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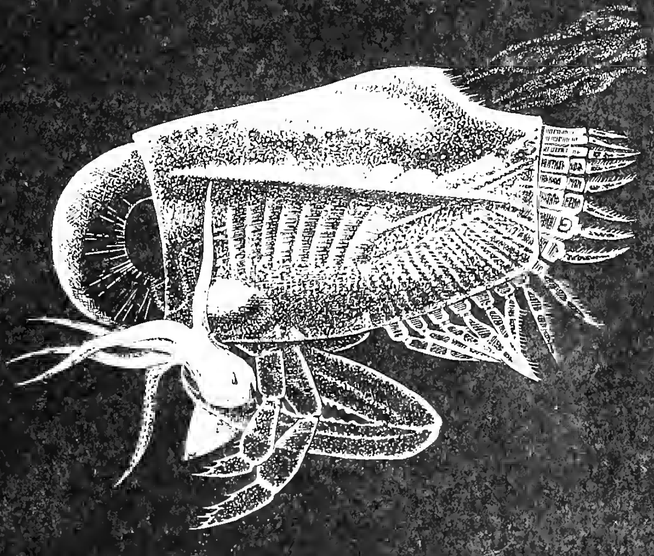

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Cover: Reconstruction of *Paraostenia voultensis* Secretan from the Middle Jurassic of the Ardèche, France, preying upon a coleoid. This is a typical thylacocephalan, a recently recognized arthropod group of uncertain, but probably crustacean, affinity, ranging from Silurian to Cretaceous, × 1.25. Reproduced by permission of the Royal Society of Edinburgh and Dr W. D. I. Rolfe from *Transactions of the Royal Society of Edinburgh*, **76**, 398, fig. 4.

# MAASTRICHTIAN SQUALOID SHARKS FROM SOUTHERN SWEDEN

*by* MIKAEL SIVERSON

ABSTRACT. The Maastrichtian of southern Sweden has yielded more than 2000 teeth of squaloid sharks. Seven species have been identified: *Microetmopterus wardi* gen. et sp. nov., *Proetmopterus hemmooriensis* gen. nov., *Eoetmopterus* cf. *E. supracretaceus*, *Centroscymnus schmidi*, *Squalus ballingsloevensis* sp. nov., *S. balsvikensis* sp. nov. and *S. gabrielsoni* sp. nov. Etmopterine sharks, now restricted to the cold bottom-waters of the outer continental and insular shelves and slopes, apparently thrived in the shallow coastal waters of the Kristianstad Basin during the earliest Maastrichtian. As indicated by its extremely small teeth, *Microetmopterus wardi* may have been the smallest known neoselachian. The Recent *Centroscyllium* could be an example of a restricted form of 'hopeful monster', by instantaneously having acquired a monognathic heterodonty in a single ancestral individual or litter. The type series of *Eoetmopterus supracretaceus* is a heterogeneous mix of *Eoetmopterus* and *Proetmopterus*. Similarly, the type series of *Centroscymnus schmidi* also includes *Proetmopterus hemmooriensis*.

THE archipelago palaeoenvironment of the Kristianstad Basin with its rocky shorelines (see Lundgren 1934; Surlyk and Christensen 1974; Surlyk 1980) was the habitat for rich selachian faunas during the Campanian and earliest Maastrichtian (Davis 1890; Siverson 1992, in press). There were several breaks in sedimentation during this interval, interpreted by Christensen (1975) as evidence of regressions. The sea remained shallow during the transgressions with a maximum water depth probably generally not exceeding 30–40 m in the Campanian and about 100 m in the earliest Maastrichtian (Gabrielson, pers. comm.). Maastrichtian strata are currently accessible at four localities within the Kristianstad Basin (Text-fig. 1), i.e. Balsvik, Bjärlången, Ballingslöv 1, and Ballingslöv 2 (Siverson in press). Placed in the NW-European belemnite stratigraphy, these sites are referred to the earliest Maastrichtian *Belemnella lanceolata* Zone (Christensen 1975; Siverson in press).

In addition to those outcrops, large glacial rafts of Maastrichtian white pelagic chalk are quarried at Kvarnby village, situated about 65 km SW of the Kristianstad Basin's SW margin (Text-fig. 1). Brood (1972), in his study of cyclostomatous bryozoans, suggested a late Early Maastrichtian age for the Kvarnby chalk. Based on Foraminifera, Holland *in* Ringberg *et al.* (1984) referred the strata to the Late, but not latest, Maastrichtian. The composition of the Kvarnby off-shore selachian fauna corresponds well with that of the mid-Maastrichtian of Hemmoor, Germany (see Herman 1982*a*). A reduced faunistic similarity is found in a comparison with a Late Maastrichtian assemblage from the bryozoan chalk at Stevns Klint, Denmark.

## SQUALOID SHARKS

The most conspicuous differential external features of Recent squaloids are their lack of an anal fin and presence of dorsal fin spines (lost in some species). Dentally they differ from other sharks mainly by their almost exclusively interlocked lower jaw teeth, with a single cusp bent towards the rear. In the *Squalus*-group genera, the lower and upper jaw dentitions are much alike. Others, in particular *Etmopterus* Rafinesque, 1810, show a very marked dignathic heterodonty with firmly interlocked cutting lower teeth and multicuspidate erect upper teeth.

The adults of Recent squaloid genera range in maximum size from about 0·25 m, e.g. *Squaliolus*

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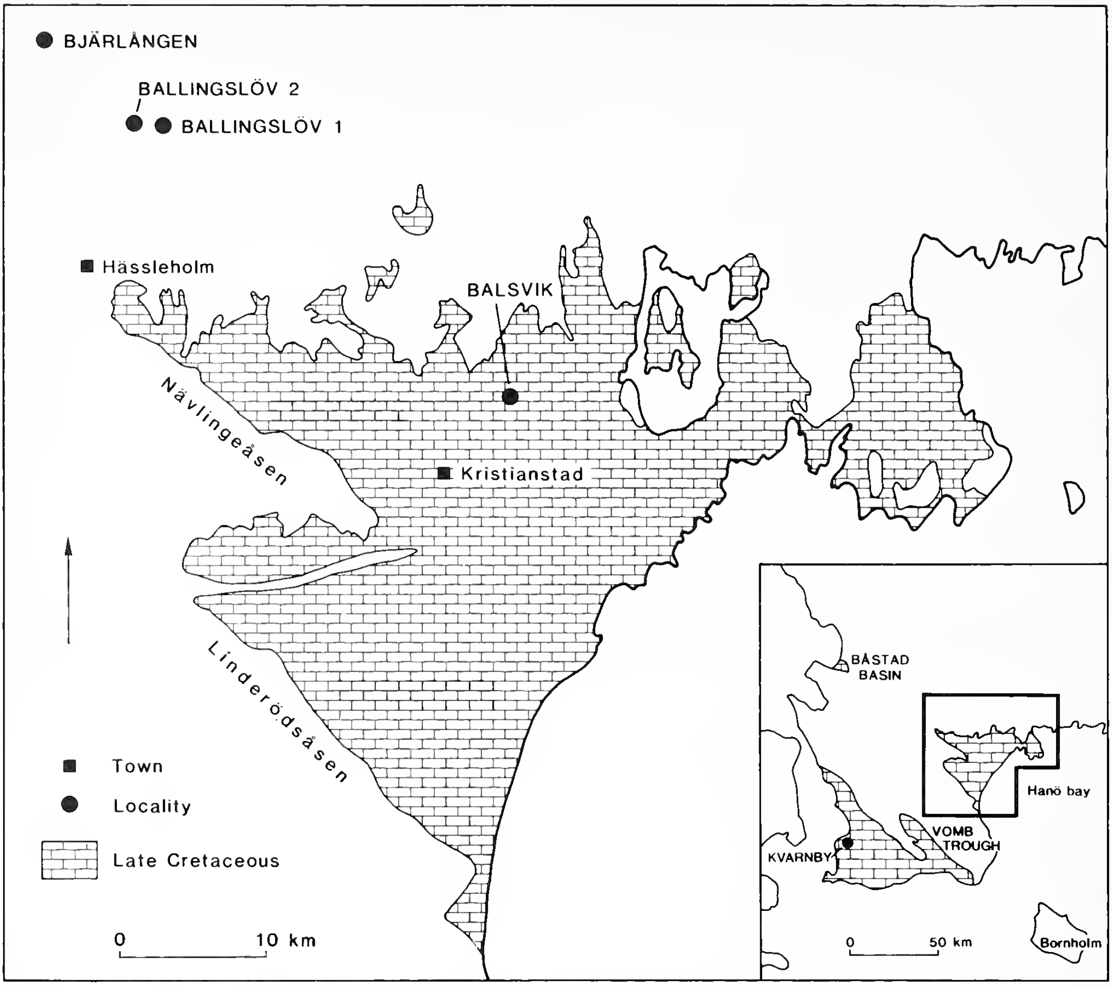

TEXT-FIG. 1. Map of the Kristianstad Basin, showing the location of the sites referred to in this work (based on SGU Ba43/Ah15, SGU Af167 and SGU Af168).

Smith and Radcliffe, *in* Smith, 1912, to more than 6 m, e.g. *Somniosus* LeSueur, 1818 (see Compango 1984). Most species live near the bottom on the temperate to tropical outer shelves and slopes (Compagno 1984). Some species, like certain *Squalus* Linnaeus, 1758 may enter shallow coastal waters at higher latitudes.

The earliest known unquestionable squaloid is *Protosqualus albertsi* Thies, 1981 from the late Middle Barremian (Early Cretaceous) of Germany. The Late Triassic *Pseudodalatias barnstonensis* (Sykes, 1971) had a dentition superficially similar to that of some Recent squaloids, e.g. *Dalatias* Rafinesque, 1810. Reif (1978) and Cappetta (1987) declined to relate it to the Squalidae on the basis of its different enameloid structure.

## PREVIOUS WORK ON CRETACEOUS SQUALOID FAUNAS

There are few records of Cretaceous squaloid faunas other than single-species occurrences of the *Squalus*-group. Dalinkevičius (1935) described (partly unaware) three squaloids from the Turonian of Lithuania, i.e. *Centrophorus*? *balticus* Dalinkevičius, 1935, a *Squaliolus*-like species, and a species of the *Squalus*-group (see Cappetta 1987, p. 53).

Cappetta (1980) redescribed skeletons of three previously poorly known squaloids from the Late Santonian of Sahel Alma, Lebanon: *Cretascymnus adonis* (Signeux, 1950) and the two *Squalus*-group taxa *Centrophoroides latidens* Davis, 1887, and *Centrosqualus primaevus* (Pictet, 1850).

Herman (1982*a*), in a study based on 80 selachian teeth (33 belonging to squaloids) from the mid-Maastrichtian of Hemmoor, Niederelbe, Germany, illustrated teeth of *Centroscymnus schmidi*, *Proetmopterus hemmooriensis*, possibly *Eoetmopterus supracretaceus* (see below), two taxa possibly related to *Scymnodon* (pl. 1, fig. 7; pl. 2, fig. 1, not fig. 2), and a species referred by him to *Centrosqualus appendiculatus* (Agassiz, 1843).

Müller and Schöllmann (1989) recorded seven nominal species (based on 270 teeth) of Squalidae from the Late Campanian of Westfalen, Germany. They figured 5 *Squalus*-group teeth from juvenile individuals referred to *Centrophoroides appendiculatus* (Agassiz, 1843) and to their new species *Squalus wondermarcki*, the latter based on a heterogeneous type-series and with insufficiently documented dental ontogeny. Their holotype differs from the Swedish *Squalus* mainly by its large cusp and small distal heel. The rest of their Squalidae fauna included *Eoetmopterus supracretaceus* with its heterogeneous type-series also including *Proetmopterus* (see below), a *Deania*-like lower jaw tooth and a *Proetmopterus*-like upper jaw tooth, both figured as Etmopterine, g. indet., n. sp., their new *Centroscymnus praecursor* and *Cretascymnus westfalicus*, and finally a tooth figured as Somniosinae? g. et sp. indet., resembling the upper jaw teeth of *Deania* Jordan and Snyder, 1902.

Considering the wide distribution of Recent *Squalus*, it may seem strange that I have been unable positively to identify any of the Swedish *Squalus* in the German faunas. However, poor quality of the illustrations and lack of documented dental ontogeny of the German *Squalus*-like taxa makes a careful comparison difficult.

## MATERIAL AND METHODS

The Kvarnby and the Kristianstad Basin samples were enriched in their content of phosphatic fossils by treatment with buffered acetic acid (see Jeppsson *et al.* 1985), heavy liquids (sodium polytungstate), and magnetic separation. Depending on the state of preservation of the sharks' teeth and the amount of non-selachian phosphatic material, the residues were sieved down to 500, 355, or 250 $\mu$m.

About 10 per cent of the teeth from Kvarnby are perfectly preserved (250 $\mu$m sieve). The corresponding figure for the more near-shore Kristianstad Basin strata is less than 1 per cent.

Relatively few *Squalus* teeth from the Kristianstad Basin sites could be identified to species level. This is a result of the generally, though not exclusively, poor state of preservation (mainly bioerosion, see Pl. 4, figs 9–12) and at least bispecific nature of the *Squalus* assemblage.

Beside their presence in the Maastrichtian, teeth of squaloid sharks occur also in the Campanian of the Kristianstad Basin, infrequently in the Early Campanian, abundantly in the Late Campanian. This material is, however, less well preserved. As far as can be determined, all of the teeth belong to species of the *Squalus*-group.

Systematics and terminology follow those of Compagno (1984) and Cappetta (1987) respectively. All illustrated teeth are deposited in the type collection of the Department of Historical Geology and Palaeontology, Lund University (LO).

## LOCALITIES

KVARNBY. *Map sheet* Bara 2C:26, Ed. 1987 (economic map 'Gula Kartan' in Swedish; 1:20,000); coordinates 6165 1330 (The Swedish National Grid 2·5 gon V system). *References*. Brotzen 1960; Brood 1972; Ringberg *et al.* 1984. *Age*. Probably mid-Maastrichtian, see Brood 1972; Holland *in* Ringberg *et al.* (1984), and discussion above. *Remarks*. East of the village of Kvarnby, glacial rafts (Schollen) of a very pure white chalk are quarried by the Malmökrita AB company. The tilted

Schollen are several hundred metres long and up to 30 m thick and are interbedded in a till. The commercial processing of the microbrecciated chalk includes washing the sediment over a 200 $\mu$m mesh. The rejected $> 200$ $\mu$m fraction is dumped into two abandoned quarries (not marked on the map) situated just west of Ängdala Farm (see Ringberg *et al.* 1984, fig. 2). One sample (S91-5-1-MS; 179 kg) of the $> 200$ $\mu$m residue was collected from the northwestern corner of the southern quarry, located immediately south of the sieving station.

BJÄRLÅNGEN. *Map sheet.* Bjärnum 3D 8e, Ed. 1 – Nov. 1975 (Swedish economical maps, 1:10,000); coordinates 624262 137120 (southern quarry). *References.* Moberg 1884; Siverson in press. *Age. B. lanceolata* Zone, earliest Maastrichtian. *Remarks.* The sample (S89-4-2-MS, 96·7 kg) was collected about 0·5–1·0 m below ground level in the northwestern corner of the small overgrown quarry.

BALSVIK. *Map sheet.* Balsby 3E 3a, Ed. 1 – Mar. 1975 (Swedish economical maps, 1:10,000); coordinates 621830 140184. *References.* Christensen 1972, 1975; Siverson in press. *Age. B. lanceolata* Zone, earliest Maastrichtian. *Remarks.* About 3 m of earliest Maastrichtian mainly fine-grained calcarenite is currently exposed in the partly overgrown quarry. Perfectly preserved teeth are rare ($< 10/100$ kg, 250 $\mu$m sieve) and mainly confined to the uppermost metre of the strata.

BALLINGSLÖV 1 and 2. For details see Siverson (in press).

## SYSTEMATIC PALAEONTOLOGY

### Order SQUALIFORMES Goodrich, 1909
### Family SQUALIDAE Blainville, 1816
### Genus SQUALUS Linnaeus, 1758

*Type species. Squalus acanthias* Linnaeus, 1758. Recent, boreal to warm-temperate, intertidal down to at least 900 m of the upper continental and insular slopes. Occurs throughout the water column but is usually found near the bottom (Compagno 1984).

*Remarks.* The overall dental morphology has remained virtually unchanged within the genus since its appearance, probably some time during the Cenomanian to Campanian interval. Recognition of palaeospecies of dentally broadly static genera like *Squalus* is no easy task. Intraspecific variation in tooth morphology for a given tooth file is to a large extent governed by ontogeny (see below) and, after maturity, also by sex. Furthermore, schools of Recent *Squalus* are commonly segregated by size and sometimes by sex (Compagno 1984, p. 112).

Much of the dental interspecific variation in the *Squalus*-group is concentrated on the basal face of the root. Unfortunately, it does not take much corrosion of the root for vital information to be lost. Descriptions of new nominal species of *Squalus* and closely related genera based on teeth of the same size which are not of the best preservation, do not help the understanding of squaloid taxonomy.

The great similarities in general tooth morphology between species of *Squalus* result in descriptions of the dentition of each species differing only slightly. Therefore, separate descriptions have been omitted here. Herman *et al.* (1989) gave a detailed description of the type species, *S. acanthias*.

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EXPLANATION OF PLATE 1

Figs 1–8. *Squalus ballingsloevensis* sp. nov. 1–2, holotype, LO 5061 T, 5·2 mm long posterior lower jaw tooth from a mature male; labial and lingual views; Ballingslöv 1, sample S89-9-1-MS, 399·2 kg, × 13. 3–4, paratype, LO 5062 t, 4·7 mm long antero-lateral tooth from a mature female; labial and lingual views; Ballingslöv 1, sample S89-9-1-MS, 399·2 kg, × 13·5. 5–6, paratype, LO 5063 t, 3·8 mm long symphyseal tooth, cusp broken off; labial and lingual views; Ballingslöv 2, sample S89-4-8-MS, 10·9 kg, × 16. 7–8, paratype, LO 5064 t, 2·62 mm long incomplete lower? jaw tooth from an immature individual, distal part of tooth broken off; labial and lingual views; Bjärlången, sample S89-4-2-MS, 96·7 kg, × 23·5.

PLATE 1

SIVERSON, *Squalus*

### *Squalus ballingsloevensis* sp. nov.

Plate 1, figs 1–8

*Type stratum.* Sample S89-9-1-MS, Ballingslöv 1 quarry (*Belemnella lanceolata* Zone, earliest Maastrichtian; for details see Siverson in press).

*Derivation of name.* After the type locality.

*Holotype.* LO 5061 T; Pl. 1, figs 1–2.

*Paratypes.* LO 5062 t–LO 5064 t; Pl. 1, figs 3–8.

*Additional material.* More than 100 poorly preserved teeth, most of them from Ballingslöv 1. The species has been found in all samples from the Swedish *B. lanceolata*-beds.

*Diagnosis.* A large, dentally primitive *Squalus*. Centrally situated apron: triangular in juveniles, but often well demarcated with parallel edges in adults. Lingual side of apron not covered by basal edge of root. Mesial expansion of basal edge of tooth root very poorly developed, particularly in juveniles. Basal face of root flat or slightly concave in profile. Axial foramina fused into large subcircular infundibulum. Teeth only moderately labio-lingually compressed.

*Comparison.* Teeth of *S. ballingsloevensis* most closely resemble those of '*Centrophoroides*' *worlandensis* Case, 1987 (Late Campanian of Wyoming). Teeth of the American species have a larger infundibulum and are slightly larger (up to at least 6·9 mm). Moreover, the lower part of the basal face of the root is incompletely mineralized in '*C*'. *worlandensis*, explaining the presence of a row of irregularly shaped foramina below the infundibulum. Normally, this area is covered by a cap of dentine. In *S. ballingsloevensis*, the mesial cutting edge is gently convex in mature females (Pl. 1, figs 3–4), and straight in mature males (Pl. 1, figs 1–2). In '*C*'. *worlandensis*, the cutting edge is straight in mature females and concave in mature males. Unfortunately, juvenile teeth of the latter species have never been illustrated.

Some teeth of mature females of the early Palaeogene *S. minor* (Leriche, 1902) and its possible ancestor *S. balsvikensis* sp. nov. have a short and poorly demarcated apron with its lingual side not covered by the basal edge of the root. Except for being more labio-lingually compressed and having a more convex mesial cutting edge, these teeth are fairly similar to the female tooth of *S. ballingsloevensis* figured herein (Pl. 1, figs 3–4). However, the development of the apron and the basal face of the root through ontogeny easily separates the latter from the former two species.

### *Squalus balsvikensis* sp. nov.

Text-fig. 2A–F

*Type stratum.* About 0–0·3 m above the upper level of white-spotted flint nodules (see Christensen 1972, fig. 5), Balsvik quarry; *Belemnella lanceolata* Zone, earliest Maastrichtian.

*Derivation of name.* After the type locality.

*Holotype.* LO 5065 T; Text-fig. 2C–D.

*Paratypes.* LO 5066 t–LO 5067 t; Text-fig. 2A–B, E–F.

*Additional material.* Several hundred teeth, most of them poorly preserved. The species has been found in all samples from the *B. lanceolata*-beds.

*Diagnosis.* Uvula very small and symmetrical in teeth from very young individuals; mesially twisted in teeth larger than about 1·1 mm. Axial foramina separated in teeth of very young individuals, otherwise fused into oblique infundibulum. Apron long and narrow with parallel edges in juveniles and mature males; relatively broad and short in large females. Basal face of root concave in profile.

TEXT-FIG. 2. *Squalus balsvikensis* sp. nov. A–B, paratype, LO 5066 t, 2·53 mm long anterior tooth from a female; lingual and labial views; Balsvik quarry, sample S90-4-1-MS, 21·35 kg, the cemented bed between the two levels of white-spotted flint nodules, × 21. C–D, holotype, LO 5065 T, 2·35 mm long upper jaw tooth from a mature male; labial and lingual views; Balsvik quarry, sample S92-2-2-MS, 47·5 kg, 0–0·3 m above the upper flint level, × 24. E–F, paratype, LO 5067 t, 1·01 mm long posterior lower jaw tooth from a very young individual; labial and lingual views; Balsvik quarry, sample S90-5-1-MS, 10·85 kg, 0·2–0·4 m above the upper flint level, × 54.

Mesial expansion of basal edge of root well developed but mostly not reaching apex of apron. Distal part of basal edge of root markedly bilobate.

*Comparison.* Teeth of *S. balsvikensis* most closely resemble those of the Palaeocene to Eocene *S. minor*

(Leriche, 1902) and the very similar Oligocene *S. alsaticus* (Andreae, 1892). Judging from illustrations (Herman 1982*b*) and specimens of *S. minor* examined, teeth from adult *S. balsvikensis* differ from those of *S. minor* by their narrower and more inclined cusp, more concave basal face of the root, generally more prominent distal lobe of the basal edge of the root, and weaker sexual heterodonty. I am not convinced that the Eocene teeth figured as *S. smithi* sp. nov. by Herman (1982*b*) belong to a species other than *S. minor*.

*Remarks*. Females of *S. acanthias*, a Recent species probably close in size to *S. balsvikensis*, reach at least 1·24 m in body length, whereas newborn offspring from presumably smaller females are sometimes no larger than 0·22 m (Compagno 1984, p. 113). Based on the illustrations and data of *S. acanthias* teeth/body length, presented by Ledoux (1970) and Herman *et al.* (1989), the relationship between body length and tooth size in that species seems to be roughly isometric. In *Squalus*, the lower jaw teeth are about 20–30 per cent larger than the otherwise similar upper ones. Using the latter figure and assuming an isometric body length/tooth size ratio, the size ratio between upper teeth of the smallest newborn and corresponding lower teeth of the largest females of *S. acanthias* would be about 7·3:1. In my collection of *S. balsvikensis*, the size range for lateral teeth is 0·94–4·11 mm, giving a 4·4:1 ratio. It thus seems reasonably likely that the greater part of the ontogeny is covered.

### *Squalus gabrielsoni* sp. nov.

Plate 2, figs 1–8

*Type stratum*. Kvarnby chalk Schollen (probably mid-Maastrichtian).

*Derivation of name*. After Jan Gabrielson, Lund, in recognition of field assistance and stimulating discussions on the Cretaceous geology of Sweden.

*Holotype*. LO 5068 T; Pl. 2, figs 3–4.

*Paratypes*. LO 5069 t–LO 5071 t; Pl. 2, figs 1–2, 5–8.

*Additional material*. About 50 teeth from Kvarnby, most of them poorly preserved.

*Diagnosis*. Axial foramina separated or fused. Apron very elongated and narrow, particularly in juveniles. Mesial expansion of basal edge of root well developed reaching apex of apron. Lingual side of mesial expansion of basal edge of root generally meeting root protuberance almost at right angle. Basal edge of root nearly straight.

*Comparison*. This species is a good example of a *Squalus* in the process of losing the thin bridge of dentine separating the two axial foramina. The species has otherwise a remarkably modern tooth morphology close to that of the Recent *S. acanthias*, a species which it resembles more than it does any fossil attributed to *Squalus*. The sexual dimorphism is, however, less marked in *S. gabrielsoni*. Further, in the latter, the apron is narrower and the distal part of the basal edge of the root does not reach the end of the apron. In contrast to *S. balsvikensis* and *S. minor*, the mesial expansion of the root commonly reaches beyond the apex of the apron

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EXPLANATION OF PLATE 2

Figs 1–8. *Squalus gabrielsoni* sp. nov. 1–2, paratype, LO 5069 t, 3·08 mm long posterior lower jaw tooth from a mature male; lingual and labial views; Kvarnby, ×22. 3–4, holotype, LO 5068 T, 2·55 mm long anterolateral lower jaw tooth; lingual and labial views; Kvarnby, ×23. 5–6, paratype, LO 5070 t, 2·31 mm long upper jaw tooth from a mature? male, basal face of root unusually flat; labial and lingual views; Kvarnby, ×27. 7–8, paratype, LO 5071 t, 1·26 mm long tooth from an immature individual; labial and lingual views, Kvarnby, ×45.

PLATE 2

SIVERSON, *Squalus*

in *S. gabrielsoni* and *S. acanthias*. The bilobated distal part of the basal edge of the root is very similar in the former two taxa. In *S. gabrielsoni* and *S. acanthias* the basal edge is more or less straight with a poorly demarcated terminal lobe. The almost straight basal root edge, often fused axial foramina in adults, and weak mesial labial interlocking hollow of the crown in *S. gabrielsoni*, easily separate it from the contemporaneous *Centrophoroides*? *appendiculatus*.

In both *S. balsvikensis* and *S. gabrielsoni*, the uvula is very small and symmetrical in teeth (about 0·94–1·1 mm long) presumably of newborn individuals. In teeth larger than about 1·1 mm, the uvula rapidly increases in size and inclination towards the symphysis.

## Genus MICROETMOPTERUS gen. nov.

*Type species. Microetmopterus wardi* gen. et sp. nov.

*Derivation of name.* Combination of '*mikros*' (Greek, small) and *Etmopterus* (lanternsharks).

*Diagnosis.* Upper jaw teeth with very large lateral cusplets, reaching half the height or more of cusp. Labial face of crown very flat, without ornamentation. Flat, V-shaped basal face of root with two axial foramina or with infundibulum. Rectangular lower jaw teeth longer than high. Separate axial foramina; occasionally forming infundibulum. No disto-lingual foramen. Interlocking hollows poorly developed, especially in juveniles.

*Comparison.* The combination of mesio-distally elongated, poorly interlocked, lower jaw teeth, and advanced, smooth upper jaw teeth with very large cusplets, separates *Microetmopterus* from *Proetmopterus* and *Etmopterus*. The upper jaw teeth of *Microetmopterus* are very close in morphology to those of *Etmopterus*, whereas the lower teeth are quite different in the two genera. In *Etmopterus*, the lower teeth are roughly quadrangular with large interlocking hollow areas.

### *Microetmopterus wardi* sp. nov.

Plate 3, figs 1–12

*Type stratum.* Kvarnby chalk Schollen (probably mid-Maastrichtian).

*Deviation of name.* After David J. Ward, Orpington, UK, in recognition of his publications on Tertiary selachians and his assistance in building me a clay-washing machine of the type described by him (Ward 1981).

*Holotype.* LO 5072 T; Pl. 3, figs 3–4.

*Paratypes.* LO 5073 t–LO 5077 t; Pl. 3, figs 1–2, 5–12.

*Additional material.* 18 less well-preserved teeth; 9 upper jaw teeth and 9 lower jaw teeth, all from Kvarnby.

*Diagnosis.* As for the genus.

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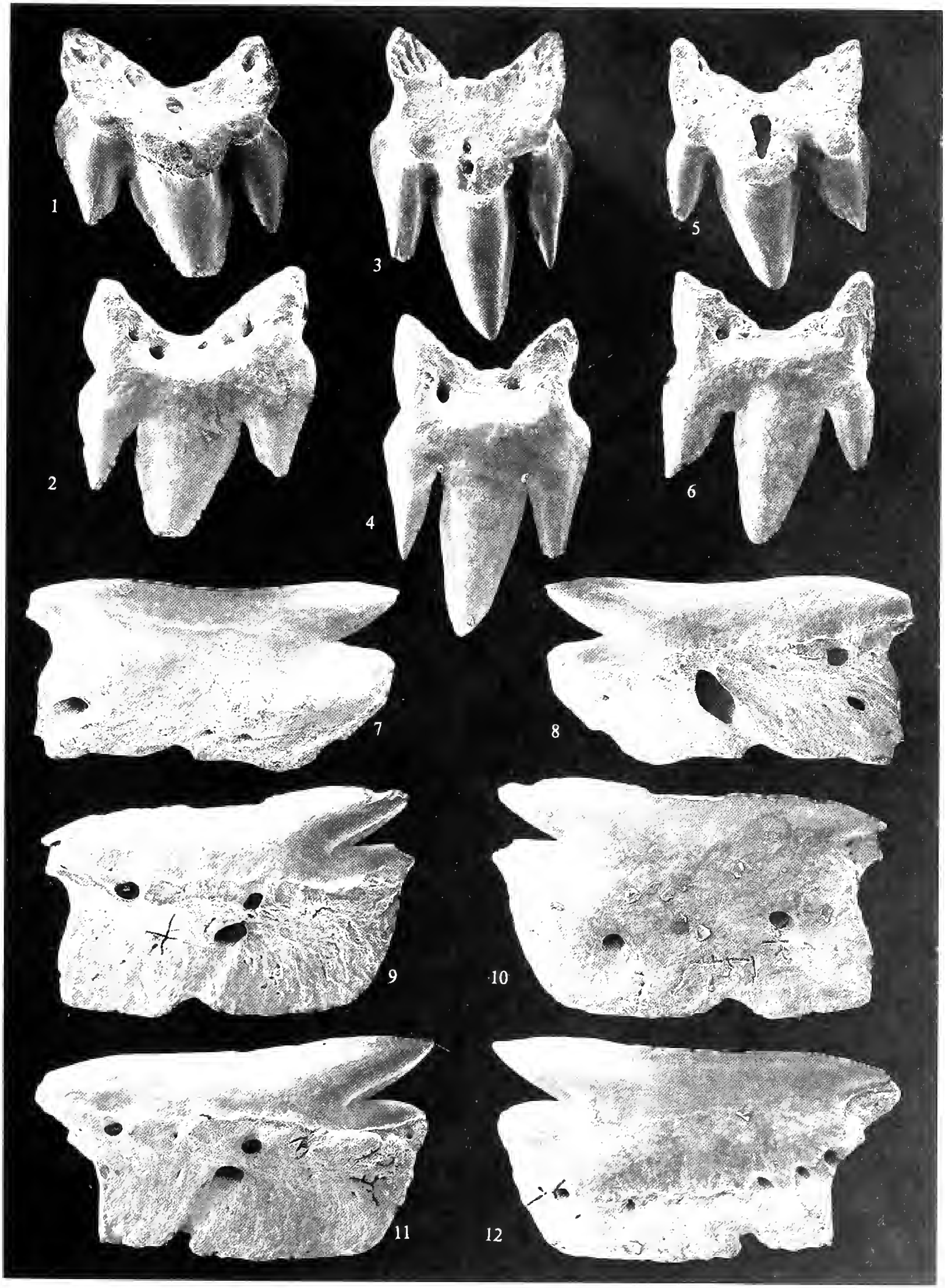
EXPLANATION OF PLATE 3

Figs 1–12. *Microetmopterus wardi* gen. et sp. nov. 1–2, paratype, LO 5073 t, 0·50 mm high upper lateral tooth; lingual and labial views; Kvarnby. 3–4, holotype, LO 5072 T, 0·57 mm high upper anterior tooth; lingual and labial views; Kvarnby. 5–6, paratype, LO 5074 t, 0·49 mm high upper lateral tooth; lingual and labial views; Kvarnby. 7–8, paratype, LO 5075 t, 0·71 mm long lower jaw tooth; labial and lingual views; Kvarnby. 9–10, paratype, LO 5076 t, 0·72 mm long lower jaw tooth; lingual and labial views; Kvarnby. 11–12, paratype, LO 5077 t, 0·75 mm long incomplete lower jaw tooth, mesial corner of root broken off; lingual and labial views. All specimens from Kvarnby, and × 80.

PLATE 3



SIVERSON, *Microetmopterus*

*Description.* Upper jaw teeth up to 0·62 mm high with one, or rarely two, pairs of erect, robust lateral cusplets, reaching two-thirds of height of main cusp. Labial face of crown smooth, very flat; lingual face convex. Crown overhangs root labially. Two or more foramina open along labial base of crown. Basal face of root flat with two axial foramina or infundibulum.

Lower jaw teeth, about 50 per cent longer than high, up to 1·1 mm long. Mesial cutting edge weakly sigmoidal; four to six times longer than distal convex cutting edge. Two separate axial foramina, rarely forming infundibulum. Mesio-lingual foramen present but no disto-lingual one. Interlocking hollows poorly developed, especially in juveniles. Two or more foramina open along labial base of crown. Basal edge of root straight.

*Remarks.* The upper jaw teeth, remarkably similar to those of *Etmopterus spinax* (Linnaeus, 1758), range in size from 0·45 to 0·62 mm in height. The variability in size is much greater for the lower jaw teeth, i.e. 0·57–1·1 mm in length. A sieve finer than 250 $\mu$m is probably needed in order to obtain upper jaw teeth of juveniles. The height of the smallest lower jaw tooth coincides with the diagonal of the aperture in a 250 $\mu$m sieve. Thus, obtaining lower jaw teeth of very young individuals may also require a sieve finer than 250 $\mu$m. The teeth of 0·30 m long individuals of the extant *E. spinax* appear gigantic if placed next to those of *M. wardi* figured herein. The latter may well be the smallest known neoselachian.

## Genus PROETMOPTERUS gen. nov.

*Type species. Etmopterus? hemmooriensis* Herman, 1982*a* (p. 137, pl. 1, fig. 6; pl. 3, fig. 1).

*Derivation of name.* Combination of '*pro*' (Greek, before in time) and *Etmopterus* (lantern sharks).

*Diagnosis.* Lower jaw teeth with mesio-labial interlocking hollow not extending below mesio-labial main foramen. Disto-lingual interlocking hollow poorly developed below lingual bulge of root. Upper jaw teeth with rectangular root, one or two pairs of cusplets, and weakly to well-developed apron.

*Comparison. Proetmopterus hemmooriensis* is a good candidate for the species ancestral to *Etmopterus.* The lower jaw teeth of the two taxa are almost identical, except for the smaller interlocking area and open median lingual duct ('sillon' of Casier 1961) of the root in the former taxon. The upper jaw teeth of *P. hemmooriensis* have a primitive morphology, retaining a rectangular root unlike the advanced scyliorhinid-like roots of *Etmopterus* and *Microetmopterus.* Passing from *Proetmopterus* to *Etmopterus*, there is an increase in the interlocking area of the lower jaw teeth coupled with a development towards scyliorhinid-like upper jaw teeth. If *P. hemmooriensis*, or a later descendant, gave rise to *Etmopterus*, scyliorhinid-like upper jaw teeth with V-shaped roots evolved at least twice in Squalidae: in the mid-Maastrichtian *Microetmopterus* and in the Early Miocene to Recent *Etmopterus.*

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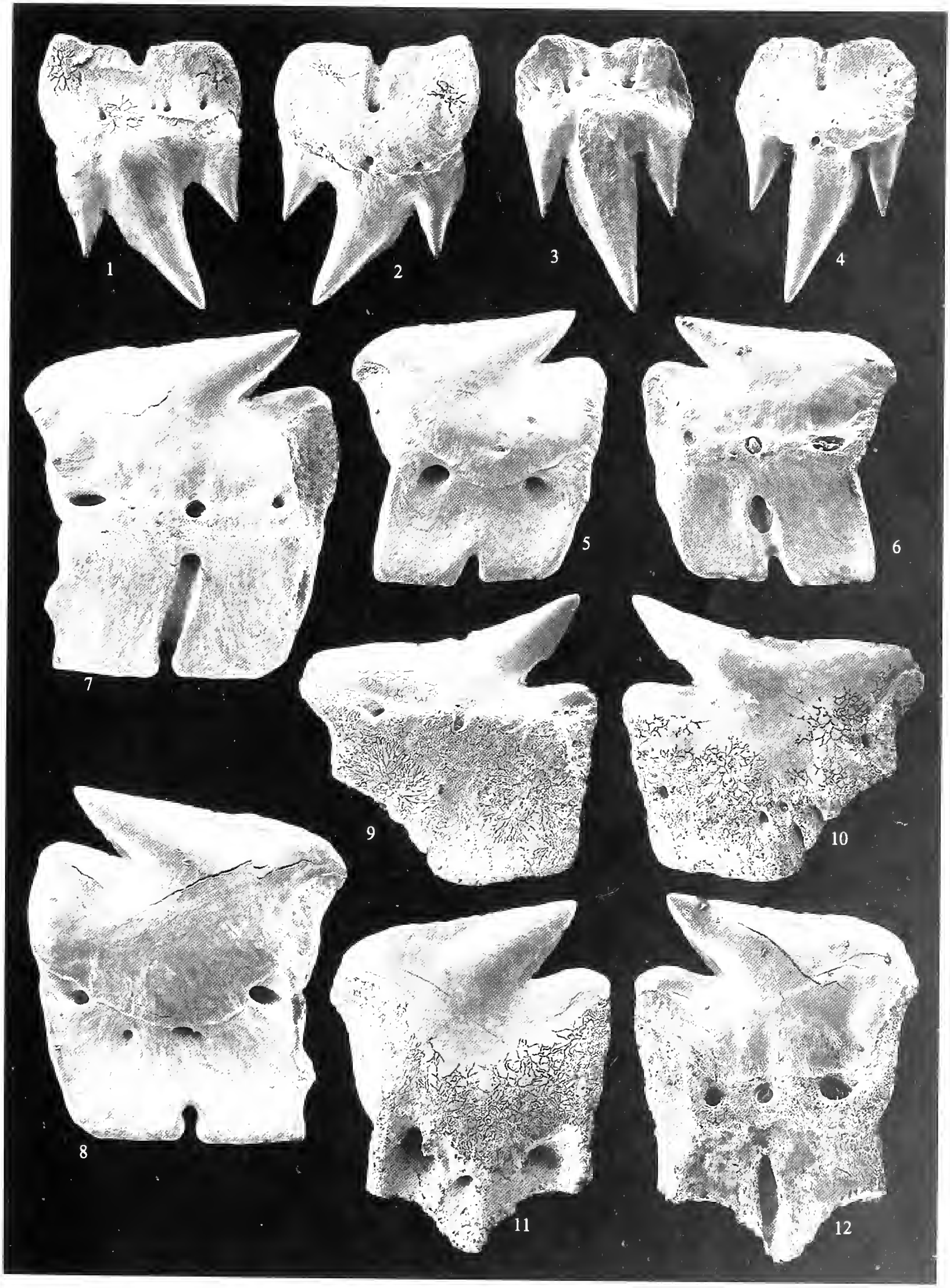
### EXPLANATION OF PLATE 4

Figs 1–8. *Proetmopterus hemmooriensis* (Herman, 1982*a*) gen. nov. 1–2, LO 5078 t, 1·09 mm high upper latero-posterior tooth; labial and lingual views; Kvarnby. 3–4, LO 5079 t, 1·08 mm high upper anterior tooth, basal bulge of labial side of cusp worn, presumably during feeding; labial and lingual views; Ballingslöv 1, sample S89-9-1-MS, 399·2 kg. 5–6, LO 5080 t, 1·01 mm high lower jaw tooth; labial and lingual views; Bjärlången, sample S89-4-2-MS, 96·7 kg. 7–8, LO 5081 t, 1·34 mm high lower jaw tooth, mesial corner of root broken off; lingual and labial views; Ballingslöv 1, sample S89-9-1-MS, 399·2 kg. All specimens × 40.

Figs 9–10. *Eoetmopterus* cf. *E. supracretaceus* Müller and Schöllmann, 1989. LO 6332 t, 1·57 mm high lower jaw tooth, large portion of mesial side of root broken off, note bioerosion; lingual and labial views; Kvarnby, × 30.

Figs 11–12. *Centroscymnus schmidi* Herman, 1982*a*. LO 6333 t, 1·4 mm high incomplete lower jaw anterior tooth, distal part of root missing, note bioerosion; labial and lingual views; Balsvik quarry, sample S90-6-1-MS, 8·4 kg, 20–30 cm below the lower flint level, × 40.

PLATE 4



SIVERSON, *Proetmopterus*, *Eoetmopterus*, *Centroscymnus*

### *Proetmopterus hemmooriensis* (Herman, 1982*a*)

Plate 4, figs 1–8

?1982*a* *Centroscymnus schmidi* Herman [*partim*], p. 135, pl. 1, fig. 5*a*, *non* figs 5*b–c*
1982*a* cf. *Centroscymnus schmidi* Herman, p. 135, pl. 1, fig. 5*d*; pl. 3, fig. 6.
1982*a* *Etmopterus*? *hemmooriensis* Herman, p. 137, pl. 1, fig. 6; pl. 3, fig. 1.
?1989 *Eoetmopterus supracretaceus* Müller and Schöllmann [*partim*], p. 11, figs 4·3*a–b*; ?4·5*a–b*; 4·6*a–b*; 4·7*a–c*; 5·1*a–c*; 5·2*a–c*; 5·93*a–c*; *non* figs 4·4*a–c* (holotype of *E. supracretaceus*).
?1990 *Eoetmopterus supracretaceus* Müller [*partim*], pl. 2. figs 5–8, pl. 3, figs 1–3; *non* pl. 2, figs 3–4.

*Type stratum*. 0·5 m above bed T100; *Belemnella junior* Zone (early Late Maastrichtian) of Hemmoor, Niederelbe, Germany (Herman 1982*a*).

*Material*. More than 1000 teeth, most of them poorly preserved. All samples from the *B. lanceolata* beds yielded *P. hemmooriensis*.

*Description*. Upper jaw teeth up to 1·27 mm high with one or two pairs of erect cusplets; inner pair reaching half or less of height of main cusp. Labial basal border of crown straight or forming median apron. Several foramina open along labial base of crown. Cutting edges sharp. Labial face of cusp mildly convex, lingual face strongly convex. Basal face of root flat or labio-lingually concave. Single median foramen opens on lingual bulge of root. Lower half of basal face of root divided by median groove. Outline of root's basal face roughly rectangular. Anterior teeth erect; laterals bent towards commissure.

Lower jaw teeth up to 1·4 mm high. Overall tooth shape quadrangular (except for commissural teeth). Cusp strongly bent towards rear. Cutting edges with irregular, weak serrations. Mesial cutting edge occasionally convex in, presumably, adult females, otherwise straight. Large mesio-lingual foramen; smaller disto-lingual one. Median lingual foramen connecting with open median lingual duct. Disto-lingual interlocking hollow apico-basally elongated; poorly developed below lingual bulge of root. Mesial labial interlocking hollow not extending below mesio-labial main foramen. Basal border of labial face of crown broadly convex. Basal edge of root straight.

*Remarks*. Herman (1982*a*) based his new species *Etmopterus*? *hemmooriensis* on an upper jaw tooth lacking the distal part of the distal root branch. In the same paper, he also described the new species *Centroscymnus schmidi* with its type series comprising three fairly well-preserved lower jaw teeth along with an incomplete upper jaw tooth. By comparison with the Swedish collection of *Proetmopterus*, it is evident that the upper jaw tooth referred to *C. schmidi* by Herman (1982*a*, pl. 1, fig. 5*d*; pl. 3, fig. 6), is a poorly preserved tooth of *P. hemmooriensis* with broken cusplets. Unlike the holotype of *E.*? *hemmooriensis*, the specimen has a relatively well demarcated apron. This is, however, a highly variable character within the species. Most imaginable intermediate forms are present in the Swedish collection. Some have a labial side like the holotype, others show a more or less well-defined apron. One of the three lower jaw teeth referred to *C. schmidi* by Herman (1982*a*, pl. 1, fig. 5*a*) probably also belongs to *P. hemmooriensis*. Unfortunately, this tooth was not illustrated by scanning electron micrographs.

### Genus EOETMOPTERUS Müller and Schöllmann, 1989

*Type species*. *Eoetmopterus supracretaceus* Müller and Schöllmann, 1989 (p. 11, figs 4·4*a–c*; *non* figs 4·3, 4·5–4·7, 5·1–5·3).

*Remarks*. The lower jaw tooth morphology alone does not justify a generic separation of *Eoetmopterus* from the Recent *Centroscymnus* (*Scymnodon*?) *crepidater* (Bocage and Capello, 1864). If my suggested recombination below of the lower jaw teeth of *E. supracretaceus* with the upper ones of Herman's Scymnorhinidae indet. n. sp. 2 is correct, then *E. supracretaceus* is a taxon generically difficult to separate from *Centroscymnus* (*Scymnodon*?) *crepidater*. The putative upper jaw teeth of

*E. supracretaceus* differ from those of other scymnorhinid squaloids by their lack of a basal constriction of the crown.

### *Eoetmopterus* cf. *E. supracretaceus* Müller and Schöllmann, 1989

Plate 4, figs 9–10

| | |
|---|---|
| ?1982*a* | Scymnorhinidae indet. n. sp. 2 Herman, p. 139, pl. 1, fig. 5*e*, and pl. 3, fig. 7. |
| *1989 | *Eoetmopterus supracretaceus* Müller and Schöllmann [*partim*], p. 11, fig. 4·4*a–c*; *non* figs 4·3, 4·5–4·7, 5·1–5·3. |
| .1990 | *Eoetmopterus supracretaceus* Müller [*partim*], pl. 2, fig. 4; *non* pl. 2, figs 3, 5–8, pl. 3, figs 1–3. |

*Type stratum*. Upper Coesfelder Schichten (Late Campanian), Westfalen, Germany.

*Material*. One lower jaw tooth from Kvarnby.

*Description*. Tooth 1·57 mm high; 1·55 mm long. Mesial corner of root broken off, otherwise fairly well preserved. Cusp narrow. Mesial cutting edge concave, distal one convex. Several foramina open along diffuse basal labial edge of enameloid. Interlocking hollows poorly developed, affecting upper half of root only. Single mesio-lingual foramen, no disto-lingual one. Median lingual duct roofed over. Basal edge of root rectilinear.

*Remarks*. The figured material originally included in *Eoetmopterus supracretaceus* Müller and Schöllmann, 1989, comprises 5 upper jaw teeth (figs 4·6–4·7 and 5·1–5·3) and 3 lower jaw teeth (figs 4·3–4·5). As far as can be determined from the drawings of the imperfectly preserved upper jaw teeth, they do not differ generically from those of *Proetmopterus hemmooriensis*. Three of them have two pairs of cusplets whereas most Swedish specimens have one pair only. This difference may be significant but could also result from sexual segregation. Females of extant *Etmopterus* were reported to have fewer cusplets than males (Ledoux 1972). Judging from Müller and Schöllmann's drawings, one of the three lower jaw teeth (1989, figs 4·3*a–b*) also belongs to a species of *Proetmopterus*. The relatively large lower jaw tooth chosen as holotype of *E. supracretaceus* by Müller and Schöllmann (1989, fig. 4·4*a–c*), has a convex mesial cutting edge, elongated cusp, and diffuse labial borderline of the crown. No such teeth have been found in the *Proetmopterus*-yielding strata of the Kristianstad Basin. Consequently, the suggested combination of the 5 etmopterine upper jaw teeth with the holotype of *E. supracretaceus* is rejected. The remaining lower jaw commissural tooth (1989, figs 4·5*a–b*) has a distinct labial crown/root boundary, and thus differs significantly from the holotype of *E. supracretaceus*. It also differs from commissural teeth of *P. hemmooriensis* by its concave rather than straight mesial cutting edge and less mesio-distally elongated overall shape. Müller (1990, pl. 2, figs 5–6) figured two additional well preserved teeth as *E. supracretaceus* which undoubtedly belong to *Proetmopterus* and possibly to *P. hemmooriensis*. From the discussion above, it follows that of the eight specimens originally figured as *E. supracretaceus*, the holotype alone remains as representative of the taxon in the Westfalen Late Campanian selachian fauna. The early Late Maastrichtian specimen figured as Scymnorhinidae indet. n. sp. 2 by Herman (1982*a*, pl. 3, fig. 7), fits much better as upper jaw tooth of *E. supracretaceus*, both in size, labial root/crown boundary, distribution of labial foramina, and overall root shape.

The holotype of *E. supracretaceus* has double marginal foramina on the lingual face of the root, whereas the Swedish specimen has a single mesio-lingual foramen but no disto-lingual one. Other than that, the two teeth are almost identical in morphology.

### Genus CENTROSCYMNUS Bocage and Capello, 1864

*Type species*. *Centroscymnus coelolepis* Bocage and Capello, 1864, Recent, on or near the bottom on the continental slopes (Compagno 1984).

### *Centroscymnus schmidi* Herman, 1982*a*

Plate 4, figs 11–12

*1982*a* *Centroscymnus schmidi* Herman, p. 135, pl. 1, fig. 5*b–c*, and pl. 3, fig. 5; *non* pl. 1, fig. 5*a*, *d*, and pl. 3, fig. 6.

*Type stratum*. 0·6 m above bed F104, *Belemnella junior* Zone (early Late Maastrichtian) of Hemmoor, Niederelbe, Germany.

*Material*. Kvarnby; 5 specifically determinable lower jaw teeth. There are probably a few dozen additional, poorly preserved, upper and lower jaw teeth in my Kvarnby collection. Balsvik; sample S90-6-1-MS, 8·4 kg, one lower jaw tooth.

*Description*. Narrow lower jaw teeth reaching more than 1·65 mm in height. Crown relatively thick; root very compressed below lingual bulge. Mesial cutting edge generally straight with weak irregular serrations; distal cutting edge mildly convex. Mesial/distal cutting edge length ratio about 3·5–4:1. Large mesio-lingual foramen; smaller median and disto-lingual ones. One mesio-labial foramen; two or less disto-labial ones. Enameloid covered apron not extending below disto-labial foramen/foramina. Unroofed median duct. Mesio-labial interlocking hollow not reaching below mesio-labial foramen; disto-lingual one extending below lingual bulge of root.

*Remarks*. *C. schmidi* was the first described Cretaceous *Centroscymnus*, followed by the Late Campanian *C. praecursor* Müller and Schöllmann, 1989, from Westfalen, Germany. The lower jaw teeth of the latter are only moderately apico-basally elongated and lack a disto-lingual foramen.

## *CENTROSCYLLIUM*, A RESTRICTED FORM OF 'HOPEFUL MONSTER'?

In the view of Compagno (1984), the subfamily Etmopterinae comprises the three Recent genera *Aculeola* de Buen, 1959 (monospecific), *Centroscyllium* Müller and Henle, 1841 and *Etmopterus*. In particular the latter two are very similar in overall body shape, whereas their lower jaw dentitions are fundamentally different (see Herman *et al*. 1989, pls 5–6). In *Centroscyllium* the upper and lower jaw teeth are very much alike, superficially resembling those of some scyliorhinids (see Herman *et al*. 1990). In complete contrast, *Etmopterus* shows a very marked dignathic heterodonty with firmly interlocked lower jaw cutting teeth with a single commissurally bent cusp, and multicuspidate erect upper jaw clutching teeth of scyliorhinid design.

Considering the observed rate of dental evolution in neoselachians, one may have to take a restricted form of 'hopeful monster' (see Goldschmidt 1940) into consideration in order to defend a close genetic relationship (e.g. a Tertiary splitting point) between *Centroscyllium* and *Etmopterus*. Let us assume a phenotypic transformation, in a mutant individual or litter, from a cutting/clutching dentition to a monognathic heterodonty with multicuspidate *Etmopterus*-like upper jaw teeth in the lower jaw as well. Instantly equipped with a basic scyliorhinid-like clutching dentition, *Centroscyllium*-phenotypes would then have been able, and certainly forced, to explore new food sources. They would simply no longer be able to cut pieces of flesh from larger prey the way their *Etmopterus*-phenotypic conspecifics could. Considering the opportunistic feeding behaviour of most Recent sharks, it is likely that *Centroscyllium*-phenotypes could change their choice of prey, if facing starvation. A resultant ecological barrier, maintained by way of different prey preference, could in time result in genotypical irreversible isolation. The otherwise typical scyliorhinid trademarks of *Centroscyllium*, such as longer jaws, strong labial folds on the tooth crowns, and divergent but rounded root lobes, may then have evolved rapidly as a response to the altered function of the food-gathering apparatus. Although undeniably speculative, this might be a possible explanation for the *Centroscyllium*/*Etmopterus* body shape/lower jaw teeth paradox. *Centroscyllium* has yet no fossil record. This is probably because very little work has been done on Tertiary small-toothed deep-water selachians. A Miocene species, probably belonging to a new squaloid genus, was erroneously referred to *Centroscyllium* by Ledoux (1972).

## PALAEOECOLOGY

As would be expected, based on the deep-water habitat of most Recent squaloids, the pelagic white chalk at Kvarnby yielded a more diverse squaloid fauna than the slightly older Kristianstad Basin shallow-water strata. Five squaloids have been identified from Kvarnby: two etmopterines (*M. wardi* and *P. hemmooriensis*), two scymnorhinids (*C. schmidi* and *E. supracretaceus*), and one *Squalus* (*S. gabrielsoni*). Fragmentary material indicates that the Kvarnby squaloid fauna may include yet another *Squalus* along with a possible *Scymnodon*. The earliest Maastrichtian Kristianstad Basin strata have yielded four squaloids, i.e. *Squalus ballingsloevensis*, *S. balsvikensis*, *C. schmidi* and *P. hemmooriensis*.

Recent species of *Etmopterus* are all small (< 1 m) deep-water sharks, mostly occurring on or near the bottom on tropical and temperate continental and insular slopes (Compagno 1984). It is therefore surprising to find an abundance of *Proetmopterus hemmooriensis* teeth in the shallow coastal water facies strata of the Kristianstad Basin. Of the four sampled localities, the species is most common at Balsvik, where planktonic foraminifera constitute no more than 0·8–16 per cent of the total foraminiferal fauna (J. Gabrielson pers. comm.). The species is less common at Ballingslöv 1, Ballingslöv 2, and Bjärlången, where up to about 40 per cent of the foraminiferal fauna consists of planktonic forms, indicating somewhat deeper water. The great abundance of orectoloboid teeth at these three localities indicates also warmer water. In the Balsvik *B. lanceolata*-beds, orectolobids comprise only a few per cent of the selachian fauna, whereas the squaloids make up more than 50 per cent.

Newborn individuals of *Etmopterus spinax* are 0·12–0·14 m long compared to 0·33–0·45 m for most of the mature females (see Compagno 1984, p. 85). The 3:1 size ratio between the largest and smallest teeth for a given tooth position for the Balsvik material indicates that most ontogenetic stages are present. It thus seems likely that *P. hemmooriensis* not only entered the shallow basin to feed, seasonally or more permanently, but also used it as a breeding area. Extant *Etmopterus* feed mainly on small bony fishes, squid and crustaceans (Compagno 1984). Schools of at least one species, i.e. *E. virens* Bigelow *et al.*, 1953, seem to attack and kill fairly large squid (Compagno 1984, p. 88). One can easily imagine individual belemnites being attacked by a school of *Proetmopterus hemmooriensis*. The shallow, temperate waters of the Kristianstad Basin archipelago, with its abundance of belemnites, may have constituted such a temptation to etmopterine sharks that they were willing to sacrifice the relative safety of deeper waters. Although belemnite rostra are very common fossils in the Campanian of the Kristianstad Basin as well, warmer water (inferred from e.g. *Squalus*-group/rhinobatid teeth ratios) combined with an abundance of large lamnoid sharks (Siverson 1992) probably provided an unhealthy environment for tiny squaloids like *P. hemmooriensis*.

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# *ORTHAMBONITES* AND RELATED ORDOVICIAN BRACHIOPOD GENERA

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ABSTRACT. In a revised diagnosis, *Orthambonites* is restricted to a small group of late lower Ordovician (latest Arenig-Llanvirn equivalent) brachiopods from Baltoscandia. *Orthambonites rotunda* is proposed as the formal type species of the genus to replace *Orthambonites transversa* which is considered a *nomen dubium*. Revision of *Orthis calligramma* suggests in turn that it is a senior subjective synonym of *O. rotunda*, and thus becomes the effective type species of *Orthambonites*. Many species included previously within the genus are assigned to *Paralenorthis*, and to three new genera – *Sulevorthis*, *Sivorthis*, and *Shoshonorthis*. *Krattorthis* is defined as a new related genus. Neotypes are proposed for *O. rotunda* and *Sulevorthis lyckholmiensis*. A lectotype is designated for *Orthis callactis*, the type species of *Orthis*, which is discussed briefly in order to clarify past confusion with *Orthambonites*.

ONE of the most commonly quoted Lower Palaeozoic brachiopod genera in recent palaeontological literature is *Orthambonites* Pander, 1830. For many years this genus was regarded generally as a junior subjective synonym of *Orthis* Dalman, 1828, until Cooper (1942, p. 229) revived the use of the name *Orthambonites* to embrace a wide range of coarsely ribbed, biconvex, orthacean species. However, the relationships of these many species to type material of the genus have remained poorly understood, not least because Pander's original collections from the Ordovician of Ingria (St Petersburg district, Russia – also known by its Swedish name as Ingermanland) have been lost for well over a century (see below, pp. 23, 33). Cooper (1956, p. 294) recognized the likelihood that in its revived concept the genus is composite, and in working mainly on various Ordovician faunas from Baltoscandia we also concluded separately that a number of stocks are involved for which there remains a great amount of taxonomic imprecision and nomenclatorial confusion at both the generic and specific levels. This paper incorporates our combined data to revise some definitions and relationships within the '*Orthambonites* group' in the Baltoscandian area, and in turn this re-evaluation has enabled us to review the wider geographical and stratigraphical limits of the taxa involved.

Of particular importance for this study have been the extensive collections of orthacean brachiopods from Ingria housed in the Naturhistoriska Riksmuseet, Stockholm, the CNIGR museum and at VSEGEI in St Petersburg, and in the Institute of Geology in Tallinn, Estonia. These collections were made at various times during the nineteenth and twentieth centuries and are mostly from sections in the type area from where Pander's species were described, between the rivers Izhora and Ligovka to the south of St Petersburg (see Pander 1830, pl. 1, figs 1–3 and his un-numbered map). Some later authors such as Murchison *et al.* (1845, pp. 20, 28) and Schmidt (1897, p. 5) gave brief additional information on these sections in sketch maps and vertical profiles and commented on the faunas, but precise locality details for Pander's taxa remain unknown. We have also studied additional collections from Ingria from around Izvos on the Volkhov river some 120 km to the east-north-east of Pander's sections, from where contemporaneous brachiopods relevant to this paper have been described more recently (e.g. Alikhova 1953; Rubel 1961).

On the basis of all these collections it has been possible to try to assess some of the probable variation encompassed within Pander's (1830) very narrow species concept, which it is otherwise difficult to interpret only from his very short descriptions and his drawings of small shells at natural size; it should be noted, however, that in most cases Pander's illustrations appear to be fairly

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accurate representations of the specimens (as opposed to species) that he described, particularly with regard to number of ribs and general outline and convexity.

From the literature, we have noted some seventy species described within Cooper's (1942) broad definition of *Orthambonites*. The majority of these differ clearly from the distinctive but restricted group of fairly large Baltoscandian late lower Ordovician species to which we restrict the genus in this paper, typified by *O. calligramma* Dalman, 1828. Many of the described biconvex species can be assigned fairly readily to other genera that we discuss here, but there still remain some twenty forms that are either poorly described, inadequately illustrated, based on poorly preserved specimens, or have somewhat deviating external features and no information on internal morphology; the generic reference of these cannot be determined at present (see also p. 58).

*Note on terminology*. In reference to stratigraphy and faunal distributions throughout this paper we use the terms 'lower', 'middle' and 'upper' for the Ordovician System only in an informal sense, but for consistency we relate this usage to the tripartite subdivision as applied commonly in Baltoscandia (for summary see Jaanusson 1982, p. 8, fig. 4). Because of imprecision in inter-regional and intercontinental correlations within the Ordovician, and in the absence of a globally applicable chronostratigraphical subdivision of the System, we record the distributions of genera and species in current local terminology appropriate to any particular region (mostly by reference to a Formation and/or to a 'regional Stage' or 'regional Series'). In some cases, where sufficiently precise data are available to allow correlation with the graptolite zonation, we refer to the graptolite succession determined in Skåne [Scania], southernmost Sweden (e.g. Jaanusson 1982, fig. 4). Apart from in the lower Ordovician, this zonation is close to that of the British standard succession, but in Skåne the definition of zonal boundaries is generally more precise, and correlation based on this region also has the advantage of giving close ties to the Ordovician North Atlantic conodont zonation (Bergström 1971*b*, 1986). For the many species referred to *Orthambonites* from the southern Appalachians of the USA (Cooper 1956), we base our age data on Ross *et al.* (1982), Jaanusson and Bergström (1980, fig. 7), and Bergström (1971*a*, fig. 10).

Morphological terminology follows that of Williams *et al.* (1965), with the addition of terms used by Jaanusson (1971) for hinge-teeth. Many papers refer to ribbing strength and patterns in brachiopods in a loose sense; differences in ribbing styles are important diagnostic characters in some of the taxa discussed here, and we emphasize our consistent differentiation between costae (first order ribs originating in the umbonal area), costellae (second order ribs arising by implantation or bifurcation beyond the umbonal area), and capillae (very fine radial ribs generally as micro-ornament on costae, costellae and in the interspaces between them). In referring to the relative dimensions of interareas, some authors use the term 'height' and others 'length' for the parameter taken sagitally from the centre of the hinge to the tip of the beak; we refer to this as the length of the interarea as it is measured sagitally along the length of the shell, and its true height is partly a function of its attitude relative to the commissural plane. All dimensions are given in millimetres (mm).

## SYSTEMATIC PALAEONTOLOGY

### Superfamily ORTHACEA Woodward, 1854
### Family ORTHIDAE Woodward, 1854
### Subfamily ORTHINAE Woodward, 1854
### Genus ORTHAMBONITES Pander, 1830

*Discussion of type species*. Under ICZN rules the formally designated type species of *Orthambonites* is *O. transversa* Pander, 1830 (subsequent designation by Schuchert and LeVene 1929, p. 90; some authorities refer to an earlier designation by Dall 1877, p. 51, but this is not valid as Dall only referred to the name as Pander's first listed species without specifying it as the type). In following previous usage, this species was in fact probably selected because it was the first in the list of seventeen nominal species of *Orthambonites* described by Pander and thus had page priority (Pander 1830, p. 81, pl. 22, fig. 1; an eighteenth species was named and figured by Pander on his pl. 16A, fig. 4 as *O. dubia*, but this was not described in the text; see also pp. 56–57 herein). However, as noted by Öpik (1934, p. 130), within each genus in his monograph Pander listed the assigned species consistently in a morphological series, beginning with what he considered as least 'typical' for the genus or even transitional to another genus. The most 'typical' representatives were normally listed in the middle of the sequence of species, and for this reason the first named taxon is usually a poor choice for the type of a brachiopod genus erected by Pander. Such an argument applies in the case of *Orthambonites*, to the extent that no author since Pander has described or illustrated material as '*O. transversa*' and it remains impossible to make such an identification with any certainty based only on the original illustrations and description. It is not unlikely that the original described and figured specimen (Pander 1830, p. 81, pl. 22, fig. 1) is an extreme variant in the morphological range of a species; in particular, the dorsal valve of this specimen is more strongly convex than is typical for Ingrian forms with the same size, outline and number of ribs. The material described in Pander's monograph is lost and is presumed to have been destroyed (L. E. Popov pers. comm.), so that without the possibility of examining characters of the original specimen that are unclear or are not shown on the figures, '*Orthambonites transversa* Pander, 1830' must be considered a *nomen dubium*.

Prior to Cooper's (1942, 1944, 1956) revival of the genus, this uncertainty as to the status of the type species was essentially academic since, as noted above, from almost immediately after its description by Pander it was generally regarded as synonymous with *Orthis*, following authorities such as Buch (1840*a*, 1840*b*), Eichwald (1840), Verneuil (*in* Murchison *et al.* 1845, p. 207), Bronn (1848, p. 852), Dall (1877, pp. 36–51), Hall and Clarke (1892, pp. 186, 236), Schuchert and LeVene (1929, p. 90), and Schuchert and Cooper (1932, pp. 75–76). Nomenclatorial confusion accompanying this synonymy was introduced by Buch (1840*a*, p. 206; 1840*b*, p. 18) when he used Pander's generic name *Orthambonites* as a specific name within the genus *Orthis*, and Pander's nominal species were all submerged within '*Orthis orthambonites*'; Eichwald (1840, p. 150) adopted Buch's usage, and then Verneuil (1845, p. 207) took the nomenclature one stage further in naming *Orthambonites* as a 'variety' of the Swedish species '*Orthis calligramma* Dalman, 1828'. Later authors tended to use only *calligramma* as a species name, with *Orthambonites* generally being synonymized within *Orthis*.

In this context it is important to note that in describing his many species for his 1830 monograph, Pander had not seen Dalman's 1828 publication and the original description of *Orthis* and *O. calligramma* (he makes no mention of Dalman's paper in the introduction, although he does refer to earlier work by the same author). Some evidence from later collections available to Pander suggests that he too subsequently accepted many of his *Orthambonites* species as synonyms of *O. calligramma* (see p. 33).

Schuchert and Cooper (1932, pl. 2, caption to figs 8, 12, 15) hinted that *Orthis* and *Orthambonites* might be separable following further study, but did not take that step at that time. With only a few exceptions, such as the brachiopod volume of the Soviet *Osnovy Paleontologii* (Alikhova *in* Sarycheva 1960, p. 187), Cooper's subsequent separation of the two genera has been generally adopted, but in the absence of data on the morphology of the type species, *Orthambonites* has usually been interpreted in relation to *O. calligramma*. Rubel (1961, p. 173) even listed *calligramma* as the type species of *Orthambonites*, but since this was not one of the taxa included originally in the genus by Pander it cannot qualify objectively as the type. Problems of generic definition have also been compounded by the fact that *O. calligramma* itself has been interpreted within rather broad morphological limits and has not been described or illustrated adequately on the basis of type material subsequent to its original description from high lower Ordovician beds in southern Sweden (Dalman 1828); the species name has been applied to numerous Ordovician and Silurian forms or 'varieties' from many parts of the world (e.g. Giovannoni and Zanfra 1979, table 1 and fig. 7).

From our examination of Ingrian collections, we consider that some material described from the region by previous writers as *Orthambonites calligramma* (Alikhova 1953; Rubel 1961) in fact closely matches Pander's description (1830, p. 82) of *Orthambonites rotunda*. In this respect there is one important anomaly between Pander's text and illustrations, despite their otherwise apparent accuracy as noted above; his description of *O. rotunda* states that it has 'at least thirty ribs', whereas on the illustration (Pander 1830, pl. 22, fig. 5) there are only 26 distinct ribs; for the following species, *O. aequalis*, he stated (p. 82) that there are 'twenty-six flat ribs', whereas in this case the illustration (pl. 22, fig. 6) has 30 (possibly 31) ribs. This is the only such anomaly of which we are aware in Pander's brachiopod descriptions. It appears to us therefore that in this example the descriptions and figures have become transposed; we here regard the description as having page priority and thus being definitive. Despite the somewhat typological application of these figures of rib numbers, it is important in this historical context to understand Pander's own concept of his species in order now to apply his nomenclature. Thus we interpret Pander's original specimen of *rotunda* as having about 30 primary ribs.

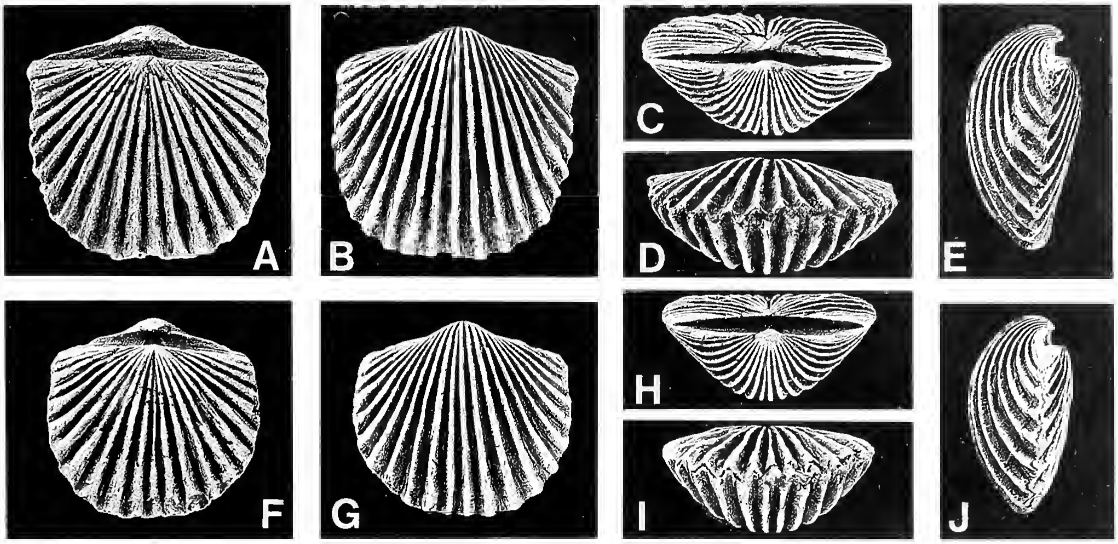
Given that specimens occurring commonly in Ingria can now be matched with *O. rotunda*, and that this is one of Pander's original species included in *Orthambonites*, with a morphology that satisfies the accustomed usage of the genus, it appears to be the best choice as a substitute type species; it is also from the middle part of the list of Pander's species of *Orthambonites* and can therefore be assumed to represent what he considered as a 'typical' form. With regard to the accustomed usage, it should be noted that, for example, this species from Ingria was used to typify the genus *Orthambonites* in the *Treatise on Invertebrate Paleontology* (Williams *in* Williams *et al.* 1965, fig. 196: 4*a–e*; taken from Alikhova 1953 and named, following her, as *O. calligramma*).

In order to stabilize the concept of the genus we are submitting an application to the ICZN to set aside previous designations and to rule that the type species of *Orthambonites* be designated as *Orthambonites rotunda* Pander, 1830.

The corollary to this formal requirement of designating one of the originally named species as the type species (ICZN 1985, Articles 67*g*, 69ai) is discussed further below (pp. 25, 33) in consideration of the relationships of *O. rotunda* and *O. calligramma*. It is sufficient at this point to note that we consider *rotunda* to be a junior subjective synonym of *calligramma*, so that the latter will effectively act as the type species for practical, comparative purposes.

It is also relevant here to discuss two further species named by Pander (1830) which have added confusion to the interpretation of *Orthambonites*. The Stockholm collections from Ingria include a number of specimens whose general size range, convexity, relative length of interareas, and number and style of ribs agree with illustrations of *Orthambonites tetragona* Pander (1830, p. 81, pl. 22, fig. 3*a–d*), and whose range of variation also encompasses shells similar to Pander's illustrations of *Orthambonites rotundata* (Pander 1830, p. 81, pl. 22, fig. 4*a–d*). It has been suggested that *O. transversa* is conspecific with *O. rotundata* (Öpik 1939, p. 122) or with both *O. rotundata* and *O. tetragona* (Alikhova 1953, p. 31). However, material of the two latter forms identified by us (all named here as *tetragona*, the senior name by page priority) clearly does not belong to *Orthambonites* of accustomed usage and as diagnosed in this paper; *tetragona* is a fairly small species (known maximum length 15 mm) with weak dorsal curvature, 20–23 strong costae, and distinct concentric fila but no trace of radial capillae. Rubel (1961, pl. 19, figs 1–5) described and figured conspecific shells as *Glossorthis* sp. a, and the exterior features certainly have a general similarity to this genus (Rubel recorded 26 costae but in the specimen in question – his pl. 19, fig. 2 – the ornament at the dorsal left cardinal angle is abnormal, possibly due to slight injury). Alikhova (1969, p. 25) questioned the reference of Rubel's specimen to *Glossorthis* and suggested that it may represent a juvenile shell of *Orthis* (i.e. including *Orthambonites* in her sense), but on the basis of the absence of capillate ornament this is certainly not correct. One reason for Alikhova's doubt was that she (1969, p. 25) considered *Glossorthis* to be restricted to the lower half of the middle Ordovician (Viru Series), whereas Rubel's specimen is from the immediately underlying beds (Kundan Stage, Aluojan Substage). However, in the Stockholm collections '*O.*' *tetragonus* occurs in association with other species indicating a basal Viru (Aserian) age, and it is likely therefore that the species ranges from the Aluojan Substage to the Aserian Stage. We have no information on the internal features of *tetragonus* so that its generic reference must remain uncertain, but on the basis of its external morphology (Text-fig. 1) we believe tentatively that Rubel's (1961) assignment of this form to *Glossorthis* is possible though not yet proved.

If *O. transversa* were to be retained as the type species of *Orthambonites*, and if Öpik's (1939) and Alikhova's (1953) views were supported as to its synonymy with '*O.*' *rotundata* and '*O.*' *tetragona*, then this would mean that *Orthambonites* would become restricted to quite a different group of



TEXT-FIG. 1. *Glossorthis? tetragona* (Pander, 1830); dorsal, ventral, posterior, anterior and lateral views of two conjoined shells demonstrating differences from *Orthambonites* in external morphology (see text for discussion). A–E, RM Br73943; F–J, RM Br73944. Both from Pulkova, Ingria, exact horizon unknown, ×2.

orthaceans than in common usage, and it may even prove to be a senior subjective synonym of *Glossorthis* Öpik, 1930. This serves further to emphasize the status of *O. transversa* as a *nomen dubium* and lends support to an unambiguous definition of *Orthambonites* based on *O. rotunda* [= *calligramma*].

### *Generic diagnosis of* Orthambonites

Subequally biconvex to ventribiconvex, curvature moderate to strong, anterior commissure rectimarginate, shells relatively large, ventral interarea short, concave, weakly apsacline to orthocline. Ornament costate or rarely with very few costellae (known range 19–37 ribs in adult specimens), fine capillae and concentric fila well developed. Ventral vascula media long, straight, closely adjacent and parallel for much of their extent proximally. Dental plates suberect to receding, ventral muscle field extends only slightly anterior to delthyrial cavity, anterior margin gently rounded to weakly lobed. Cardinalia stout, notothyrial platform thickened; brachiophores simple, blunt bosses, cardinal process a simple ridge.

### *Species assigned to* Orthambonites

*Orthis calligramma* Dalman, 1828 (defined and described below as a basis for comparison of the many forms that have been identified as this species; *Orthambonites rotunda* Pander, 1830 and *Orthambonites lata* Pander, 1830 are regarded here as junior subjective synonyms of *O. calligramma*, and they are thus discussed further below following the description of the latter); *Orthambonites aequalis* Pander, 1830; *Orthis kreklingensis* Öpik, 1939; *Orthambonites majusculus* Rubel, 1961; *Orthambonites fundata* Rubel, 1961; ?*Orthis novitas* Öpik, 1939.

*Remarks.* We have examined all available type material to confirm these assignments to *Orthambonites*. In his description of *O. fundata*, Rubel (1961, p. 178) mentioned only the presence of concentric fila as micro-ornamentation on the costae, but re-examination of Rubel's type material confirms that radial capillae are present both on and between the primary ribs; most of the specimens are worn and the capillae are thus not readily apparent, but where developed they closely match the pattern seen in *O. calligramma* (Pl. 1, figs 1*f*–*g*, 2*f*). The dorsal valve of *O.*? *novitas* resembles that of *O. kreklingensis* except that it has a few costellae developed medially (Pl. 3, fig. 6);

the taxonomic significance of this difference is difficult to assess without the availability of a larger sample of *O.*? *novitas*, but we provisionally include this species within *Orthambonites* and include a restricted development of costellation within our generic diagnosis. All other species assigned above to *Orthambonites* show no costellation. The long, closely adjacent ventral vascula media that characterize *Orthambonites*, and which help to distinguish the genus from others described in this paper, are particularly well illustrated in Plate 2, figure 1, and by Schuchert and Cooper (1932, pl. 2, fig. 18) and Rubel (1961, pl. 15, fig. 8).

*Occurrence*. The above group of species is restricted geographically to Baltoscandia, within a narrow time interval of the late lower Ordovician (latest Arenig to early-mid Llanvirn equivalent; Kundan Stage; uppermost *Didymograptus hirundo* to *Didymograptus* '*bifidus*' Zone; southern and central Sweden, northern Estonia, Ingria, and the Oslo region of Norway). No undoubted representatives of the genus are known from outside Baltoscandia.

### *Orthambonites calligramma* (Dalman, 1828)

Plate 1, figs 1–3; Plate 2, figs 1–7; Plate 3, fig. 1

| | |
|---|---|
| v*1828 | *Orthis calligramma* Dalman, p. 30, pl. 2, fig. 3*a–d*. |
| 1830 | *Orthambonites rotunda* Pander, p. 82, pl. 22, fig. 6 [*non* fig. 5; see text above]. |
| 1830 | *Orthambonites lata* Pander, p. 82, pl. 22, fig. 7*a–d*. |
| v.1837 | *Orthis calligramma* Dalman; Hisinger, p. 71, pl. 20, fig. 10*a–c*. |
| 1932 | *Orthis* cf. *calligramma* Dalman; Schuchert and Cooper, pl. 2, figs 7, 9, 11, 13. |
| ?1932 | *Orthis rotunda* (Pander); Schuchert and Cooper, pl. 2, figs 10, 16, 18. |
| v.1953 | *Orthis calligramma* Dalman; Alikhova, p. 30, pl. 2, figs 1–5. |
| v.1960 | *Orthis calligramma* Dalman; Alikhova *in* Sarycheva, pl. 9, figs 12–14. |
| v.1961 | *Orthambonites calligramma* (Dalman); Rubel, p. 177 *pars* [*non* pl. 15, fig. 1]. |
| v.1965 | *Orthambonites calligramma* (Dalman); Williams *in* Williams *et al.*, fig. 196: 4*a–e*. |
| *non* 1985 | *Orthis calligramma* Dalman; Cocks, p. 56, pl. 5, fig. 2.2A–C [= *O. callactis* Dalman, 1828] |

*Holotype* (by monotypy). RM Br102501, conjoined valves, figured Pl. 1 fig. 2*a–g*; from Skarpåsen, Östergötland, Sweden; almost certainly from the lower part of the zone of *Asaphus* (*Asaphus*) *raniceps* ('Raniceps Limestone'), topmost lower Ordovician (Kundan Stage, lower Valastean Substage, lower *D.* '*bifidus*' Zone); the original specimen collected by Olivecrona and figured both by Dalman and Hisinger (see synonymy). Dalman's description (1828, p. 30) appears to refer to a single specimen and in the absence of evidence to the contrary we thus consider that this is the holotype rather than a lectotype.

*Material*. The species is not particularly common in the topotype area in Östergötland and specimens from there are normally not well preserved; the Stockholm collections from this region are mostly from localities at Borghamn and Husbyfjöl. Our description is based in addition on samples from the lower part of Valastean age beds on northern Öland, and particularly on well-preserved specimens from sections at Hälludden and Hagudden (e.g. RM Br106189-Br106195). The

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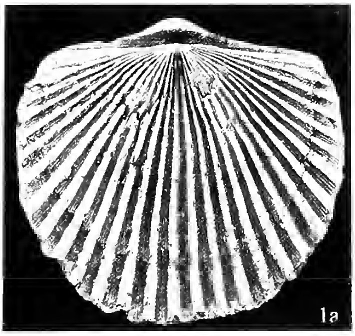
EXPLANATION OF PLATE 1

Figs 1–3. *Orthambonites calligramma* (Dalman, 1828). 1*a–g*, neotype of *Orthambonites rotunda* Pander, 1830; RM Br66169; Voka Beds, Kundan Stage, lower Valastean Substage ($B_{III}\beta$); Pulkova, Ingria, Russia; dorsal, ventral, lateral, posterior and anterior views of conjoined valves, with details of capillate ornament on left anterolateral and right anterolateral flanks of dorsal valve; *a–e* × 2, *f–g* × 10. 2*a–g*, holotype; RM Br102501; figured Dalman 1828, pl. 2, fig. 3*a–d* and Hisinger 1837, pl. 20, fig. 10*a–c*; probably from the Raniceps Limestone, Kundan Stage, lower Valastean Substage; Skarpåsen, Östergötland, Sweden; dorsal, ventral, lateral, posterior and anterior views of conjoined valves, with details of fine capillae and fila on right anterolateral and left anterolateral flanks of ventral valve; *a–e* × 2, *f* × 8, *g* × 10. 3*a–d*, RM Br106189; lower Raniceps Limestone, Kundan Stage, lower Valastean Substage; Hagudden (level +45 +20D), Öland, Sweden; dorsal, ventral, lateral and anterior views of conjoined valves, × 2.

PLATE 1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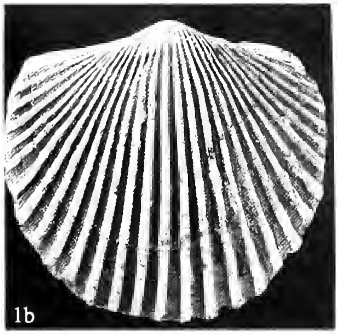
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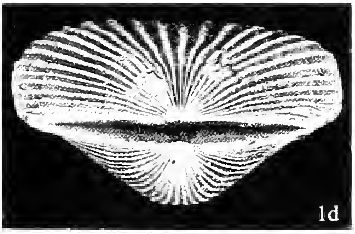
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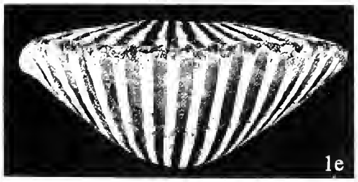
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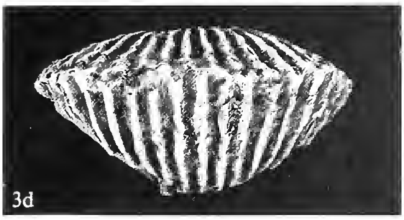
1g


2f


2g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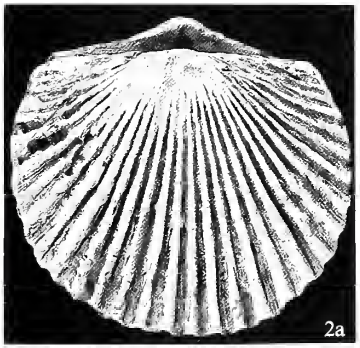
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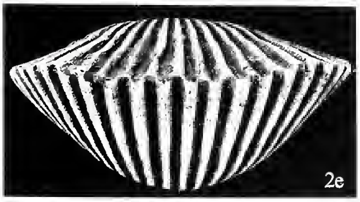
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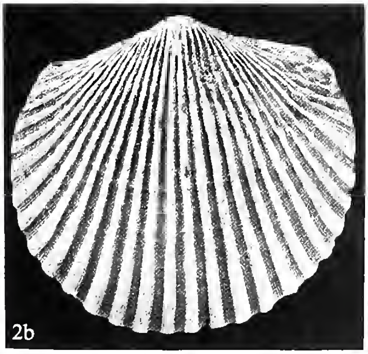
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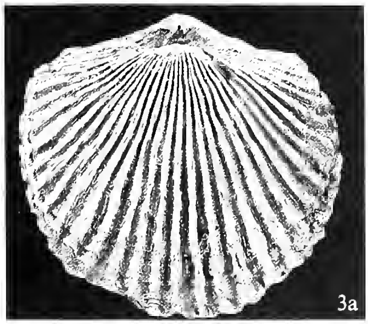
2c


3c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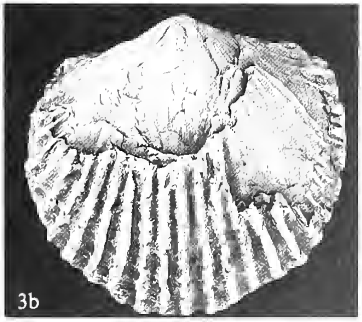
3b

JAANUSSON and BASSETT, *Orthambonites*

range of *O. calligramma* at Hälludden was shown by Jaanusson and Mutvei (1982, fig. 7). The contemporaneous specimens described by Alikhova (1953) and Rubel (1961) from Ingria have also been examined, together with smaller samples from Pulkova in Ingria and from Tsitre in northern Estonia.

*Description*. Initially ventribiconvex, mature shells subequally biconvex to only slightly ventribiconvex, with uniform transverse and longitudinal curvature or with dorsal valve flattening slightly peripherally, maximum depth 52–67 per cent of maximum width in three mature shells. Subcircular at maturity, some juvenile dorsal valves approaching subtriangular, 95 per cent as long as wide (OR 91·1–96·6; n = 4), dorsal valve about 90 per cent as long as ventral valve. Cardinal angles obtuse to rounded, hinge width 76–97 per cent (mean 84 per cent; n = 4) of maximum width, which is close to the mid-length. Lateral and anterior margins evenly curved, commissures crenulate, anterior commissure rectimarginate or very weakly deflexed ventrally in peripherally flattened shells. Umbones low, inconspicuous, ventral beak suberect, not curved over the hinge line. Ventral interarea short, gently concave, weakly apsacline, delthyrium open with a rounded apex, delthyrial angle from about 50° to 75°. Dorsal interarea plane, anacline, notothyrium open.

Ornament costate and capillate, ribs initially relatively slender, rounded, 11 in a 10 mm arc at the 10 mm growth stage of the dorsal valve, widening gradually anteriorly to become subrounded to subflattened at the anterior margin of mature shells. Commonly 30–32 ribs on mature dorsal valves (OR 29–37). The costae are straight with an amplitude close to 0·5 mm and a wavelength anteriorly of up to 2 mm, interspaces and ribs of subequal width. In the available material there is only one example of a rib originating outside the umbonal area, arising on the flanks of a costa at the 2·5 mm growth stage. Both costae and interspaces bear slender, rounded capillae with a mean spacing of 4 to 5 per mm (Pl. 1, figs 1*f*–*g*, 2*f*), though they are commonly worn on the rib crests. Growth lines normally weak to inconspicuous, but very fine, slightly lamellose fila are present over the whole surface (Pl. 1, fig. 2*g*).

Delthyrial cavity large and deep, with a thick, concave pedicle collar lining about half the height of the posterior wall. The collar is buttressed anteriorly by a subflattened, tapering median septum that extends anteriorly for about 30 per cent of the length of the delthyrial cavity. Teeth relatively large, deltidiodont, bluntly rounded in outline, supported by thick, suberect dental plates; lateral cavities shallow. Muscle field deeply impressed, subpentagonal, extending anteriorly beyond the delthyrial cavity for about 30% of the valve length, widest at the base of the dental plates (25 per cent of maximum valve width) then tapering anteriorly to a straight anterior margin. Anterior to the dental plates the muscle field is unbounded by ridges, but is confined within a hollow defined by swollen, rounded margins. Diductor scars large, oval, divided posteriorly by the median ridge, adductor scars not clearly preserved on the material available but probably confined to a small area immediately anterior to the ridge. Across its full width the anterior margin of the muscle field merges smoothly into a broad, slightly raised ridge of shell that tapers anteriorly to about the mid-length of the valve and is grooved along its mid length; the raised lateral areas of the ridge represent the inner margins of thick vascular media of a saccate mantle canal system. From the anterior margin of the muscle field the vascula media extend anteriorly beyond the median ridge as long, closely adjacent, parallel, straight to slightly

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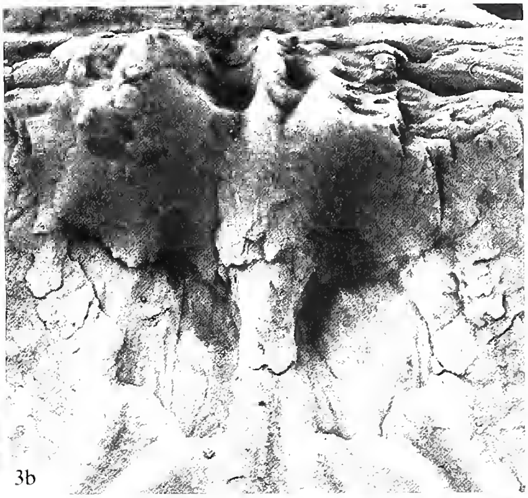
EXPLANATION OF PLATE 2

Figs 1–7. *Orthambonites calligramma* (Dalman, 1828). 1, RM Br20218; lower Raniceps Limestone, Kundan Stage, lower Valastean Substage; Hälludden, northern Öland, Sweden; mould of interior of exfoliated ventral valve showing long, parallel, proximally adjacent vascula media, ×2. 2, RM Br106191; horizon and locality as for fig. 1; interior of dorsal valve, ×2. 3*a*–*b*, RM Br106190; horizon and locality as for fig. 1, level +41 +46D; interior of dorsal valve (×2) and oblique-anterior detail of cardinalia showing the thickened brachiophores and notothyrial platform (×6). 4*a*–*b*, RM Br106192; horizon and locality as for fig. 1; interior of dorsal valve (×2) and oblique-lateral detail of cardinalia (×4; right hand brachiophore broken away). 5*a*–*b*, RM Br106193; horizon and locality as for fig. 1; loose in section; interior of ventral valve (×2) and oblique-anterior detail of delthyrial chamber showing the distinctive pedicle collar. 6, CNIGR 21/7135; figured Alikhova 1953, pl. 2, fig. 5; Kundan Stage; Volkhov River between Obukhovo and Simonkovo, Ingria, Russia; interior of dorsal valve, ×2. 7*a*–*e*, CNIGR 17/7135; figured Alikhova 1953, pl. 2, fig. 1*a*–*e*; horizon and locality as for fig. 6; dorsal, ventral, lateral and anterior views of conjoined valves (×1·5), with detail of capillate ornament on left anterolateral flank of dorsal valve (×5).

# PLATE 2


1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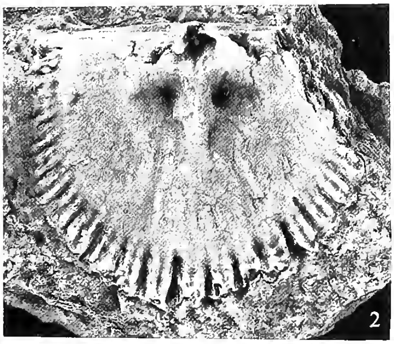
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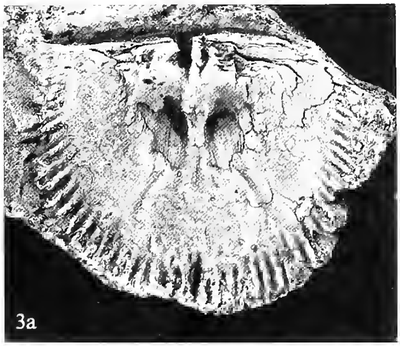
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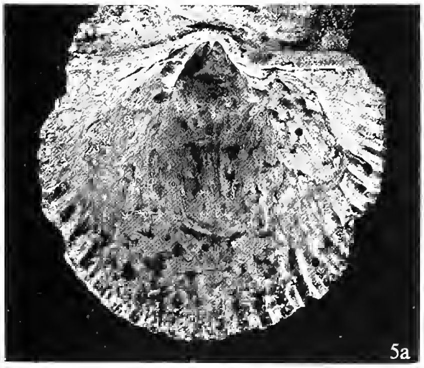
4a


4b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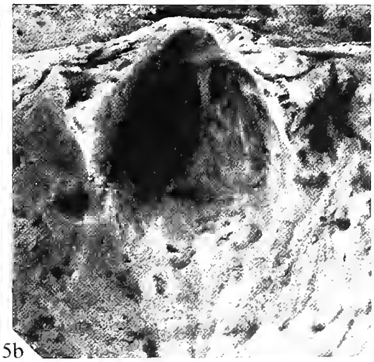
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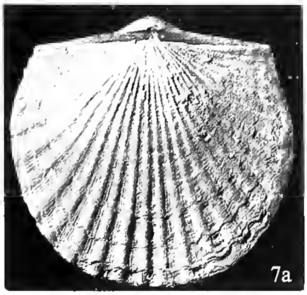
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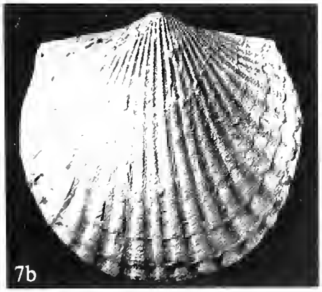
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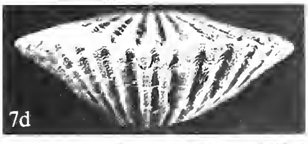
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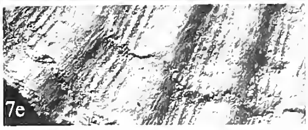

7e

JAANUSSON and BASSETT, *Orthambonites*

arcuate tracks that reach to well over 80 per cent of the valve length, curving laterally and then posteriorly only close to the anterior margin around the crenulated rim formed by the impress of the external ribbing (Pl. 2, fig. 1).

Cardinalia robust, increasingly thickened with growth, raised on a stout notothyrial platform that occupies up to 25 per cent of the valve length and merges smoothly anteriorly with a broad, swollen, longitudinal median ridge that decreases gradually in height to the anterior margin of the muscle field just posterior to the mid-length of the valve; the ridge occupies up to about 13 per cent of the valve width and may be weakly carinate along its length, though it is usually rounded by secondary shell in mature individuals, and anteriorly it may pass into a broad, shallow groove. Notothyrial cavity broad and deep, cardinal process a simple, thick ridge with a rounded to subcarinate cross-section, produced anteriorly to merge smoothly with the posterior end of the median ridge. The deep muscle attachment hollows adjacent to the cardinal process may each be divided in two by a transverse, rounded ridge. Brachiophores thick, grooved along inner faces, sub-erect or with tops convergent relative to bases, divergent anterolaterally at about 100–120° to one another, originally bluntly triangular distally but becoming increasingly thickened and rounded with growth, with thick bases that swell out from the notothyrial platform and median ridge. Sockets large, suboval with well rounded floors. Dorsal muscle field deep, occupying about 30–37 per cent of valve width and 50 per cent of the length, bisected longitudinally throughout by the median ridge. Posterior scars set in deep, rounded hollows excavated partly below the notothyrial platform, separated from the smaller and less deeply impressed anterior pair in some specimens by short, transverse swellings from the median ridge. Vascular system apocopate, with broad, well impressed vascula media diverging anterolaterally from the centre of the anterior margin of the adductor muscle scars.

The internal periphery of both valves is crenulated strongly by broad, flat ridges with a shallow central groove, separated by deep, narrow, rounded intergrooves.

*Dimensions of figured specimens*

| | Maximum length ventral valve | Maximum length dorsal valve | Maximum width | Hinge width | Maximum thickness | Maximum number of ribs along commissure |
|---|---|---|---|---|---|---|
| RM Br102501, conjoined valves (Holotype) | 21·3 | 19·2 | 22·5 | 17·2 | 11·9 | 31 |
| RM Br106189, conjoined valves | 20·3 | 18·6 | 21·0 | 16·4 (est.) | 11·4 | 31 |

## EXPLANATION OF PLATE 3

Fig. 1. *Orthambonites calligramma* (Dalman, 1828). 1*a–c*, RM Br134535; Voka Beds, Kundan Stage, lower Valastean Substage ($B_{III}\beta$); Tsitre, Estonia; dorsal, ventral and lateral views of conjoined valves, ×2.

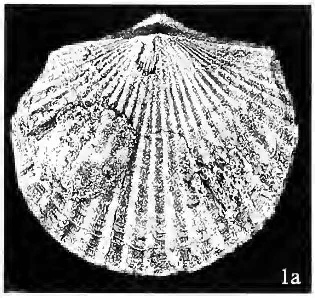
Figs 2–5. *Orthambonites* sp. All from Vokhovian Stage ($B_{II}$); Volkhov, Izvos, Ingria, Russia. 2*a–c*, RM Br116438; dorsal, ventral and lateral views of conjoined valves, ×2. 3*a–c*, RM Br116434; exterior of ventral valve (×2), detail of capillate ornament on left anterolateral flank (×5), and interior of valve (×3). 4*a–b*, RM Br116435; interior and exterior of dorsal valve, ×3. 5, RM Br116429; interior of ventral valve showing proximally adjacent vascula media, ×2.

Fig. 6. *Orthambonites*? *novitas* (Öpik, 1939). Holotype; PMO 2338; figured Öpil 1939, pl. 5, fig. 5; Expansus Shale (3c$\beta$; Arenig); Rokstadåsen, Hedenstad, Oslo Region, Norway; latex cast of mould of dorsal valve and ventral interarea, ×2·5.

Figs 7–8. *Orthambonites kreklingensis* (Öpik, 1939). 7, holotype; PMO 61090*b*; figured Öpik 1939, pl. 1, fig. 1; horizon as for fig. 6; Krekling, Oslo Region, Norway; latex cast of interior of dorsal valve; ×3. 8*a–b*, PMO 61090*a*; horizon and locality as for Fig. 7; latex cast of exterior of dorsal valve (×2) and detail of capillate ornament on right anterolateral flank (×5).

Figs 9–13. *Paralenorthis proava* (Salter, 1866). All from Carmel Formation, Arenig Series; coarse sandstones in low scarp 90 m north-east of ruined cottage, Prys-Owain-Bach, Carmel, 2 km south-west of Llanerchymedd on B5112 road, Anglesey, north Wales, SH 3986 8282. 9, NMW 88.17G.1; internal mould of ventral valve, ×3. 10*a–b*, NMW 88.17G.2; internal mould of dorsal valve and latex cast, ×2. 11, NMW 88.17G.3; latex cast of internal mould of dorsal valve, ×2. 12, NMW 88.17G.4; internal mould of ventral valve, ×2. 13*a–b*, NMW 88.17G.5; internal mould of dorsal valve and latex cast, ×2.

PLATE 3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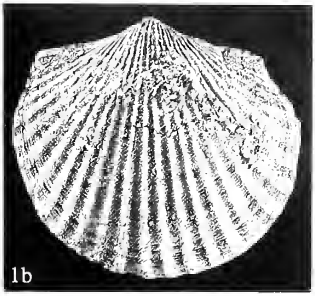
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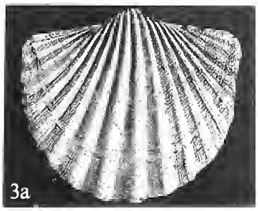
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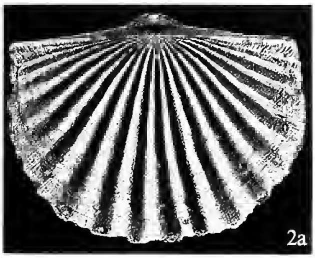
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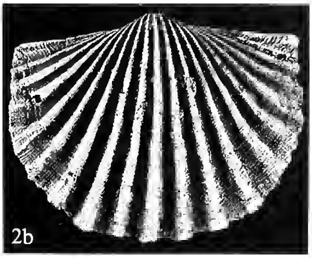
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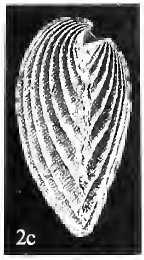
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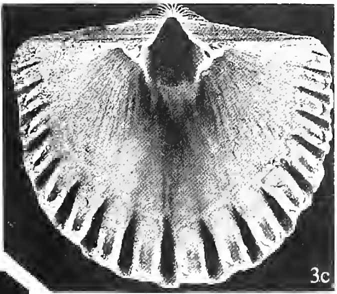
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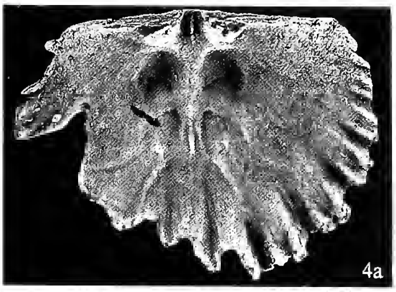
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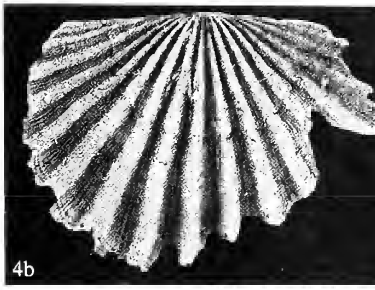
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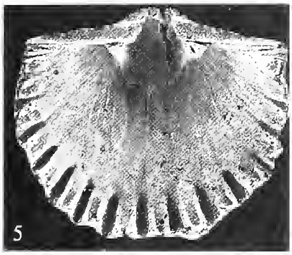
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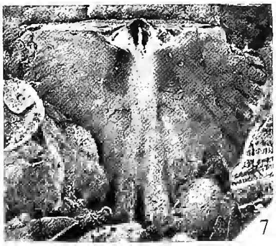
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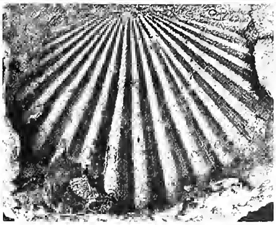
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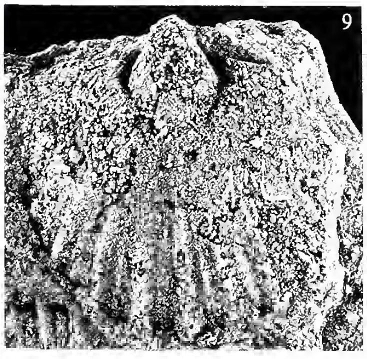
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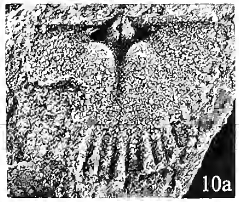
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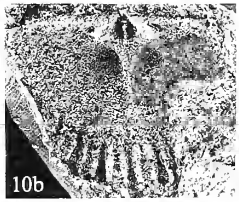
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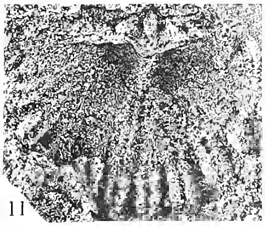
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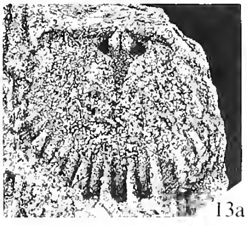
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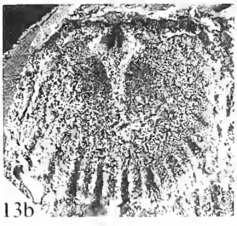
13b

JAANUSSON and BASSETT, *Orthambonites*, *Paralenorthis*

| | | | | | | |
|---|---|---|---|---|---|---|
| RM Br106193, ventral valve | 20·6 | — | 22·6 | — | 7·4 | > 33 |
| RM Br106190, dorsal valve | — | 18·8 | — | 22·0 (est.) | — | — |
| RM Br106191, dorsal valve | — | 19·2 | 22·5 | 21·8 (est.) | — | — |
| RM Br106192, dorsal valve | — | 15·8 | 16·9 | 14·1 | — | — |
| RM Br20218, internal mould of ventral valve | 30·5 | — | 32·9 | — | — | — |
| RM Br134535, conjoined valves | 23·2 | 20·9 | 24·6 | 20·5 (est.) | 11·3 | 29 |
| RM Br66169, conjoined valves [= Neotype of *O. rotunda*] | 20·5 | 18·8 | 21·3 | 17·7 | 9·9 | 30 |
| CNIGR 17/7135, conjoined valves | 24·0 | 21·9 | 25·7 | 20·5 | 19·1 | 30 |
| CNIGR 21/7135, dorsal valve | — | 15·8 | 18·2 | 13·0 | 9·9 | 32 |

*Occurrence.* Despite being recorded from many areas and stratigraphical levels throughout the world, *O. calligramma* is known with certainty only from the lower Valastean Substage of the Kundan Stage in Sweden, northern Estonia, and Ingria.

*Comparison. O. fundata* and *O. majuscula* are approximately contemporaneous species in different facies of Valastean beds at a slightly higher lithostratigraphical level than that at which *O. calligramma* occurs. *O. fundata* from the Pakri Sandstone has only 22–26 primary ribs and a weakly to moderately convex dorsal valve, contrasting with the relatively strong dorsal curvature of *O. calligramma* in which typical populations have 30–32 primary ribs as a mean, and in which only one specimen that we have examined has fewer than 30 ribs (29). *O. majuscula* also differs from *O. calligramma* in its weak dorsal convexity and in having fewer primary ribs; in the latter respect, Rubel (1961, p. 175) reported a range of 20 to 33 ribs in *majuscula*, but examination of the type series (by M. G. B.) shows that 22 or 23 is the most common figure (23 on the dorsal valve of the holotype). The higher number of ribs in some larger specimens suggests some overlap with *O. calligramma*, but apart from the differences in convexity, *majuscula* also differs in having somewhat flatter costae, smaller, less robust teeth, only a very weak ridge anterior to the ventral muscle field, and a cardinal process that is swollen at its mid length. Both *majuscula* and *fundata* have the radial and concentric micro-ornament typical of *calligramma*, and both have the long, subparallel ventral vascula media and stout brachiophores diagnostic of the genus. *O. kreklingensis* and *O*? *novitas* are both readily separable from *O. calligramma* by their weaker dorsal convexity and more slender ribbing, and as noted above (p. 25), *novitas* also differs in having costellae developed medially.

Rubel (1961, p. 177, fig. 9) examined the variation in number of ribs in *Orthambonites* specimens through successive stratigraphical levels in the Kundan of the Volkhov river section in Ingria, ranging from the base of the Valastean Substage to the lower part of the Aluojan Substage; he interpreted the pattern as variation within a single species, *O. calligramma*, showing upward decrease in rib numbers from 30–34 in the lower Valastean to 19–22 in the uppermost Valastean to lower Aluojan. No specimens were recorded with 23–24 or 27–29 ribs, and our comparison of Ingrian specimens in the Stockholm collections also suggests that the variation is discontinuous; unfortunately these latter collections lack stratigraphical control. Swedish specimens of *O. calligramma* from lower Valastean beds mostly have 31–33 ribs (OR 29–34), matching closely with Rubel's material from the same level in Ingria, and since there are no consistent differences in other morphological features these forms are considered to be conspecific (note that the full range of our Ingrian collections assigned to *calligramma* is 29–37 ribs). Ingrian specimens with 25–26 ribs from the middle part of the Valastean Substage may be a separate species; in rib number, outline and convexity they resemble Pander's figure of *Orthambonites aequalis* Pander, 1830, pl. 22, fig. 5 (but not fig. 6, see p. 23). Rubel's forms with only 19–22 ribs at the top of his section are present in our collections, and they might again represent a separate species. However, in order to define the differences between these forms more precisely a statistical study would be required, for which adequate collections are not available.

*Remarks.* We have commented above on the likely synonymy of *O. calligramma* and *O. rotunda*, which we base on the close similarity in outline, convexity, attitude and relative lengths of the interareas, and number of ribs. From a study of the original description and illustrations we also consider that *O. lata* Pander, 1830, p. 82, pl. 22, fig. 7 is a probable synonym of *O. calligramma*. Alikhova (1953, p. 30) also synonymized these three species (note that her inclusion of Pander's name *aequalis* is a reference to the original figure, which as we have noted above on pp. 23–24 was transposed with that of *rotunda*).

L. E. Popov (VSEGEI, St Petersburg) has confirmed for us that the whereabouts of all the specimens used by Pander for his 1830 monograph have been unknown for over a century, and that they must be regarded as lost. In view of our recommendation and pending application to the ICZN to recognize *O. rotunda* as the formal type species of *Orthambonites*, it is desirable to stabilize the specific name by designation of a neotype. We here designate RM Br66169 accordingly; it is from Pulkova, Ingria, and some limonitic ooids in the adhering matrix indicate that it is from the Voka Beds (Kundan Stage, lower Valastean Substage; Pl. 1, fig. 1*a–g*). In outline, convexity, and rib number (30) this specimen matches Pander's original illustration and description in close detail; it is also from one of the sections described by Pander in his original study area. The presence of this form in the Voka Beds of Ingria reinforces the view that it is a junior synonym of *O. calligramma*, as this is the level from where Rubel (1961, fig. 9, lowest part of graph) recorded what we take to be typical specimens of *calligramma*.

In searching for Pander's original material in St Petersburg, L. E. Popov discovered some collections now housed in the Palaeontological Museum of the Institute of Technical Geology (Gorny Institut), and these were studied by M.G.B. in 1983. The specimens were probably not collected by Pander himself, but most likely he obtained them as late as the 1850s from P. Jeremeyev, a State Captain in the Engineering Corps of the Russian Army; included are brachiopods from well known localities in Ingria, including Popovka and Izvos, and the associations suggest that they are mostly from the Volkhovian, Kundan, and Aserian stages. Although not the type material, these collections have some relevance to Pander's own concept of *Orthambonites* and to the possible synonymy of *O. rotunda* and *O. calligramma*. Among the orthacean brachiopods present are specimens of *Orthambonites*, *Nicolella*, *Orthis*, *Glossorthis*?, and *Cyrtonotella*. All the *Orthambonites* specimens are named as *Orthis calligramma* and they were probably identified and named as such by Pander himself (L. E. Popov pers. comm.); in a number of cases some of the other genera are also included within samples identified as *calligramma*. The evidence from these collections suggests that at that time Pander probably believed all his *Orthambonites* species to be synonyms of *O. calligramma*. Suppression of *O. transversa* as the formal type species of the genus, and even the possible synonymy of *O. rotunda* with *O. calligramma* does not therefore alter the concept of the genus as seen subsequently by Pander himself.

### Genus PARALENORTHIS Havlíček and Branisa, 1980

*Type species. Paralenorthis immitatrix* Havlíček and Branisa, 1980; from un-named upper Arenig or Llanvirn beds of San Lucas, Bolivia.

*Diagnosis.* Subequally biconvex with only moderate curvature, ventral valve slightly carinate, dorsal valve weakly sulcate, shells comparatively small, ventral interarea apsacline. Ornament costate or rarely sparsely costellate, and capillate. Ventral muscle field extending anteriorly only slightly beyond the delthyrial cavity, anterior margin rounded or faintly lobate; ventral vascula media diverge immediately in front of the muscle field. Cardinal process a simple ridge, brachiophores blunt bosses.

*Nomenclatorial history of the genus.* Andreeva (*in* Andreeva and Nikiforova 1955) erected *Lenorthis* based on material from the middle Ordovician of the Siberian Platform, but reported subsequently (Nikiforova and Andreeva 1961, p. 73) that the type species of *Lenorthis*, *L. girardi*, had been based by mistake on a combination of a ventral valve of a *Mimella* species and a dorsal valve of a *Hesperorthis*. As based on the lectotype of the type species (designated subsequently by Havlíček and Branisa 1980, p. 16), *Lenorthis* is a junior subjective synonym of *Hesperorthis*. Unfortunately the taxonomic status of *Lenorthis* as corrected by Nikiforova and Andreeva (1961) escaped the attention of many brachiopod specialists for a number of years.

Williams (*in* Williams *et al.* 1965, p. H311) redefined *Lenorthis* for *Orthambonites*-like forms with ventral vascula media that diverge from immediately in front of the muscle field. It should be noted that the species used by him to illustrate the genus – *L. mostellerensis* (Cooper, 1956) – is included in this paper (p. 38) in our new genus *Sulevorthis*. Williams's concept of *Lenorthis* was used subsequently by several writers (e.g. Bates 1968, 1969; Williams 1974). Because *Lenorthis* is not now available for this group of species (see also Neuman and Bates 1978, p. 588), Havlíček and Branisa (1980) established *Paralenorthis* as a replacement for *Lenorthis* in the sense of Williams (*in* Williams *et al.* 1965), with a type species from Bolivia.

Our survey of *Orthambonites*-like genera reveals that a number of species groups have ventral vascular media which diverge widely from their proximal extremities close to the anterior margin of the muscle field; for example, in addition to *Paralenorthis* this feature is typical of *Sulevorthis* gen. nov. and may also be a constant characteristic of *Shoshonorthis* gen. nov. In redefining *Paralenorthis* therefore we recognize a combination of characters, of which the nature of the ventral vascula media is just one; the divergent pattern referred to above does appear to be useful consistently as a contrast from the long, subparallel tracks of *Orthambonites*.

*Species assigned to* Paralenorthis

*Paralenorthis immitatrix* Havlíček and Branisa, 1980; *Productus orbicularis* Pander, 1830; *Spirifer alatus* J. de C. Sowerby *in* Murchison, 1839; *Orthis calligramma* var. *proava* Salter, 1866; *Orthis panderiana* Hall and Clarke, 1892; *Orthis calligramma* var. *serica* Martelli, 1901 [*Orthis calligramma* var. *chinensis* Chang, 1934 and

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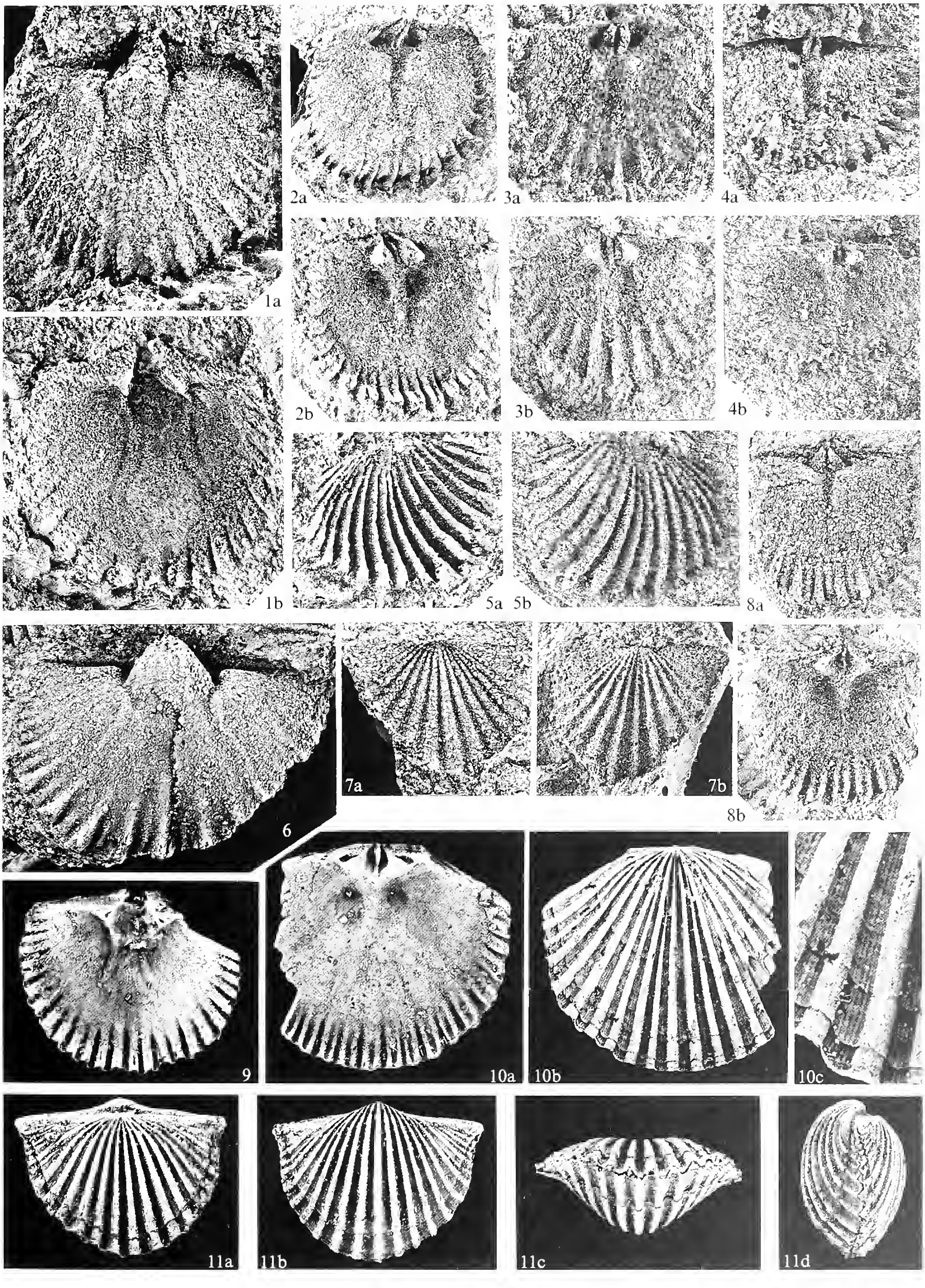
EXPLANATION OF PLATE 4

Figs 1–5. *Paralenorthis robusta* (Neuman, 1964). All from R. B. Neuman syntype collection; Shin Brook Formation, Whiterock Series; falls in Crommet Brook, Penobscot County, Shin Pond quadrangle, north-eastern Maine, USA (USGS locality CO-3608; locality E of Neuman 1964, p. E12). 1*a*–*b*, USNM 423930*a*; internal mould of ventral valve and latex cast, showing posteriorly separated and divergent vascula media, × 3. 2*a*–*b*, USNM 423933*a*; internal mould of dorsal valve and latex cast, × 2. 3*a*–*b*, USNM 423932; internal mould of dorsal valve and latex cast, × 2. 4*a*–*b*, USNM 423931*a*; internal mould of dorsal valve and latex cast, × 2. 5*a*–*b*, USNM 423931*b*; external mould of ventral valve and latex cast, × 2.

Figs 6–8. *Paralenorthis proava* (Salter, 1866). All from Carmel Formation, Arenig Series; coarse sandstones in low scarp 90 m north-east of ruined cottage, Prys-Owain-Bach, Carmel, 2 km south-west of Llanerchymedd on B5112 road, Anglesey, north Wales, SH 3986 8282. 6, NMW 88.17G.6*a*; internal mould of ventral valve showing posteriorly separated and divergent vascula media, × 3. 7*a*–*b*, NMW 88.17G.6*b*; external mould of dorsal valve and latex cast, × 2. 8*a*–*b*, NMW 88.17G.6*c*; internal mould of dorsal valve and latex cast, × 2.

Figs 9–11. *Paralenorthis orbicularis* (Pander, 1830). All from Volkhovian Stage; Izvos, Ingria, Russia. 9, RM Br73924; interior of ventral valve showing posteriorly separated and divergent vascula media, × 3. 10*a*–*c*, RM Br73923; interior and exterior of dorsal valve ( × 3) and detail of capillate ornament on left posterolateral flank ( × 10). 11*a*–*d*, RM Br73922; dorsal, ventral, anterior and lateral views of conjoined valves, × 3.

PLATE 4



JAANUSSON and BASSETT, *Paralenorthis*

*O. calligramma* var. *hupehensis* Chang, 1934 were regarded by Xu and Liu (1984, p. 68) as synonyms of *P. serica*]; *Orthis marshalli* Wilson, 1926; *Orthis buttsi* Schuchert and Cooper, 1932 [*pro O. crassicosta* Butts, 1926 *non Orthambonites crassicosta* Pander, 1830]; ?*Orthis minusculus* Phleger, 1933; *Orthis alabamensis* Ulrich and Cooper, 1938; ?*Orthambonites angulatus* Cooper, 1956; *Orthambonites robustus* Neuman, 1964; *Orthambonites riojanus* Levy and Nullo, 1973; *Orthambonites mollesensis* Levy and Nullo, 1973.

*Discussion.* Of the above fourteen species assigned to *Paralenorthis*, four were recorded by Williams (1974, p. 53) as *Lenorthis* (*P. orbicularis*, *P. alata*, *P. proava*, and *P. panderiana*). Two further species (*P. immitatrix* and *P. marshalli*) were included in *Paralenorthis* by Havlíček and Branisa (1980). The other species referred to *Lenorthis* or *Paralenorthis* in these two papers are here assigned to *Sulevorthis* gen. nov. According to Ross (1970, p. 54), *Orthis subalata* Ulrich and Cooper, 1938, is a junior subjective synonym of *P. marshalli* Wilson, 1926.

Specimens in which the ventral vascula media are divergent from their proximal ends are known in *Paralenorthis orbicularis* (Pl. 4, fig. 9), *P. alata* (Bates 1969, pl. 3, fig. 3; pl. 5, figs 3, 5), *P. proava* (Bates 1968, pl. 2, figs 3, 6; Pl. 4, fig. 6; *cf.* Williams 1974, pl. 8, fig. 2), *P. marshalli* (Ross 1970, pl. 3, fig. 9), *P. angulata* (Cooper 1956, pl. 36, fig. 20), *P. robusta* (Neuman 1964, pl. 1, figs 1, 3, 5; Pl. 4, figs 1*a*–*b* herein), *P. immitatrix* (Havlíček and Branisa 1980, pl. 1, figs 2, 4) and *P. mollesensis* (Levy and Nullo 1973, pl. 1, figs 11–19).

Levy and Nullo (1973) compared one of their new species ('*Orthambonites*' *riojanus*) from the Molles Formation in the Famatina Range of the Argentinian Precordillera with one North American species that we assign here to *Paralenorthis* (*P. buttsi*), and a second that we assign (see p. 38) to *Sulevorthis* (*S. blountensis*). They also compared their second species ('*O.*' *mollesensis*) with a North American species assigned here to *Sulevorthis* (*S. rotundiformis*). Although we have not examined the Argentinian specimens we consider that the descriptions and illustrations of both *riojanus* and *mollesensis* suggest an assignment to *Paralenorthis*, particularly in features of ornament, convexity, attitude of interareas, musculature, and nature of the ventral vascula media. The vascular pattern in Argentinian material was well illustrated originally by Kayser (as *calligramma*) as long ago as 1876 (pl. 3, fig. 18*a*). It is not unlikely that the two nominal species are conspecific. They are from the same Formation and locality and the described minor differences may be due to state of preservation. Minor variation in the described number of costae (18 in *riojanus* and 14–17 in *mollesensis*) is well within the range observed in other species of *Paralenorthis*. According to Levy and Nullo (1973, p. 140), the Molles Formation is of late Llanvirn to early Llandeilo age; other assessments suggest that the late Llanvirn correlation is most likely (e.g. Turner 1960, p. 96; Cuerda 1973, p. 285; Aceñolaza 1976, p. 483).

Martelli's (1901) original illustrations of '*Orthis*' *serica* from Hanzhong in southern Shaanxi Province, China, do not show the nature of the vascularia, but we assign this species to *Paralenorthis* on the assumption that specimens described and illustrated under the same name by Li *et al.* (1975, p. 103, text-fig. 51, pl. 11, figs 1–4) from the Xiliangsi Formation in the same general region are conspecific; in these specimens the ventral vascula media diverge laterally before the mid length of the shell, and in other details of convexity, ornament, attitude of interareas, and internal morphology the material conforms closely with *Paralenorthis*. Examination (by M.G.B.) of similar specimens from Guizhou Province identified as *O. serica* also confirms the general features of the genus and a close similarity with the British *O. proava*, although in the Guizhou collections the vascular tracks were again not preserved. In the other species included here within the genus the course of the main ventral vascular tracks has also not been observed because of poor preservation, so that generic assignment is only provisional on the basis of overall morphological similarity.

Micro-ornament is not always preserved in silicified specimens and in those embedded in coarse clastic matrix. In *Paralenorthis*, radial capillae have been observed in *P. orbicularis*, *P. alata*, *P.* cf. *proava* (Williams 1974, pl. 8, fig. 3), *P. panderiana*, *P. serica*, *P. buttsi*, *P. alabamensis* (traces, personal observations), and *P. immitatrix*.

The Baltoscandian *P. orbicularis* differs somewhat from other species assigned to the genus in having a shorter ventral interarea (Pl. 4, fig. 11*d*; Rubel 1961, pl. 14, figs 7, 11), a relatively more strongly convex dorsal valve, and shorter cardinalia and ventral muscle field. This species is provisionally retained in the genus because in several species of *Paralenorthis* the available information on relative valve convexities and interarea length and attitude is insufficient for further taxonomic discrimination.

*Paralenorthis* differs from *Orthambonites* in normally having a smaller adult shell (known maximum length of *Paralenorthis* is 18 mm; *Orthambonites* is consistently a relatively large genus, with a known maximum length up to 33 mm), a more distinctly sulcate dorsal valve, a somewhat carinate ventral valve, longer ventral interarea, and ventral vascula media that diverge anterolaterally from their proximal extremities. *Sivorthis* has proximally parallel ventral vascula media, is more finely ribbed, and the brachiophores appear to have a more elaborate morphology.

*Occurrence.* The above species are distributed widely through strata of mid lower to mid middle Ordovician age (*Didymograptus extensus* to *Glyptograptus teretiusculus* Zones):

SOUTH AMERICA: Bolivia, un-named upper Arenig or Llanvirn beds (*P. immitatrix* and *P.* cf. *alata*; Havlíček and Branisa 1980). Argentina, Precordillera, Famatina Range, Molles Formation of Famatina Group, probably upper Llanvirn (*P. riojanus* and *P. mollesensis*; Levy and Nullo 1973).

NORTH AMERICA: Northern Appalachians, Maine, Shin Brook Formation, Whiterock (*P. robusta*; Neuman 1964). Southern Appalachians, Blount belt, *G. teretiusculus* equivalents, Tennessee, Arline Formation (*P.*? *angulata*; Cooper 1956) and Alabama, Little Oak Formation (*P. buttsi*; Cooper 1956); Southern Appalachians, Alabama, Odenville Limestone, upper Ibexian (*P. alabamensis*; Ulrich and Cooper 1938). Quebec, Canada, limestone boulders in Levis Shale and Solomons Corners Formation, upper Ibexian (*P. panderiana*; Ulrich and Cooper 1938). British Columbia, Canada, Skoki Formation, Whiterock (*P. marshalli*; Wilson 1926; see also Ross 1970, p. 55). Great Basin of western USA, Nevada and California, Antelope Valley Formation, Whiterock (*P. marshalli* and *P.*? *minusculus*; Ross 1970); Utah, Juab Limestone, basal Kanosh Shale and dolomite equivalent of Swan Peak Quartzite, Whiterock (*P. subalata* [= *P. marshalli*]; Ulrich and Cooper 1938; Jensen 1967, p. 89).

CHINA: Hanzhong, southern Shaanxi Province, Siliangssu [Xiliangsi] Formation, Arenig equivalent above *D. protobifidus* and *D.* cf. *deflexus* faunas (*P. serica*; Martelli 1901; see also Li *et al.* 1975, p. 103; also Yang and Wang 1955, p. 125, pl. 66, figs 11, 14–17, 21; Wang *et al.* 1964, p. 91, pl. 9, figs 16–22); western Hupeh Province, Dawan Formation (*P. serica*; Zeng 1977, p. 37, pl. 10, figs 13–14); Sinan, Guizhou Province, Meitan Formation, Arenig (*P. serica*; M.G.B. personal observations with Rong Jia-yu); Sichuan Province, Arenig equivalent beds (*P. serica*; Xu *et al.* 1978, p. 285, pl. 115, fig. 6).

BALTOSCANDIA: Ingria and northern Estonia, upper Volkhovian – middle Kundan, Langevojan to Valastean substages (*P. orbicularis*; Rubel 1961, p. 175); Öland, Sweden, Kundan, Hunderumian to lower Valastean substages (*P.* sp. A; Jaanusson and Mutvei 1982, fig. 7).

BRITISH ISLES: All known occurrences are of Arenig age: Anglesey, Wales, Carmel Formation (*P. proava*; Bates 1968); Dyfed, Wales, Ogof Hen Formation and equivalents (*P. alata*; Bates 1969); Shelve inlier, Welsh Borderland, Mytton Flags (*P.* cf. *proava*; Williams 1974); Tourmakeady, Co. Mayo, Ireland, Tourmakeady Limestone (*P.* cf. *panderiana*; Williams and Curry 1985).

FRANCE: Montagne Noire, Couches du Foulon and lower Schistes du Landeyran (*P.* cf. *robusta*; Melou 1982).

### Genus SULEVORTHIS gen. nov.

v.1948 *Sulevorthis* Jaanusson and Martna, p. 186, *nomen nudum.*
v.1982 *Sulevorthis* Jaanusson, pp. 28, 30, 33, 35, 39 (fig. 7), *nomen nudum.*

*Type species. Orthis lyckholmiensis* Wysogórski, 1900; from the Nabalan, Vormsian, and lower Pirguan stages (*Pleurograptus linearis* – *Dicellograptus complanatus* Zones) of Estonia.

*Derivation of name.* From Sulev, a man's name in Estonian mythology.

*Diagnosis.* Shell comparatively small, dorsal valve moderately convex, non-sulcate or only faintly sulcate, ventral interarea short, weakly apsacline. Ornament with simple costae (known range in adult specimens 13–24) and fine concentric fila. Ventral muscle field limited to delthyrial cavity, most proximal parts of ventral vascula media either adjacent over a short distance and then divergent, or separated by a ridge and divergent from their origins. Brachiophores tabular, generally thick and elaborate with a flattened process; cardinal process a thick, simple ridge or swollen with a median crest.

*Species assigned to Sulevorthis*

*Orthis lyckholmiensis* Wysogórski, 1900 (redescribed below in order to clarify details of the type species of the genus); *Orthis playfairi* Reed, 1917; *Orthambonites bielsteini* Cooper, 1956; *Orthambonites blountensis* Cooper, 1956; *Orthambonites mostellerensis* Cooper, 1956; *Orthambonites parvicrassicostatus* Cooper, 1956; *Orthambonites rotundiformis* Cooper, 1956; *Orthambonites tennesseensis* Cooper, 1956; *Orthambonites cessatus* Williams, 1963; *Orthambonites humilidorsatus* Wright, 1964; *Orthambonites exopunctatus* Williams, 1974; *Orthambonites humilidorsatus albidus* Harper, 1984; *Orthambonites humilidorsatus primadventus* Harper, 1984; *Orthambonites humilidorsatus ultimus* Harper, 1984; ?*Orthambonites rectangulatus* Cooper, 1956 (assigned with doubt as the internal features are unknown).

*Remarks*. This genus has long been recognized in Baltoscandia as distinct from *Orthambonites*, and this recognition has been expressed previously in use of the generic name as a *nomen nudum* (see synonymy). In all species with the external characteristics of *Sulevorthis*, the proximal ends of the ventral vascula media are either subparallel and then divergent after a short distance, or are separated by a ridge or elevation of varying width and are divergent from their origins. The former condition is shown in *S. exopunctatus* (Williams 1974, pl. 8, fig. 15) and *S. rotundiformis* (Cooper 1956, pl. 34, figs 27, 38). Williams (1974) apparently thought that this feature in *S. exopunctatus* matched the course of the vascula media in *Orthambonites*, but as noted above (p. 36), in that genus the ventral vascula media are adjacent and subparallel for most of the valve length. A ridge anterior to the ventral muscle field is developed in many species of *Sulevorthis*, and its position relative to the vascula media is shown in *S. lyckholmiensis* (Pl. 6, fig. 3*a*), *S. playfairi* (Williams 1962, pl. 7, fig. 41) and *S. mostellerensis* (Cooper 1956, pl. 35, figs 7, 9).

At least two described species of *Sulevorthis* show distinctive exopunctation in a pattern offset along the rib crests (*S. lyckholmiensis*, Pl. 5, fig. 1*f*; *S. exopunctatus* Williams 1974, pl. 8, figs 10–12). This feature may be diagnostic of the genus as a whole but has not yet been reported in other named species, possibly because of poor preservation through silicification for example; we can confirm the presence of exopunctae in numerous specimens of undescribed species from middle and upper Ordovician successions in Norway, Sweden, and Estonia. *Orthambonites* as defined in this paper has a much larger shell (the smallest true *Orthambonites* is larger than the largest known *Sulevorthis*, which has a maximum length of 12 mm) and a different micro-ornament (*Sulevorthis* lacks radial capillae). There is a conspicuous difference in the structure of the brachiophores, which in *Orthambonites* form simple, blunt bosses but which are tabular in *Sulevorthis* and in well preserved specimens have moderately long, flattened brachiophore processes that reach far beyond the socket

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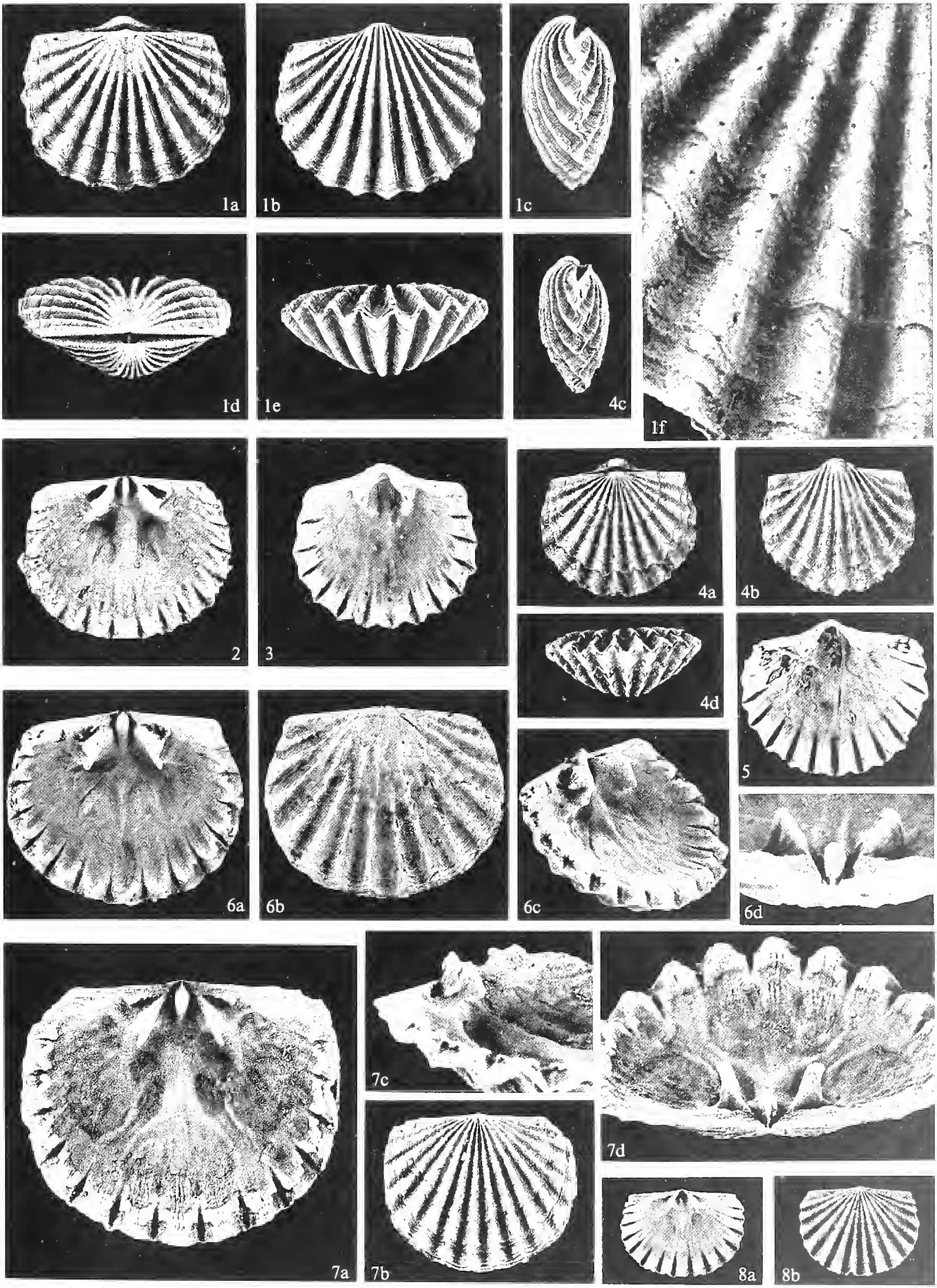
EXPLANATION OF PLATE 5

Figs 1–6. *Sulevorthis lyckholmiensis* (Wysogórski, 1900). All from Vormsian Stage (F$_1$b); Kõrgessaare, Hiiumaa, Estonia. 1*a–f*, neotype; TAGI BR4475; dorsal, ventral, lateral, posterior and anterior views of conjoined valves, with detail of exopunctuation on ribbing on left anterolateral flank of dorsal valve, *a–e* × 3, *f* × 12. 2, RM Br106198; interior of dorsal valve, × 3. 3, RM Br106199; interior of ventral valve, × 3. 4*a–d*, RM Br106196; dorsal, ventral, lateral and anterior views of conjoined valves, × 3. 5, RM Br106197; interior of pedicle valve, × 3. 6*a–d*, RM Br108633; interior and exterior of dorsal valve, oblique-lateral view of interior, and posterior view of cardinalia, *a–c* × 3, *d* × 5.

Figs 7–8. *Sulevorthis* cf. *S. lyckholmiensis* (Wysógorski, 1900). Both specimens from erratic blocks, Öland, Sweden (Hulterstad fauna, Harju Series, ?Pirguan Stage). 7*a–d*, RM Br4502; block 1; figured Wiman 1907, pl. 2, fig. 12–12*a*; interior and exterior of dorsal valve, oblique-lateral view of brachiophores, and posterior view of cardinalia, *a* × 5, *b* × 3, *c–d* × 6. 8*a–b*, RM Br4501; interior and exterior of juvenile dorsal valve, block 1, × 3.



JAANUSSON and BASSETT, *Sulevorthis*

area (Pl. 5, figs 2, 6*a*, *c–d*, 7*a*, *c–d*). It should be noted that in isolated valves of *Sulevorthis* the processes are not always preserved in their original shape, because these projections were easily worn off. However, even then the elaboration of the brachiophores is usually discernible. *Sulevorthis* is also readily distinguished from *Paralenorthis* in being non-capillate. In several regions *Sulevorthis* occurs in association with *Sivorthis* gen. nov. but it can be recognized immediately by its coarse, simple ribbing and its short ventral interarea.

*Occurrence*. *Sulevorthis* is a common genus in the Blount and Tazewell belts of the Appalachians, in the British Isles, and in Baltoscandia. Its known age range is from the mid middle to the late upper Ordovician (*Glyptograptus teretiusculus* to *Glyptograptus persculptus* Zones). In all regions it has generally previously been reported as *Orthambonites* or *Lenorthis*.

ESTONIA: Northern Estonia, Nabalan and Vormsian stages, Nybyan Substage of Pirguan Stage (*S. lyckholmiensis*; Wysogórski 1900; Oraspõld 1959, p. 59). *Sulevorthis* is notably absent from the middle Ordovician of the North Estonian confacies belt.

SWEDEN: The genus occurs widely through the central confacies belt in the middle-upper Ordovician of Sweden, including several different undescribed species (V.J. and M.G.B. unpublished data); Öland, erratic boulders with Hulterstad fauna, ?Pirguan Stage (*S.* cf. *lyckholmiensis*; Wiman 1907; this paper), and lower Dalby Limestone at Böda Hamn; Östergötland, Skagen Limestone and Jonstorp Formation, and in the Hirnantian Borenshult fauna; Siljan district, Dalarna, uppermost Dalby, Skagen, Skålberg and lower Jonstorp formations, flank facies of stromatactis-bearing carbonate mounds of Kullsberg Limestone (Wiman 1907, pl. 2, fig. 10) and Boda Limestone.

NORWAY: Oslo Region, Hugbergoya Shale Formation, Ashgill, Rawtheyan (*Sulevorthis* sp.; Cocks 1982, p. 758, pl. 78, fig. 5 as *Orthambonites* sp.); Hadeland, Gagnum Limestone Formation, early Ashgill (*Sulevorthis* sp. nov.; M.G.B. unpublished).

BRITISH ISLES: Shelve inlier, Welsh Borderland, Whittery Shales, Caradoc (*S. exopunctatus*; Williams 1974); Bala district, North Wales, Gelli Grin Group, Caradoc (*S. cessatus*; Williams 1963); Berwyn Hills, North Wales, Dolhir Formation, Ashgill, Rawtheyan, (*S.* cf. *humilidorsatus*; Hiller 1980); Girvan district, Scotland, Myoch Formation and Mill Formation of Whitehouse Group, Quarrel Hill Formation of Drummock Group, Caradoc-Ashgill, Onnian-Cautleyan (*S. humilidorsatus primadventus*, *S. humilidorsatus albidus*, *S. humilidorsatus ultimus*; Harper 1984); Girvan district, top of Stinchar Limestone to Craighead Limestone, Llandeilo-Caradoc (*S. playfairi* and *S.* aff. *humilidorsatus*; Reed 1917; Williams 1962); Ireland, Portrane Limestone, Ashgill, Cautleyan (*S. humilidorsatus*; Wright 1964); Ireland, Pomeroy, Killey Bridge Formation, Ashgill, Cautleyan (*S. humilidorsatus*; Mitchell 1977).

NORTH AMERICA: Southern and central Appalachians, Blount and Tazewell Belts only, *G. teretiusculus* to *D. multidens* equivalents, inclusive: Tennessee and Virginia, Arline Formation (*S. blountensis*; Cooper, 1956); Virginia, Maryland and Pennsylvania, Martinsburg, Oranda, Benbolt and Shippensburg Formations (*S. bielsteini*; Cooper 1956); Virginia, Benbolt, Effna, Botetourt and Chatham Hill Formations (*S. parvicrassicostatus*; Cooper, 1956); Alabama, Little Oak Formation (*S. mostellerensis*; Cooper 1956); Tennessee, Athens Formation (*S. rotundiformis*; Cooper 1956); Tennessee, Alabama and Virginia, Arline, Little Oak and Botetourt Formations (*S. tennesseensis*; Cooper 1956); Maryland, Shippensburg Formation (?*S. rectangulatus*; Cooper 1956).

Specimens described as '*Orthambonites*' *parvicrassicostatus* Cooper, 1956 by Nikitin and Popov (1984, p. 134, pl. 15, figs 1–2, 4, 7–8), from the middle Ordovician of the Chingiz mountains, Kazakhstan, do not appear to belong to this species; they differ from Cooper's material in having a more strongly convex dorsal valve and, particularly, a distinctly longer ventral interarea. On the basis of the latter feature we doubt that the Kazakhstan specimens belong to *Sulevorthis*, but their true generic identity requires further study.

### *Sulevorthis lyckholmiensis* (Wysogórski, 1900)

Plate 5, figs 1–6; Plate 6, fig. 3

| | |
|---|---|
| *1900 | *Orthis lyckholmiensis* Wysogórski, p. 12, pl. 8. |
| cf.v.1907 | *Orthis lyckholmiensis* Wysogórski; Wiman, p. 8, pl. 2, figs 9, 11–12*a* [*non* fig. 10 = *Sulevorthis* sp. nov.]. |
| cf.v.1948 | *Sulevorthis* cf. *lyckholmiensis* (Wysogórski) Jaanusson and Martna, p. 186 [generic name as *nomen nudum*]. |

v.1956 '*Orthis*' *lyckholmiensis* Wysogórski; Jaanusson, p. 382 [name only].
v.1959 *Orthis*(?) *lyckholmiensis* Wysogórski; Oraspõld, p. 57, pl. 2, figs 1–4.
1964 *Orthambonites lyckholmiensis* [(Wysogórski)] Wright, p. 161 [name only].

*Neotype* (designated here). TAGI Br4475, conjoined valves.; Pl. 5, fig. 1*a–f*; from Kõrgessaare, island of Hiiumaa, Estonia; Kõrgessaarean Substage, lower part of Vormsian Stage ($F_1b$), upper Ordovician (*Pleurograptus linearis* Zone); this horizon is equivalent to the low middle part of the Lyckholm Beds of former usage (Jaanusson 1944, 1956).

*Discussion*. Wysogórski's original material of *Orthis lyckholmiensis* is lost, but his brief description and illustration leave no doubt that it is the species that occurs fairly commonly in the 'Lyckholm Beds' of northern Estonia. In the absence of collections from Estonia, the species has generally been interpreted in terms of material described by Wiman (1907) under the same name from erratic blocks of upper Ordovician Hulterstad limestone (Jaanusson and Mutvei 1982) on Öland, Sweden. Our studies, however, indicate that the Öland material differs slightly from the Estonian forms (see Remarks below), and we consider it necessary to choose a neotype to clarify the definition of the species in its original sense. Apart from studying large collections in Estonia, including the material described by Oraspõld (1959), our interpretation is also based on further material housed in Stockholm (RM Br106196-Br106201, Br108633-Br108634).

*Description*. Subequally biconvex to slightly ventribiconvex, ventral valve uniformly curved, dorsal valve with very weak sulcus at the umbo, tending to die out anteriorly, maximum thickness close to 45 per cent of maximum width. Outline slightly transverse, suboval, 90 per cent as long as wide (OR 87·15–91·74; n = 4 pedicle valves), dorsal valves about 92 per cent as long as ventral valves. Cardinal angles obtusely rounded, produced as very short ears in some specimens, hinge width 85 per cent (OR 78·7–92·7; n = 6) of maximum width which is close to the mid-length. Lateral margins evenly curved or with a slight constriction immediately anterior to the hinge, anterior margin smoothly rounded. Commissures crenulate, anterior commissure rectimarginate. Ventral umbo rounded, beak suberect to weakly curved up to the hinge, dorsal umbo flattened, beak protruding slightly above lateral areas of cardinal margin. Ventral interarea short, flat to very gently concave, weakly apsacline, dorsal interarea flat, anacline. Delthyrium broad, open, apex rounded, delthyrial angle about 80°–90°, notothyrium open; both the notothyrium and base of the delthyrium are occupied by the posterior tip of the cardinal process.

Ornament costate, almost invariably with 14 or 15 costae in mature shells. Six costae in a 5 mm arc at the 5 mm growth stage of the dorsal valve. Ribs are initially low and rounded, becoming more angular but with slightly rounded crests, wavelength *c*. 1·5 mm in mature shells, amplitude *c*. 0·7–0·8 mm, interspaces weakly rounded to subflattened. Concentric ornament of fine, slightly lamellose fila and coarser growth lines. In well preserved specimens, minute but distinct exopunctae are visible just below the rib crests, normally arranged in offset pairs alongside the crests (Pl. 5, fig. 1*f*), but also singly in some specimens.

Delthyrial chamber broad and deep, with a small pedicle callist visible in some specimens. Teeth deltidiodont, weakly hollowed on their dorsal faces, which are bluntly triangular in outline, inner faces merging smoothly with delthyrial margins and bearing elongated, anteriorly widening fossettes. Dental plates short, receding and inclined gently inwards onto the floor of the valve. Lateral cavities shallow.

Ventral muscle field large, cordate, well impressed, widest at the base of the dental plates, unbounded outside the delthyrial chamber, occupying about 27 per cent of the valve width and up to 45 per cent of the length. Diductor scars large, tapering anterior to the dental plates, separated posteriorly by a very low flat ridge bearing the adductor scars; anterior to the adductors the elongated extensions of the diductor scars are set slightly lateral to the ridge, which in some specimens is produced into the anterior half of the valve as a low, rounded swelling. Ventral vascular system saccate, with broad, weakly divergent vascular media in shallow grooves arising at the elongate terminations of the diductor scars and branching well before the crenulations around the periphery of the valve.

Cardinalia fairly robust, set on a low notothyrial platform that is produced anteriorly either as a low, broad swelling or as a broad, rounded median ridge extending just beyond the mid-length of the valve; in some specimens the ridge tapers and extends beyond this point. Cardinal process with a simple, stout, rounded shaft merging smoothly into the median ridge, and a posteriorly directed attachment face that may protrude well above the valve margin and in some specimens is crenulated with a carinate crest.

Brachiophores robust, suberect, divergent anterolaterally at about 75° to one another, inner faces tabular, tops straight, distal edges straight to gently curved. Weakly swollen bases support the brachiophores for about

80 per cent of their length and merge smoothly into the floor of the valve to form posterolateral boundaries to the muscle field. Sockets deep, well developed, widening anterolaterally where they are bounded by rounded fulcral plates that extend as swellings onto the lateral faces of the brachiophores leaving a deep hollow in the face in its distal half. Muscle field subquadrate to subrounded, weakly quadripartite, well impressed, set in a hollow with no lateral and anterior bounding ridges, occupying about 40 per cent of the valve width and 50–55 per cent of the length. Vascular system apocopate, with well preserved intervascular ridges extending back across the muscle field.

The periphery of both valves is scored by long, strong crenulations that occupy about 25 per cent of the total length. The crenulations form broad, flat to weakly hollowed, scalloped ridges separated by narrow deep grooves.

*Dimensions of figured specimens*

| | Maximum length ventral valve | Maximum length dorsal valve | Maximum width | Hinge width | Maximum thickness | Maximum number of ribs along commissure |
|---|---|---|---|---|---|---|
| TAGI Br4475, conjoined valves, Neotype | 9·5 | 8·8 | 10·9 | 10·1 | 4·8 | 14 |
| RM Br106196, conjoined valves | 7·3 | 6·7 | 8·1 | 7·1 | 3·5 | 14 |
| RM Br106197, ventral valve | 8·3 | — | 9·7 | — | 2·7 | 15 |
| RM Br106198, dorsal valve | — | 8·7 | 10·7 | 8·7 | 1·9 | 15 |
| RM Br106199, ventral valve | 8·8 | — | 9·6 | 7·8 | 3·8 | 14 |
| RM Br108633, dorsal valve | — | 10·4 | 12·2 | 9·6 | 2·8 | 15 |
| RM Br108634, ventral valve | 10·0 | — | 10·9 | 9·6 | 3·5 | 15 |

*Occurrence. S. lyckholmiensis* is a common species through the Vormsian Stage of northern Estonia, and was also recorded by Jaanusson (1956) and Oraspõld (1959) from the underlying Nabalan Stage and the overlying Nybyan Substage of the Pirguan Stage.

*Remarks.* Wiman (1907, p. 8) described *lyckholmiensis* from Öland, Sweden in silicified material

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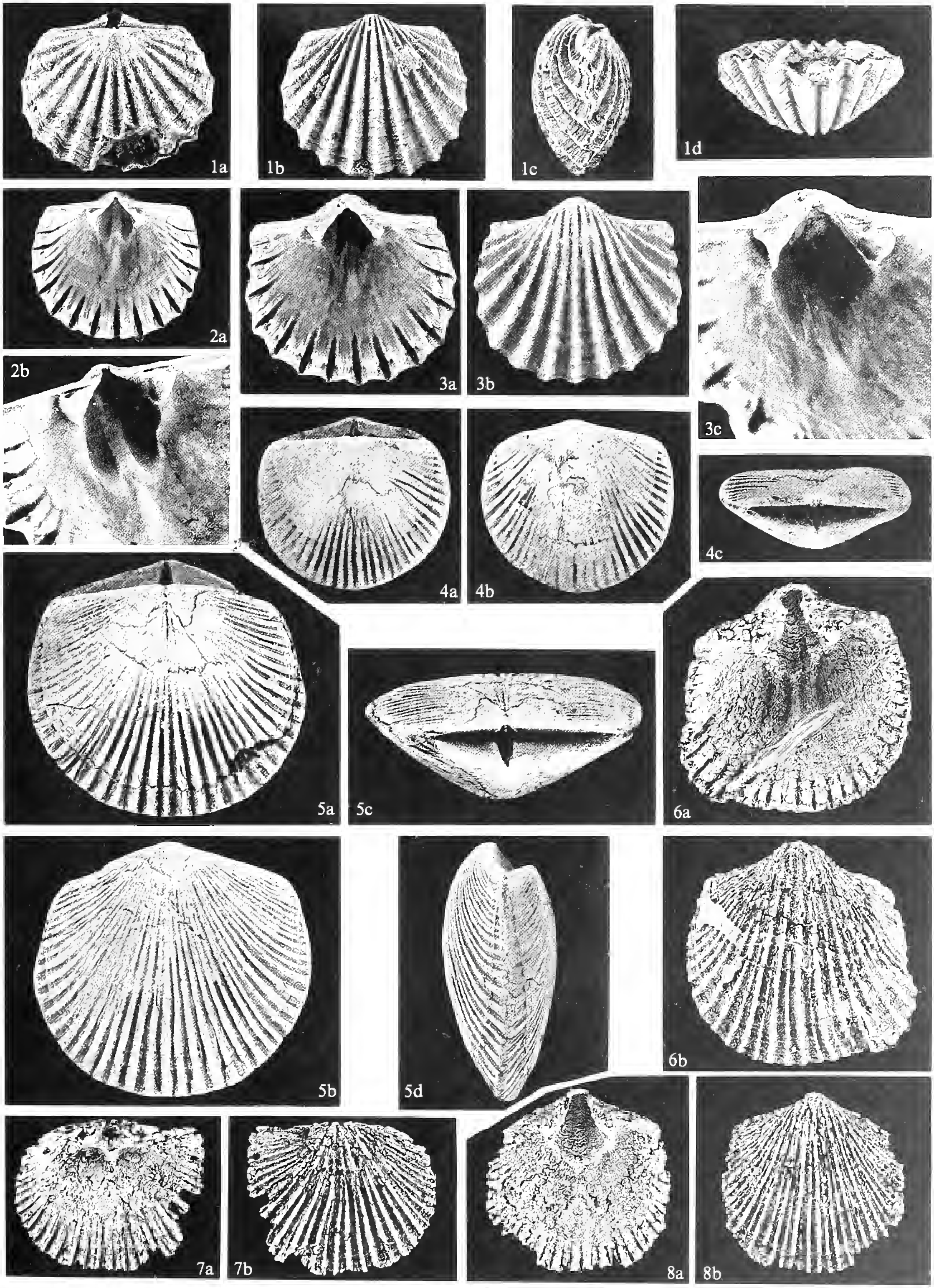
## EXPLANATION OF PLATE 6

Figs 1–2. *Sulevorthis* cf. *S. lyckholmiensis* (Wysogórski, 1900). Both specimens from erratic blocks, Öland, Sweden (Hulterstad fauna, Harju Series, ?Pirguan Stage). 1*a–d*, RM Br4503; block 54; figured Wiman 1907, pl. 2, fig. 9; dorsal, ventral, lateral and anterior views of conjoined valves, × 3. 2*a–b*, RM Br5004; block 1; figured Wiman 1907, pl. 2, fig. 11–11*a*; interior of ventral valve ( × 3) with oblique view showing stout dental plates and fossettes on inner faces of teeth ( × 6).

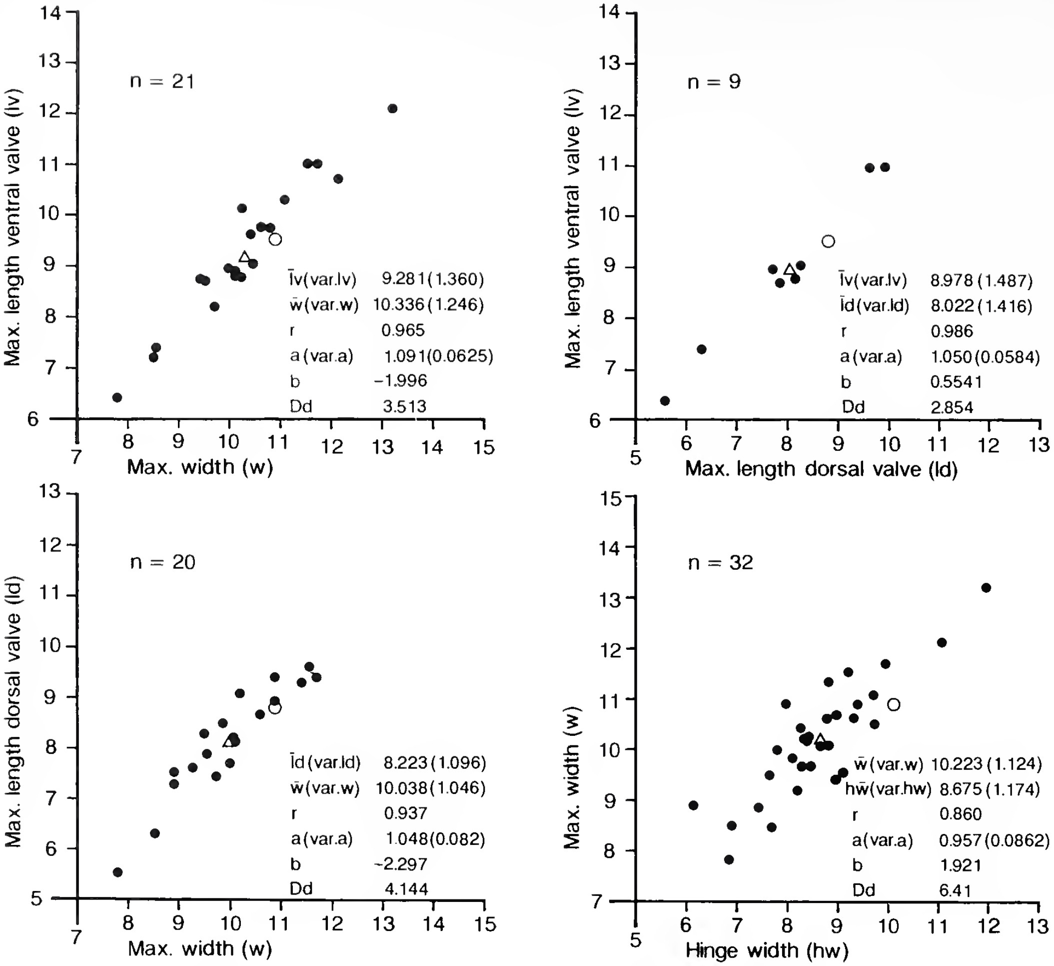
Fig. 3. *Sulevorthis lyckholmiensis* (Wysogórski, 1900). 3*a–c*, RM Br108634; Vormsian Stage ($F_Ib$); Kõrgessaare, Hiiumaa, Estonia; interior and exterior of ventral valve, with oblique view of delthyrial area (note the posteriorly separated vascular tracks), *a–b* × 3, *c* × 6.

Figs 4–5. *Shoshonorthis? ovata* Pander, 1830. 4*a–c*, RM Br73933; Kundan Stage; Ingria, Russia (exact horizon and locality unknown); dorsal, ventral and posterior views of conjoined valves; × 2·5. 5*a–d*, neotype; RM Br116406; horizon and locality as for fig. 4; dorsal, ventral, posterior and lateral views of conjoined valves; × 2·5.

Figs 6–8. *Sivorthis eucharis* (Ulrich and Cooper, 1938). All from upper Pogonip Group, Whiterock Series; ridge east of Frenchman Flat, Las Vegas quadrangle, Nevada, USA. 6*a–b*, RM Br87636; interior and exterior of ventral valve, × 3. 7*a–b*, RM Br87639; interior and exterior of dorsal valve, × 3. 8*a–b*, RM Br87637; interior and exterior of ventral valve, × 3.



JAANUSSON and BASSETT, *Sulevorthis*, *Shoshonorthis*?, *Sivorthis*



TEXT-FIG. 2. Bivariate plots and statistical characterization of a topotype sample of 32 specimens of *Sulevorthis lyckholmiensis* (9 conjoined valves, 12 ventral valves, 11 dorsal valves); same sample as used for Table 1. The open circle represents the plot of the neotype in each graph, with other specimen values plotted as solid circles; the triangle is a plot of the mean value for the sample.

etched from erratic blocks containing the Hulterstad fauna; the precise age of this material is uncertain, but it is possibly from Pirguan equivalents in Estonia (Ashgill, *Dicellograptus complanatus* and *D. anceps* Zones; Jaanusson and Mutvei 1982, p. 9) and thus slightly younger than the type material of *S. lyckholmiensis*. The small sample and silicified preservation of the Öland specimens makes comparison uncertain, but there is some suggestion that they are slightly more globose, with more elaborate brachiophore processes and a more anteriorly lobate ventral muscle field than the Estonian material; these relatively small differences may be of only intraspecific significance, but until the uncertainties and age relationships are resolved we identify the Öland specimens as *S.* cf. *lyckholmiensis* (Pl. 5, figs 7–8; Pl. 6, figs 1–2). Wright (1964, p. 163) similarly drew attention to differences between *lyckholmiensis s.s.* and the Swedish material described by Wiman (1907), and he considered that the latter might be related more closely to or even conspecific with *S. humilidorsatus* (Wright) from the Portrane Limestone (Ashgill) of Ireland. Some of the differences described by Wright are somewhat variable in the full range of material available from Öland, over and above that figured by Wiman, and in the light of the uncertainties mentioned above we consider an

TABLE 1. Statistics from a sample of 32 topotype specimens of *Sulevorthis lyckholmiensis*; Vormsian, Kõrgessaare, Hiiumaa, Estonia; sample housed in the Geological Institute, Estonian Academy of Sciences, Tallinn; lv = maximum length ventral valve, ld = maximum length dorsal valve, w = maximum width, hw = hinge width, t = thickness (conjoined or single valves as appropriate).

A CONJOINED VALVES; n = 9

| Variates | lv | ld | w | hw | t |
|---|---|---|---|---|---|
| Means | 8·99 | 8·04 | 10·10 | 8·73 | 4·72 |
| Variance-covariance matrix | 2·21 | 2·07 | 1·90 | 1·46 | 1·22 |
| | | 2·00 | 1·81 | 1·52 | 1·12 |
| | | | 1·68 | 1·37 | 1·02 |
| | | | | 1·50 | 0·72 |
| | | | | | 0·72 |

B VENTRAL VALVES; n = 12

| Variates | lv | w | hw | t |
|---|---|---|---|---|
| Means | 9·52 | 10·60 | 9·18 | 3·52 |
| Variance-covariance matrix | 1·62 | 1·48 | 1·36 | 0·61 |
| | | 1·50 | 1·42 | 0·50 |
| | | | 1·53 | 0·50 |
| | | | | 0·30 |

C DORSAL VALVES; n = 11

| Variates | ld | w | hw | t |
|---|---|---|---|---|
| Means | 8·41 | 10·0 | 8·15 | 1·90 |
| Variance-covariance matrix | 0·59 | 0·59 | 0·44 | 0·37 |
| | | 0·72 | 0·53 | 0·32 |
| | | | 0·70 | 0·36 |
| | | | | 0·39 |

identification as *S.* cf. *lyckholmiensis* to be more appropriate. Wright's text (1964, p. 163) implies that all of Wiman's (1907) material is from Dalarna in Sweden; in fact, of the figured specimens, only Wiman's pl. 2, fig. 10 is from Dalarna (Kullsberg Limestone, late Caradoc), with the remainder from the Hulterstad fauna of Öland. We consider that the Kullsberg Limestone *Sulevorthis* belongs to a new species (see p. 40 and synonymy, p. 40). Reed (1932, pp. 116, 117, 132, pl. 20, fig. 18) described a species as cf. *lyckholmiensis* from the upper Ordovician of the Trondheim region, Norway, but his reported presence of 'fine radial striae' on the ornament (i.e. capillae) suggests that this material does not belong to *Sulevorthis*.

## Genus SIVORTHIS gen. nov.

*Type species. Sivorthis filistera* sp. nov.; from the lower Dalby Limestone (near base of *Nemagraptus gracilis* Zone), Böda Hamn, Öland, Sweden.

*Derivation of name.* From Siv, the wife of Thor in Scandinavian mythology.

*Diagnosis.* Shell small to medium sized, dorsal valve moderately convex, non-sulcate to weakly sulcate, ventral interarea relatively long, fairly strongly apsacline. Costellate (known range of ribs 27–46 in adult valves), one or two generations of costellae intercalated in front of the umbo. Ventral muscle field relatively small, anterior margin almost straight to slightly rounded. Ventral vascula media parallel for about half of their extent between the muscle field and anterior valve margin, then broadly curved laterally (in at least two species). Brachiophores with relatively slender bases and a laterally compressed process; cardinal process a simple ridge, mostly slender.

*Species assigned to* Sivorthis

*Sivorthis filistera* sp. nov. (see description below); ?*Orthis* (*Plectorthis*) *ardmillanensis* Reed, 1917; *Orthis eucharis* Ulrich and Cooper, 1938; *Orthambonites bellus* Cooper, 1956; *Orthambonites friendsvillensis* Cooper, 1956; *Orthambonites multicostellatus* Cooper, 1956; *Orthambonites occidentalis* Cooper, 1956; *Orthambonites tenuicostatus* Cooper, 1956; ?*Orthambonites minus* Cooper, 1956; ?*Orthambonites minutus* Cooper, 1956.

*Discussion.* With a maximum recorded shell length of 15 mm, *Sivorthis* is typically much smaller than known species of *Orthambonites*, from which it is also readily distinguished externally by its considerably longer and more strongly apsacline ventral interarea and by the consistent development of costellae. The stout, simple brachiophores and long, subparallel ventral vascula media of *Orthambonites* contrast with the more compressed to tabular brachiophores and divergent vascular tracks of *Sivorthis*. Similar differences in ornamentation and in the cardinalia also separate *Sivorthis* from *Paralenorthis*. From *Sulevorthis*, which has adult shells of about the same maximum size, *Sivorthis* differs in having a relatively longer and more strongly apsacline ventral interarea, finely costellate ribbing, and more delicately constructed brachiophore bases; in *Sulevorthis* the tabular brachiophores are invariably supported by massive bases with thick secondary shell developed. The costellate ribbing of *S.*? *ardmillanensis* (Reed, 1917; Williams 1962, pl. 8, fig. 8) is of *Sivorthis* type, but this small species is otherwise poorly known.

The parallel course of the proximal portions of the ventral vascula media is indicated in specimens of *S. bella* (Cooper, 1956, pl. 35, fig. 48) and *S. friendsvillensis* (Cooper, 1956, pl. 36, fig. 8), and can be observed clearly in *S. eucharis* (Pl. 6, fig. 6*a*) and *S. filistera* (Pl. 7, figs 3*a*, 6*b*), in which the laterally curved continuation of the medial vascular tracks is also preserved in some ventral interiors.

Most of the known specimens of species assigned above to *Sivorthis* are silicified and the micro-ornament is obliterated or very poorly preserved. However, *S. tenuicostatus* has well defined concentrically lamellose fila (Pl. 7, figs 8*b*, 9), and examination of specimens of *S. bella* in the United States National Museum has revealed traces of similar sculpture. In other North American species no undoubted trace of the micro-ornament could be observed to compare with the fila and capillate pattern of *S. filistera*.

The distal part of the brachiophores is preserved only exceptionally in silicified specimens of *Sivorthis*. A specimen of *S. bella* shows somewhat compressed brachiophore processes (Cooper 1956, pl. 35, fig. 49 and personal observations), and the presence of a similar brachiophore structure is indicated in *S. friendsvillensis* (Cooper 1956, pl. 36, fig. 1). The general tabular shape of the processes resembles that of *Sulevorthis*.

*Occurrence.* With the exception of occurring also in the Great Basin of the western USA and in Oklahoma, known species of *Sivorthis* appear to have roughly the same geographical distribution as *Sulevorthis*. However, *Sivorthis* appears earlier, in rocks of Whiterock (Llanvirn equivalent) age and is not known to continue into the upper Ordovician. Occurrences in the southern Appalachians are restricted to the Blount confacies belt.

SWEDEN: Öland (central Baltoscandian confacies belt), lower Dalby Limestone, Viruan (*S. filistera* sp. nov.; see below).

BRITISH ISLES: Girvan district, Scotland, basal Ardwell Mudstones, Caradoc, lower *Diplograptus multidens* Zone (*S*? *ardmillanensis*; Reed 1917; Williams 1962).

NORTH AMERICA: Whiterock Series: Nevada, Antelope Valley Limestone (*S. occidentalis*; Cooper 1956) and upper Pogonip Group (*S. eucharis*; Ulrich and Cooper 1938); Utah, upper part of Garden City Formation (*S.* cf. *eucharis*; Ross 1968, p. H6, pl. 3, figs 1–7); Oklahoma, *G. teretiusculus* Zone equivalents, Tulip Creek Formation (*S.*? *minus*; Cooper 1956) and McLish Formation (*S.*? *minutus*; Cooper 1956). Southern Appalachian occurrences are all in *G. teretiusculus* to *D. multidens* Zone equivalents: Virginia, Chatham Hill Formation (*S. bella*; Cooper 1956), and Edinburg and Oranda Formations (*S. multicostellata*; Cooper 1956);

Tennessee, Arline Formation (*S. friendsvillensis*; Cooper 1956); Alabama, Pratt Ferry Formation (*S. tenuicostata*; Cooper 1956).

### *Sivorthis filistera* sp. nov.

Plate 7, figs 1–7

*Derivation of name.* Latin '*filum*', a thread – provided with threads; referring to the fine capillae and well developed, lamellose growth fila.

*Holotype.* RM Br116395, conjoined valves, lower Dalby Limestone (Viruan, approximately at base of *Nemagraptus gracilis* Zone), Böda Hamn, north-east Öland, Sweden; Pl. 7, fig. 1*a–e*.

*Paratypes.* RM Br116371-Br116394, Br116396-Br116405, Br17368, Br18287, Br16013-Br16015, all from same locality and horizon as holotype. RM Br18086-Br18087, from loose blocks of lower Dalby Limestone at Bocketorp, Oland, Sweden.

*Diagnosis.* Finely costellate (40–46 ribs observed) with well developed lamellose growth fila. Ventral interarea relatively long. Sockets confined within notothyrial platform, fulcral plates absent, dorsal median ridge tapering almost to anterior margin.

*Description.* Ventribiconvex, ventral valve uniformly curved transversely and longitudinally, dorsal valve only weakly to moderately convex with slightly swollen umbo and faint sulcus occupying median half of valve behind the umbo; maximum thickness approximately 45 per cent of maximum width. Outline subtriangular in some juvenile shells, becoming subrounded to subquadrate at maturity, subequally as long as wide (OR 82·96–104·61 per cent in 14 ventral valves), lateral margins almost straight to weakly curved, anterior margin smoothly curved; dorsal valves 83–91 per cent as long as ventral valves (n = 8 conjoined specimens). Cardinal angles gently rounded, hinge width equals maximum width in young shells, but at maturity the point of maximum width is close to mid length and hinge width is then approximately 90 per cent of maximum width (OR 82·3–100; n = 12). Commissures crenulate, anterior commissure weakly sulcate. Ventral umbo rounded, beak erect, dorsal umbo obscure to slightly swollen; ventral interarea relatively long, apsacline, plane to weakly concave, from about three to six times as long as the plane, anacline dorsal interarea. Delthyrium and notothyrium open, delthyrium narrow with rounded apex, delthyrial angle generally less than 45°, margins approaching subparallel in some specimens; cardinal process extends up into notothyrium.

Ornament costellate, most commonly with only one generation of branching. Ribs are low and rounded, equally spaced with an amplitude of about 0·7 mm at the commissure of mature shells, and number 14 to 16 in a 5 mm arc at the 5 mm growth stage of the dorsal valve. Interspaces subrounded. Fine capillae present on costellae and in interspaces, with a maximum of three observed between ribs, of which the central capilla then tends to be slightly stronger; fine but distinctly lamellose growth fila are preserved over and between the costellae (often worn away in the available samples).

Delthyrial chamber relatively broad and deep. Teeth blunt, deltidiodont with triangular dorsal faces which may be weakly concave; inner faces merge smoothly with delthyrial margins which bear elongated anteriorly widening fossettes. Dental plates short and blunt, erect, receding, lateral cavities shallow.

Ventral muscle field well impressed, subcordate, widest at the base of the dental plates from where low,

TABLE 2. Statistics from 20 syntype specimens (all conjoined valves) of *Sivorthis filistera*; lower Dalby Limestone (Viru), Böda Hamn, Öland, Sweden; sample housed at Naturhistoriska Riksmuseet, Stockholm; lv = maximum length ventral valve, ld = maximum length dorsal valve, w = maximum width, hw = hinge width, t = thickness.

| Variates | lv | ld | w | hw | t |
|---|---|---|---|---|---|
| Means | 11·10 | 9·93 | 12·0 | 10·4 | 5·11 |
| Variance-covariance matrix | 3·09 | 2·63 | 2·58 | 1·55 | 1·09 |
| | | 2·42 | 2·42 | 1·40 | 0·96 |
| | | | 2·91 | 1·59 | 0·84 |
| | | | | 1·27 | 0·52 |
| | | | | | 0·81 |

curved, rounded bounding ridges converge toward the anterior margin of the scars; the ridges die out anteriorly and the anteromedial part of the muscle field is either unbounded or rimmed by a very low flat pad of shell, with the anterior ends of the diductor scars separated by a shallow, broad hollow. The muscle field is slightly longer than wide, occupying about 25 per cent of the valve width and some 33 per cent of the length. Diductor scars large, longitudinally oval, widening anteriorly, separated by and extending beyond slender parallel adductor scars which are unbounded anteriorly. Ventral vascular system poorly preserved in available material, saccate with large gonadal areas bounded by weak vascula media which appear to be subparallel immediately anterior to the muscle field but curve anterolaterally at about the mid length of the valve.

Cardinalia raised on a wide platform, notothyrial cavity long, occupied by a slender, simple cardinal process which may be only slightly swollen anteriorly; the process merges smoothly into the anterior edge of the notothyrial platform which is produced anteriorly as a broad, rounded median ridge. Brachiophores poorly preserved in available material, but apparently simple and tabular. Sockets small, slightly elongated and relatively deep, excavated entirely within the lateral area of the notothyrial platform. No fulcral plates. Dorsal muscle field relatively large, subquadrate, occupying up to 30 per cent of valve width, unbounded laterally and anteriorly. Posterior adductor scars set immediately under anterior end of notothyrial platform, suboval, larger and deeper than the weakly impressed anterior scars. The broad, low, rounded median ridge occupies almost 50 per cent of the width of the muscle field, becoming lower between the anterior scars where it tapers to a narrow pad that extends almost to the anterior margin of the valve. Mantle canal system only weakly impressed but apparently digitate, with long vascula media extending from anterior muscle scars almost to anterior margin and only weakly divergent from median ridge, and large vascula genitalia occupying most of the posterolateral quarters of the valve.

The periphery of both valves is crenulated by strong, flat ridges separated by narrower, rounded grooves.

*Dimensions of figured specimens*

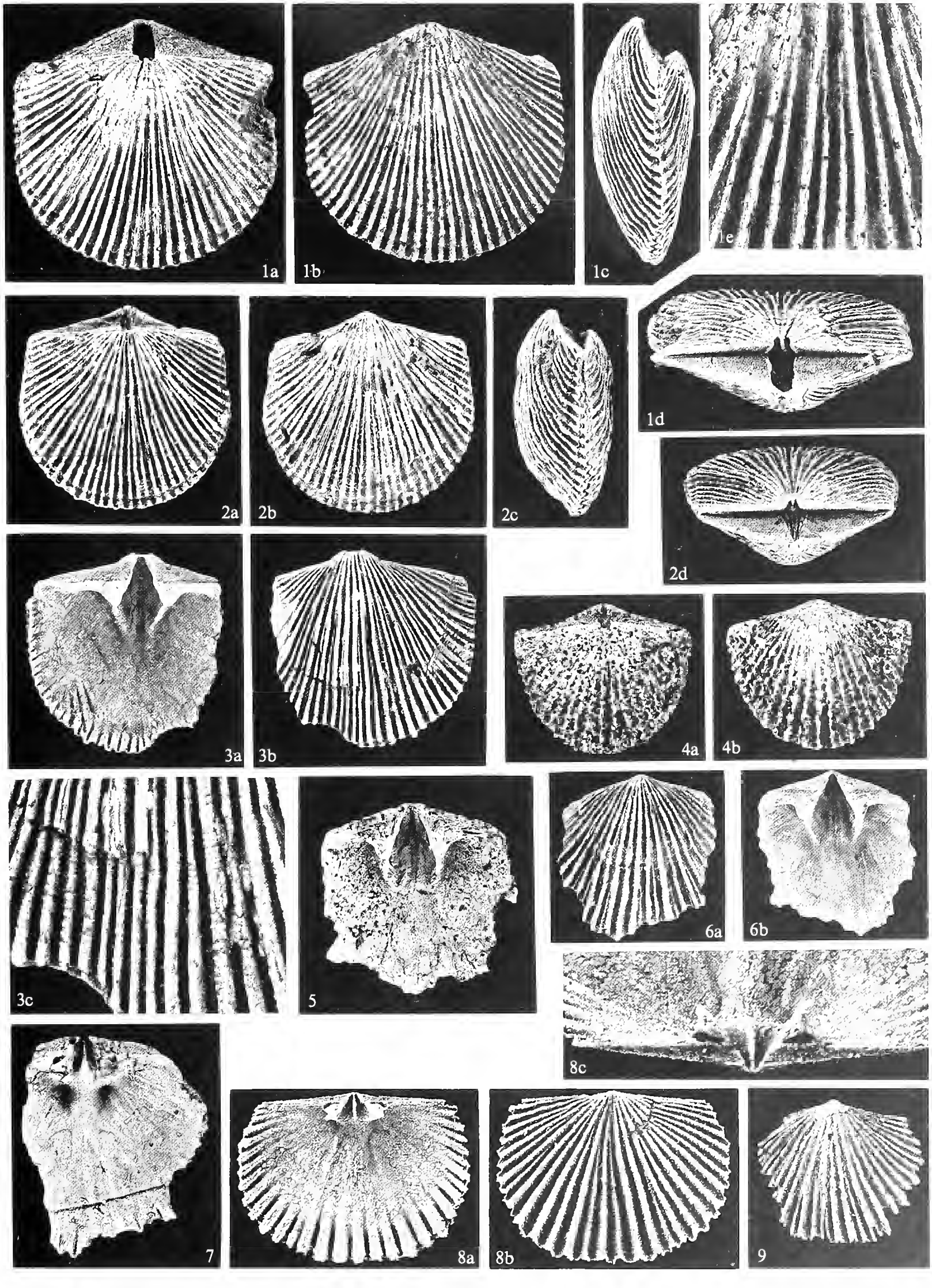
| | Maximum length ventral valve | Maximum length dorsal valve | Maximum width | Hinge width | Maximum thickness | Maximum number of ribs along commissure |
|---|---|---|---|---|---|---|
| RM Br116395, conjoined valves, Holotype | 13·3 | 11·5 | 13·7 | 12·9 | 5·5 | 44 |
| RM Br116397, conjoined valves, Paratype | 11·0 | 9·9 | 11·2 | 10·0 | 5·0 | 46 |
| RM Br116390, ventral valve, Paratype | — | — | — | — | 2·3 | — |
| RM Br116391, ventral valve, Paratype | 10·5 | — | — | — | 3·1 | — |
| RM Br116392, ventral valve, Paratype | — | — | — | — | 2·6 | — |
| RM Br116393, dorsal valve, Paratype | — | — | — | — | 1·3 | — |
| RM Br116371, conjoined valves, Paratype | 7·9 | 7·2 | 9·5 | 9·5 | 4·1 | — |

## EXPLANATION OF PLATE 7

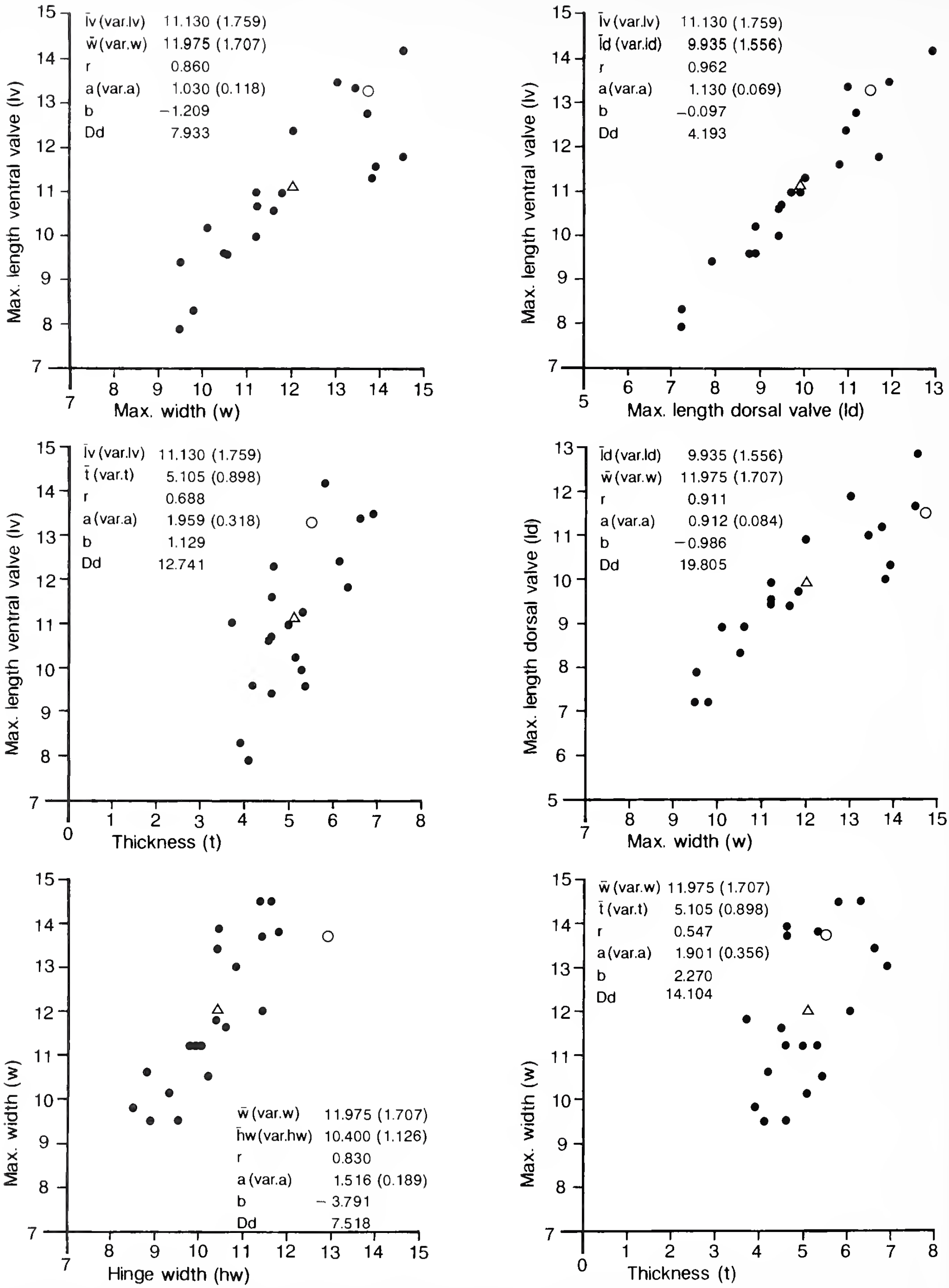
Figs 1–7. *Sivorthis filistera* sp. nov. All from lower Dalby Limestone, Viru Series; Böda Hamn, north-east Öland, Sweden. 1*a–c*, holotype; RM Br116395; dorsal, ventral, lateral and posterior views of conjoined valves, with detail of branching costellae, *a–d* × 3, *e* × 8. 2*a–d*, paratype; RM Br116397; dorsal, ventral, lateral and posterior views of conjoined valves, × 3. 3*a–c*, paratype; RM Br116391; interior and exterior of ventral valve, with detail of lamellose micro-ornament, *a–b* × 3, *c* × 8. 4*a–b*, paratype; RM Br116371; dorsal and ventral views of juvenile conjoined valves, × 3. 5, paratype; RM Br116390; interior of ventral valve, × 3. 6*a–b*, paratype; RM Br116392; exterior and interior of ventral valve, × 3. 7, paratype; RM Br116393; interior of dorsal valve, × 3.

Figs 8–9. *Sivorthis tenuicostata* (Cooper, 1956). Both from Pratt Ferry Formation; Pratt Ferry, Alabama, U.S.A. 8*a–c*, RM Br135164; interior and exterior of dorsal valve (× 3), with posterior view of cardinalia (× 6). 9, RM Br135165; exterior of ventral valve, × 3.

PLATE 7



JAANUSSON and BASSETT, *Sivorthis*



TEXT-FIG. 3. Bivariate plots and statistical characterization of a sample of 20 syntype conjoined valves of *Sivorthis filistera*; same sample as used for Table 2. Symbols as for Text-fig. 2 (but with open circle here as holotype).

*Remarks. S. filistera* is distinct from other species referred to *Sivorthis* in having finer ribbing. It appears to be closest to *S. tenuicostata* (Cooper), in which 34–40 costellae are typically developed, and which has a slightly more convex ventral valve and a posteriorly more convex dorsal valve. Other species are distinguished readily by still coarser ribbing.

*Occurrence. S. filistera* is currently known only from the lower Dalby Limestone on Öland, Sweden.

## Genus SHOSHONORTHIS gen. nov.

*Type species. Orthis michaelis* Clark, 1935; from the Swan Peak Formation (Whiterock) of Utah, USA.

*Derivation of name.* From Shoshone, a North American Indian group.

*Diagnosis.* Shell medium sized to fairly large, strongly ventribiconvex, non-sulcate to weakly sulcate, ventral interarea fairly long and apsacline. Ornament costate (known range 18–36 rounded ribs in adult valves), fine radial capillae developed in most species. Ventral muscle field long, extending considerably beyond the delthyrial cavity. Cardinalia relatively long, brachiophores developed as slender rods. Cardinal process a slender ridge without a clearly differentiated myophore. Dorsal musculature with posterior pair of scars considerably larger than the anterior pair.

*Species assigned to* Shoshonorthis

*Orthis michaelis* Clark, 1935; *Orthambonites swanensis* Ulrich and Cooper, 1938; *Orthambonites subconvexus* Cooper, 1956; *Orthambonites dinorthoides* Cooper, 1956; *Orthambonites perplexus* Ross, 1967; *Orthambonites tifletensis* Havlíček, 1971; ?*Gonambonites ovata* Pander, 1830.

*Discussion. Shoshonorthis* is typically a medium sized to fairly large shell (recorded maximum length up to 21 mm). Its relatively long ventral interarea distinguishes it immediately from *Orthambonites*, and internally the former genus is also recognized easily by its considerably longer ventral muscle field and relatively longer cardinalia; similarities in other general external features are probably due to parallel development. Distinction between *Shoshonorthis* and early species of *Plectorthis* is less clear, partly because the internal characters of the latter are poorly known. The dorsal valve of *Shoshonorthis* is normally less convex than in *Plectorthis*, and the brachiophore supports are not developed as discrete plates. *Plectorthis* also lacks the capillate micro-ornament present in most species assigned here to *Shoshonorthis*.

*S. michaelis*, *S. swanensis*, *S. dinorthoides*, *S. tiftelensis* and *S*? *ovata* have well developed radial capillae. In *S. perplexa* there is a single capilla in each interspace between the costae (Ross 1970, p. 57); capillate micro-ornament has not been reported in *S. subconvexa*.

Cooper (1956, p. 301) emphasized the similarity in the shape of the ventral muscle field between *S. dinorthoides* and species of *Dinorthis*, obviously based on a ventral interior that he figured (1956, pl. 33, fig. 27). However, in another figured ventral interior (1956, pl. 33, fig. 26) the configuration of the muscle field is very similar to that of *S. subconvexa* (see Cooper 1956, pl. 34, fig. 26), indicating some variation in this feature. One specimen of *S. subconvexa* shows faint traces of the ventral vascula media (Cooper 1956, pl. 34, fig. 35), which diverge anterolaterally directly from the muscle field. In other species of *Shoshonorthis* the course of the ventral vascula media is unknown.

The configuration of the dorsal muscle field is known in *S. michaelis* (Ulrich and Cooper 1938, pl. 14, fig. 26) and *S. subconvexa* (Cooper 1956, pl. 34, fig. 22); in both cases the posterior pair of scars is considerably larger than the anterior pair. In *S. tifletensis* the structure of the cardinalia is poorly known and the assignment of this species to *Shoshonorthis* must therefore remain somewhat uncertain.

Two specimens from Pulkova (RM Br116406, Br73933) agree clearly with Pander's (1830) brief description and illustration of *Gonambonites ovata*. Pander probably included this species in *Gonambonites* because of its relatively long ventral interarea; there are no other species that he described with which this distinctive form could be confused. Although somewhat worn, the external character of both specimens conforms with the morphology of *Shoshonorthis*, but until internal features are known the generic assignment is only tentative.

*Occurrence*. All described species that we assign to *Shoshonorthis* appear to be confined to rocks of Whiterock-Llanvirn age. The genus is known currently from the Great Basin of the western USA, Oklahoma, from Ingria, and from North Africa. In addition to these occurrences of described taxa, one of us (M. G. B.) has examined specimens resembling *S. michaelis* in undescribed faunas from the early-mid Arenig age Meitan Formation of Sinan County, Guizhou Province, south-west China; this material, which occurs in association with *Paralenorthis serica*, may belong to *Shoshonorthis*, and is currently being described by Dr Rong Jia-yu (Nanjing) and his colleagues.

NORTH AMERICA: All occurrences are of Whiterock age: Utah, Swan Peak Formation (*S. michaelis*; Clark 1935; Ulrich and Cooper 1938, p. 101, pl. 14, figs 11–12, 21, 23, 25–29: Ross 1967, p. D3, pl. 1, figs 1–2; *S. swanensis*; Ulrich and Cooper 1938; Ross 1967, pl. 1, fig. 8); Utah, Kanosh Shale (*S. michaelis*; Jensen 1967, p. 90, pl. 4, figs 1–5); Nevada, Antelope Valley Limestone (*S. perplexa*; Ross 1967); Utah, Crystal Peak Dolomite (*S. perplexa*; Jensen 1962, p. 91, pl. 4, figs 6–10); Oklahoma, Oil Creek Formation (*S. dinorthoides*; Cooper 1956; and *S. subconvexus*; Cooper 1956).

INGRIA: Kundan, exact locality and horizon unknown (*S*? *ovata* (Pander, 1830) herein).

MOROCCO: Un-named Llanvirn or Llandeilo beds (*S. tifletensis*; Havlíček 1971).

## Genus ORTHIS Dalman, 1828

*Type species*. *Orthis callactis* Dalman, 1828; from the zone of *Asaphus* (*Asaphus*) *expansus* ('Expansus Limestone'; high lower Ordovician, Kundan Stage, Hunderumian Substage, high *Didymograptus hirundo* to lowest *Didymograptus 'bifidus'* Zone), Husbyfjöl, Östergötland, Sweden.

*Diagnosis*. Plano-convex to weakly concavo-convex, anterior commissure rectimarginate, shells relatively large at maturity. Ornament costate and finely capillate. Interareas short, ventral beak low. Cardinalia very short and low, notothyrial platform aligned subparallel to the hinge, brachiophores widely divergent, cardinal process a simple ridge. Dental plates short, receding, ventral muscle field extended only slightly beyond the broad, shallow, delthyrial cavity, no ventral median ridge. Ventral vascula media adjacent and parallel for about half the length of the valve.

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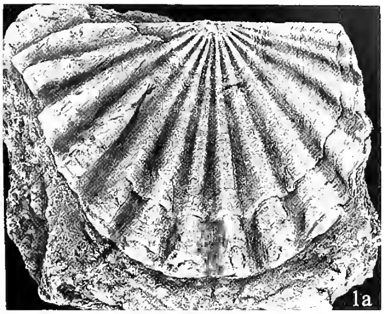
### EXPLANATION OF PLATE 8

Figs 1–8. *Orthis callactis* Dalman, 1828. All specimens are from the 'Expansus Limestone', lower Kundan Stage, Hunderumian Substage. 1*a*–*b*, lectotype; RM Br21959; figured Dalman 1828, pl. 2, fig. 2 and Hisinger 1837, pl. 20, fig. 9; Husbyfjöl, Östergötland, Sweden; exterior of dorsal valve (×2·5) and detail of fine fila (×10) on posterolateral flank. 2, paralectotype; RM Br21958; locality as for fig. 1; exterior of dorsal valve, ×2. 3, RM Br22129; Omberg, Östergötland, Sweden; interior of dorsal valve, ×2. 4*a*–*c*, RM Br135876; Borghamn, Ostergötland, Sweden; dorsal, ventral and lateral views of juvenile conjoined valves; ×2. 5*a*–*b*, RM Br134536; Locality unknown, Siljan district, Dalarna, Sweden; partly exfoliated ventral valve (×1·5) and detail of finely capillate ornament on left posterolateral flank (×10). 6, RM Br135165; locality as for fig. 1; interior of ventral valve, ×1·5. 7, RM Br135166; locality as for fig. 4; interior of fragment of dorsal valve, ×4. 8, RM Br21971; locality as for fig. 3; dorsal view of conjoined valves, ×1.

Figs 9–11. *Glossorthis tacens* Opik, 1930. All from Kukruse Stage ($C_{II}\alpha$); Kohtla-Järve, Estonia. 9*a*–*c*, RM Br135877; interior and exterior of ventral valve (×2), with oblique view of interior (×3) to show elevation of muscle platform, stout dental plates and fossettes on inner faces of teeth. 10, RM Br92206; interior of ventral valve, ×2. 11, RM Br108635; interior of dorsal valve, distal portion of brachiophores not preserved, ×2.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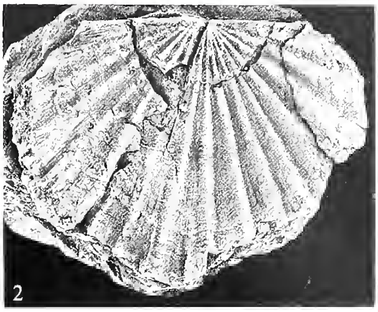
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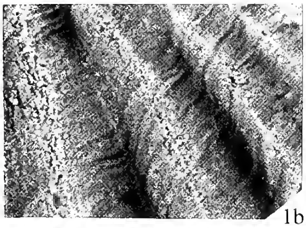
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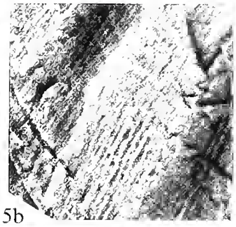
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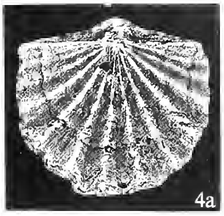
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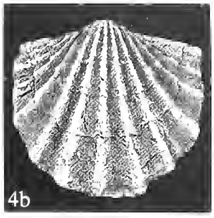
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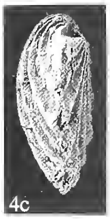
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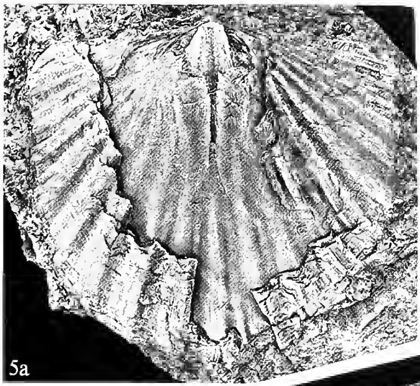
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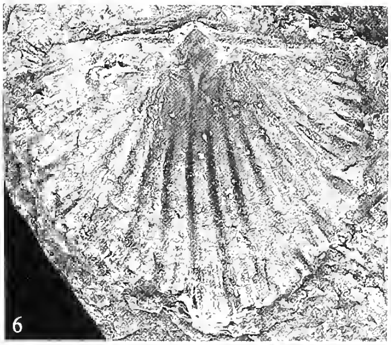
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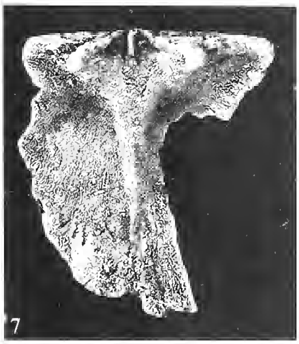
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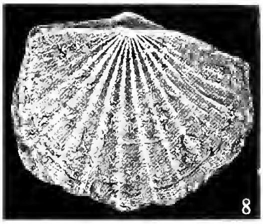
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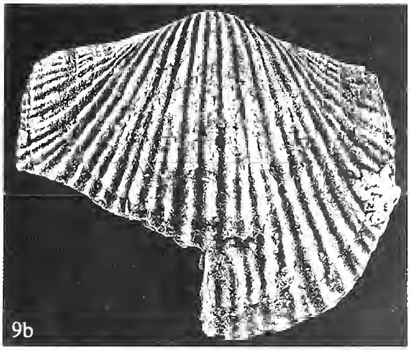
9a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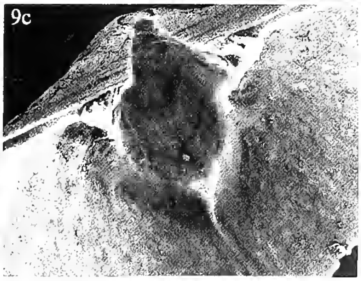
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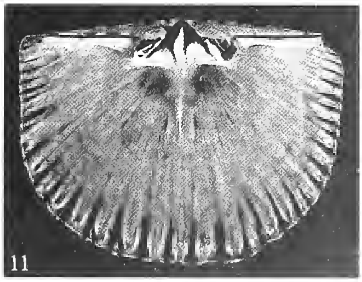
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JAANUSSON and BASSETT, *Orthis*, *Glossorthis*

*Species assigned to* Orthis

Although the name *Orthis* has been assigned in the past to an extremely wide range of species, we have not identified any that we consider with certainty to be congeneric with *O. callactis.*

*Remarks.* Dalman's (1828) syntypes of *Orthis callactis* are housed in the Riksmuseum in Stockholm, which allows us to select a lectotype in order to stabilize the identity of the species and hence the type genus for the family Orthidae. Although *O. callactis* has always been interpreted fairly consistently, Dalman's material has not been illustrated or revised subsequent to its original description.

The genus *Orthis* has long been defined in an extremely wide sense, to include not only *O. callactis* but also species of *Orthambonites* and related genera. *Orthis* is readily distinguished from all other taxa described in this paper by having a plane to weakly concave dorsal valve, a very short dorsal interarea, and very short cardinalia with widely divergent brachiophores and the notothyrial platform aligned subparallel to the hinge.

### *Orthis callactis* Dalman, 1828

Plate 8, figs 1–8

v*1828 *Orthis callactis* Dalman, p. 112, pl. 2, fig. 2.
1830 *Orthis crassicosta* Pander, p. 82, pl. 21, fig. 1.
1830 *Orthis eminens* Pander, p. 82, pl. 21, fig. 2.
v.1837 *Orthis callactis* Dalman; Hisinger, p. 70, pl. 20, fig. 9.
v.1880 *Orthis callactis* Dalman var.; Lindström *in* Angelin and Lindström, p. 26, figs 2–3.
1932 *Orthis callactis* Dalman; Schuchert and Cooper, p. 75, pl. 2, figs 8, 12, 15, 17.
v.1953 *Orthis callactis* Dalman; Alikhova, p. 28, pl. 1, figs 13–16.
v.1961 *Orthis callactis*(?) Dalman; Rubel, p. 172, pl. 14, figs 16–17.
1965 *Orthis callactis* Dalman; Williams *in* Williams *et al.*, p. H311, fig. 197.7*a–d*.
v.1985 *Orthis calligramma* Dalman; Cocks, p. 56, pl. 5.2.2.A–B.

*Lectotype* (here selected). RM Br21959, Dalman Collection, dorsal valve, figured Pl. 8, fig. 1*a–b*; from Husbyfjöl, Östergötland, Sweden, zone of *Asaphus* (*Asaphus*) *expansus* ('Expansus Limestone'), high lower Ordovician (lower Kundan Stage, Hunderumian Substage – high *Didymograptus hirundo* to lowest *Didymograptus 'bifidus'* Zone); the original specimen figured by Dalman (1828, pl. 2, fig. 2) and refigured by Hisinger (1837, pl. 20, fig. 9).

*Paralectotype.* RM Br21958, Dalman Collection, dorsal valve, figured Pl. 8, fig. 2; same locality and horizon as lectotype.

*Diagnosis.* Shell relatively large (maximum recorded length 30 mm). Costae low, rounded, widely spaced (OR 13–19). As the only confirmed species of the genus, other characteristic features of *O. callactis* apply equally to the generic diagnosis given above.

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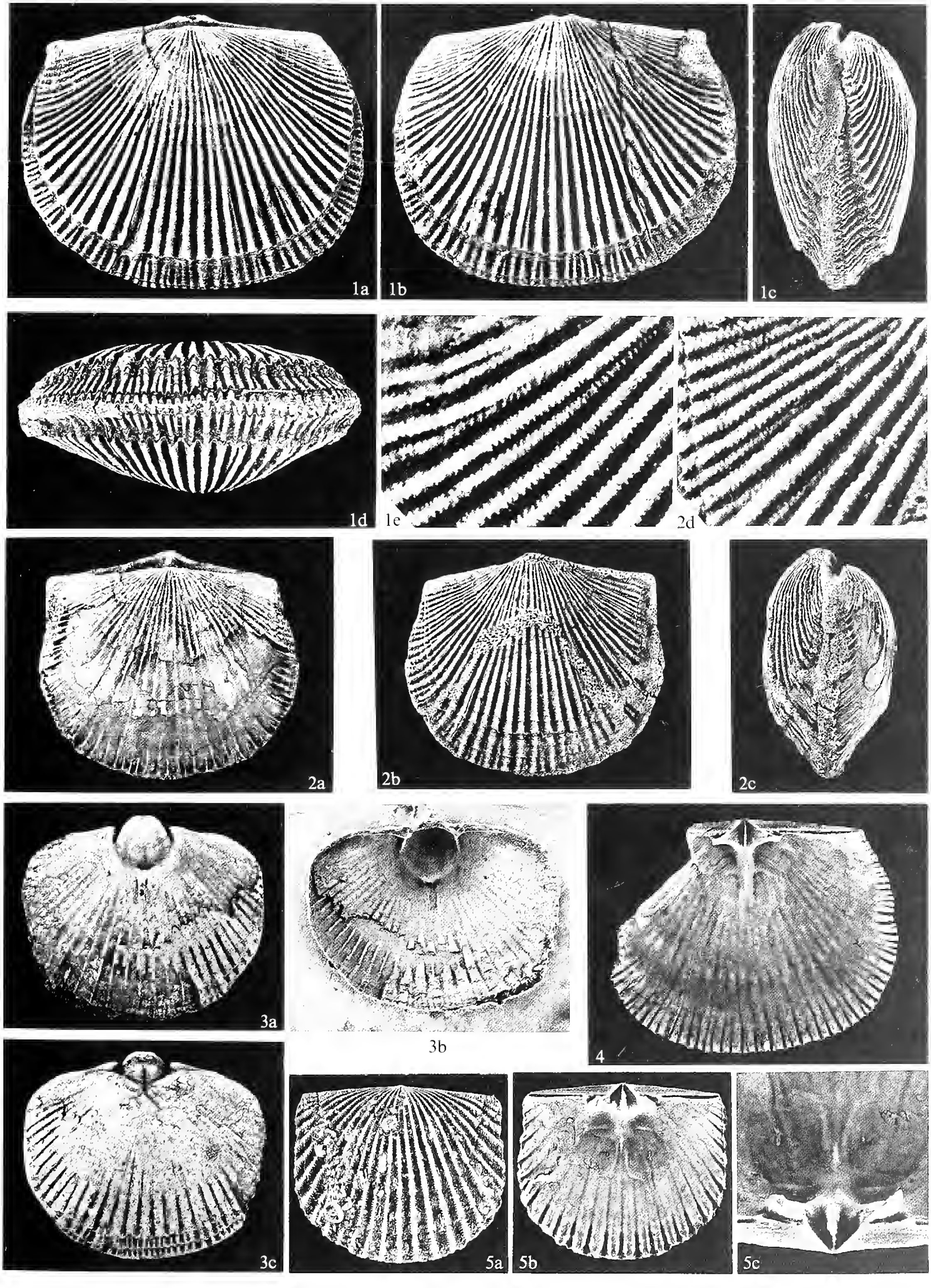
EXPLANATION OF PLATE 9

Figs 1–4. *Krattorthis verneuli* (Rubel, 1961). 1*a–e*, RM Br74764; Aserian Stage ($\mathrm{C_1}$a); Archangelskoje, Ingria, Russia; dorsal, ventral, lateral and anterior views of conjoined valves, with detail of lamellose micro-ornament on left lateral flank of dorsal valve, *a–d* × 2, *e* × 5. 2*a–d*, RM Br74424; probably Aserian Stage; Pulkova, Ingria, Russia; dorsal, ventral and lateral views of conjoined valves, with detail of lamellose micro-ornament on left lateral flank of ventral valve, *a–c* × 2, *d* × 5. 3*a–c*, RM Br74014; horizon and locality as Fig. 2; conjoined valves with shell heated and scraped away to reveal interiors, ventral valve with latex cast, dorsal valve, × 2. 4, RM Br74762; Aserian Stage ($\mathrm{C_1}$a); Duboviki, Ingria, Russia; interior of dorsal valve, × 2.

Fig. 5. *Glossorthis tacens* Öpik, 1930. 5*a–c*, RM Br68424; Uhakuan Stage ($\mathrm{C_1}$c$\beta$); Türpsalu, Estonia; exterior and interior of dorsal valve, with posterior view of cardinalia, distal portion of brachiophores not preserved, *a–b* × 2, *c* × 4.

PLATE 9



JAANUSSON and BASSETT, *Krattorthis*, *Glossorthis*

*Distribution. O. callactis* is known with certainty only from the lower Kundan beds (zone of *A. expansus*) in Baltoscandia (Östergötland, Öland, and Siljan district in Sweden; lower Voka beds of north-western Estonia; and Ingria).

### Genus KRATTORTHIS gen. nov.

*Type species. Glossorthis verneuili* Rubel, 1961; from the upper Kundan and Aserian Stage (Llanvirn) of northern Estonia and Ingria, Russia.

*Derivation of name.* Kratt, a kind of troll in Estonian folklore.

*Diagnosis.* Subequally biconvex to slightly ventribiconvex, multicostellate with densely spaced, distinct concentric to lamellose fila. Interareas very short, anterior commissure rectimarginate. Dental plates slender, ventral muscle field situated on an elevated platform with a rounded anterior margin which is produced only slightly anterior to the delthyrial cavity. Cardinalia relatively small and delicate; brachiophore process slender, somewhat flattened laterally and slightly curved posteroventrally, supported by plates which are undercut and converge dorsomedially onto a ridge; cardinal process high and slender. Shells relatively large.

*Remarks. Krattorthis verneuili* is a distinctive, relatively large (known maximum length 23 mm) and fairly common species that was first figured by Verneuil (*in* Murchison *et al.* 1845, pl. 13, figs 11*a–c*) but referred incorrectly by him to *Orthis extensa* Pander, 1830; the latter species was described originally as a *Productus* and belongs to *Panderina* (see Schuchert and Cooper 1932, p. 78, n. 38). Schuchert and Cooper (1932, p. 78) referred *O. extensa sensu* Verneuil *non* Pander to *Glossorthis*. However, the specimen figured by them (1932, pl. 4, figs 3, 6, 10) has a distinct dorsal sulcus and is stated to come from much older beds ($B_2$; upper Arenig Volkhov Stage). We have not observed a comparable dorsal sulcus among the numerous examined specimens of *K. verneuili*. Rubel (1961, p. 184, pl. 18, figs 5–10) named the species figured by Verneuil *Glossorthis verneuili* nom. nov., but in reality he established a new species and the type designated by him is a holotype not a neotype.

It is possible that the specimen named and figured by Pander (1830, pl. 16A, fig. 4) as *Orthambonites*, but without a description, is a synonym of *K. verneuili*. This is suggested particularly by the very short interareas, not known in any other biconvex orthacean from Ingria. The size and relative convexities of the valves are also similar, although the multicostellate ornament of Pander's figure appears to be irregular and finer than that in *K. verneuili*. Although the name *O. dubia* is valid as an indication under Article 12(b)(7) of the ITZN Code (1985), we propose that it should be treated as a *nomen oblitum* in terms of previous editions of the code since its senior synonymy cannot be proved and the name *verneuili* has now become established in the literature based on a validly designated type specimen.

Externally *Krattorthis* differs from *Glossorthis* in its much finer multicostellate ornament and far more strongly convex dorsal valve. For a full description of the external characters of *K. verneuili* see Rubel (1961, p. 184, pl. 18, figs 5–10).

The interior of *K. verneuili* has not been described previously, but examination of a well-preserved dorsal interior collected by G. Holm (Pl. 9, fig. 4) confirms that it differs from *Glossorthis*, and this is supported further by preparations of ventral interiors (Pl. 9, figs 3*a–b*). The ventral muscle field forms an anteriorly-elevated platform but it lacks a tongue-like anterior projection (Pl. 9, fig. 3*b*). A characteristic feature for *Glossorthis* is the position of the maximum length of the hinge-teeth far lateral of the delthyrial margins, associated with a distinct growth line which defines a triangular area on the interarea (Schuchert and Cooper 1932, p. 79). No free ventral valves of *K. verneuili* have been available and it is not known whether the hinge-teeth in *Krattorthis* have a similar position relative to the delthyrial margins. However, no comparable growth line on the interarea has been observed. The cardinalia of *K. verneuili* are remarkably small relative to the size of the valve (Pl. 9, fig. 4), much smaller than in *Glossorthis* (Pl. 8, fig. 11; Pl. 9, fig. 5*b–c*).

In all figured dorsal interiors of *Glossorthis* (Öpik 1930, pl. 3, figs 28–32, pl. 4, figs 34, 36, 39;

Schuchert and Cooper 1931, pl. 4, fig. 8; Alikhova *in* Sarycheva 1960, pl. 12, fig. 8; Williams *et al.* 1965, fig. 194:8*b*) the brachiophore processes appear to be partly or completely broken off, as they are in the majority of specimens examined by us (see also Pl. 8, fig. 11). In addition, the broken ends of the processes in most specimens have been worn by depositional processes or, when exposed, to recent subaerial weathering. This gave an impression in the past that in *Glossorthis* the brachiophores are 'blunt, rather short' (Schuchert and Cooper 1932, p. 78). Preparation of a juvenile dorsal valve of *Glossorthis tacens* revealed a virtually complete brachiophore process (Pl. 9, figs 5*b–c*). It is fairly long, laterally flattened and with a distinct posteroventral curvature. In *Krattorthis verneuili* (Pl. 9, fig. 4) the process is subtriangular in cross section with a medially flattened surface; it is narrower than in *Glossorthis tacens* and only slightly curved posteroventrally. The brachiophores are supported by plates that converge onto a median ridge; they are undercut and resemble the plectorthid type. In *Glossorthis* the brachiophores are supported by adventitious shell substance which forms a prominent notothyrial platform (Pl. 8, fig. 11).

*Occurrence.* As currently known the genus is monotypic. Rubel (1961, p. 185) gave data on the distribution of *K. verneuili* in middle Llanvirn equivalent strata of northern Estonia and Ingria (Aluojan Substage of the Kundan Stage, and the Aserian Stage).

## APPENDIX: OTHER SPECIES ASSIGNED PREVIOUSLY TO *ORTHAMBONITES*

### 1. *Pander's (1830) species*

Of the 18 species originally named by Pander as *Orthambonites*, it is likely that no more than five belong in the genus as now restricted in this paper. Even within these we emphasize that their identification remains only tentative, based on a typological assessment of Pander's illustrations and brief descriptions, but supported by a comparison with the collections from Ingria available to us. Of the five, we have commented earlier (pp. 23–26, 33) on relationships and the possible synonymy groupings of *O. rotunda*, *O. lata*, *O. aequalis*, and *O. semicircularis*. Pander considered that *O. plana* (1830, p. 82, pl. 22, fig. 8*a–d*) is very similar to *O. semicircularis*, but *plana* has fewer primary ribs (21) and is less convex, so that we doubt the similarity and consider its generic relationships to remain uncertain. In addition, *O. ovata* Pander, 1830, p. 85, pl. 16A, fig. 9 has the convexity and general costate ribbing pattern (23 ribs) of *Orthambonites*, and its suboval outline may be an end-variant in the range of shape displayed by one of Pander's other taxa.

We have also commented on *O. transversa*, which is the previously designated type species of *Orthambonites*, but which we propose should be regarded as a *nomen dubium*, and on *O. tetragona* and *O. rotundata* which are probably synonyms and represent a *Glossorthis*-like form. *Orthambonites dubia*, figured but not described by Pander, resembles *Krattorthis verneuili*, and we propose here (p. 56) to regard it as a *nomen oblitum*.

Alikhova (1953, p. 28) suggested that *O. crassicosta* Pander, 1830, p. 82, pl. 21, fig. 1 and *O. eminens* Pander, 1830, p. 82, pl. 21, fig. 2 are junior synonyms of *Orthis callactis* Dalman, 1828, and this appears to be probable (see synonymy, p. 54). Pander's figures of *Orthambonites convexa* (1830, p. 82, pl. 25, fig. 8) and *O. alta* (1830, p. 82, pl. 25, fig. 17) show a *Nicolella*-like exterior and should be considered when Ingrian species of early *Nicolella* are revised. Pander himself pointed out that *Orthambonites flexuosa* (1830, p. 83, pl. 16B, fig. 8) differs in several characters from other species of *Orthambonites*; it is clearly a clitambonitacean.

Three further species included by Pander (1830, p. 83) in *Orthambonites* were assigned only with some hesitation. Of these, *O. parva* Pander, p. 83, pl. 26, fig. 10 was subsequently made the type species of the enteletacean genus *Paurorthis* Schuchert and Cooper, 1931, p. 231 (see also Schuchert and Cooper 1932, p. 79, pl. 3, figs 5–8, 10; Öpik 1933, p. 12, pls 3–4; pl. 5, fig. 4; neotype designated by Rubel 1961, p. 196). Schuchert and Cooper (1932, p. 79) also assigned *Orthambonites trigona* Pander, p. 83, pl. 26, fig. 11 to *Paurorthis*. The relationships of the third species, *O. sphaerica* Pander, 1830, p. 84, pl. 16B, fig. 11, remain unclear.

It is beyond the scope of this paper to discuss these relationships further; in each case, the identity and use of Pander's species names should await a full taxonomic study of the relevant groups based on collections from Pander's type area in Ingria, and involving the designation of neotypes as appropriate in order to stabilize the concept of the various taxa.

### 2. *Species excluded from* Orthambonites

Several species assigned originally to *Orthambonites* have either been transferred subsequently by other authors to other genera, or do not appear to us to belong to the genus or to any of the related genera described in this paper.

*Orthambonites bifurcatus* Cooper, 1956, p. 297, pl. 34, figs 1–6, from the upper Pogonip Group (Whiterock), Nevada, USA (see also Ross 1970, p. 54, pl. 3, fig. 20) was assigned by Neuman (*in* Neuman and Bruton 1974, p. 78, fig. 7A–K) to *Trondorthis*.

*Orthambonites brachiophorus* Cooper, 1956, p. 298, pl. 36, figs 32–39; from the Effna and Rich Valley Formations, Virginia, USA was assigned by Jaanusson and Bergström (1980, p. 98) to *Dolerorthis*. In this species the relative length of the ventral interarea, the general type of ribbing, the conspicuous concentric fila, and particularly the structure of the brachiophores and the thin cardinal process so closely resemble those of some north-west European middle Ordovician species currently referred to *Dolerorthis*, that we have little doubt that they are congeneric.

*Orthambonites neumani* Cooper, 1956, pl. 37, figs 19–28, is from the Tellico Formation, Tennessee, USA. This species (maximum known length 19 mm) closely resembles *Dinorthis* in its internal characters but differs externally in having a strongly convex ventral valve (Cooper 1956, p. 308); its affinities may be with the Plaesiomyidae. The long, lobate ventral muscle field, the presence of conspicuous concentric fila, and the relatively long ventral interarea distinguish it from *Orthambonites*. Williams (1962, p. 100) pointed out similarities between *O. neumani* and *Orthis* (*Plectorthis*) *subplicatella* Reed, 1917 (Williams 1962, pl. 8, figs 12–14) from the Balclatchie Mudstones of the Girvan district, but the characters of the latter species remain too poorly known to allow a firm generic reference to be made.

*Orthambonites tuloicus* Andreeva, 1982, p. 54, pl. 3, fig. 6-3, from the Stretinskaya(?) Formation (middle Ordovician?), Altai region, USSR, is certainly not *Orthambonites*. Its affinities appear to be with *Hesperorthis* as witnessed particularly by the long ventral interarea, the narrow delthyrium, and the position of the hinge teeth set somewhat lateral to the delthyrial margin (Andreeva 1982, pl. 3, fig. 7).

*Orthambonites*? *inaequalis* Rubel, 1961, p. 179, pl. 12, figs 8–10, is from the Kundan Stage, northern Estonia. The flat, faintly sulcate dorsal valve, comparatively short cardinalia, and the micro-ornament consisting solely of distinct concentric fila, exclude this species from *Orthambonites*. Further knowledge of internal morphology is required before its generic assignment can be determined.

*Orthambonites roquebrunensis* Melou, 1982, p. 27, pl. 4, figs 1–5 from the lower Schistes de Landeyran (Arenig), Montagne Noire, France, may be related to *Paralenorthis*, but differs in having pronouncedly costellate ribbing, a longer, anteriorly bilobate ventral muscle field, and a poorly-defined cardinal process. It cannot be assigned confidently to any known genus.

### 3. *Species requiring further investigation*

There is, finally, a small group of species that we have encountered in the literature that were either identified originally by their authors as *Orthambonites* or were transferred subsequently to the genus, but which we believe to be too poorly known to allow any meaningful comments to be made as to their relationships. For the most part these species are based on poorly preserved material or are described and illustrated inadequately; additional taxonomic investigation of either the original material or of new collections would be necessary to comment further on these forms, which are recorded here to complete the coverage of literature dealing with previous interpretations of *Orthambonites*. On balance, the limited information available suggests to us that it is unlikely that any of these species belongs within the genus.

*Orthis decipiens* Phleger, 1933, p. 17, pl. 1, fig. 2; Barrel Spring Formation (Whiterock), California, USA. Assigned by Ross (1967, p. D2, pl. 1, figs 31–36) to *Orthambonites*, although Cooper (1956, p. 351) questionably assigned it to *Hesperorthis*.

*Orthambonites divaricatus* Cooper, 1956, p. 302, pl. 33, figs 1–3; Effna and Rich Valley Formations, Virginia, USA.

*Hebertella exfoliata* Raymond, 1905, p. 370; Day Point Formation, New York State, USA. Assigned tentatively to *Orthambonites* by Cooper (1956, p. 303), although he suggested that the external morphology resembles that of *Desmorthis*.

*Orthambonites fraternus* Havlíček, 1971, p. 31, pl. 3, figs 7–10, pl. 23, fig. 3; Llandeilo beds, Morocco.

*Orthambonites jaboganicum* Severgina, *in* Petrunina and Severgina 1962, p. 88, pl. 3, figs 1–4; Khankharinsky Group (Caradoc), Altai Mountains, USSR (see also Kulkov and Severgina 1989, p. 65, pl. 8, figs 15–18).

*Orthambonites tuvensis* Andreeva, 1982, p. 53, pl. 3, figs 1–5; Tarlyk Formation (?Whiterock), Tuva, Russia.

*Orthambonites planus* Bondarev, 1968, p. 65, pl. 1, figs 1–4; Yngor beds (middle Ordovician), Vaigach and Pai-Khoy, Russia.

*Orthambonites pseudomonetus* Bednarczyk, 1964, p. 63, pl. 12, figs 1–4, 7, 8, 13; Bukówka and Dyminy beds (lower Ordovician), Kielce region, Holy Cross Mountains, Poland.

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## *Note Added in Proof*

Subsequent to the submission of the manuscript, we have noted two further species assigned to *Paralenorthis*, both described by Herrera and Benedetto (1989) from the lower Ordovician of the Argentinian Precordillera. *P. vulgaris* Herrera and Benedetto (1989, pl. 4, figs 8, 14–15, 20) shows distinctly the proximally separated and divergent vascula media typical of the genus (p. 34 herein); it is from late Arenig beds of the Huaco Anticline and upper levels of the San Juan Formation (early Llanvirn) in the Cerro Viejo Range. Their second species, recorded under open nomenclature, is also from the upper San Juan Formation, apparently occurring at a single locality in association with *P. vulgaris*; the authors comment that the material is too poorly preserved to make a specific determination, but suggest that the disposition of the vascula media support an assignment to *Paralenorthis*.

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# THE EPIDERMAL STRUCTURE OF THE CARBONIFEROUS GYMNOSPERM FROND *RETICULOPTERIS*

*by* E. L. ZODROW *and* C. J. CLEAL

ABSTRACT. The epidermal structure of Upper Carboniferous *Reticulopteris* fronds is documented for the first time. It is shown to be very similar to that of *Neuropteris obliqua*, confirming earlier stratigraphical and gross-morphological evidence of a phylogenetic link between the two frond-types. The evolution of *Reticulopteris* fronds with their anastomosed venation from typical open-veined *Neuropteris* probably reflects the drier climate in the middle Westphalian. *Barthelopteris* gen. nov. is proposed for the Stephanian and Autunian species '*Reticulopteris*' *germarii*, which has a very different epidermal structure from type *Reticulopteris*.

THE trigonocarpaleans form a group of gymnosperms abundantly represented in the Upper Carboniferous fossil record. They were mainly shrubs and smaller trees that favoured drier habitats such as raised levée-banks, within equatorial swamps. One of the few exceptions is a liana-like trigonocarpalean recently reconstructed from coal ball petrifactions (Hamer and Rothwell 1988). The foliage, which is the part of the plant most commonly found fossilized, consisted of large dissected leaves superficially resembling fern fronds. These leaves were mostly between 0·5 and 2 m long, although examples up to 7 m long have been reported (Laveine 1986). In most form-genera, the ultimate segments of the fronds (usually referred to as pinnules, thus continuing the analogy with fern fronds) had a venation consisting of a midvein from which were emitted simple or dichotomous lateral veins. In a few cases, the venation was anastomosed.

One such frond-type with reticulate veining belongs to the form-genus *Reticulopteris* Gothan, 1941. This was established for reticulate-veined fronds, which in all other characteristics resemble the imparipinnate neuropterids. It is of particular interest as being the only example of a reticulate-veined frond that can be directly linked with a non-reticulate ancestor, through a reasonably convincing phylogenetic model: the transition from *Neuropteris obliqua* (Brongniart) Zeiller, through *N. parvifolia* Stockmans and *N. semireticulata* Josten, to *Reticulopteris muensteri* (Eichwald) Gothan documented in the Westphalian record by Josten (1962) and Laveine (1967).

The position of *Reticulopteris* as a reticulate-veined counterpart of *Neuropteris* was until recently relatively straightforward and unchallenged. However, the taxonomy of neuropterids has been revised by Cleal *et al.* (1990) using new evidence of frond architecture and epidermal structure. Where there was originally just one form-genus, at least five can now be clearly identified and delineated. The question thus arises, of which of these form-genera (if any) is *Reticulopteris* the reticulate-veined counterpart? The Josten (1962) model clearly suggests a link with *Neuropteris* in its restricted sense, as *N. obliqua* has recently been shown to belong there (Cleal and Shute 1992). Establishing phylogenetic relationships using stratigraphical distributions can be risky and should normally be supported by more concrete morphological evidence. Frond architecture is in this case of little help, since no large specimens of *Reticulopteris* with critical features have been reported, and so epidermal structure appears the only way of resolving the problem.

Cuticles from the type species of *Reticulopteris* are documented to see if they confirm the taxonomic position suggested by the Josten model (Josten 1962). They were prepared from specimens from Cape Breton Island, Nova Scotia, Canada, which has previously proved a good area for Carboniferous cuticle studies (Cleal and Zodrow 1989). Bell (1938) first recognized and

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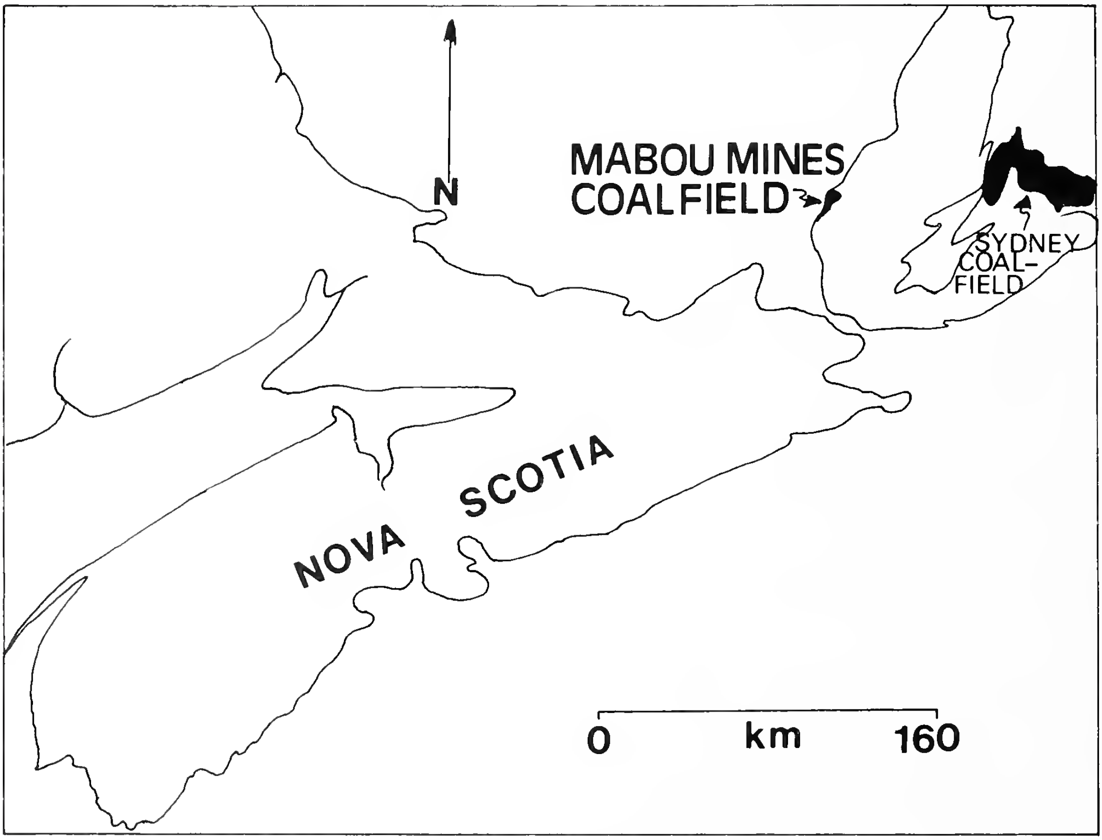
mapped the stratigraphical range of *R. muensteri* from the Maritime Provinces of Canada, describing specimens from the Sydney Coalfield, with later records coming from the Pictou Coalfield (Bell 1940) and New Brunswick (Bell 1962). Most recently, specimens have been reported from the small Mabou Mines Coalfield (Zodrow and Vasey 1986) and it is these that form the basis of the present study.

## MATERIAL AND METHODS

Specimens studied are from the Mabou Mines Coalfield on the west coast of Cape Breton (Text-fig. 1). The stratigraphy is summarized in Text-figure 2, and further details are in Zodrow and Vasey (1986). The entire section is fossiliferous, *R. muensteri* being particularly abundant in the roof rocks of the coals and in the silty shale lithologies. The specimens described in this paper are all from the lower Westphalian D.

The specimens are preserved in an extremely soft matrix. Many are naturally macerated, with little more than the cuticle remaining, resulting in a very low colour-contrast between fossil and matrix. Obtaining good photographs of hand specimens thus proved extremely difficult. To document details of venation, we prepared transfers using the method of Walton (1923).

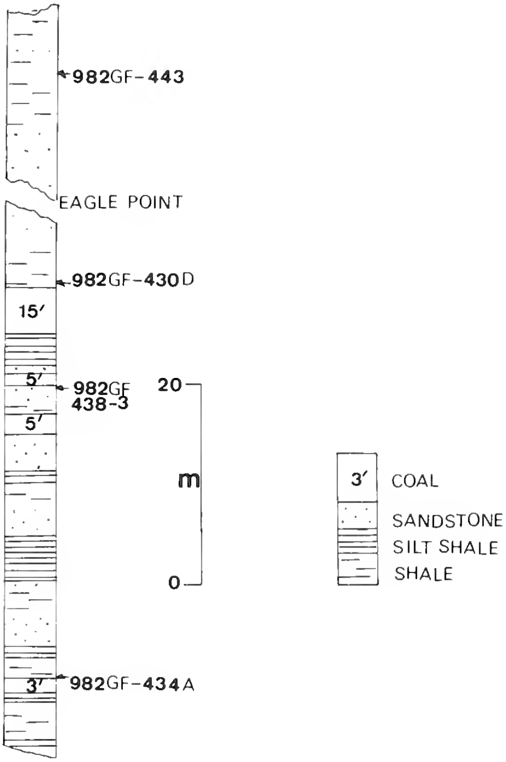
Cuticles were prepared from a specimen (University College of Cape Breton Collections, Number 982GF-443) which still retained some carbonized phytoleim. Naturally macerated cuticles in the Upper Carboniferous rarely preserve details of the epidermal structure. The matrix was removed by hydrofluoric acid. The fossils were then macerated in Schulze's Solution for about three hours and then washed in 5 per cent ammonium hydroxide and finally in distilled water. The cuticles were mounted in glycerine jelly containing safranin on



TEXT-FIG. 1. Outline map of Nova Scotia, showing location of Mabou Mines Coalfield.

glass slides. The slides were examined under a Leitz Ortholux II microscope, using both brightfield and Nomarski (interference phase) illumination. Fourteen slides were prepared, and are stored in the collections of the University College of Cape Breton.

TEXT-FIG. 2. Lithostratigraphical section through Mabou Mines Coalfield, showing horizons where the described specimens were found. Based on Zodrow and Vasey (1986, fig. 1).



## DESCRIPTIONS

### *Gross morphology*

The material consists mainly of isolated pinnules, or of small fragments of ultimate pinnae. Rachides are thick and longitudinally striated. Pinnae are more or less parallel-sided and terminated by a single apical pinnule. Apical pinnules are all about 10 mm long and may either be elongate and subtriangular (5 mm wide) or more isodiametric and rhomboidal (10 mm wide).

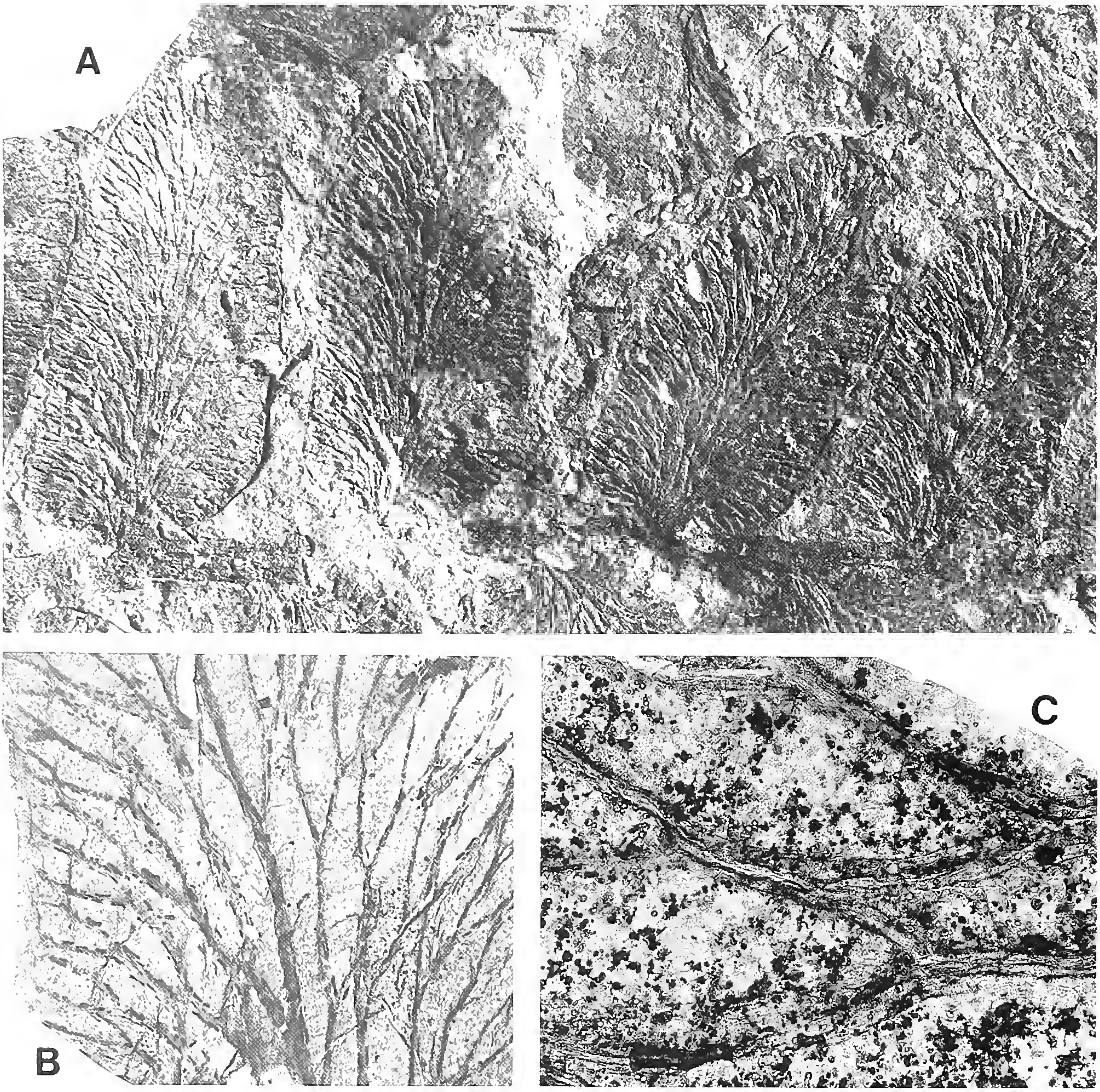
Lateral pinnules are quite variable in shape, but can be grouped into two broad categories. The most common are oval to linguiform, up to 25 mm long and 10 mm wide (Text-fig. 3A). Near the pinna apex they are broadly attached to the rachis; lower in the pinna they have a more constricted base, being attached to the rachis by only a narrow band of lamina on either side of the midvein, and often with an acroscopic auricle. These are probably the pinnules from the main part of the frond, above the main dichotomy.

Pinnules of the second category are larger, up to 60 mm in length, with a rounded to subtriangular aspect. These are probably the forma *impar*-type pinnules from the basal parts of the frond.

The venation pattern is shown in Text-figure 4. The midvein enters the pinnule on the basiscopic side. It initially lies at a low angle to the rachis, until it reaches the centre of the pinnule. It then bends and extends along the long axis of the pinnule. In the smaller pinnules near the pinna apex, the midvein extends for about 50% of the pinnule length; in the larger pinnules lower in the pinna, it extends for about 90% of the length.

The lateral veins are attached to the midvein at 10–20°, and are loosely anastomosed (Text-figs 3B–C,4). The anastomoses are produced in three different ways:

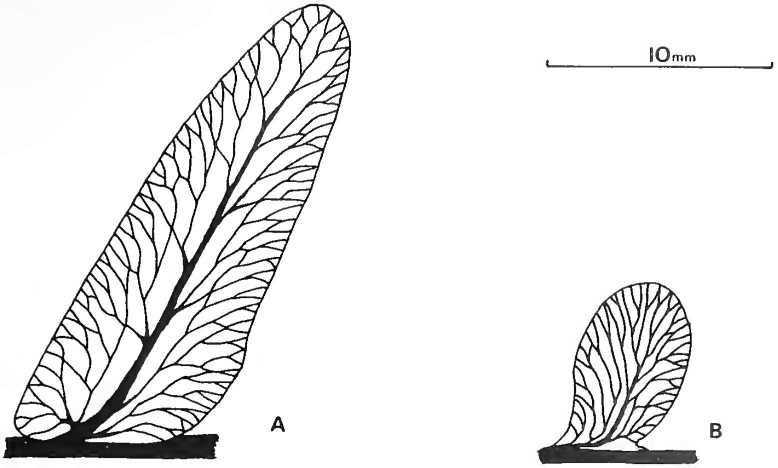
1. by undulating or highly flexuous veins approaching each other but remaining separate by several cell-widths (i.e. pseudoanastomoses);



TEXT-FIG. 3. *Reticulopteris muensteri* (Eichwald) Gothan. Features of gross morphology. A, UCCB, 982GF-438-3; unmacerated specimen, showing shape and venation of pinnules, × 6. B, UCCB, 982GF-434A; naturally macerated pinnule, separated from rock, showing detail of venation, × 25. C, UCCB, CCB/982GF-443/4; pinnule macerated in Schulze's solution but not washed with alkali, showing close-up of venation, × 50.

2. by tangential anastomoses, where the veins come into intimate contact;
3. by full anastomoses, where the veins appear to cross over on contact.

Anastomosis types 2 and 3 predominate in the larger pinnules; in the smaller pinnules, type 1 are more common, especially on the acroscopic side of the pinnule. The veins meet the pinnule margin at about right-angles, and produce a vein density of 4·5–5·0 per mm. Further details of the variation in the venation in these specimens are in Zodrow and Vasey (1986).



TEXT-FIG. 4. *Reticulopteris muensteri* (Eichwald) Gothan. Venation diagrams, based on Zodrow and Vasey (1986, fig. 8). A, fully developed pinnule. B, small pinnule from near pinna apex.

### *Cuticles*

The adaxial epidermis is differentiated between the costal and intercostal fields (Pl. 1, fig. 1; Text-fig. 5A). Costal cells are elongate and subrhomboidal, up to 200 μm long and 20 μm wide. Intercostal cells are significantly shorter and more irregularly polygonal, up to 120 μm long and 30 μm wide (Pl. 2, fig. 1). No trichomes were observed. Two examples of small, round structures, 20 and 25 μm in diameter, were observed attached to intercostal cells on one cuticle. The larger of the two is damaged and shows little structure. The other seems to be ovoid with a central fold (Pl. 2, fig. 6). The nature of these structures is unclear.

The abaxial epidermis is also differentiated between the costal and intercostal fields (Pl. 1, fig. 4; Text-fig 5B). Costal cells are elongately subrhomboidal, up to 160 μm long and 30 μm wide. Intercostal cells are irregularly polygonal and more or less isodiametric, up to 35 μm in size (Pl. 2, fig. 2). Most of the intercostal cells are neighbour cells to the stomata (Pl. 2, fig. 2). The cuticle covering the costal cells seems often to be in a different plane to the intercostal cells (Pl. 1, fig. 3). However, it is unclear whether the stomatiferous areas were sunken, or there is merely a taphonomic wrinkling of the cuticle, perhaps reflecting differential cuticle thicknesses in different parts of the pinnule.

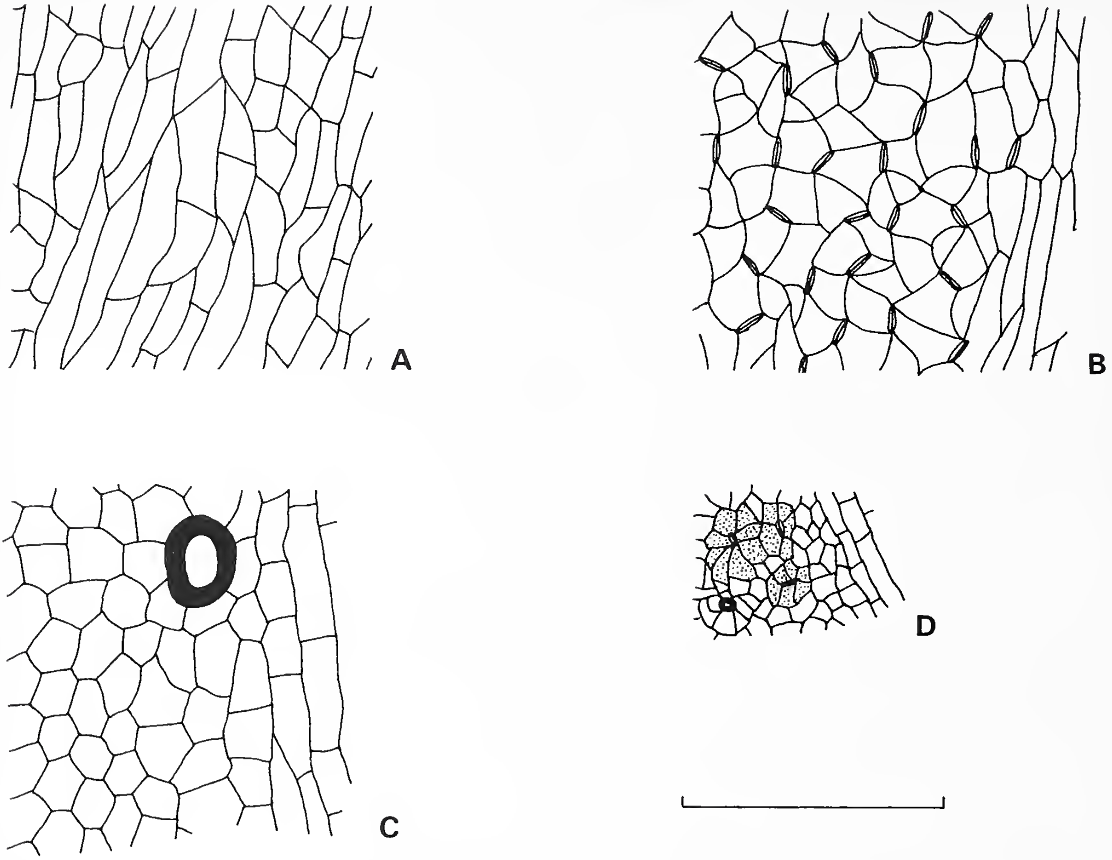
Trichome bases 25–30 μm in diameter are present on the abaxial cuticle (Pl. 2, fig. 5). They are sparsely distributed and occur mainly but not exclusively in the costal fields. There also seems to be a greater concentration of hair bases near the pinnule margin. No trichomes were found attached, but they evidently had a splayed base and were often attached to the middle of a single epidermal cell.

Stomata are anomocytic and restricted to the intercostal fields of the abaxial epidermis (Pl. 2, figs 2–4). In some parts of the abaxial cuticle, the cuticle of the guard cells is lost and all that remains is a hole (Pl. 1, fig. 2). Where preserved, however, they show the guard cells to have been about 25 μm long and 6 μm wide (Pl. 2, fig. 4). The alignment of the polar axes of the guard cells is somewhat irregular, but there seems a general tendency for them to be arranged parallel to what is probably the long axis of the pinnule (Text-fig. 5B). Some stomata seem to be covered by a small fold of cuticle, which may be the remains of a stomatal pit (Pl. 2, fig. 3).

## COMPARISONS

### *Neuropteroid taxa*

In the revised classification of neuropteroid foliage form-genera proposed by Cleal *et al.* (1990), the cuticles clearly indicate that *R. muensteri* lies closest to *Neuropteris sensu stricto* (i.e. the Group II species of Cleal and Zodrow 1989). Particularly significant characters are: (1) clear differentiation between costal and intercostal fields on the adaxial cuticle; (2) well-developed anticlinal walls on the



TEXT-FIG. 5. Epidermal features separating *Reticulopteris* from *Barthelopteris*. A–B, *Reticulopteris muensteri* (Eichwald) Gothan. UCCB, CCB/982GF-443/1, drawn directly from slides using camera-lucida; Westphalian D, Mabou Mines Coalfield, Nova Scotia. A, adaxial cuticle. B, abaxial cuticle, showing stomata without subsidiary cells. C–D, *Barthelopteris germarii* (Giebel) Zodrow and Cleal, comb. nov. Based on Barthel (1962, figs 45–46). C, adaxial cuticle showing hair base (in black). D, abaxial cuticle showing stomata with subsidiary cells (stippled) and hair base (in black). Scale bar = 200 μm.

abaxial cuticle; (3) anomocytic stomata; and (4) presence of multicellular trichomes on the abaxial cuticle. In contrast, the laveineopterids show an essentially uniform distribution of epidermal cells on the adaxial surface, and have no trichomes with poorly-cutinized anticlinal walls on the abaxial surface. Both the macroneuropterids and neurocallipterids are readily distinguishable from

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EXPLANATION OF PLATE 1

Figs 1–6. *Reticulopteris muensteri* (Eichwald) Gothan. Cuticles photographed using brightfield illumination; Westphalian D; Mabou Mines Coalfield, Nova Scotia. 1, UCCB, CCB/982GF-443/1; adaxial cuticle, × 100. 2, UCCB, CCB/982GF-443/3; abaxial cuticle showing relationship between costal and intercostal field, × 100. 3, UCCB, CCB/982GF-443/7; abaxial cuticle including midvein area in upper part of figure, × 100. 4, UCCB, CCB/982GF-443/1; abaxial cuticle showing stomata with missing guard-cells, × 100. 5, UCCB, CCB/982GF-443/7; adaxial cuticle, × 100. 6, UCCB, CCB/982GF-443/3; abaxial cuticle showing stomata with guard-cells, × 100.

PLATE 1

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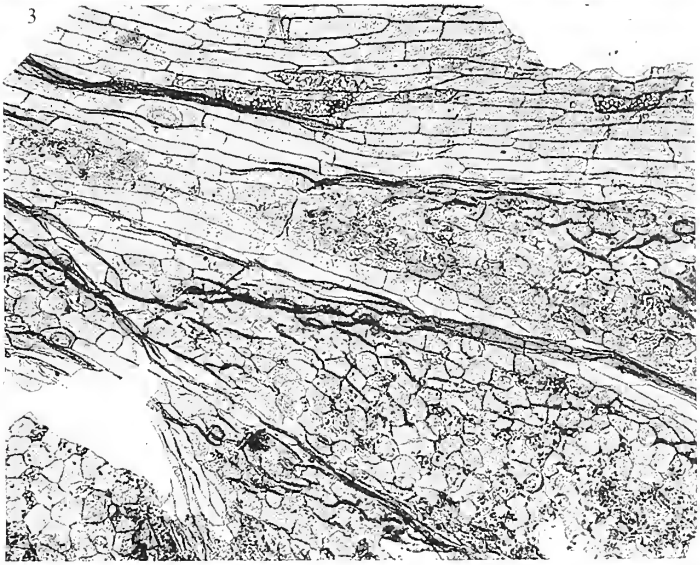

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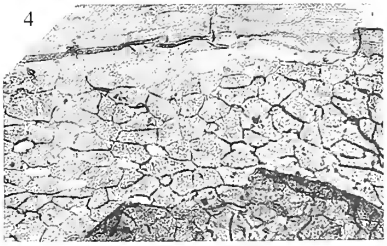

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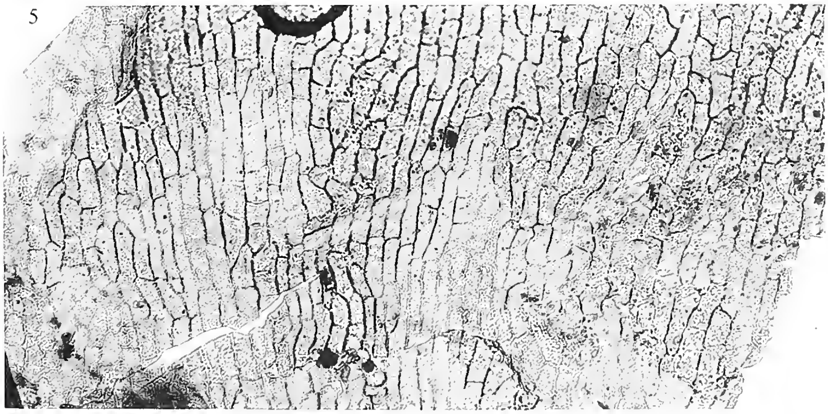

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*R. muensteri* by their stomatal apparatuses having from two to four well-developed subsidiary cells in the brachyparacytic, or rarely, cyclocytic arrangement.

### *Other reticulopterids*

Only one other well-documented species has been assigned to *Reticulopteris* – namely *R. germarii* (Giebel) Gothan. It is known from the upper Baruellian to the Autunian of Portugal, Spain, France, Italy, Germany and Yugoslavia (see Wagner 1964, for further details of its distribution). Cuticles have been described by Barthel (1962, 1976).

*R. germarii* has some of the obvious, gross morphological characters of *Reticulopteris*, including lateral pinnules with a constricted base, an anastomosed venation, and pinnae terminated by a single apical pinnule (Gothan 1941; Barthel 1958, 1976). The venation is far more consistently anastomosed over the entire width of the pinnule, with none of the pseudo- or tangential anastomoses that occur so commonly in *R. muensteri*, but this could be due merely to the venation of the later species having reached a more 'advanced' condition. However, the differences in epidermal structure are far more marked (Text-fig. 5). According to Barthel (1962), the adaxial epidermis of *R. germarii* is virtually undifferentiated between the costal and intercostal fields, except for the midvein, while on the abaxial epidermis the stomata are cyclocytic. Prominent trichome bases were reported on both sides of the pinnule, particularly near the midvein, but no attached trichomes were found.

The epidermal structure of *R. germarii* in fact stands far nearer to that of *Neurocallipteris* Sterzel *emend.* Cleal *et al.*, 1990, than that of *R. muensteri*. According to Cleal *et al.* (1990), the neurocallipterids have an adaxial epidermis with weakly differentiated costal and intercostal fields, and stomata on the abaxial epidermis that are cyclocytic or amphicyclocytic. There are differences, most notably the presence of prominent papillae on the abaxial epidermis of neurocallipterids. However, there are clearly more similarities than differences in the epidermal structures of the two taxa. There is furthermore an interesting correlation in the general shape and symmetry of the *R. germarii* pinnules with one of the species currently assigned to *Neurocallipteris*, i.e. *N. planchardii* (Zeiller) Cleal *et al.*, 1990. For instance, a large fragment of a *R. germarii* frond figured as a drawing by Langiaux (1984, fig. 228) compares closely with photographs of *N. planchardii* in Reichel and Barthel (1964, pl. 1, fig. 1; pl. 4, figs 1–2) and Vetter (1968, pl. 34, figs 1, 7–8). Such relatively subtle characters of pinnule form would not normally be considered of taxonomic significance at the rank of form-genus but, taken together with the cuticular evidence, the similarities cannot be ignored. Thus, gross morphological, cuticular and stratigraphical evidence all point to *R. germarii* being a mesh-veined analogue of *Neurocallipteris*, rather than being a true reticulopterid (i.e. a mesh-veined analogue of *Neuropteris*). For this reason, a formal proposal is made below to transfer *R. germarii* to a new form-genus, *Barthelopteris*.

## SYSTEMATIC PALAEONTOLOGY

The classification of supra-generic taxa follows that of Cleal (in press), and incorporates the satellite-taxon

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### EXPLANATION OF PLATE 2

Figs 1–7. *Reticulopteris muensteri* (Eichwald) Gothan. Cuticles photographed using Nomarksi illumination, except fig. 2 which is with brightfield illumination; Westphalian D, Mabou Mines Coalfield; Nova Scotia. 1, UCCB, CCB/982GF-443/3; adaxial cuticle, × 250. 2, UCCB, CCB/982GF-443/7; enigmatic oval structures on adaxial cuticle, × 500. 3, UCCB, CCB/982GF-443/3; trichome base on abaxial cuticle, × 500. 4, UCCB, CCB/982GF-443/1; detail of stomata showing guard cells, × 500. 5, UCCB, CCB/982GF-443/1; abaxial cuticle showing stomata, × 250. 6, UCCB, CCB/982GF-443/1; detail of stomata showing 'flap' of cuticle which may be evidence of a stomatal pit, × 500. 7, UCCB, CCB/982GF-443/3; abaxial cuticle showing stomata, × 500.


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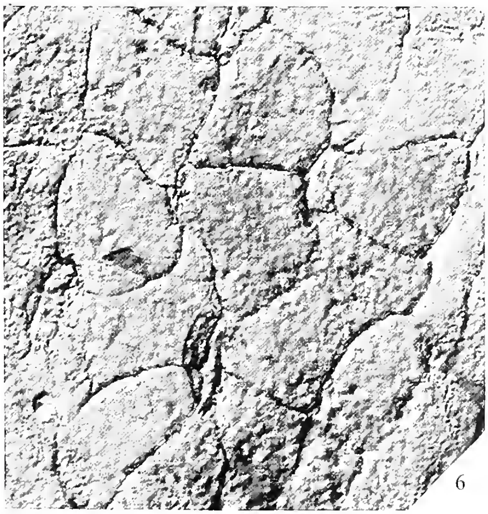
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ZODROW and CLEAL, *Reticulopteris*

concept outlined by Thomas and Brack-Hanes (1984). The synonymy lists, which are not complete, use the system of annotations summarized by Matthews (1973) with two additions. One is specific to palaeobotany, and is the prefix of the letter 'k' to a synonym if it includes cuticular evidence. The second is of more general use; entries prefixed by the dagger sign (†) are the most recent references which include a reasonably full synonymy and extensive illustration.

### Class CYCADOPSIDA Barnard and Long, 1975
### Order TRIGONOCARPALES Seward, 1917 *emend.* Meyen, 1984
### Satellite form-genus RETICULOPTERIS Gothan, 1941 emend.

p*1941 *Reticulopteris* Gothan, p. 427.
†1967 *Reticulopteris* Gothan; Laveine, p. 215.

*Type species. Reticulopteris muensteri* (Eichwald) Gothan, 1941, p. 428.

*Emended diagnosis.* Pinnules entire-margined, oval to linguiform, with lateral margins parallel or slightly tapered. Pinnule apex round or slightly acuminate. Pinnule base cordiform, generally narrowly attached to rachis, but sometimes more broadly attached, particularly high in a pinna. Midvein usually extends for half to two-thirds the pinnule length, except in the largest pinnules, where it extends for most of the pinnule length. Lateral veins clearly marked, anastomosed, with dimension of the meshes diminishing towards the pinnule margin. Ultimate pinnae terminated by single apical pinnule. Frond probably bipartite, each primary segment being tri- or occasionally quadri-pinnate with intercalated monopinnate segments attached to the two primary rachis branches. Adaxial foliar epidermis clearly differentiated between costal and intercostal fields. Well-developed anticlinal walls on abaxial foliar cuticle. Anomocytic stomata found only in intercostal fields of abaxial epidermis. Multicellular trichomes on the abaxial epidermis.

*Remarks.* The above emended diagnosis is adapted from that given by Laveine (1967), with the addition of the foliar epidermal details. The nomenclature of frond architecture follows that of Cleal and Shute (1991).

### *Reticulopteris muensteri* (Eichwald) Gothan, 1941, emend.

Plates 1–2; Text-figs 3–5A–B

*1840 *Odontopteris Münsteri* Eichwald, p. 87, pl. 3, fig. 2.
1849 *Dictyopteris Münsteri* (Eichwald) Brongniart, p. 19.
1862 *Dictyopteris Hoffmanni* Roemer, p. 29, pl. 7, fig. 3.
1868 *Dictyopteris cordata* von Roehl, p. 50, pl. 15, fig. 6; pl. 21, fig. 7*b*.
1880 *Dictyopteris rubella* Lesquereux, p. 145, pl. 23, figs 7–10.
1899 *Linopteris Münsteri* (Eichwald) Zeiller, p. 48, pl. 4, fig. 13.
1913 *Linopteris major* Goode, p. 265, pl. 27, figs 1, 3.
1941 *Reticulopteris Münsteri* (Eichwald) Gothan, p. 428.
†1967 *Reticulopteris münsteri* (Eichwald) Gothan; Laveine, p. 218, pls 58–60; pl. 61, figs 1–4.

*Type specimen.* Holotype figured with protologue originated from a sandstone exposed in the Lougan Mine, Donets Coalfield, Ukraine. Stratigraphical details were not given, but the specimen probably originated from the lower Moscovian. Its present location is unknown.

*Emended diagnosis.* Pinnules oval to elongately linguiform, sometimes somewhat triangular, 6–25 mm long, 4–8 mm wide; obliquely attached to rachis. Midvein flexuous and extends for up to two-thirds the pinnule length, except in the larger pinnules near the base of the frond where they extend for most of the pinnule length. Near the midvein, lateral veins are pseudoanastomosed or form only large meshes; nearer the pinnule margin, veins are more fully anastomosed, producing smaller and more numerous meshes. Veins meet pinnule margin at about 90° and produce vein density of 4·5–5·0 per mm on pinnule margin. Adaxial costal epidermal cells elongate, subrhomboidal, up to 200 μm long and 20 μm wide; adaxial intercostal cells shorter, more irregularly polygonal, up to 120 μm long and 30 μm wide. Abaxial costal epidermal cells elongately subrhomboidal, up to 160 μm long and 30 μm wide; abaxial intercostal cells irregularly polygonal, more or less isodiametric, up to 35 μm in size. Anomocytic stomata restricted to abaxial intercostal fields; guard cells 25 μm long and 6 μm wide. Trichomes only on abaxial surface, 25–30 μm in diameter at base.

*Remarks*. The above emended diagnosis is based mainly on Laveine (1967), with the addition of epidermal features.

*Distribution*. Bolsovian and lower Westphalian D (*Paripteris linguaefolia* and *Linopteris bunburii* Zones *sensu* Cleal 1991) of the so-called paralic-belt of coalfields, that extends from Cape Breton (Nova Scotia) in the west, through Britain, northern France, Belgium, The Netherlands, northern Germany and Poland, to the Ukraine in the east.

## Satellite form-genus BARTHELOPTERIS gen. nov.

p1941 *Reticulopteris* Gothan, p. 427.

*Type species*. *Barthelopteris germarii* (Giebel) Zodrow and Cleal comb. nov.

*Diagnosis*. Pinnules entire-margined, oval to linguiform, with lateral margins parallel or slightly tapered. Pinnule apex round. Pinnule base cordiform, generally narrowly attached to rachis. Midvein usually extends for two-thirds or more of pinnule length, except in the smallest pinnules where it extends for half or less of their length. Lateral veins clearly marked, anastomosed, with dimension of the meshes diminishing towards the pinnule margin. Ultimate pinnae terminated by single apical pinnule. Frond composed of at least bipinnate segments. Isodiametric, polygonal epidermal cells more or less uniformly distributed on adaxial surface of pinnules, except near midvein where they are more elongate. Well-developed anticlinal walls on abaxial foliar cuticle. Cyclocytic stomata found only in intercostal fields of abaxial epidermis. Multicellular trichomes on both surfaces of pinnules.

### *Barthelopteris germarii* (Giebel) Zodrow and Cleal comb. nov.

Text-fig. 5C–D

*1857 *Lonchopteris Germari* Giebel, p. 301, pl. 1.
1862 *Dictyopteris Schützei* Roemer, p. 30, pl. 12, fig. 1.
1864 *Sagenopteris taeniaefolia* Göppert, p. 127, pl. 9, figs 11–13.
1897 *Linopteris Germari* (Giebel) Potonié, p. 154.
1941 *Reticulopteris germari* (Giebel) Gothan, p. 428.
k1962 *Linopteris germari* (Giebel) Potonié; Barthel, p. 31, pl. 27, figs 1, 4, 6; pl. 28, figs 1–6.
†1964 *Reticulopteris germari* (Giebel) Gothan; Wagner, p. 26, pl. 17, figs 35–37.
†1968 *Linopteris germari* (Giebel) Potonié; Vetter, p. 105, pl. 27, fig. 5; pl. 33, fig. 3; pl. 35, figs 6–7.
k1976 *Reticulopteris germari* (Giebel) Gothan; Barthel, p. 94, pl. 32, figs 7–8.

*Type specimen*. Holotype figured with protologue originated from the Löbejün Mines in the Saale Trough, near Halle, southern Germany. Stratigraphical details were not given, but the specimen probably came from the Stephanian C Wettiner Schichten (*Sphenophyllum angustifolium* Zone *sensu* Cleal 1991). Its present location is unknown.

*Emended diagnosis*. Mainly elongate, linguiform to subfalcate pinnules 20–60 mm long, 3–13 mm wide, attached alternately or sub-oppositely to the rachis by a short pedicle; lateral margins parallel or slightly converging, apex obtuse, and base cordate. Prominent midvein extending for most of pinnule length. Anastomosed lateral veins form on average four small meshes between the midvein and the pinnule margin. Lateral veins narrowly attached to midvein, and meet pinnule margin at about right-angles. Adaxial foliar epidermal cells mostly isodiametric and polygonal, 30–50 μm in size, except near midvein where they are more elongate, 50–80 μm long by 15–20 μm wide. On abaxial foliar surface, costal cells elongate, 30–60 μm long by 15–20 μm wide; intercostal cells small and irregular in shape, 14–20 μm in size. Stomata dense, irregularly orientated, probably sunken; guard cells 12–15 μm long by 7–9 μm wide; each stoma surrounded by 6–10 small subsidiary cells. Hair bases thickly cutinized, 50–80 μm in diameter.

*Remarks.* The above diagnosis has been adapted mainly from Vetter (1968), with some additional gross-morphological characters mentioned by Wagner (1964), and details of the epidermal structures given by Barthel (1962).

*Distribution.* Upper Barruelian to Autunian of the intra-montane basis of southern Portugal, southern and central France, southern Germany, Italy and Yugoslavia. In northern Spain, it ranges down to the upper Cantabrian. This stratigraphical discrepancy of the Spanish records may be because they represent drifted remains from extra-basinal ('hillside') vegetation, not normally preserved in the other areas (Knight 1974).

## DISCUSSION

The evidence presented here is further confirmation that *Reticulopteris* Gothan is closely related to *Neuropteris* Sternberg *emend.* Cleal *et al.* (1990), differing significantly only in having anastomosed veins. We further provide evidence that *Neurocallipteris* Sterzel *emend.* Cleal *et al.* (1990) also had an anastomosed veined counterpart, which we have named *Barthelopteris.* These are not unique among the trigonocarpalean fronds (Wagner 1958), other well-documented form-genus couplets with anastomosed and open venation being *Lonchopteris/Alethopteris* and *Linopteris/Paripteris.* Some of the other examples quoted by Wagner are less well established. For instance, he proposed the form-genus *Anastomopteris* as a counterpart to *Odontopteris*, but it was described from a single small specimen of uncertain affinities from Turkey (Laveine 1967). The evidence put forward by Asama (1981) also undermines the link between the Cathaysian *Emplectopteridium* and the mainly Euramerian *Callipteridium*, since the former seems not to have possessed a bipartite frond architecture. Nevertheless, the general thesis that many of the open-veined trigonocarpalean fronds had anastomosed-veined counterparts still holds good.

At least among gymnosperms, such form-genus couplets appear to be unique to the trigonocarpaleans, perhaps reflecting that they are the oldest known plants to develop this style of venation. The only extant order with both types of venation is the Gnetales (as currently defined by e.g. Martens (1971)) with *Gnetum* being anastomosed and *Welwitschia* open veined. However, they cannot be regarded as couplets in the same sense as the trigonocarpalean form-genera; *Gnetum* has oval leaves with a midvein and anastomosed lateral veins, not unlike some dicot angiosperms, while *Welwitschia* has elongate, strap-like leaves with parallel veins. Indeed there is now some suggestion from rRNA data that the two genera are only distantly related and that the Gnetales is not a natural order (Troitsky *et al.* 1991). In the fossil record, the nearest comparison is with the Arberiales ('glossopterids'), where there are leaves with anastomosed (e.g. *Glossopteris*) and open (*Rhabdotaenia*) veining. Even here the anastomosed and open-veined leaves are not otherwise virtually identical as in the Trigonocarpales.

Apart from the gymnosperms, the existence of open and anastomosed veining in closely related genera is known only in ferns. Bower (1923) mentioned examples among the Ophioglossaceae, Marattiaceae, Schizaeaceae and Dennstaedtiaceae. However, anastomosed veining seems to have evolved rather later (probably in the early Mesozoic) and in quite a different way than in the gymnosperms. According to Bower, it first developed by the fusion of the distal vein-endings to form loops, and only later developed in more proximal positions in the pinnule. This contrasts with the lateral fusion of flexuous veins, which Josten (1962) showed in the gymnosperms.

The change from open to anastomosed venation occurred independently in several phylogenetic lineages within the Trigonocarpales, but in only one has the actual transition been observed directly in the fossil record, i.e. from *Neuropteris* to *Reticulopteris* (Josten 1962; Laveine 1967). This is of general interest, as being one of the very few examples of phyletic gradualism to be documented in the plant fossil record. However, it is also of major importance for understanding the evolutionary processes taking place within the trigonocarpaleans. The gradual increase in flexuousness of the veins, which culminated in the anastomosed condition, seems to have started in the early to mid Duckmantian, and full anastomosis appeared in the early Bolsovian. It thus coincides with changes occurring in the flood-plain swamps documented by DiMichele *et al.* (1985), in which lycophyte trees favouring the wettest conditions (e.g. *Lepidophloios*, *Diaphorodendron*) were progressively replaced by trees favouring somewhat drier substrates (e.g. *Paralycopodites*). DiMichele *et al.* (1985) interpret this in terms of climatic change, referring to the Duckmantian/Bolsovian as their First Dry Interval. It is thus clearly tempting to relate the change from open anastomosed veining as a response to this climatic change.

According to the DiMichele *et al.* (1985) model, the Westphalian D experienced a reversion to wet conditions when the diaphorodendrids and lepidophloiids return to the main parts of the swamps. This is again mirrored by developments among the trigonocarpaleans, with the introduction of a second group of neuropterids, often referred to as the *N. ovata* Group. *Reticulopteris* persisted through part of the Westphalian D, but this may reflect ecological partitioning within the raised habitats (levées, etc.) favoured by the trigonocarpaleans. The areas that were topographically higher, or had drier substrates, perhaps favoured *Reticulopteris*, the lower or wetter parts, *Neuropteris*. By the middle Westphalian *Reticulopteris* disappears from the fossil record. This may reflect the elimination of the slightly drier sub-habitats of the levées, as wetter conditions became more prevalent. Alternatively, *Reticulopteris* may have been displaced by another group of trigonocarpalean plants, which bore fronds known as *Odontopteris* Brongniart, and which may have been better-adapted to the drier parts of the levées.

The evidence thus suggests that the development of anastomosed veining was a response to the climate becoming drier. However, this veining pattern did not appear suddenly, and the adaptive significance of the change must be sought in the morphological changes that preceded it, i.e. the increasing flexuousness of the veins. If this group of plants was being placed under increased physiological stress due to reduced water-availability, any improvement in the plant's water transport system for example by increasing the area of interface between the veins and the mesophyll would be an advantage. This could be achieved by either increasing the number of veins in the leaf, or increasing the length of an individual vein in a particular area of leaf. The *N. obliqua* group of species appears to have followed the latter route, by making the veins sinuous along their length. The degree of sinuosity progressively increased, in turn increasing the vein–mesophyll contact area and thus the efficiency of water distribution, until eventually adjacent veins met to form the anastomosed pattern seen in *Reticulopteris*.

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# A NEW FERN FROM THE LOWER PERMIAN OF CHINA AND ITS BEARING ON THE EVOLUTION OF THE MARATTIALEANS

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ABSTRACT. A fertile marattialean fern from the Lower Shihhotse Formation, Lower Permian of Taiyuan, north China is ascribed to a new genus, *Taiyuanitheca*, as *T. tetralinea* sp. nov. The fronds are *Pecopteris*-like with two rows of synangia arranged on each side of the midvein on the adaxial surface of the pinnules. The synangia are sessile and ring-like with elliptical sporangia that are fused together along their full length. The new fern is compared with fossil and extant marattialeans and new evolutionary pathways are proposed for this group of plants.

PERMIAN strata are well developed in the Taiyuan area in north China and have been used as an index section for stratigraphical correlation in China. The Cathaysian flora proposed by Halle (1927, 1937) was based on the late Palaeozoic plants from this area. The Permo-Carboniferous plants of Taiyuan belong to the North Cathaysian flora which is characterized by lobatunnularias, tingias, emplectopterids and marattialeans (Li and Yao 1983; Zhang and He 1985). The present specimens were discovered during the course of a study on the Lower Permian plants from Taiyuan (Gao 1988). Re-evaluations of *Tingia* and *Tingiostachya*, cycadalean remains, and the enigmatic *Shuangnangostachya* have been published elsewhere (Gao and Thomas 1987, 1989*a*, 1989*b*, 1991).

Marattialean ferns are characterized by exannulate sporangia grouped into synangia. They have a long history and can be dated back to the Carboniferous. Extant genera have unbranched stems, large and fleshy adventitious roots and usually large fronds; all grow in tropical or sub-tropical areas.

During the Early Permian of North China, marattialeans played an important role in vegetation. Apart from this new fertile fern, there is also a number of associated sterile *Pecopteris* species: *P. orientalis* (Schenk) Potonié, *P. tuberculata* Halle and *P. wongii* Halle (Gu and Zhi 1974; Gao 1988).

## MATERIAL AND METHODS

The specimens were collected by G.Z. in the summer of 1986 from the Lower Shihhotse Formation of Simugedong, Dongshan (East Hills), Taiyuan, north China. They are preserved in a grey shale as compressions with impression counterparts. Some *dégagement* of the specimens was achieved with the aid of tungsten needles sharpened by heating and subsequent dipping into molten sodium nitrite. Maceration of portions of the laminae and sporangia with Schultze solution unfortunately yielded neither cuticles nor spores. Sporangia were prepared for SEM observation by coating with gold, using an Emscope sputter coater, prior to examination with a Jeol T100 Scanning Electron Microscope.

The specimens (prefixed with GP) will be deposited in the Beijing Graduate School, China Institute of Mining.

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## SYSTEMATIC PALAEONTOLOGY

### Order MARATTIALES G. Bitter *in* Engler and Prantl, 1902
### Family MARATTIACEAE Berthtold and Presl, 1802
### Genus TAIYUANITHECA gen. nov.

*Derivation of name.* Taiyuan is the city nearest to the type locality; Greek '*theca*', case or container.

*Type species. T. tetralinea* sp. nov., Lower Shihhotse Formation, Lower Permian, north China.

*Diagnosis.* Fertile frond at least bipinnate; pinna normally elliptical with truncated base; pinnule of *Pecopteris* type; midvein of pinnule almost to apex of pinnule. Two rows of synangia on each side of midvein; synangium sessile, ring-like. Sporangia elliptical, fused together along full length.

### *Taiyuanitheca tetralinea* sp. nov.

Text-figs 1–2

*Derivation of name.* For the feature of four rows of synangia on each pinnule.

*Locality.* Simugedong, Dongshan (East Hills), Taiyuan, China.

*Horizon.* Lower Shihhotse Formation, Lower Permian.

*Holotype.* GP0112 (Text-fig. 2).

*Diagnosis.* Pinnule oblong, 12–16 mm long, 5–7 mm wide, apex rounded, attached almost perpendicularly to rachis by entire base. Margin of pinnule entire, with abaxially recurved edge about 1 mm wide. Lateral veins once dichotomized. Synangia ring-like, sessile, about 1 mm in diameter. Two rows of synangia, each with about 15 synangia, situated on each side of midvein. Sporangia elliptical, fused together along their entire length; approximately 12 sporangia in each synangium.

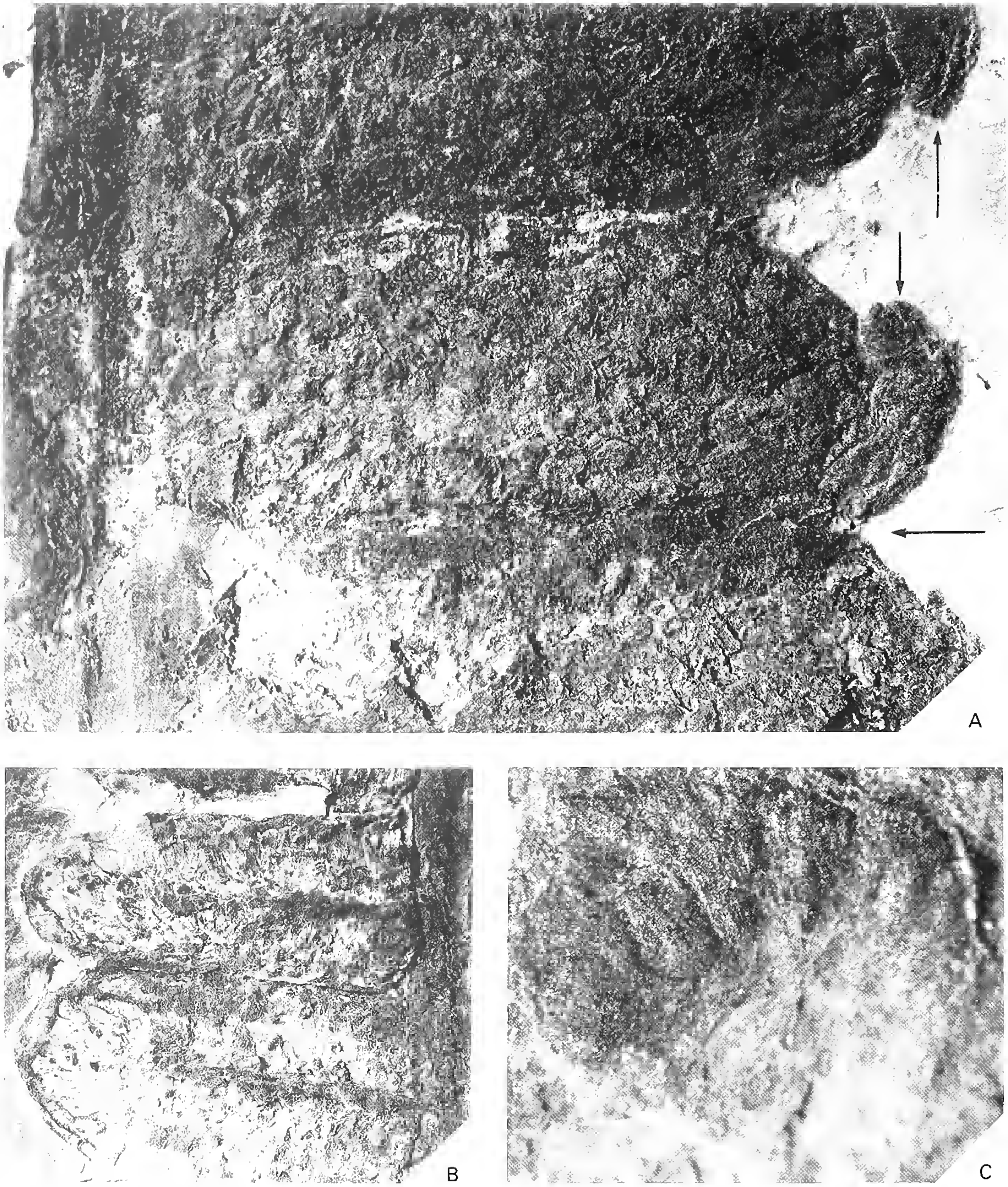
*Description.* Eight specimens (GP0032–34, 0066, 0111–0114) are compressions; some of them with their impression counterparts. The longest pinnate frond portion (GP0113) is about 220 mm long (Text-fig. 1A). The rachis is about 16 mm wide in the basal part and 6 mm in the upper part. The pinna raches are about 4 mm wide, with two longitudinal ridges, and attached alternately at a 40°–60° angle to the rachis. The overall shape of the pinnae is linear-lanceolate. The longest pinna is about 120 mm long, although not complete. The pinnules alternate on the pinna rachis and are attached almost at right angles by their entire basal widths. They are 12–16 mm long and 5–7 mm wide, with parallel and entire lateral margins and rounded apices. The pinnules basipetally overlap each other very slightly. Another noticeable feature is a black coalified layer, about 1 mm wide, extending around the entire margin of the abaxial surface of the pinnule including the apex (Text-fig. 2A). This is interpreted as an abaxially incurved margin. In some pinnules the venation is seen to consist of a straight midvein almost reaching the pinnule apex and once-dichotomizing lateral veins (Text-fig. 2B). Two rows of about 15 ring-like synangia occur regularly along both sides of pinnule midveins (Text-fig. 2A) and each synangium has approximately 12 sporangia (Text-fig. 2C). The sporangia are entirely laterally fused like those of the living marattialean fern *Christensenia* Maxon.

The exact attachment of the synangia to the pinnule is difficult to interpret because of the nature of the compression. Although the impression counterparts are badly preserved, it seems clear that the specimens are generally preserved with the abaxial surface of the pinna embedded into the matrix. During the splitting of the rock, the laminae of some of the pinnules have been lost so that the bases of the embedded synangia become visible. Occasionally, parts of a lamina compression, with midveins and lateral veins, have been preserved together with the synangia in the same compression. After carefully removing the midvein and lateral veins of the pinnule with a tungsten needle, the synangia can be observed beneath them. From this it seems certain that the synangia had constricted bases and were sessile on the pinnule lamina.

TEXT-FIG. 1. *Taiyuanitheca tetralinea* gen. et sp. nov. A, GP0113; bipinnate portion of frond with prominent rachis, pinna raches and the broken apex of the frond (arrowed), × 1. B, GP0112; adaxial view of linear pinnules with thick pinna rachis, × 1.

*Comparison.* The present specimens of *Taiyuanitheca tetralinea* show certain similarities to some other Permian compression marattialean ferns (*Rajahia* Konno, *Bifarinsotheca* Zhao, *Gemellitheca* Wagner *et al.* and *Dizeugotheca* Archangelsky and de la Sota).

Five species of *Rajahia* were described from the Late Permian of the Gunong Blumut area, Johore, Malaysia (Konno *et al.* 1970). The synangia of *Rajahia* are smaller than those of *Taiyuanitheca tetralinea*, and differ in being arranged in rows on both sides of the lateral veins running from the midvein to the pinnule margin, i.e. two rows of synangia occur between the lateral veins. Furthermore there is no visible pore on the apical part of the sporangium of *Taiyuanitheca tetralinea* unlike that in *Rajahia*.



TEXT-FIG. 2. *Taiyuanitheca tetralinea* gen. et sp. nov., GP0112. A, adaxial view of pinnules with incurved margins (arrowed) and four rows of synangia, ×6. B, adaxial view of pinnules showing exposed veins, ×4. C, synangium on the adaxial surface of a pinnule, ×4.

*Bifariusotheca* was described from the Late Permian of Qinglong, Guizhou Province, south-west China (Zhao *et al.* 1980). The type species, *B. qinglongensis*, has two rows of synangia on each side of the midvein, as in *Taiyuanitheca tetralinea*, but the synangia are elliptical with their long axis at right angles to the pinnule midvein.

*Gemellitheca* was described from the Upper Permian of Saudi Arabia and Turkey with *G. saudica* as its type species (Wagner *et al.* 1985). Its pecopterid foliage has synangia that are exannulate, elongate in shape and situated at the distal end of the lateral veins. Each synangium is composed of two sporangial compartments (loculi), orientated at right angles to the pinnule midvein and margin that extend almost half-way across the pinnule before curving away from the lamina at their tips. The margins of the pinnules are abaxially infolded and cover a third to half of the pinnule half-width. From these characters it can be seen that the two genera have only a general overall resemblance, with their synangia and lamina margins being quite different.

*Dizeugotheca* was described by Archangelsky and de la Sota (1960) from Patagonia as having sori with sporangia consistently in groups of four, two of each group being largely overlapped by the other two. It differs therefore from the present specimens of *Taiyuanitheca tetralinea* in its sporangial arrangement.

There are several Euramerian marattialean ferns that bear some resemblance to *Taiyuanitheca*. *Ptychocarpus* Weiss, 1869, which was first described from the Upper Carboniferous of Breitenbach, Rhenish Prussia, is the closest. Following Weiss's original diagnosis, we understand *Ptychocarpus* to have bipartite and bilaterally symmetrical synangia, which appear to have elliptical outlines, that are arranged in one or two rows along each side of the midvein. Most distinctively the sporangia are fused along their full length such that there is a slight terminal elliptical depression at the top of the synangium. This differs considerably from the more hollow feature of the present specimens of *Taiyuanitheca tetralinea*. Furthermore, the outline of the synangia is also different, being rounded in *T. tetralinea* and elliptical in *Ptychocarpus*.

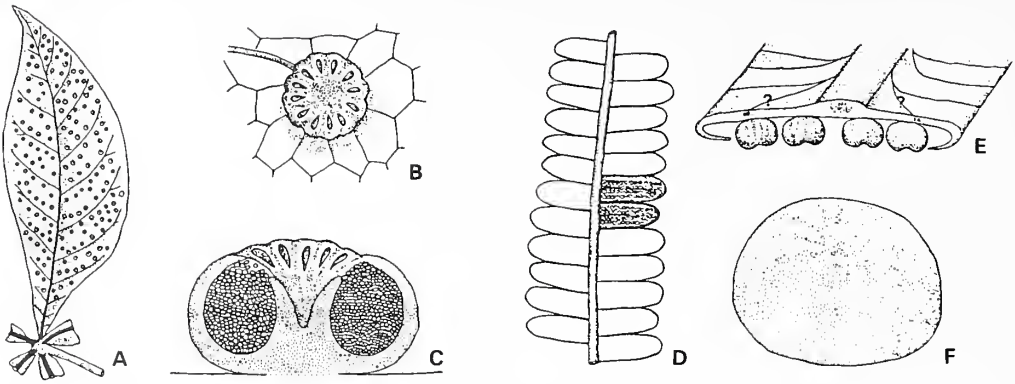
Many fertile specimens of *Pecopteris unita* Brongniart have been incorrectly named as *Ptychocarpus*. In fact, *Pecopteris unita* is a marattialean fern with both fertile and sterile pinnules. Its synangia, with a short pedicel at the base, are borne in two rows, one on each side of the pinnule midvein. Elongate sporangia are radially arranged and appear to be laterally free for a relatively short distance. The apices of the sporangia taper to an acute point. Therefore, *Taiyuanitheca tetralinea* shares certain features with *Pecopteris unita*, but differs in having its sporangia entirely fused.

Many Mesozoic marattialean ferns have been reported (e.g. Harris 1961; Van Cittert 1966; Hill 1987), but unfortunately they are usually poorly preserved compression specimens. Most of the Mesozoic marattialean ferns are difficult to distinguish from modern taxa and specimens most commonly found are similar to the extant *Marattia*, *Angiopteris* and *Danaea*.

Among the extant marattialean ferns, *Christensenia* shows the most similarity to *Taiyuanitheca tetralinea* for they both have circular and sessile synangia and almost the same number and shape of sporangia in each synangium (Text-fig. 3). The synangia of *Christensenia* are, however, irregularly distributed between the main veins on the abaxial surface whereas those of the *T. tetralinea* are regularly arranged into two rows on each side of the midvein. Furthermore *Christensenia* differs from *T. tetralinea* in having palmately compound fronds and also in having reticulate venation. Although the sporangia dehiscence mechanism of *T. tetralinea* is not perfectly understood, *Christensenia* is unusual in that each sporangium has an apical dehiscence slit for dispersing its spores rather than a longitudinal one as in some of the extant genera e.g. *Angiopteris* or a terminal pore as in *Danaea*.

## DISCUSSION

*Dehiscence*. Dehiscence in the marattialean ferns may be by one of three methods (Bierhorst 1971). In the extant *Christensenia* Corda, dehiscence occurs by an apical slit in each sporangium. In the extant *Angiopteris*, *Macroglossum*, *Archangiopteris* and perhaps *Marattia*, dehiscence is by a longitudinal slit. In the extant *Danaea*, dehiscence is by a terminal pore. Dehiscence in the Carboniferous permineralized *Scolecopteris* can be apical (Millay 1979) or longitudinal (Mamay 1950; Millay 1977) as in *Acaulangium* (Millay 1977, 1987). In *Millaya* the sporangia probably separated distally and then dehisced through longitudinal slits on the inner-facing sporangial walls.



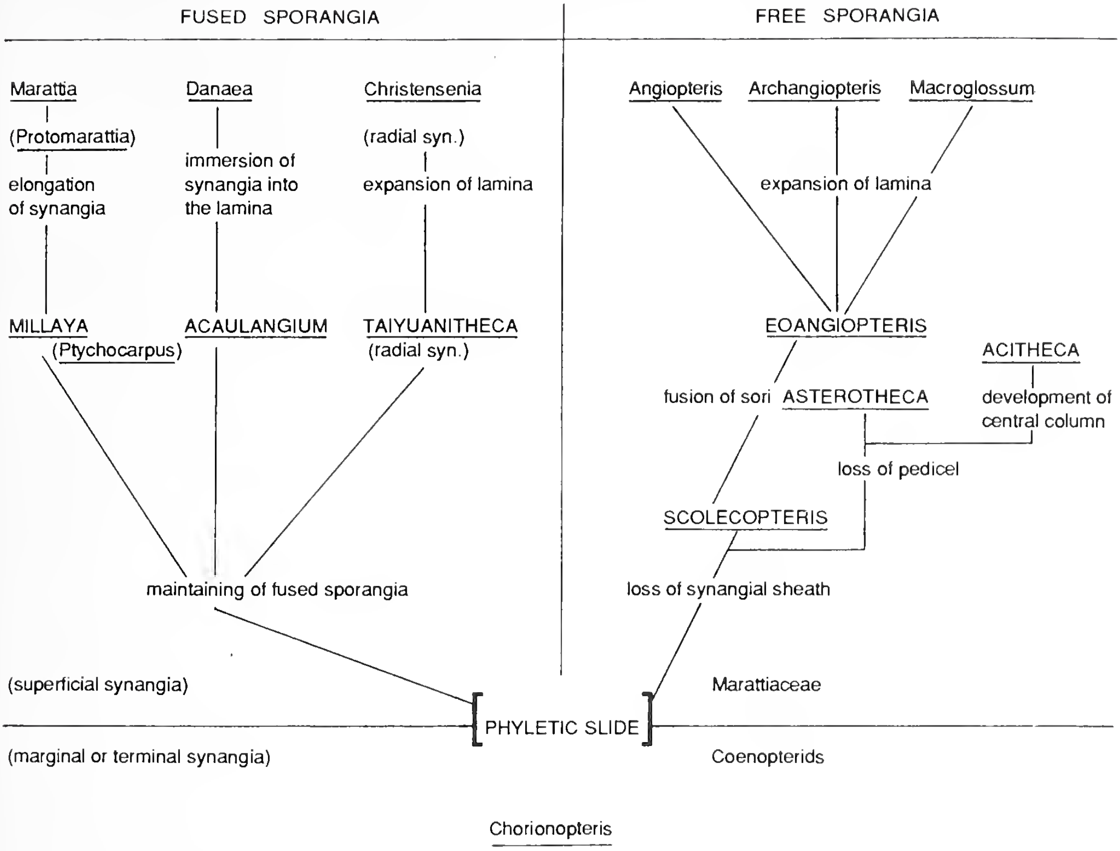
TEXT-FIG. 3. Comparison of *Taiyuanitheca* and *Christensenia*. A–C, *Christensenia* Maxon. (after Bower 1926, from Engler and Prantl). A, single leaf palmately attached to a stalk with synangia distributed between the lateral veins, ×0·25. B, single circular synangium viewed from its top showing sporangial composition and dehiscence split at the inside of upper part of each sporangium, ×5. C, section of a synangium showing its sessile attachment to the lamina, ×14. D–F, *Taiynanitheca tetralinea* gen. et sp. nov. D, sketch drawing based on GP0112 and 113, showing the alternative arrangement of the pinnules and four rows of synangia with two on each side of midvein, ×0·5. F, reconstruction of part of a pinnule, showing the synangial arrangement and incurved marginal lamina, ×5. F, reconstruction of a single synangium showing the sporangial arrangement with depression in the centre, ×25.

*Araiangium* also had its sporangia longitudinally separated for dehiscence (Millay 1982*a*). According to Bower (1908) dehiscence in *Ptychocarpus* was by terminal pores, although the specimens on which Bower's suggestion was based may belong to *Pecopteris unita* as discussed earlier. No special dehiscence structures can be seen in the sporangia of *Taiynanitheca tetralinea*, although the longitudinal striations along the sporangia might indicate that the sporangia of *T. tetralinea* also dispersed their spores through a longitudinal opening in each sporangium.

*Evolution*. Mamay (1950) proposed two evolutionary pathways for the derivation of the *Asterotheca*-like fructifications. He considered *Chorionopteris* to be the ancestor. The *Ptychocarpus* type may have evolved from this by the retention of the pedicel and synangial sheath, along with the development of a central column. *Cyathotrachus* (*Scolecopteris* of Millay 1982*b*) would have been an intermediate. Then the *Asterotheca*-type may have been derived by the reduction of both the synangial sheath and the pedicel. Alternatively the *Scolecopteris* type could have been evolved by the reduction of the synangial sheath accompanied by the retention of the pedicel. With the development of a central column in a synangium of the *Asterotheca* type, an *Acitheca*-like fructification might have been produced. Although Mamay (1950) suggested that the radial sori (synangia) were more primitive than linear ones, he also stated that the radial sori (synangia) of *Christensenia* are apparently the most highly evolved form. Therefore *Christensenia* seems to occupy the highest position among those genera with fused sporangia. This seems to be supported by the fact that *Christensenia* possesses large laminae, reticulate leaf venation and creeping rhizomes (Sporne 1975; Hill and Camus 1986).

Mamay's phylogenetic hypothesis for the marattialean ferns has received little reaction although many workers have published on both fossil and extant marattialean ferns. As shown in Text-figure 3, the synangia of *Christensenia* and *Taiynanitheca* show striking similarities. If *Christensenia* is taken, as generally accepted, to be advanced, the *Taiynanitheca* form could then be interpreted to be an intermediate between *Ptychocarpus* and *Christensenia* in Mamay's 'phyletic slide'. Mamay's evolutionary diagram can then be modified as in Text-figure 4, taking into account the synonymy of *Cyathotrachus* and *Scolecopteris* (Millay 1982*b*; Stubblefield 1984).

Millay (1978, 1979), like Mamay (1950), considered *Eoangiopteris* to be the ancestor for the free-



TEXT-FIG. 4. Phylogenetic chart of marattialean ferns (based on Mamay 1950). Marattialean ferns are proposed as having been derived from the coenopterid fern *Chorionopteris* Corda. The superficial marattialean synangia and sori may have developed in one of two ways: those with fused sporangia (synangia) at the left of the vertical line, and those with free sporangia (sori) at the right. Three groups of the extant marattialean ferns with synangia (*Marattia* including *Protomarattia*, *Danaea* and *Christensenia*) may have evolved from three different groups, exemplified by *Millaya*, *Acaulangium* and *Taiyuanitheca*, as explained on left side of the chart.

sporangiate genera of marattialean ferns, because it shows many features in common with free-sporangiate extant genera like *Angiopteris* and *Macroglossum*. This idea is reproduced here in the phylogenetic chart.

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# THE ORIGIN OF ARTICULATE CRINOIDS

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ABSTRACT. Cladistic analysis of various Palaeozoic and post-Palaeozoic crinoids indicates that the latter constitute a monophyletic clade, the Articulata, whose origins lie among the late Palaeozoic Ampelocrinidae of the inadunate order Cladida. The Cladida, raised to subclass alongside the Disparida and Camerata, is extended to include the Flexibilia and Articulata. Early articulates differ from some Palaeozoic cladids only in the absence of an anal plate in the adult cup, but a suite of characters can be used to identify progressively more derived members of the articulate stem group. Re-evaluation of two stem-group articulate families, the Ampelocrinidae and Cymbiocrinidae, indicates that there is little to justify retaining them as distinct families and that fewer than half of the constituent genera should be retained there. The remainder have been either wrongly assigned (*Allosocrinus*, *Halogetocrinus* and *Paracymbiocrinus*) or are based on material inadequate for establishing phylogenetic position (*Armenocrinus*, *Arroyocrinus*, *Moundocrinus*, *Oklahomacrinus*, *Polusocrinus*, *Sphensicocrinus*, *Aenigmocrinus* and *Lecobasicrinus*). Furthermore, several genera (including *Nowracrinus* and *Tribrachycrinus*) currently excluded show clear affinities with the Ampelocrinidae.

IN his seminal work of 1821, J. S. Miller erected the 'Division' Articulata for a number of Mesozoic and extant taxa. Since that time there has been a general consensus amongst crinoid workers that most, if not all, post-Palaeozoic crinoids can be assigned to the Articulata (since afforded the status of subclass) while all Palaeozoic crinoids are excluded. Although Miller included only a selection of Mesozoic and extant taxa in his Articulata, nowhere did he state that Palaeozoic taxa were excluded from this group. In fact, Miller's original description (see below) is sufficiently imprecise that it encompasses a range of late Palaeozoic forms.

Since Miller's work, the articulates have remained a rather poorly-defined group, almost invariably regarded as synonymous with post-Palaeozoic crinoids. Previous diagnoses have utilized characters which, although ubiquitous among post-Palaeozoic taxa, are by no means unique to them. Partly as a consequence of this, the relationship of articulates to late Palaeozoic taxa has never been investigated adequately and they have, at various times, been considered to have affinities with a wide variety of Palaeozoic taxa. Much of this confusion has arisen as a result of the inadequate documentation of many Palaeozoic crinoid taxa, thereby hindering the compilation of a comprehensive database by which to compare articulates with their putative ancestors. This is further compounded by the huge diversity of crinoids in the Carboniferous and Permian so that at present it is impossible to produce an overall phylogeny of, for instance, families within the paraphyletic subclass Inadunata.

Despite these obstacles, we have attempted, by cladistic analysis, to reinterpret the relationship of post-Palaeozoic crinoids to the various Palaeozoic crinoid taxa with which affinities have been suggested in the past. This is based upon a re-examination of the morphology and relationships of Triassic crinoids and of various Palaeozoic taxa whose taxonomic position is critical to our understanding of the phylogeny of stem articulates.

## DEFINITION OF THE SUBCLASS ARTICULATA

The currently accepted crinoid classification, as used in the *Treatise on Invertebrate Paleontology* (Moore and Teichert 1978), recognizes four main taxonomic groupings, each accorded subclass rank. The Articulata are exclusively post-Palaeozoic whilst the Camerata, Inadunata and Flexibilia are confined to the Palaeozoic. The camerates comprise two orders, the Monobathrida and

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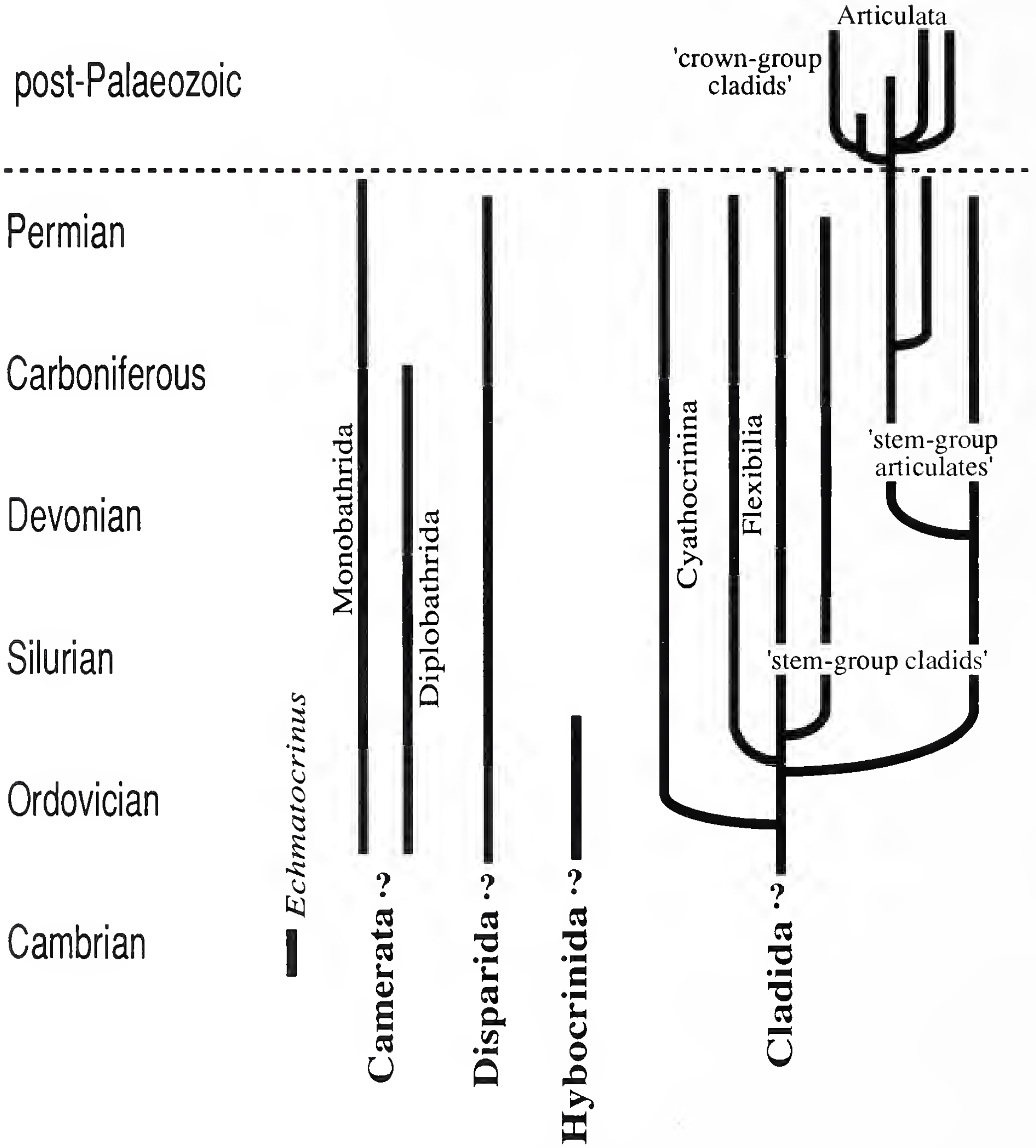
Diplobathrida. The inadunates contain three orders, the Disparida, Cladida and Hybocrinida, with the Cladida further subdivided into the suborders Cyathocrinina, Dendrocrinina and Poteriocrinina. The Coronata have been transferred from the Inadunata to the Blastozoa (Brett *et al.* 1983). Increasingly it has been recognized that not all of these divisions can justifiably be retained as natural taxa. The broad relationships of the various taxa are summarized in Text-figure 1.

The Articulata, the earliest of the four major crinoid taxa to be established, is also the one to have experienced the least revision. In his original description Miller (1821, p. 17) stated: 'The joints resting on the first or superior columnar joint, and forming the cup containing the viscera, articulate by liplike and transverse processes, having a minute perforation.' The 'liplike and transverse



TEXT-FIG. 1. Stratigraphical distribution and inferred relationships of the major crinoid clades recognized herein.

processes' we interpret to refer to the fulcral ridge and the muscular and ligament fossae on the radial plates, while the 'minute perforation' presumably refers to the axial canal, which pierces this articulation. Although his description implies that only a single canal is present, his inclusion within the Articulata of *Encrinus*, which has paired axial canals, suggests that he considered the presence, rather than the number, of axial canals to be the critical character. However, he described another division (Miller 1821, p. 66), the Crinoidea Semiarticulata, in very similar terms: 'The plate-like joints resting on the superior columnar joint, and forming the cup containing the viscera, articulate by transverse processes having a minute central perforation.' From this it is clear that the primary character which Miller used to define the Articulata was the presence of well-developed muscular and ligament fossae on the radial–brachial articula rather than the presence of an axial canal in the radials. Significantly, he did not mention in either description whether the cup is perfectly symmetrical or instead has the pentaradiate symmetry interrupted by the addition of one or more anal plates. It is the lack of an anal plate in the cup of adult post-Palaeozoic crinoids that is considered now to be one of the primary diagnostic characters of the Articulata (Simms 1988).

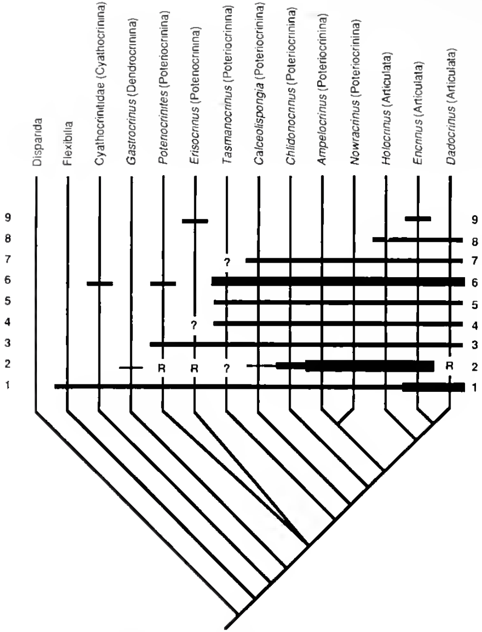
It is clear from the characters listed by Miller (1821), and from reference to our cladogram (Text-fig. 2), that the Articulata, as defined by Miller, must encompass a significant number of Palaeozoic taxa in addition to the post-Palaeozoic forms, which without exception can be assigned to his original concept. However, it would appear that all subsequent attempts to define the Subclass Articulata have, in fact, been based upon the morphology of post-Palaeozoic crinoids without direct reference to Miller's original description. Attempts to produce a concise and unambiguous definition of the articulates (in the sense of workers since Miller and hence synonymous with post-Palaeozoic crinoids) repeatedly have proven problematic, and it has been necessary to refer to a variety of characters additional to those listed by Miller. The definition given by Rasmussen (*in* Moore and Teichert 1978, p. 816) incorporates most of the diagnostic characters of post-Palaeozoic crinoids, but it lacks conciseness and cites so many exceptions found in highly derived taxa that its usefulness is obscured. At present no single character can be considered diagnostic of post-Palaeozoic crinoids, since examples of Palaeozoic taxa can be found which also possess such characters, either through convergence or through shared common ancestry. Nonetheless, articulate crinoids possess an apparently unique combination of characters and it is this character suite which establishes their monophyly. Each of these characters defines an increasingly inclusive clade, the crown group of which is characterized by the absence of an anal plate in the adult cup and corresponds to the articulates (post-Palaeozoic crinoids) as interpreted by later authors.

## MORPHOLOGICAL CHARACTERS OF ARTICULATES

The characters which we have found useful in defining the crown group and various plesions within the stem group of post-Palaeozoic crinoids, and which are incorporated in the cladogram of Text-figure 2, are discussed below.

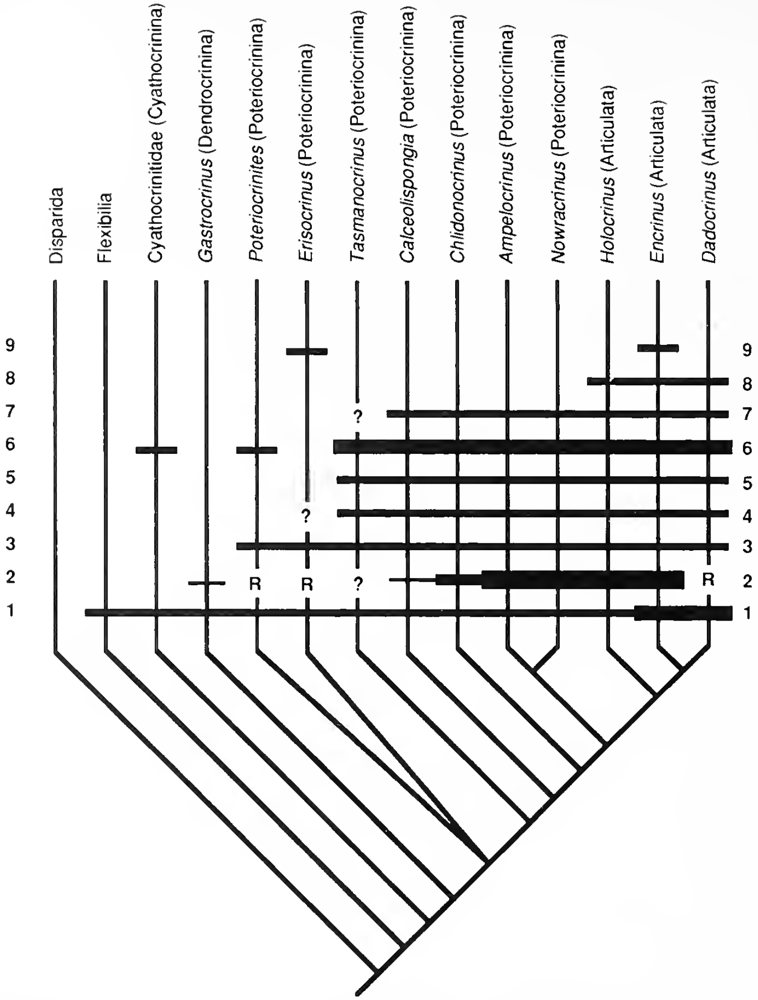
*Cup dicyclic or cryptodicyclic*. Crinoid cups can be grouped into two main types on the basis of the number of circlets, primitively each of five plates, of which they are constructed; those in which the cup comprises two circlets of plates are termed monocylic, while those in which a third circlet is present are termed dicyclic. In some dicyclic taxa it can be proven that the lowermost circlet (termed infrabasals) are vestigial or secondarily lost; in such cases the cup is termed cryptodicyclic or pseudomonocyclic. All post-Palaeozoic crinoids, and their stem group, have a cup which is either dicyclic or cryptodicyclic, as do other cladids, flexibles and diplobathrid camerates.

The primitive condition among post-Palaeozoic crinoids, found also in the Palaeozoic taxa mentioned above, is for the cup to be dicyclic with the infrabasals clearly exposed, as in the early Triassic *Holocrinus*. In virtually all other articulates the infrabasals are greatly reduced in size and lie concealed between the overlying circlet (termed basals) and the top of the stem (Clark 1908; Simms 1989, pl. 10, fig. 34); hence they are cryptodicyclic. Although derivation of articulates from monocyclic ancestors has been suggested on more than one occasion (Wachsmuth and Springer 1886, 1889; see below), the presence of infrabasals in the former group does not



TEXT-FIG. 2. A cladogram for some early articulate crinoids and various Palaeozoic taxa which have been proposed as ancestral to the articulates or whose morphology suggests close affinities with them. Character states as listed below (R = character reversal).

| Primitive | Derived |
|---|---|
| 1. Cup monocyclic | Cup dicyclic (thin line)<br>Cup cryptodicyclic (thick line) |
| 2. No cirri on stem | Cirri with multiradiate articula throughout (thin line)<br>Cirri with multiradiate articula distally and transverse ridge articula proximally (medium line)<br>Cirri with transverse ridge articula throughout (thick line) |
| 3. Arms non-pinnulate | Arms pinnulate |
| 4. Brachial articular without fossae | Brachial articula with ligamentary and clearly defined muscular fossae |
| 5. First arm division variable | First arm division on IBr2 |
| 6. Entoneural system open | Entoneural system enclosed in single canal (thin line)<br>Entoneural canal enclosed in paired canal (thick line) |
| 7. No syzygial articula in arms | Syzygial brachial pairs in arms |
| 8. Anal plate(s) in/above adult cup | Anal plates absent from adult cup |
| 9. Uniserial arms | Biserial arms |



TEXT-FIG. 2. A cladogram for some early articulate crinoids and various Palaeozoic taxa which have been proposed as ancestral to the articulates or whose morphology suggests close affinities with them. Character states as listed below (R = character reversal).

| Primitive | Derived |
|---|---|
| 1. Cup monocyclic | Cup dicyclic (thin line)<br>Cup cryptodicyclic (thick line) |
| 2. No cirri on stem | Cirri with multiradiate articula throughout (thin line)<br>Cirri with multiradiate articula distally and transverse ridge articula proximally (medium line)<br>Cirri with transverse ridge articula throughout (thick line) |
| 3. Arms non-pinnulate | Arms pinnulate |
| 4. Brachial articular without fossae | Brachial articula with ligamentary and clearly defined muscular fossae |
| 5. First arm division variable | First arm division on IBr2 |
| 6. Entoneural system open | Entoneural system enclosed in single canal (thin line)<br>Entoneural canal enclosed in paired canal (thick line) |
| 7. No syzygial articula in arms | Syzygial brachial pairs in arms |
| 8. Anal plate(s) in/above adult cup | Anal plates absent from adult cup |
| 9. Uniserial arms | Biserial arms |

support this. Such a scenario would require the convergent evolution of a third circlet of plates in Palaeozoic and in post-Palaeozoic crinoids, for which there is no supporting evidence.

*Cirri.* Although true cirri are absent from many post-Palaeozoic crinoid taxa, they are present in *Holocrinus* and are considered to represent the primitive condition for articulate crinoids (Schubert *et al.* 1992). Brett (1981) suggested that cirri evolved independently in several groups. Certainly, it seems probable that the cirri of camerates were derived independently of those in inadunates. In both groups the presence of cirri is a derived trait and they are lacking in early taxa. Within the inadunates, which is a demonstrably paraphyletic group (see discussion below), it is highly probable that cirri evolved more than once. Cirri are found in the disparid genus *Pisocrinus* and in the Myelodactylidae, though considering the aberrant morphology of the latter group it is quite possible that cirri evolved independently in these two groups. Since there is little evidence for a close phylogenetic relationship between disparids and cladids (Donovan 1988), it is probable also that the cirri in these disparid taxa were derived independently of the cirri found in the cladid orders Dendrocrinina and Poteriocrinina. However, since the present distinction between dendrocrinine and poteriocrinine cladids is largely artificial, with the Poteriocrinina best regarded as a 'grade group' comprising a variety of the more derived cladids, it is more parsimonious to suggest that cirri evolved only once in the dendrocrinine–poteriocrinine clade.

This cannot be assumed unequivocally since documentation of the morphology of cirri is lacking for most taxa. Furthermore, initial observations suggest a striking morphological distinction between the cirri of most articulates and those of most cirri-bearing cladids. This has been interpreted as evidence for an independent origin for cirri in the two groups (Simms 1988). In the slender cirri of articulates, such as those of isocrinids and comatulids, the articula bear a prominent transverse ridge which articulates with a corresponding groove on the proximal face of the next cirral ossicle (Pl. 1, figs 2–3). This type of cirral articulation is found in *Holocrinus*, the earliest articulate (Schubert *et al.* 1992) and in some encrinids (Hagdorn 1982), but occurs also in several late Palaeozoic genera such as *Ampelocrinus*, *Cymbiocrinus* and *Nowracrinus*. However, in many other poteriocrinine cladids the cirral articulations are essentially the same as those of the columnals, typically taking the form of a multiradiate symplectial articulum (Pl. 1, fig. 9). Even in *Calceolispongia*, which in several other respects appears to lie close to the common ancestry of articulate crinoids (Text-fig. 2), the cirral articula are symplectial (Webster 1990). Nonetheless, the synapomorphies which *Calceolispongia* shares with *Ampelocrinus* and its allies suggest that transverse-ridge cirri may have been derived from the symplectial-type cirri rather than having an independent origin. *Calceolispongia* is of importance, therefore, in lying close to the common ancestry of all crinoids with transverse ridge cirri. Critical evidence that the transverse-ridge-type cirri were derived from the multiradiate symplectial-type cirri comes from a series of specimens from the Pennsylvanian (upper Bashkirian–lower Moscovian) Marble Falls Formation of Texas, described by Strimple and Watkins (1969) as *Chlidonocrinus echinatus*. In this species the nodal columnals each bear five cirral scars with prominent transverse-ridge-type articula (Pl. 1, fig. 1). The first four cirral ossicles have similar depressed elliptical articula, with the same groove-and-ridge style of articulation clearly visible in lateral view (Pl. 1, figs 1, 10). The fifth cirral ossicle is unique in having on its proximal face a depressed elliptical articulum with transverse ridge, tapering distally to a circular articulum with a multiradiate symplectial type of articulation (Pl. 1, fig. 10). From the sixth cirral ossicle distally the ossicles are cylindrical with multiradiate articula, although in more distal parts of the cirri (which may comprise more than 40 ossicles) the crenulae may be very weakly developed or absent. Multiradiate cirral articula also occur in several Triassic isocrinid taxa, but it remains to be ascertained whether this character arose through convergence in these taxa or represents a heterochronic trait related to the ancestral character state. Cirri are absent from the stem of many articulates, including a number of Triassic taxa such as *Dadocrinus* (Text-fig. 2), but it can be demonstrated that this represents a secondary loss and is no indication of a close phylogenetic relationship with any Palaeozoic taxa which lack cirri.

*Pinnulate arms.* Traditionally, branches which arise from opposite sides of alternate brachials, and which do not branch themselves, are termed pinnules, whereas side branches which show further branching, and typically are more widely spaced, are termed ramules. The relative size of these side branches also is of importance; pinnules are significantly smaller than the arms from which they arise, whereas ramules typically are of comparable diameter to that of the arm. More recent attempts to define these types of side branching have judged the most significant difference to be the presence of a muscular articulation at the base of each pinnule, where it articulates with the arm, whereas ramules lack such muscular articula (Lane and Breimer 1974; Broadhead 1988). However, neither definition is entirely satisfactory, since the former would exclude the branched pinnules of *Nowracrinus* (Willink 1979), while in the case of the latter it is difficult to establish the nature of such articula, whether muscular or ligamentary, in most fossil material (see discussion below). Furthermore, since pinnules are a derived trait in both camerates and cladids they evidently are not homologous structures. Consequently, the precise definitions cited above are unwarranted unless separate terms are coined for the 'pinnules' of camerates and cladids. We consider that the term 'pinnule' should be applied more informally to small side branches which arise from a majority of the brachials in a crinoid arm. No sense of homology is implied in this definition, and each case should be treated on its own merits in any phylogenetic study.

Pinnules are absent from the Hybocrinida, Flexibilia, Cyathocrinina and most Disparida and Dendrocrinina. The pinnules of Poteriocrinina and advanced Dendrocrinina, although probably homologous with each other and with those of articulates, almost certainly are convergent with those of camerates, since they are found only in the more derived cladids which appeared long after they had diverged from the camerates. Without exception the arms of adult post-Palaeozoic crinoids bear pinnules at regular intervals (Text-fig. 3). In all cases a single pinnule arises from alternate sides of successive brachials, though they are not developed on axillary brachials or on proximal brachials of pairs united by ligamentary articulations (hypozygal brachials). No examples of hyperpinnulation (more than one pinnule per brachial) or branching pinnules (ramules) are known among post-Palaeozoic crinoids. Pinnules in the majority of the more derived Poteriocrinina which lie close to the articulate stem group do not differ significantly from those of articulates themselves, though the Permian *Nowracrinus* represents a notable exception since the pinnules dichotomize several times (Willink 1979), and hence equally may be termed ramules.

*Muscular articula in arms.* Muscular brachial articula of the type characteristic of articulates, with a transverse ridge bounded by muscular and ligament fossae, are well developed in most post-Palaeozoic crinoids. The presence of these features was the primary criterion in Miller's (1821) original description. Among Palaeozoic taxa, muscular brachial articula appear confined to certain Poteriocrinina though their presence, or absence, is difficult to prove conclusively (Lane and Macurda 1975) and is rarely stated in descriptions of Palaeozoic taxa. Ausich (1977) suggested, on the basis of variations in stereom type on the articula of the radial–brachial articulation, that muscles may have been present between the radials and arms

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## EXPLANATION OF PLATE 1

Figs 1, 8, 10. *Chlidonocrinus echinatus* Strimple and Watkins, 1969 ('Cladida'; stem-group Articulata). Pennsylvanian, Lemons Bluff Member, Marble Falls Formation (upper Bashkirian/lower Moscovian); San Saba County, Texas, USA. 1, USNM S5136; part of stem and cirri of paratype showing the transverse ridge by which the cirri articulate on the cirrinodal and the ridge-and-groove arrangement by which the proximal ossicles of the cirri articulate with each other, × 7·5. 8, USNM S5136; syzygial articulum on secundibrach, × 12. 10, USNM S5174; proximal region of cirrus showing the ridge-and-groove style of articulation between the first five ossicles and the development of a multiradiate symplectial type of articulation between the fifth and sixth ossicles and further distally, × 6·5.

Figs 2, 6. *Isocrinus robustus* (Wright, 1858) (Articulata). Jurassic, Carixian; Humberside, England. 2, BM E70492; pluricolumnal showing the transverse ridge on the cirral scar characteristic of articulates and more advanced representatives of the articulate stem group, × 6. 6, BM E70485; distal articulum of proximal secundibrach showing development of distinct ligament and muscular fossae and a single axial canal, × 4.

Figs 3–4. *Balanocrinus gracilis* (Charlesworth, 1847) (Articulata). 3, BM E70331; part of stem and cirri showing the ridge-and-groove style of articulation between cirral ossicles; Jurassic, Domerian; Dorset, England, × 3. 4, BM E70344; proximal stem and crown showing the concealment of the infrabasals, arm branching on the second primibrachial (IBr2) and the presence of both muscular and syzygial/synarthrial articulations in the arms; the two arms on the left-hand side terminate at the syzygies on the distal articula of IIBr3; Jurassic, Domerian; Gloucester, England, × 2·5.

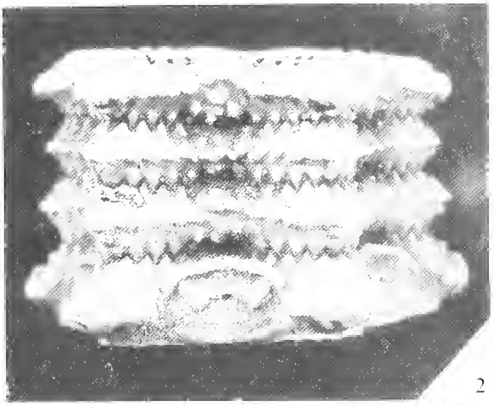
Fig. 5. *Encrinus liliiformis* Lamarck, 1801 (Articulata), BM E49926; distal articulum of radial plate pierced by paired axial canals; Triassic, Ladinian, Germany, × 3·5.

Fig. 7. BM E70631; syzygial articulum on brachial of indeterminate isocrinid (Articulata). Jurassic, Carixian, Gloucestershire, × 15.

Fig. 9. BM E14306; pluricolumnal of indeterminate ? cladid crinoid showing the multiradiate symplectial type of cirral articulation characteristic of most Palaeozoic crinoid taxa; Dinantian, Ironstone Beds; Ridsdale, Northumberland, England, × 4.

PLATE 1


1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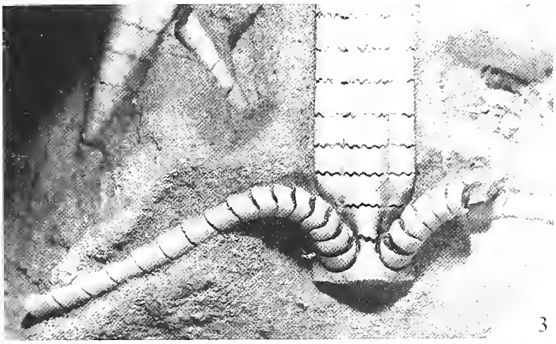
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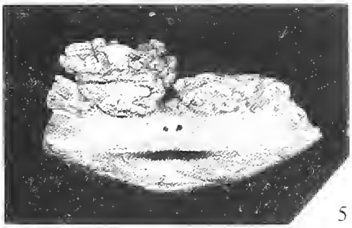
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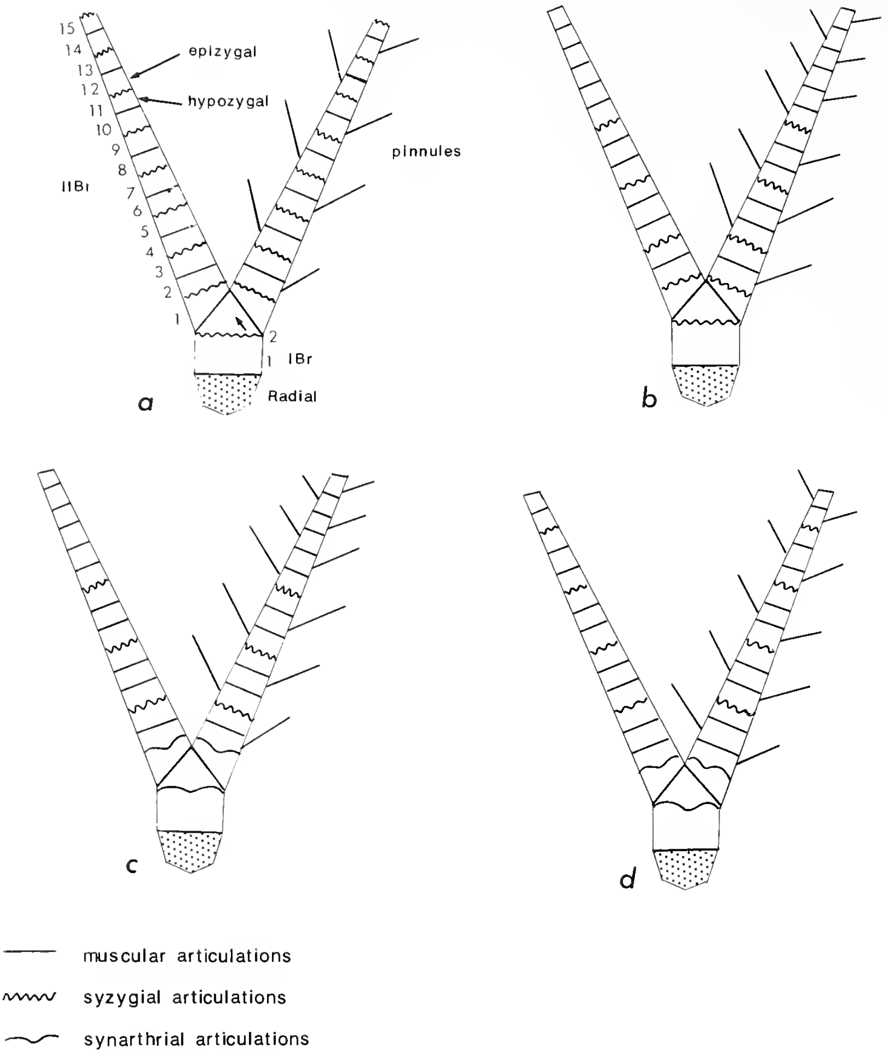
SIMMS and SEVASTOPULO, *Chlidonocrinus*, *Isocrinus*, *Balanocrinus*, *Encrinus*



TEXT-FIG. 3. Distribution of pinnules and syzygial articulations in the arms of an ampelocrinid (Cladida; stem-group Articulata) and representative articulate taxa. *a*, *Nowracrinus* (Ampelocrinidae). *b*, *Holocrinus* (Articulata: early Triassic). *c*, Isocrinida (Articulata: late Triassic to Recent). *d*, Millericrinida (Articulata: ?mid-Triassic to Recent).

in the disparid *Pisocrinus*. This may have been true of other disparids (Ubaghs *in* Moore and Teichert 1978, p. 164) and has been suggested also for the camerate *Planacrocrinus* (Ubaghs *in* Moore and Teichert 1978). However, although in extant crinoids there is some correlation between stereom type and tissue type, there still exists considerable variation between species in the morphology of the stereom associated with muscle attachment (Ausich 1977). Furthermore, Smith (1980) has shown that, in echinoids, muscular tissue is found associated with five out of the seven main stereom types. Considering the phylogenetic distance between articulate crinoids and certain of the Palaeozoic groups, such as camerates or disparids, it is perhaps to be expected that considerable differences might exist between the stereom types associated with muscular tissue in the various major Palaeozoic clades. This is even more likely if it is considered that muscular arms may have evolved more than once in the Crinoidea, and so it is perhaps unrealistic to expect to find the same stereom type associated with muscular tissue throughout the history of the group. On purely functional grounds, we find it difficult to visualize how most Palaeozoic crinoids could have operated in the absence of muscular articulations in the arms, since ligamentary tissue, even of the catch-connective type (Wilkie and Emson 1988), cannot move parts of the skeleton actively but can only hold them in a particular position. The currently accepted notion, that most Palaeozoic crinoids lacked any musculature in the arms, seems incompatible with their remarkable success in late Palaeozoic times even if catch-connective tissue did play a more important role early in the history of echinoderms (Wilkie and Emson 1988). We believe that muscular arms were far more prevalent in Palaeozoic crinoids than generally has been accepted, but that details of this musculature, and the associated stereom, may have differed significantly from that of articulates and hence may prove difficult to identify in fossil material.

*Arms branching on the first primibrach* (*IBr2*). With the exception of a few highly derived taxa, the arms branch on IBr2 in all post-Palaeozoic crinoids (Pl. 1, fig. 4), this being the primitive state for Triassic and later taxa. This character appears much more strongly fixed than in any Palaeozoic taxon other than the camerates, which also have arms branching almost invariably at IBr2. Only in a small minority of articulate taxa do the arms remain unbranched or divide at any other position, but in all instances it can be demonstrated that such taxa are comparatively derived. Few examples are known prior to the Cretaceous and, with the exception of one morphotype (?species) of *Dadocrinus*, in which the arms remain unbranched, arm branching at IBr2 is ubiquitous among Triassic crinoids.

Among late Palaeozoic cladids considerable variation exists in the position of the first arm division, although it occurs most frequently at IBr1. The Erisocrinidae are one such example with the first axillary at IBr1 and this, together with other characters, suggests their biserial arms and bowl-shaped cup to be convergent with the morphology of the Triassic family Encrinidae rather than indicating any close phylogenetic relationship between these taxa (see below). A significant proportion of the remaining cladid genera have arms which branch at IBr2, although in many cases this is more probably due to convergence and they otherwise share few, if any, synapomorphies with articulates. However, in those taxa which share several 'articulate' characters the arms usually branch at IBr2. These include the Permian *Nowracrinus* (Willink 1979) as well as a number of other genera (see Table 1).

*Perforate brachials and thecal plates*. All post-Palaeozoic crinoids have enclosed entoneural canals piercing the brachial and thecal plates. The presence of these entoneural canals, enclosed and clearly differentiated from the ventral groove, was one of the main characters which Miller (1821) used in his definition of the Articulata and Semiarticulata. All early Triassic and the great majority of Middle Triassic crinoid taxa have paired axial canals (Pl. 1, fig. 5), or in some cases fused pairs, but by late Ladinian and early Carnian times, a significant proportion of taxa had unpaired canals (Pl. 1, fig. 6), the dominant condition in post-Carnian crinoids. Pairing of axial canals in the brachial and thecal plates evidently is the primitive condition among articulates. Single entoneural canals have been documented for the brachials of a variety of Palaeozoic taxa, including the cyathocrinitids, and a few camerates and flexibles. However, in only a relatively small number of late Palaeozoic taxa have paired entoneural canals been observed. A triple entoneural canal system has also been documented in the brachials of an unidentified cladid from the Brigantian (Lower Carboniferous) of Scotland (Sevastopulo and Keegan 1980), though the relationship of this material to articulates, or their stem group, remains unclear. In flexibles, camerates, disparids, hybocrinids and most cladids the entoneural system was not enclosed in the thecal plates (Ubaghs *in* Moore and Teichert 1978, p. 193), though in many taxa a very short entoneural canal was developed through the distal part of the radial and the most proximal brachial or, in some taxa, extended farther along the arms. However, although it is known that the entoneural system was not enclosed in the thecal plates of most Palaeozoic crinoids, data on the presence or absence of this character is lacking for many of the more derived cladids and so it is impossible to ascertain when this character first appeared.

Teichert (1949) documented a series of canals located just beneath the inner surface within the thecal plates of the Permian *Calceolispongia*. The largest of these canals, which he termed primary canals, appear to correspond fairly closely to the expected position of the entoneural system in extant crinoids. Certainly, the canals in *Calceolispongia* show a remarkable similarity to those of *Marsupites* (see Sieverts 1927), the most obvious difference being that the primary canals are paired in *Calceolispongia* and single in *Marsupites* (see Moore and Teichert 1978, p. 193, fig. 163).

It is possible that the presence of entoneural canals penetrating the thecal plates will prove to be a critical character in tracing the phylogeny of the articulates and their stem group, though at present this character is too poorly documented for its value to be realized fully. However, enclosure of the entoneural system within

TABLE 1. Data on character distribution for genera included within the Ampelocrinidae and Cymbiocrinidae by Moore and Teichert (1978) and for other taxa considered here to have close affinities with *Holocrinus* and stem-group articulates. Taxa marked with an asterisk are those which we consider can be justifiably included within the emended Ampelocrinidae.

| | Cup | Cirri | Pinnules | Muscular arms | Arm branching | Axial canal | Syzygial pairs | Anal plates | Arm type |
|---|---|---|---|---|---|---|---|---|---|
| Ampelocrinidae | | | | | | | | | |
| **Ampelocrinus* | dicyclic | transverse | alternate | yes | IBr2 | paired | common | 1 | uniserial |
| *Armenocrinus* | dicyclic | ? | ? | ? | IBr2/4 | ? | ? | 1 | uniserial |
| *Arroyocrinus* | dicyclic | ? | alternate | ? | IBr1 | ? | absent | 3 | uniserial |
| **Chlidonocrinus* | dicyclic | transverse | alternate | yes | IBr2 | ? | some | 1 | uniserial |
| *Halogetocrinus* | dicyclic | present | present | ? | IBr3/4 | ? | some | 1 | uniserial |
| *Moundocrinus* | dicyclic | ? | alternate | yes | IBr2 | ? | ? | 1 | uniserial |
| *Polusocrinus* | dicyclic | ? | alternate | ? | IBr2 | ? | ? | 3 | uniserial |
| *Spheniscocrinus* | dicyclic | ? | alternate | yes | IBr2 | ? | absent | 1 | uniserial |
| Cymbiocrinidae | | | | | | | | | |
| **Cymbiocrinus* | dicyclic | present | alternate | yes | IBr2 | ? | common | 1 | uniserial |
| *Aenigmocrinus* | dicyclic | ? | alternate | yes | IBr2 | ? | ? | 2 | uniserial |
| **Aesiocrinus* | dicyclic | present | alternate | yes | IBr2 | paired | ? | 1 | uniserial |
| *Allosocrinus* | dicyclic | absent | alternate | yes | no | ? | common | 1 | uniserial |
| *Lecobasicrinus* | dicyclic | ? | alternate | ? | IBr2 | ? | ? | 1 | uniserial |
| *Oklahomacrinus* | dicyclic | present | alternate | yes | IBr2 | ? | ?present | 1 | uniserial |
| *Paracymbiocrinus* | dicyclic | ? | hyper. | yes | IBr2 | ? | ? | 1 | uniserial |
| **Proallosocrinus* | dicyclic | ? | alternate | yes | IBr2 | paired | some | 1 | uniserial |
| Miscellaneous | | | | | | | | | |
| **Tribrachyocrinus* | dicyclic | present | alternate | yes | IBr2 | paired | common | 3/4 | uniserial |
| *Calceolispongia* | dicyclic | multiradiate | alternate | yes | no | paired | common | 1 | uniserial |
| *Jimbacrinus* | dicyclic | absent | alternate | yes | no | paired | some | 1 | uniserial |
| *Meganotocrinus* | dicyclic | multiradiate | alternate | yes | IBr3/4 | ? | some | 1 | uniserial |
| *Araeocrinus* | dicyclic | ? | alternate | yes | IBr4/5 | ? | common | 3 | uniserial |
| *Charientocrinus* | dicyclic | in pairs | alternate | ? | IBr17+ | ? | ?present | 3 | uniserial |
| **Nowracrinus* | dicyclic | transverse | branching | yes | IBr2 | paired | common | 1 | uniserial |
| *Tasmanocrinus* | dicyclic | ? | alternate | yes | IBr2 | paired | ? | 1 | uniserial |
| *Corythocrinus* | dicyclic | absent | alternate | yes | IBr3 | ? | common | 1 | uniserial |
| *Holocrinus* | dicyclic | transverse | alternate | yes | IBr2 | paired | common | 0 | uniserial |

the brachials appears more prone to convergence, having occurred independently on a number of occasions, though the presence of paired entoneural canals appears to have been restricted to the articulates and their immediate stem group. Although this character too has been largely overlooked in most descriptive work, enough is known of its taxonomic distribution for it to be of considerable importance in elucidating the phylogeny of articulate crinoids.

*Syzygial pairs of brachials in arms.* All post-Palaeozoic crinoids have a muscular articulation between the radial and first brachial (Pl. 1, fig. 5) (although this may be greatly modified, by enlargement of the aboral ligament fossa, in certain highly derived taxa, e.g. *Seirocrinus* and *Apiocrinites*), followed by a ligamentary articulation between the first and second brachial (IBr1–2). In the primitive state among articulates this articulation is syzygial (Pl. 1, fig. 7) and followed by further syzygial articulations at IIBr1–2, IIBr3–4, IIBr5–6, etc., alternating with muscular articulations at IBr2–IIBr1, IIBr2–3, IIBr4–5, etc. (Text-fig. 3). In every instance pinnules arise only from the distal brachial (epizygal) of a syzygial pair, and the proximal brachial (hypozygal) lacks a pinnule. In virtually all post-Palaeozoic taxa this regular alternation of syzygial and muscular articulations is present only in the proximal part of the arms and is lost as syzygies become more widely spaced in the distal parts of the arms. In most articulates syzygial articula typically are developed at IIBr3–4 and

IIBr6–7 as well as more irregularly distal to this, although in the Millericrinida they are found instead at IIBr4–5 and IIBr7–8 (Taylor 1983; Text-fig. 3D). Furthermore, the most proximal syzygies (at IBr1–2 and IIBr1–2) are often modified into a synostosial or synarthrial articulation in more derived members of the Articulata (Pl. 1, fig. 4).

Among Palaeozoic crinoids this pattern of alternating muscular and syzygial articulations, with pinnules restricted to the epizygals, is uncommon and confined to a subset of those Poteriocrinina which have typical 'articulate-type' muscular articulations in the arms (Pl. 1, fig. 8). Furthermore, in descriptions of Palaeozoic taxa, syzygies often have been identified only by the arrangement of pinnules on the arms rather than by direct observation of the brachial articula, so in some instances their presence must remain equivocal. The taxonomic treatment, within Moore and Teichert (1978), of genera considered to possess syzygial pairs of brachials is symptomatic of the chaos which currently surrounds the taxonomy of Palaeozoic crinoids. It includes representatives of the Ampelocrinidae, placed within the Superfamily Agassizocrinacea; the Cymbiocrinidae in the Texacrinacea; the Corythocrinidae in the Scytalocrinacea; and *Araeocrinus*, placed in the Rhenocrinidae of the Superfamily Rhenocrinacea. Cladistic analysis of certain of these from both the Ampelocrinidae and Cymbiocrinidae demonstrates them to constitute the stem members of a monophyletic clade incorporating the post-Palaeozoic crinoids as crown group (Text-fig. 2). The present separation into disparate superfamilies is, therefore, quite unjustified. Furthermore, a reappraisal of the morphology of constituent genera currently placed within the Ampelocrinidae and Cymbriocrinidae reveals that for at least half of them there is, at best, insufficient data to establish their phylogenetic position or, at worst, clear evidence that they bear no close phylogenetic relationship with either family (Table 1).

*Anal plate in adult cup.* The dorsal cup in adult articulates characteristically exhibits an unbroken pentameral symmetry, comprising two, or sometimes three, circlets of five plates each. In contrast, this symmetry is interrupted in most cladid crinoids by the presence of one or more additional plates, termed anal plates, in the posterior, or CD, interray of the cup. Ubaghs (*in* Moore and Teichert 1978) questioned whether anal plates are homologous throughout the Class Crinoidea although their homology within the Cladida seems probable. However, it is clear that their reduction and loss from the cup has occurred independently on several occasions (Simms 1990*a*). Among the Poteriocrinina the anal series usually includes two major elements, the radianal and the anal X. Although absent in adult articulates an anal plate does occur in the cystidean and pentacrinoid stages of some comatulids, and presumably other post-Palaeozoic crinoids. Ubaghs (*in* Moore and Teichert 1978) discussed the origin and development of the radianal and anal plates and concluded that the single anal plate in juvenile articulates is homologous with the radianal, rather than with the anal X.

It is only the absence of an anal plate in the adult cup which distinguishes the post-Palaeozoic crown group (articulates) from their stem group representatives among Palaeozoic taxa. However, the absence of an anal plate is not, in itself, sufficient to establish that a given crinoid can be referred to the crown group, since this character shows convergence in a number of Palaeozoic taxa. Taxa lacking an anal plate in the cup are known among camerates and flexibles, and there are numerous other examples among the inadunates. Among late Palaeozoic Poteriocrinina several groups exhibit a reduction in the number of anal plates in the cup. Many genera retain only a single plate, the anal X, whilst some lose it. A large proportion of the latter taxa are aberrant, highly neotenous forms which can be shown, from other aspects of their morphology, to have no close phylogenetic relationship to post-Palaeozoic crinoids. Certain of the Erisocrinacea represent a notable exception to this. In *Erisocrinus* and *Sinocrinus* the anal plate is vestigial or absent and this, together with the biserial arms and bowl-shaped cup, renders both genera superficially similar to the Triassic Encrinidae. However, in all of those taxa which lie close to the stem group of post-Palaeozoic crinoids the cup retains at least one anal plate, the anal X (Text-fig. 2; Table 1); thus it is the eventual loss of this plate which has been taken as the critical diagnostic character for the crown group articulates and identifies the monophyletic clade which encompasses all post-Palaeozoic crinoids.

Although the final loss of the anal X appears to have occurred very late in the Palaeozoic, no post-Palaeozoic crinoids are known in which an anal X is present in the adult cup, and even in the juvenile stages it is rare for both the radianal and anal X to be present (Clark 1915). Only two fossil specimens, both from the Anisian Stage of the Middle Triassic, are known to us in which the pentameral symmetry of the cup is interrupted by the presence of an additional plate. The more striking of these is a crown of *Encrinus carnalli* (BM E14868) in which a roughly quadrate element occupies a position between the upper edge of two of the basals and the lower edge of the overlying radials. The second example occurs in a specimen of *Dadocrinus kunischi* (BM E6072), in which one of the basals has a square outline above which an irregular pentagonal plate occupies a position between adjacent basals and the overlying radials. In both instances these plates apparently are homologous with the radianal in juvenile articulates rather than the anal X in Poteriocrinina. Hence these two

Triassic examples represent merely the aberrant retention of a juvenile character into the adult state, and cannot be considered as evidence for any direct link between these taxa and the stem group of post-Palaeozoic crinoids.

*Biserial arms.* Among post-Palaeozoic crinoids truly biserial arms have developed only once, in certain of the Triassic Encrinidae, and in all other taxa the arms are uniserial. Cladistic analysis of Triassic crinoids, undertaken by one of us (M.J.S.) in collaboration with Hans Hagdorn, shows the encrinids to be a highly derived clade within the articulates rather than sister group to all other post-Palaeozoic crinoids (Simms 1988). The development of biserial arms in encrinids has a purely functional explanation; increasing the number of pinnules on the arms improves the effectiveness of the filtration fan (Simms 1990*b*). Similarities to Palaeozoic taxa with biserial arms, such as the Erisocrinacea, appear due to convergence and do not indicate any close phylogenetic relationship.

## THE RELATIONSHIP OF PALAEOZOIC CRINOIDS TO POST-PALAEOZOIC TAXA

The most recent classification of the Class Crinoidea (Moore and Teichert 1978) divides them into four subclasses: the Camerata, Inadunata, Flexibilia and Articulata. Sprinkle and Moore (*in* Moore and Teichert 1978) created a fifth subclass, the Echmatocrinea, for the Middle Cambrian *Echmatocrinus brachiatus*, though the taxonomic position of this species remains enigmatic and its status as a distinct subclass is questionable. The broad relationships of the major crinoid groups, and their stratigraphical distribution, are depicted in Text-figure 1.

Our analysis of post-Palaeozoic crinoids confirms their monophyletic status and suggests close affinities with the inadunate order Cladida as currently understood (Text-fig. 2). Similarly, the Flexibilia represents another monophyletic clade also derived, via *Archaetaxocrinus*, from the Cladida (Lewis 1981). Thus the Cladida, Flexibilia and Articulata together constitute a monophyletic clade (Sevastopulo and Lane 1988), with the cladids as an obviously paraphyletic group within this clade.

Two other orders, the Disparida and Hybocrinida, have been included within the Inadunata, while the Coronata, considered by Moore (*in* Moore and Teichert 1978) to be a distinct inadunate order, are now regarded as blastozoans (Brett *et al.* 1983). The relationship of both disparids and hybocrinids to the clade comprising cladids, flexibles and articulates remains unclear. The disparids almost certainly are not closely related to the cladids and may lie even farther from them than from the camerates (Kelly 1986; Donovan 1988). In hybocrinids the presence of a supposed radianal plate in the cup may perhaps indicate affinities with the Cladida (Sevastopulo and Lane 1988), though there is little other evidence to support this.

Our current understanding of the Camerata suggests that they are a monophyletic clade which was already quite distinct from other crinoids at its first appearance early in the Ordovician. The orders Monobathrida and Diplobathrida may be monophyletic too, but it is doubtful that many of the sub-ordinal taxa currently recognized within these clades will, upon closer inspection, prove to be natural taxa. Camerates possess several autapomorphies, in particular the possession of a rigid theca incorporating fixed brachials and interbrachials together with a usually rigid tegmen forming a vaulted ceiling over the thecal cavity. The camerates are excluded from the cladogram (Text-fig. 2) since it is evident from even the most preliminary comparison that no close relationship exists between camerates and articulates. Although many camerates resemble articulates in the possession of pinnulate arms branching on the second primibrach, it is clear that this is a convergent trait. Since both the earliest camerates and the earliest cladids are non-pinnulate, pinnules must have evolved independently in the two groups. Similarly, a few camerates have enclosed axial canals piercing the radials and brachials, but this too must be an isolated character which has arisen through convergence.

It is obvious that the presently accepted higher-level classification of crinoids is unsatisfactory. Although the present interpretation of the Articulata clearly differs from Miller's original concept, it is desirable to retain this taxon in its currently understood form since it represents one of the few major monophyletic clades whose limits within the Crinoidea are clearly defined. Of greater concern is the growing awareness among crinoid workers that the Inadunata is an unnatural paraphyletic, or even polyphyletic, grouping. Within the Inadunata, the Cladida includes the stem representatives of the articulates, flexibles and possibly hybocrinids, and hence is itself paraphyletic, while the Disparida can no longer justifiably be considered to have a close phylogenetic relationship with the cladids. Even within the Cladida the Dendrocrinina and the Poteriocrinina are largely artificial 'grade groups' and their true phylogeny is obscured. Only the cladid suborder Cyathocrinina can perhaps be considered a monophyletic clade, though its relationship to other cladids remains unclear.

## PREVIOUS SUGGESTIONS FOR THE ORIGIN OF POST-PALAEOZOIC CRINOIDS

The considerable morphological diversity of post-Palaeozoic crinoids has led to many suggestions concerning their relationship to Palaeozoic taxa. Both monophyletic and polyphyletic origins from any of the major Palaeozoic groups have been invoked at different times, with more recent accounts (Taylor 1983) favouring an origin among the derived cladids ('suborder Poteriocrinina'). We have included most of these proposed articulate stem groups in our cladogram (Text-fig. 2) and discuss each below.

*Disparida.* Wachsmuth and Springer (1886) considered the Anisian (Middle Triassic) *Holocrinus beyrichi* to be related to the disparid family Belemnocrinidae, which at that time was monotypic. Subsequently the extant *Holopus*, *Hyocrinus* and *Bathycrinus* were referred to the Disparida (Wachsmuth and Springer 1889; Jaekel 1918). This appears to have been based only on superficial similarities between otherwise disparate taxa. In particular, the dicyclic or cryptodicyclic cup and pinnules of post-Palaeozoic taxa contrast markedly with the monocyclic cup and non-pinnulate arms of disparids, indicating a close relationship to be unlikely. As already discussed, it is quite possible that the disparids are even less closely related to *Holocrinus* than are the camerates. Furthermore, it is by no means certain that *Belemnocrinus* has been assigned to the Disparida correctly. It may well be a cryptodicyclic cladid.

*Flexibilia.* Various post-Palaeozoic crinoid taxa have, at different times, been referred to the Subclass Flexibilia. Wanner (1916) compared the extant *Holopus* to the Permian *Palaeoholopus* and *Brachypus*, in the family Lecanocrinidae. The late Cretaceous *Marsupites* and *Uintacrinus* have also been referred to the Flexibilia on a number of occasions (Schlüter 1878; Neumayr 1889; Zittel 1895). More recently Klikushin (1983) assigned the Triassic encrinid *Traumatocrinus* to the Sagenocrinitidae, although he himself later cast doubt on this (Klikushin 1987). Again, any similarities between particular articulates and representatives of the Flexibilia are based on convergent or plesiomorphic characters, notably the presence of interbrachial plates in the latter three genera. Representatives of the Flexibilia lack nearly all of the critical articulate synapomorphies, notably the pinnulate arms with syzygial pairs of brachials.

*Cyathocrinitidae* (*Cladida, Suborder Cyathocrinina*). Jaekel (1892) suggested that the extant *Hyocrinus* and the Jurassic *Plicatocrinus* and *Saccocoma* were derived from the Cyathocrinitidae. Although the Cyathocrinitidae possess a dicyclic cup and have the entoneural system enclosed in the brachials (though apparently not in the thecal plates), they otherwise lack the characters used to diagnose articulates and possess a number of distinct autapomorphies, notably the presence (primitively) of goniospires, or traces of them, in the cup. Any close phylogenetic relationship between cyathocrinitids and articulates is, therefore, highly improbable.

*Botryocrinidae* (*Cladida, 'Suborder Dendrocrinina'*). Rasmussen (*in* Moore and Teichert 1978) suggested that the Triassic Holocrinidae might have evolved from, amongst others, the dendrocrinine family Botryocrinidae. *Gastrocrinus* is similar to holocrinids in the possession of a dicyclic cup and cirriferous stem but lacks other synapomorphies of the articulate stem group, such as the pinnulate arms with syzygial pairs of brachials. Hence a close phylogenetic relationship between these taxa is unlikely.

*Poteriocrinites*. Hildebrand (1926) considered the structure of the cup in Triassic Dadocrinidae and Holocrinidae to be more similar to the late Palaeozoic *Poteriocrinites* than to the Triassic Encrinidae. However, the cup in *Poteriocrinites* retains several anal plates and, although the radial articula have enclosed entoneural canals in both articulates and *Poteriocrinites* (Miller 1821), the latter has only a single canal, unlike the paired canals of the Triassic taxa. Furthermore, *Poteriocrinites* lacks the syzygial pairs of brachials characteristic of post-Palaeozoic crinoids, lacks well-developed muscular fossae of the articulate type on other brachial articula (Miller 1821), has arms which divide at positions as high as IBr14, and lacks cirri. The enclosed entoneural system of *Poteriocrinites* may be homologous with that in articulates, perhaps representing an earlier evolutionary stage prior to the development of paired canals, but equally it may represent a convergent trait. This hypothesis is difficult to test since, although *Poteriocrinites* clearly is a member of the articulate stem group, the absence of certain characters (Text-fig. 2) indicates that the genus lies away from the main line of descent.

*Erisocrinidae*. The Triassic Encrinidae have often been compared with the late Palaeozoic cladid Erisocrinidae on account of the biserial arms found in both groups. A close phylogenetic relationship between these taxa, though not necessarily with other articulates, has been suggested on several occasions (Jaekel 1892; Hildebrand 1926; Pisera and Dzik 1979; Simms 1988). The Encrinidae were even placed in the superfamily Erisocrinacea by Moore *et al.* (*in* Moore and Teichert 1978). Koenen (1895) also considered the Triassic *Dadocrinus* to be related to *Erisocrinus* despite the obviously uniserial arms of the former. However, although erisocrinids have a bowl-shaped cup and biserial arms superficially similar to those of encrinids, these clearly are convergent traits and they otherwise lack many other encrinid synapomorphies, such as the entoneural system enclosed in the thecal plates, arm branching at IBr2 and syzygial articula in the arms.

*Ampelocrinidae*. Strimple (*in* Moore and Teichert 1978, p. 301) suggested that the late Carboniferous ampelocrinids, particularly *Chlidonocrinus*, might lie close to the stem group of post-Palaeozoic crinoids on account of the arms branching at IBr2, the presence of syzygial pairs of brachials and the pentaradiate stem with cirrinodals. As can be seen from the cladogram (Text-fig. 2) and Table 1, it is clear that *Ampelocrinus*, along with several other closely allied genera, possess several other critical characters in addition to those listed by Strimple, notably the transverse-ridge type of cirri and the paired entoneural canals in the brachials. Indeed, it can hardly be doubted that a close phylogenetic relationship exists between certain late Palaeozoic Ampelocrinidae and the early Triassic *Holocrinus*.

*Nowracrinus and Tasmanocrinus*. In his description of these two monotypic Permian genera, Willink (1979) noted their highly derived morphology and similarities to post-Palaeozoic crinoids. However, he was reluctant to assign them to any established crinoid family or comment on their relationship to articulates, other than to conclude that they belonged to the cladid suborder Poteriocrinina. It is clear from our analysis (Text-fig. 2) that both lie much closer to the ancestry of post-Palaeozoic crinoids than do members of the Erisocrinacea, despite earlier assertions to the contrary (Simms 1988); it is equally evident that they do not lie on the direct line of ancestry, since both possess distinctive autapomorphies. In *Nowracrinus* the branching of the pinnules is a trait apparently unique to this genus, while the unusual structure of the cup in *Tasmanocrinus* (see Willink 1979 for a fuller description) is unlike that of any post-Palaeozoic crinoid.

*Polyphyletic origin*. A polyphyletic origin for the articulates has been suggested on several occasions. Rasmussen (*in* Moore and Teichert 1978) considered it unproven whether the articulates were monophyletic or polyphyletic, while Ubaghs (*in* Moore and Teichert 1978) advocated a 'moderate polyphyletism' of the articulates from more than one poteriocrinine ancestor. The strongest statement proposing articulate polyphyly was given by Moore (*in* Rhodes 1967, p. 63) in which it was suggested that the articulates comprised 'a hodge-podge of derivatives from all three Palaeozoic crinoid subclasses, though typical representatives of each and all have disappeared'. However, in all instances the similarities between post-Palaeozoic groups and the Palaeozoic taxa which he cites are clearly attributable to convergence, and there is no justification for advocating a polyphyletic origin for the articulates.

## A REVISED HIGHER-LEVEL CLASSIFICATION OF CRINOIDS

Our analysis has been concerned primarily with post-Palaeozoic crinoids and those Palaeozoic taxa which lie close to the stem group of the articulates Hence we confine ourselves to only brief comments concerning the recognition of major monophyletic clades among Palaeozoic crinoids. Nonetheless, our research has highlighted some of the inadequacies of the generally accepted classification (Moore and Teichert 1978), and has identified some of the problems which would appear to be inherent in any attempt to undertake a phylogenetic analysis of Palaeozoic crinoids.

Problems with the current classification are evident at all taxonomic levels from at least generic level upwards. In Moore and Teichert (1978) representatives of the articulate stem group are distributed primarily in two cladid families, the Ampelocrinidae Kirk, 1942 and the Cymbiocrinidae Strimple and Watkins, 1969, which are further separated into distinct superfamilies. However, the only character, of those listed, which differs between these two families is that the radial facets are directed outwards in the ampelocrinids and inwards in the cymbiocrinids. On the basis of other characters (see Table 1) we consider that *Ampelocrinus* does not differ sufficiently from *Cymbiocrinus* to warrant their separation into different families, or superfamilies, and we regard the Cymbiocrinidae as a junior synonym of the Ampelocrinidae. However, from Table 1 it is also evident that only five (*Ampelocrinus*, *Chlidonocrinus*, *Cymbiocrinus*, *Aesiocrinus* and *Proallosocrinus*) out of the sixteen genera currently included within these two families can, with any confidence, be retained in the emended family Ampelocrinidae (the monotypic *Proampelocrinus* Gupta and Webster, 1974, has been excluded from this analysis) although other taxa currently excluded (*Nowracrinus* and *Tribrachycrinus*) could justifiably also be included in the Ampelocrinidae. For most of the remainder there is insufficient data available for them to be assigned to a particular family, whilst in some cases (*Allosocrinus*, *Halogetocrinus* and *Paracymbiocrinus*) it is almost certain that genera have been assigned to this family incorrectly. Reference to original descriptions of taxa rarely provides any significant information additional to that contained in the *Treatise*. Furthermore, re-examination of much type material preserved in museums in the UK and the USA has revealed that in a majority of cases critical detail of character states is obscured by poor preservation and/or over-zealous mechanical preparation of specimens. Such factors will pose a considerable problem in any future attempts to revise the low-level taxonomy of Palaeozoic crinoids.

At higher taxonomic levels we recognize several major clades. We assign traditional categorial rank to these clades but appreciate that the choice of rank is entirely arbitrary. Future work may produce a more phylogenetically consistent classification of the Crinoidea.

*Class Crinoidea*. Like most previous authors, we accept that the Crinoidea constitutes a monophyletic clade whose common ancestry probably can be traced back to the Cambrian. However, the Middle Cambrian *Echmatocrinus brachiatus*, supposedly the oldest known crinoid, remains of uncertain phylogenetic position pending further investigation. Of the four subclasses currently recognized within the Crinoidea we retain only one, the Camerata, at subclass level. We recommend the abandonment of the Inadunata, a paraphyletic taxon, but retain the Flexibilia and Articulata as taxa of lower rank.

*Subclass Camerata.* The camerates, with their distinctive thecal morphology, almost certainly represent a monophyletic clade. Two orders, the Monobathrida and the Diplobathrida, are recognized. Both are morphologically distinct from their earliest appearance and hence, on current understanding, constitute monophyletic clades pending further evidence concerning their relationship to each other.

*Subclass Disparida.* Although the disparids have been grouped with the cladids, as an order within the Inadunata, there is no evidence for a close phylogenetic relationship between cladids and disparids and already it is recognized that they may be farther removed from cladids than from the camerates (Kelly 1986; Donovan 1988). They are regarded here as a monophyletic clade, for convenience classified at subclass level.

*Subclass Cladida.* As discussed earlier, the order Cladida, in the sense of Moore and Teichert (1978), is an obviously paraphyletic taxon incorporating stem-group representatives of several monophyletic clades, including the Articulata, Flexibilia and Cyathocrinina of earlier classification schemes. To remedy this unsatisfactory situation we recommend elevation of the Cladida to the level of subclass, and to include within this subclass all representatives of the Articulata and Flexibilia of earlier classification schemes, now reduced to the level of Infraclass, and the Cyathocrinina, elevated to Infraclass. The remaining taxa comprise stem-group representatives of these three major clades as well as almost certainly containing additional monophyletic clades. Formerly these were divided among the suborders Dendrocrinina and Poteriocrinina, two obviously paraphyletic groups, but we recommend the abandonment of these formal terms and instead group them together informally as 'stem-group cladids' pending further work on relationships within this group.

Incertae Sedis (*Subclass*) *Hybocrinida.* Sevastopulo and Lane (1988) considered the hybocrinids to be a monophyletic group, but were unable to resolve their phylogenetic position. This situation has not changed, and we tentatively accord them the rank of subclass pending further investigation.

- Class CRINOIDEA Miller, 1821
  - Subclass CAMERATA Wachsmuth and Springer, 1885
    - Order MONOBATHRIDA Moore and Laudon, 1943
    - Order DIPLOBATHRIDA Moore and Laudon, 1943
  - Subclass DISPARIDA Moore and Laudon, 1943
  - Subclass CLADIDA Moore and Laudon, 1943
    - 'stem-group cladids'
    - Infraclass CYATHOCRININA Bather, 1899
    - Infraclass FLEXIBILIA Zittel, 1895
    - Infraclass ARTICULATA Miller, 1821
  - Incertae Sedis ('Subclass') HYBOCRINIDA Jaekel, 1918

## THE ARTICULATE PROBLEM

As already demonstrated, currently understood definitions of articulate crinoids have relied more on our understanding of post-Palaeozoic crinoid morphology than upon Miller's (1821) original description of the group. Our reassessment of Miller's diagnosis indicates that a number of late Palaeozoic taxa could justifiably be included within the Articulata. A case might be made, therefore, for extending the taxonomic range of the Articulata to incorporate these Palaeozoic forms and thereby conform to Miller's original description. However, in view of the clear monophyly of post-Palaeozoic crinoids it is perhaps more desirable that recognition is given to articulate crinoids in the sense of later authors. Consequently, we recommend that the Articulata, reduced to the level of

Infraclass, be retained in its presently understood sense of post-Palaeozoic crinoids. Miller's original diagnosis of the group was not based on any phylogenetic methodology, and the characters which he considered important are often difficult to identify in fossil material. Consequently, we redefine the Articulata on the basis of characters which are confined to post-Palaeozoic crinoids, i.e. a dicyclic or cryptodicyclic cup lacking any anal plates in the adult and with the entoneural system enclosed within the thecal plates. Those Palaeozoic taxa, such as *Nowracrinus*, *Ampelocrinus*, *Cymbiocrinus* and *Aesiocrinus*, which appear to lie close to the common ancestry of the Articulata are perhaps best referred to informally as 'stem-group articulates', while the monophyletic clade which encompasses all post-Palaeozoic taxa constitutes the 'crown-group articulates'.

## CONCLUSIONS

Reassessment of Miller's (1821) original definition of the Articulata suggests that this group has been widely misinterpreted by subsequent authors, and that a variety of Palaeozoic cladid taxa might justifiably be assigned to the Articulata alongside the post-Palaeozoic articulates of later authors. However, cladistic analysis has demonstrated that all post-Palaeozoic crinoids belong to a monophyletic clade derived from a common ancestor of probable late Permian or early Triassic age, and hence we recommend that the Articulata, reduced to the level of infraclass, be retained in the currently understood sense of post-Palaeozoic crinoids only. This clade is characterized by the absence of an anal plate from the adult cup and an entoneural system enclosed within the thecal plates, together with a suite of characters found in progressively more crownward members of the stem-group of this clade. Miller's definition incorporates a number of Palaeozoic taxa which lie close to the common ancestry of articulates and are best referred to informally as 'stem-group articulates'.

Our analysis of the articulates and their Palaeozoic sister taxa highlights, once again, the inadequacy both of the current classification scheme and of the documentation of many Palaeozoic crinoid taxa. Without a radical revision of many Palaeozoic taxa at generic level, which would necessitate re-examination of much of the original material, it is impossible for us to attempt any more than the most preliminary revision of crinoid classification. Nonetheless, we recommend the abandonment of the Inadunata as an obviously paraphyletic group, and the raising of the Disparida and Cladida to subclass level alongside the Camerata. We take the Cladida to include the Articulata and Flexibilia, both reduced to infraclass level; the Cyathocrinina, raised to infraclass level; and an unresolved group which we refer to informally as 'stem-group cladids'. The Hybocrinida are nominally assigned subclass status pending further investigation of their phylogenetic position.

Although such a classification is clearly still far removed from the ideal of phylogenetic systematics (see Craske and Jefferies 1989), with the retention of four groups at subclass level implying a common origin, it is the best that can be achieved in the present state of knowledge of early crinoid morphology. We simply do not know how the major groups of Palaeozoic crinoids are related. It is to be hoped that future discoveries, and reassessment of existing material, may help to resolve these problems, and that the classification scheme which we have proposed here will be superseded by one which more closely reflects the phylogeny of crinoids.

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# XIPHOSURID TRACE FOSSILS FROM THE WESTBURY FORMATION (RHAETIAN) OF SOUTHWEST BRITAIN

*by* GUANZHONG WANG

ABSTRACT. The abundant and diverse trace fossils attributed to xiphosurid activity on sandstone soles at Westbury on Severn are described and interpreted. The xiphosurids seem to have been active in this area mainly after major storm event sedimentation. Two patterns of scratches, three types of lunate marks, and a bilobate furrow assignable to *Cruziana perucca* are distinguished. The lunate marks and one pattern of the scratch marks are assigned to *Selenichnites* isp. The marks were produced either during carnivorous feeding or burrowing for concealment. Variation in the traces is attributed to variable formation and preservation, sediment grain size, mud cohesiveness, as well as sediment thickness above the trace-taking sole surface, which modified the behavioural activity of the trace maker.

THE fossils believed to have been formed by xiphosurid arthropods have long been known from the Westbury Formation (Upper Triassic, Rhaetian) at the much frequented section at Westbury Garden Cliff (SO 717132), located on the north bank of the River Severn, 13 km (8 miles) west-southwest of Gloucester (Text-fig. 1). The section, described in detail by Richardson (1905, 1911), is readily accessible and displays the upper part of the late Triassic Mercia Mudstone Group, which dips gently towards the southeast. This contrasts with the more or less horizontal (though faulted) attitude of the better-known section at Aust Cliff (Savage 1977). The xiphosurid marks are associated with the upper of two sandstones in the section, blocks of which litter the beach. Recognition of the traces has been only by brief mention (Magor 1978; Ager and Edwards 1986).

Traces interpreted as those produced by xiphosurids are not rare in the geological record, especially those included in the ichnogenus *Kouphichnium* (Caster 1938, 1944; King 1965; Bandel 1967; Goldring and Seilacher 1971; Wright and Benton 1987); they are xiphosurid walking tracks, often accompanied by telson or genal spine marks. Traces attributed to xiphosurid resting burrows have been reported by Hardy (1970), Fisher (1975), Miller (1982) and Romano and Whyte (1987). Chisholm (1986) described a xiphosurid burrow which he interpreted as the product of intrastratal feeding activity. The present material, however, records a more complex relation of the animals with the substrate in what must have been a marginal marine environment.

The object of this paper is to document the traces found at Westbury Garden Cliff and to discuss problems related to the formation and interpretation of the traces. Material illustrated is deposited in the PRIS (University of Reading) Archive Collection. A specimen in the National Museum of Wales, Cardiff is numbered 88.72G.

## STRATIGRAPHY AND SEDIMENTOLOGY

The Westbury Formation at Westbury Garden Cliff rests directly on the mudstones and thin sandstones of the Mercia Mudstone Group (Text-fig. 2). As is generally the case, some 4 m of greenish mudstones are present below the base of the Westbury Formation. This base is an almost planar erosion surface, except for local elevations of a few centimetres, perforated by *Diplocraterion parallelum* filled with black mud or pebbly clasts and indicating firmground colonization (Text-fig. 2). A thin layer of small rounded, pebble-sized clasts derived from the underlying mudstone and some

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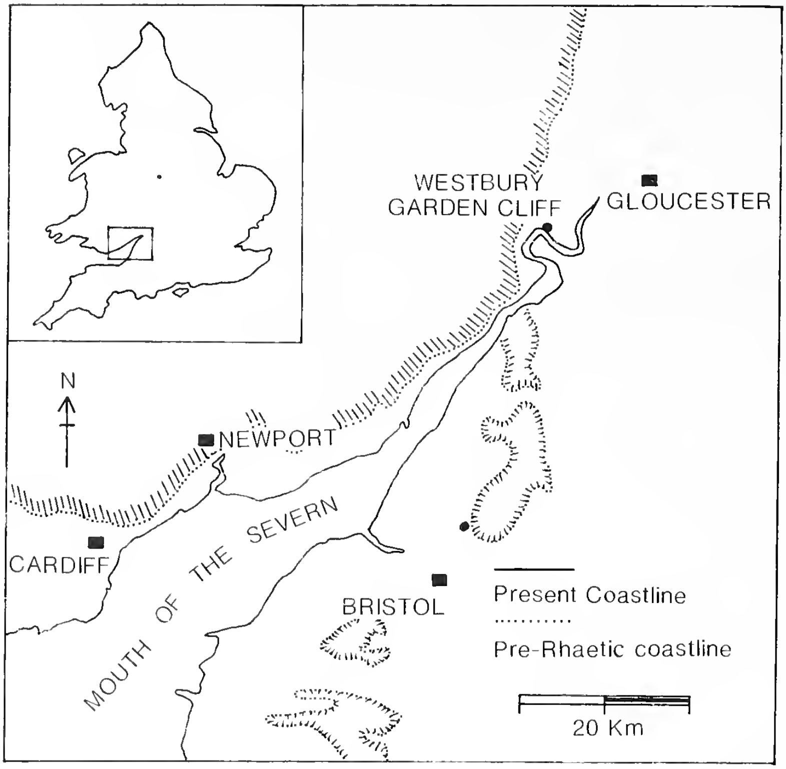


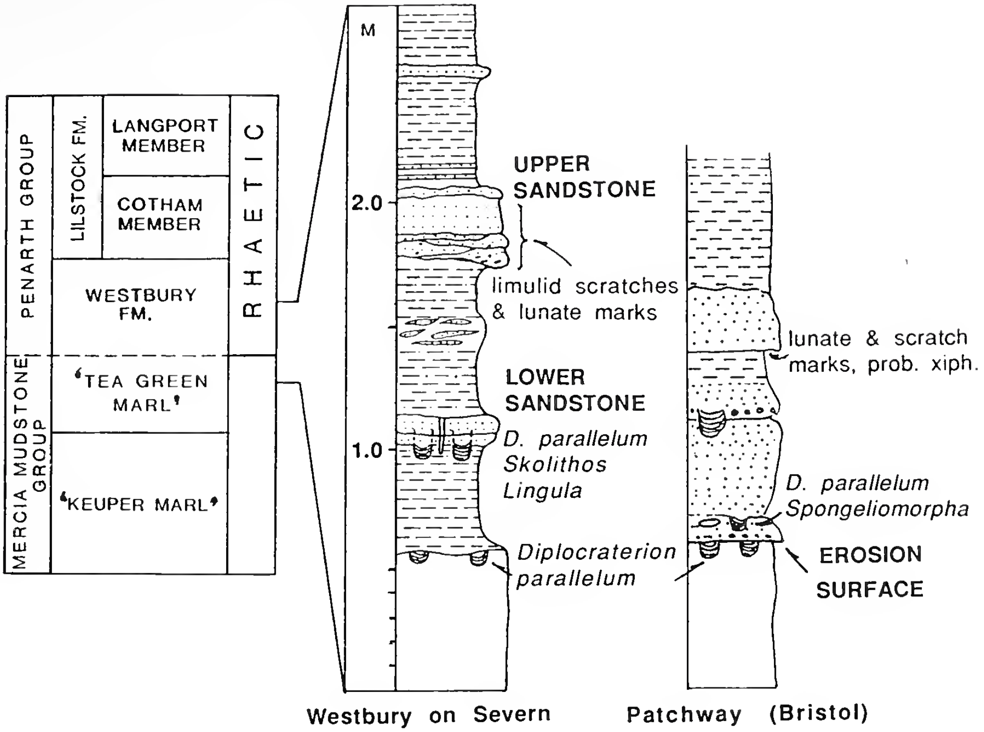
TEXT-FIG. 1. Location map of Westbury Garden Cliff with pre-Rhaetic coastline (from Audley-Charles 1970). Dot in the centre of inset indicates location of Needwood Basin, Staffordshire (Wright and Benton 1987) and the dot north of Bristol, the location of Patchway.

bone fragments mark the base. A black, finely laminated shale, some 0·4 m thick follows, from which no fossils have been recorded.

The black shale is terminated by a 10–25 mm thick, poorly cemented siltstone, above which is a 90 mm sandstone. The siltstone contains fragmental bivalve shells, fish teeth and scales, and well-preserved *Lingula*. The sandstone generally splits into two layers. The lower layer (20–30 mm thick) contains small bivalves, bones and teeth (including teeth of the lungfish *Ceratodus latissimus* and plesiosaur vertebrae) and the trace fossil *Diplocraterion*, which extends into the underlying siltstone. The upper layer is thicker (50–60 mm) and more fossiliferous, with numerous fish scales and teeth as well as spines. The upper surface of the unit is slightly undulose and bears a shell pavement of convex, dissociated bivalves including *Rhaetavicula contorta*, *Protocardia rhaetica* and *Schizodus* sp. Both sandstones have been extensively bioturbated. But the only recognizable traces are *D. parallelum*, and simple vertical and oblique burrows (*Skolithos*) filled with clean sand.

Above the Lower Sandstone is another unit (0·58 m) of black shale, the basal 10–20 mm of which is a silt containing small pieces of broken shell. Individual laminae in the shale are thicker than in the lower shale and the unit includes thin, wavy to lenticularly bedded, fine-grained sand, with opposed current directions suggesting tidal influence.

The Upper Sandstone (about 0·2 m thick) rests sharply on black shale. Bone material and bivalve shells are abundant. It is compound, with a few interbedded impersistent muddy seams and partly amalgamated units of sand that individually fine upwards and frequently have a rippled upper surface. The several leaves are markedly impersistent and separated by distinct erosion surfaces. The sandstone is calcareous and well sorted. Clasts range from coarse bone material (average 2–4 mm)



TEXT-FIG. 2. Stratigraphy (Penarth Group after Warrington *et al.* 1980) and summary logs of the sections at Westbury Garden Cliff and Patchway (Bristol) with occurrence of trace fossils indicated.

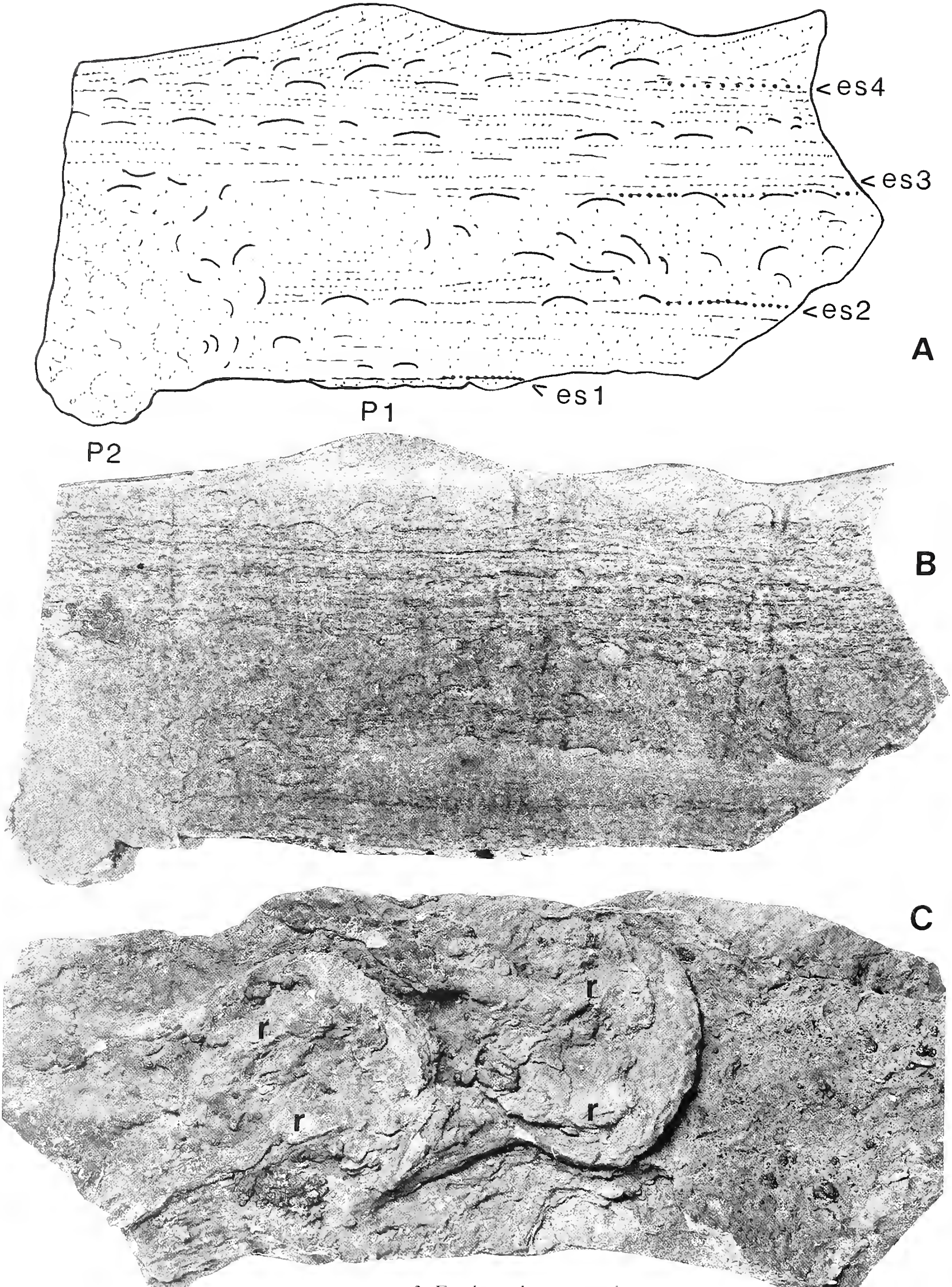
and intraformational mud chips, to very fine to fine-grained sand. Dissociated bivalves of small size, usually pyritized, occur throughout, with a notably higher concentration on each of the upper rippled surfaces. The patterns of ripple are variable, ranging from symmetrical or nearly so, to straight or sinuous, but usually low-crested with ripple crests peaked or rounded or of spill-over form.

In a representative section, the Upper Sandstone can be divided into three parts. The lower part (40–60 mm) is composed of four layers of sandstone containing abundant coarse bone debris, that laterally change in thickness and are separated by muddy drapes or leaves. Scratch marks can be seen on each lower interface, and especially on the lowest sole surface where the bone bed is in contact with the underlying black shale.

The middle part is a thicker (0·12–0·16 m), fine- to coarse-grained sandstone, which is harder and more compact and has less vertebrate debris. Slabs seen in section show at least four sedimentation events (Text-figs 3, 5D). Scratch marks are less abundant and not as sharp as seen on the sole of the lower part, but sharply outlined lunate marks are more common.

The upper part comprises two to three thin fine-grained sandstones with mud partings and includes occasional lunate marks of type *c*. The sandstone was locally highly biotubated, but only as a result of xiphosurid activity, except for occasional *Lockeia* and some small unidentified traces, identical to, but less abundant than, those described from the Needwood Basin (Wright and Benton 1987).

The sharp contact with the underlying shales, graded bedding, spill-over ripples (Seilacher 1982), and the mud-filled scours, suggest a storm-event origin for each unit of the Upper Sandstone.



TEXT-FIG. 3. For legend see opposite.

## DESCRIPTION OF TRACE FOSSILS

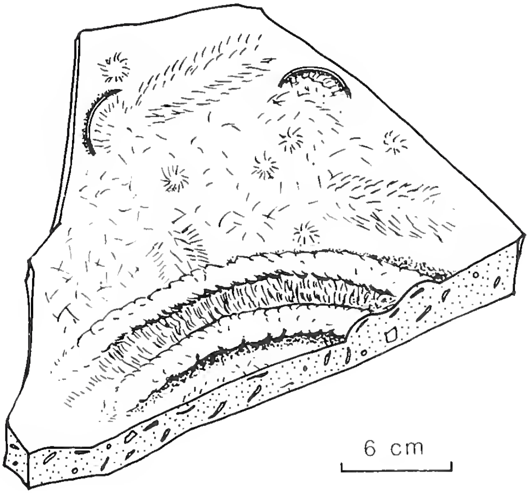
The trace fossils are all positive hypichnia and include two patterns of scratch marks, three types of lunate marks and a bilobate ridge.

*Scratch marks.* Distinct scratch marks are of only one kind: they are sharp, up to 15 mm in length and V-shaped, and may bifurcate towards the outer end. The latter feature indicates a bifid claw. Scratch marks show two patterns of arrangement and stratigraphical distribution in the Westbury Formation. The first pattern is found on the sole of the Upper Sandstone. The second is present on soles within this sandstone, following a thin mud interface.

*Pattern 1* (Pl. 1, figs 2–3; Text-fig. 5A) are sharp scratches, randomly arranged or in paired rows which cover extensive areas of the sole of the Upper Sandstone. The paired scratches have a V-arrangement: the low relief of each row being separated by a wide and shallow furrow. The scratches tend to bifurcate laterally and diverge posteriorly (in contrast to the posteriorly converging scratches of most *Cruziana*).

*Pattern 2* (Pl. 1, figs 4, 7; Text-fig. 5C) are ovoid to subtriangular outlines with a low relief, and short scratches on lower surfaces within the Upper Sandstone. Some show a superficial resemblance to *Rusophycus* but there is no median groove. They resemble Miller's (1982) *Limulicubichnus* but lack posterior ridges. Others recall Seilacher's model (1985, p. 233, figs 2*g*, 3*b*) where *Rusophycus* was formed below an appreciable thickness of sand cover.

*Bilobate furrow.* A bilobate positive hypichnial ridge (Pl. 1, fig. 2; Text-fig. 4) found on the sole of the Upper Sandstone, associated with pattern 1 scratch marks. The two broad and relatively smooth ridges (each 20 mm wide) are separated by a broad furrow (20 mm wide) with sharper scratches. The two ridges were probably produced by modification by the appendages of a groove cut by the prosoma, as illustrated by the ridges (*r*) in Text-fig. 3C. The measurable length of the whole trace is 200 mm.



TEXT-FIG. 4. Sketch of sole of upper sandstone showing a bilobate positive hypichnion (bottom) resembling *Cruziana perucca* (see Pl. 1, fig. 2), pattern 1 scratch marks, and mounds which may represent the feeding activity of the trace-maker. The layer is composed of pebble-size fish bones, teeth and spines, and fine-grained sand.

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TEXT-FIG. 3. A, B. Sketch and vertical section (× 1) through middle part of the Upper Sandstone showing amalgamation of event layers each separated by an erosional surface. Prosoma mark P1 (type *b*) was truncated by erosion surface (es) 1. Erosion surfaces 2 and 3 record the truncation of two subsequent units. Erosion surface 4 may represent a change in hydraulic regime. It is uncertain when prosoma mark P2 (type *a*) was emplaced, possibly prior to erosion surface 3 or even higher. (Specimen number PRIS. S33820). C, Positive hypichnia from high in Upper Sandstone with two prosoma marks (type *c*) probably made by a single individual twisting somewhat over substrate surface. Paired ridges (*r*) cast grooves formed by appendages. Genal spines have not left any appreciable groove, ×0·5. (PRIS. S33821).

The trace recalls *Arthrophycus*, but the latter has a smooth surface. A cruzianiform furrow thought to have been produced by xiphosurans was reported from the Rhaetic Sandstone of Pfrondorf near Tübingen (Seilacher 1985, p. 233, fig. 2*i*). There the high relief of the two lobes is separated by a narrower and deeper furrow and the trace shows head shield impressions. The leg scratch marks are less distinct but clearly diverge posteriorly. The bilobate trace described here, however, is much like *Cruziana perucca* Seilacher (1970, p. 469, figs 10*d–e*). Seilacher (1970) attributed this ichnospecies in trinucleid trilobites though later (Seilacher 1985, p. 234) commented on the possibility of xiphosurans producing similar traces.

*Lunate (prosoma) marks and associated burrows.* Three types of lunate mark are present.

*Type a* (Pl. 1, figs 1, 5; Text-fig. 5D (3)) is a crescent-shaped prosoma mark formed by the anterior part of the prosoma, forming a smoother band without enclosing scratches. Typically the mark exhibits several ridges parallel to the margin, which may be interpreted as repeated thrusts of the animal to push into a cohesive substrate. The area enclosed varies from smooth to rough. This kind of mark is found on lower surfaces, within the Upper Sandstone, specially of the sole of the middle part of the Upper Sandstone, sometimes at intervals in a linear sequence (Ager and Edwards 1986, fig. 4), similar to those illustrated by Hardy (1970). The sole surfaces follow mud drapes over rippled surfaces with convex-up dissociated bivalves.

*Type b* (Pl. 1, figs 1, 6; Text-fig. 5D, (1–2)) is a prosoma mark which is an almost complete impression of the doublure, with a median carina often evident. The prosoma mark encloses scratch marks and a telson mark may be evident. This trace closely resembles *Selenichnites hundalensis* (Romano and Whyte 1987), and is found mainly on the sole of the middle part of the Upper Sandstone and within the sandstone.

*Type c* (Text-figs 3C, 5B) is a lunate sole mark corresponding in outline with a limulid prosoma; it occurs mostly widely separated and without preferred orientation. The anterior margin is deep (15 mm) but seldom sharply defined. The mark is prolonged and shallows towards the marks of the genal spines. This mark may or may not enclose an area of rather obscure scratches. In section (Text-fig. 5B) the mark passes upwards into a broad asymmetrical burrow, posteriorly sloping upwards at about 10° with a relatively sharp margin. The anterior slope is sharper and steeper (approx. 50°). The bioturbated sediment of the burrow fill often carries mud flakes at the base, and abuts against bioturbated sand.

This mark is found on soles within the middle part of the Upper Sandstone, where the bone layer covers fine-grained, laminated sandstone (Text-fig. 5D) and in the upper part of the Upper Sandstone.

*Dimensions.* Most specimens are between 70 and 80 mm in width, and length including telson mark, 110 mm. An exceptionally large specimen (130 mm width) was recorded by D. V. Ager (personal communication).

The palaeolimulid responsible for the various marks at Westbury on Severn was probably *Limulitella* which has a prosomal outline and size in agreement with the trace fossils. *Limulitella* is well known from the Late Triassic (Stormer 1952).

## FORMATION AND PRESERVATION

There has been considerable discussion on the origin of *Cruziana* and *Rusophycus*, as to whether they were formed epigenically, or endogenically and intrastratally. While Seilacher (1955, 1970,

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### EXPLANATION OF PLATE 1

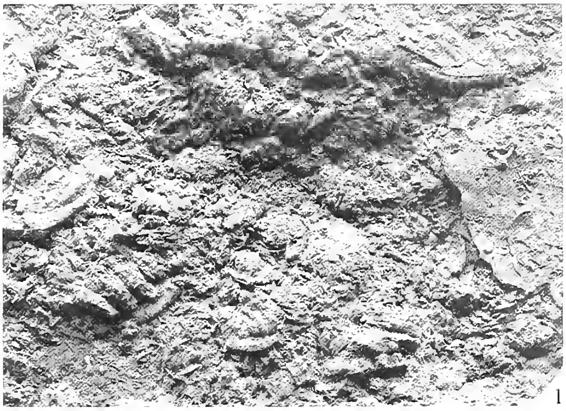
All specimens were collected from the Rhaetian of Westbury Garden Cliff.

Figs 1, 4–7. *Selenichnites* isp. 1; PRIS. S33815; lunate mark type *a* (upper right) on a rippled lower surface and lunate mark type *b* (left) on a split lower surface of a sandstone block. The split surface was extensively scratched, ×0·4. 4, PRIS. S33819; converging scratch marks of pattern 2 within a diamond-shaped outline, ×0·5. 5, lunate mark type *a* on a rippled surface on the same block as shown in fig. 1. This surface has abundant external moulds of convex-up bivalves, ×0·5. 6, PRIS. S33818; lunate marks of type *b* on the lower surface of a sandstone block from the middle part of the Upper Sandstone, showing scratches, marks of prosoma and telson (below), ×0·6. 7, scratch marks of pattern 2, also on same block, within an ovoid-shaped outline, ×0·4.

Fig. 2. *Cruziana perucca* Seilacher, 1970. PRIS. S33817; bilobate furrow and scratch marks on the sole of the Upper Sandstone, ×0·4.

Fig. 3. *Selenichnites*? isp.; PRIS. S33816; scratch marks of pattern 1 on the sole surface of the Upper Sandstone, ×0·35.

PLATE 1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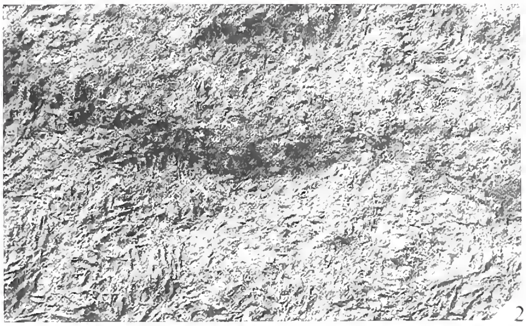
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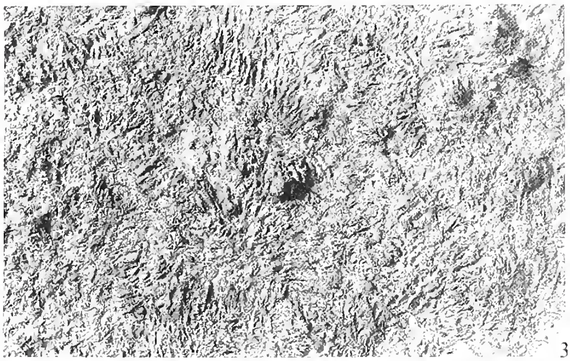
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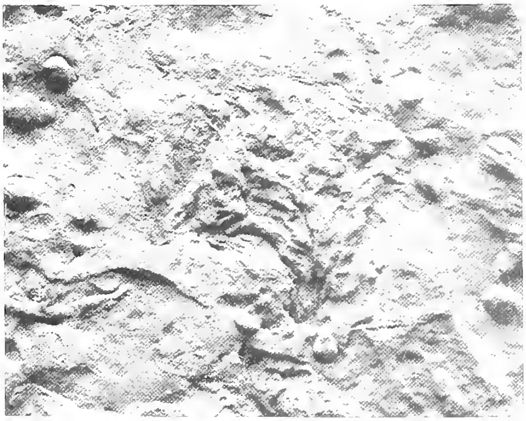
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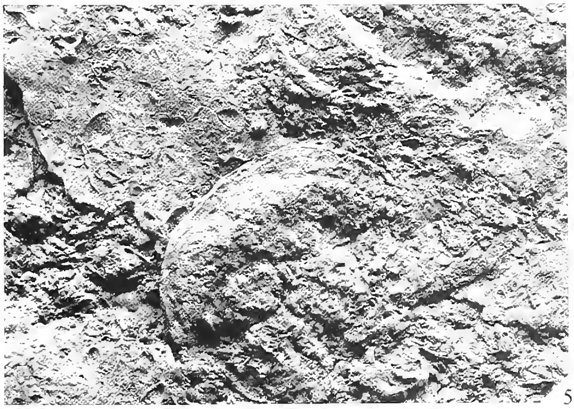
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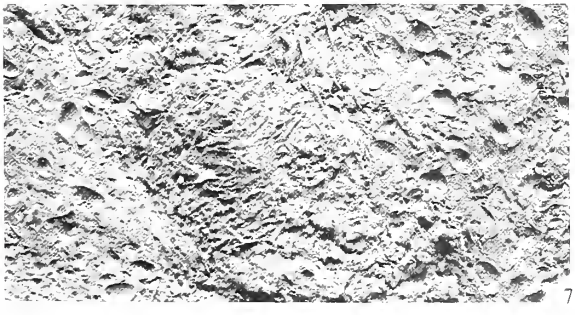
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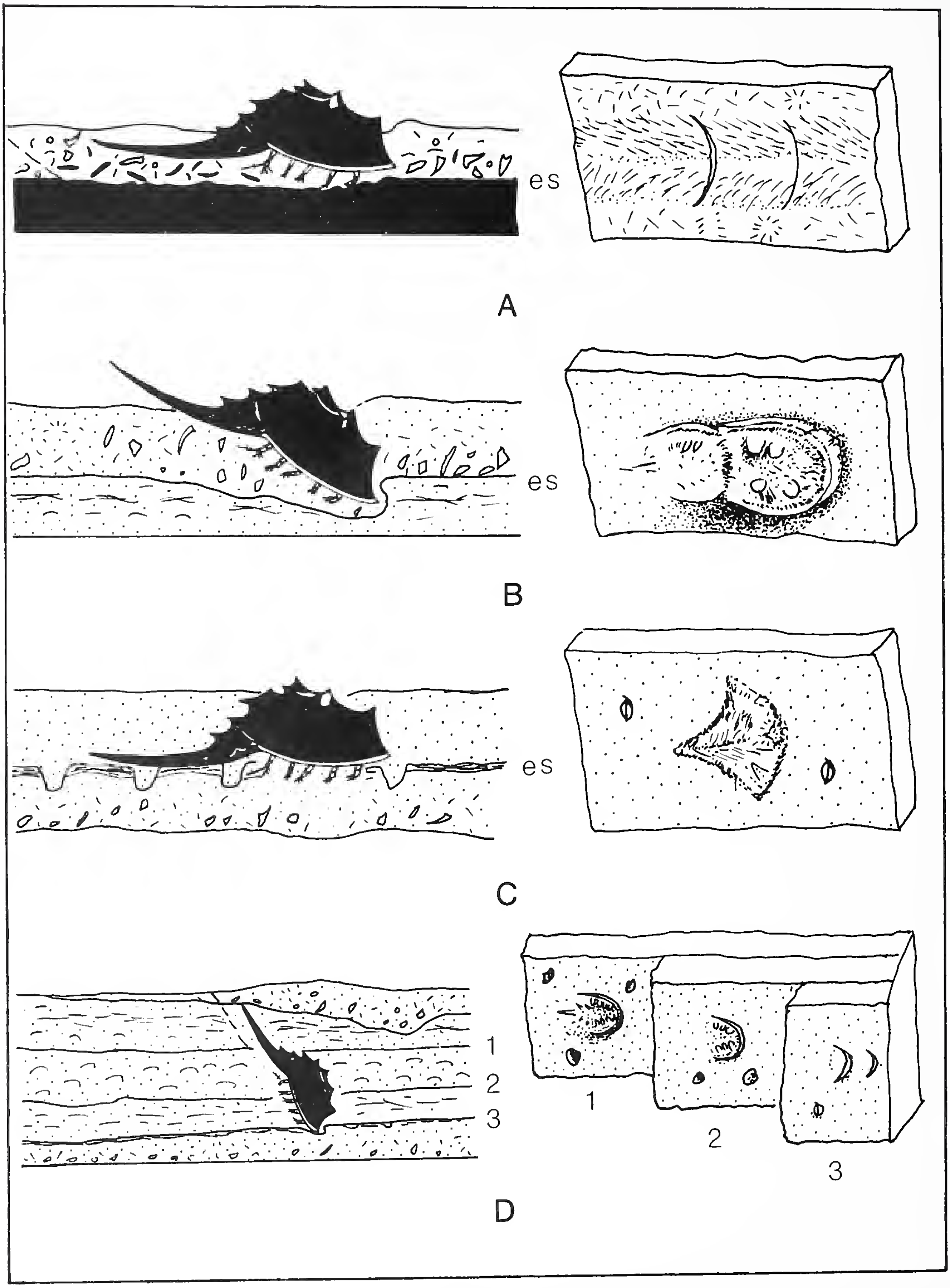
WANG, *Selenichnites*



TEXT-FIG. 5. For legend see opposite.

1985) has maintained that *Cruziana* was cut intrastratally, Crimes (1975) and Baldwin (1977) presented evidence in support of an epigenic mode of formation, whereby the mark was cut at the sediment–water interface and then cast by a subsequently deposited sand. Sectioning material firmly demonstrates an interstratal mode of formation for *Cruziana* (Goldring 1985), though he was not able to determine the thickness of the sand layer and Seilacher (1970) only presented a rough model for variation in *Cruziana* reflecting bed thickness.

Only by sectioning the rock, therefore, is it possible to understand the way in which the hypichnial traces were formed and preserved, and to interpret the behavioural activity of the animals responsible. Each trace reflects the relationships between the type of behavioural activity, the depth of the mud–sand interface below the original sediment–water interface, any lateral variation in this depth (as between ripple crest and trough), the cohesiveness of the mud below the sand, and the grain size and texture of the sand. Scratch mark of pattern 1 (Pl. 1, figs 2–3; Text-fig. 5A) and the bilobate furrow (Pl. 1, fig. 2; Text-fig. 4) were formed when the animal could move freely through the coarse-grained, loose sand trying to locate food. Where the sand was fine and cohesive, the activity of the animal was restricted and only scratch mark type of pattern 2 could form. Lunate mark type *b* (Pl. 1, figs 1, 6; Text-fig. 5D (1–2) and lunate mark type *c* were possibly produced at different levels by limulids burrowing down from the same sediment–water interface (Text-fig. 5D).

Where the trace is a sole mark directly above mud it is evident that degradation of the mud had taken place before sand deposition was initiated so that the mud was relatively firm. Evidence for this is the common occurrence of mud flakes ripped up by the animal in the bottom of the burrows (Text-fig. 5A). No tool marks have been observed at any level of the sandstone, though it is possible that any present were subsequently obscured by scratches. The nature of the mud also seems to have controlled the sharpness of the scratches. The silty mud below the main sandstone unit favoured the formation of sharper, higher relief scratches compared with scratches associated with the mud leaves within the sandstone bed.

This mode of formation contrasts with *Konphichnium* resulting from undertrack fallout through laminated siltstone (Goldring and Seilacher 1971). *Konphichnium* reflects the relationship between the animal's activity and the fall-out principle enunciated by Seilacher (in Goldring and Seilacher 1971). The trace was formed by the animal moving over laminated sediment so that the fossil trace firstly reflects the particular lamina along which the rock has split. Occasionally traces may have been cut exogenically into a sandy substrate without a thin mud drape (Wright and Benton 1987).

## ETHOLOGY OF TRACES

Limulids have been filmed during concealment when the animal pushes into loose sediment at a low angle, using a backward movement of its pushers with spread dactyli to effect. Some of the Westbury marks might be expected to result from this movement, with the prosoma impacting on the cohesive mud. In other instances the prosoma mark is repeated at intervals as in *Selenichnites rossendalensis*. But this type of trace is only present where the mark appears to have been formed below a thin layer of sand. No pusher marks have been observed. The reason is almost certainly because the pushers did not normally reach the sand/mud interface. On extensively scratched surfaces the pushers may not have splayed to give digitate impressions. In thicker layers (Text-fig. 5D) the prosoma impinged on the mud layer at a high angle. This trace probably represents activity

TEXT-FIG. 5. Interpretation of formation of different limulid traces. A, sharp scratch marks. The xiphosurid dug into the coarse sand and readily moved along the sand/mud interface, perhaps in search for food. The underlying mud was firm due to degradation, resulting in deep and sharp scratches. B, as in A, erosion surface (es) cuts fine-grained sand which was loose when intruded by limulid. The traces (type *c* lunate mark) are of high and rough relief. Associated scratches are not as sharp as in A. C, formation of type 2 scratches. Here the variation is largely due to body attitude, but consistency of the underlying sediment probably also exerted an influence. The thin mud between the two sandstones was readily disrupted. D, the animal dug down steeply from a high level and left, on split surfaces, lunate marks with different details.

in locating food. On the same sole surface where abundant scratches and a bilobate furrow appear, small hollows with scratch marks (Text-fig. 4; Pl. 1, fig. 2) are better interpreted as feeding traces.

## TAXONOMY

Although xiphosurid trace fossils are well represented in the fossil record the nomenclature has grown in a haphazard way following individual discoveries. Like trilobites, xiphosurids must have performed a variety of activities (as limulids do today), generating a range of different types of trace. Further diversification of the marks is due to toponomic and preservational processes: amount of penecontemporaneous erosion and extent of bed amalgamation, grain size variation, bed thickness, and diagenesis. These factors are not nowadays accepted as having taxonomic significance (Bromley 1990).

It is these factors, however, that seem to have determined the main differences between the traces described here and have indeed influenced the form of the traces to an extent greater than that exerted by purely ethological influences. Seilacher (1970, p. 449, fig. 1; p. 451, fig. 3; 1985, p. 233, fig. 3) discussed the variation in *Cruziana* associated with bed thickness. The scratch marks described here are somewhat analogous to the traces *Rusophycus* and *Diplichnites* and to some extent also to *Cruziana*. The grain size of the sediment or the thickness of the mark-forming layers have never been considered aspects that might serve to differentiate between *Rusophycus* and *Diplichnites*. The Westbury marks appear to represent only two types of activity, either to burrow into the sediment, most likely for feeding on the abundant small bivalves or annelid or annelid-like animals, or for concealment.

*Kouphichnium* is typically applied to a series of appendage marks that are clearly heteropodous and also commonly include the telson mark and occasionally marks of genal spines. Higgs (1988) has shown that the supposed genal spine marks, without tenson or appendage marks, described by King (1965) are attributable to fish activity. *Koupichnium* does not display scratch marks and only minimal sideways movement of each appendage in the sediment is indicated.

*Cruziana* and *Rusophycus* have been used to include traces left by trilobites and xiphosurids (Seilacher 1970, 1985; Shone 1978; Wright and Benton 1987). They are somewhat similar to some of the scratch marks described here but the differences in overall morphology are against assigning the marks to either ichnogenus. However, the cruzianiform furrow (Pl. 1; fig. 2, Text-fig. 4) described here may be assigned to *Cruziana perucca* Seilacher, 1970 unless the posterior divergence of the appendage marks is given greater weight to warrant a separate ichnogenus.

*Selenichnites* was proposed by Romano and Whyte (1990) as a new name for *Selenichnus* Romano and Whyte (1987), *Selenichnus* being pre-occupied by a vertebrate footprint. The diagnosis for *Selenichnites* (as given in Romano and Whyte 1987) emphasizes the mark of the prosoma but also indicates that scratch marks and a posterior ridge may or may not be present. Romano and Whyte (1987) considered the mark to have been formed at the sediment–water interface rather than interstratally. The single specimen (not found *in situ*) was not slabbed to prove this. Romano and Whyte (1987) considered the object of the animal in making the trace was in burrowing into a resting position. They also included *K. rossendalensis* (Hardy 1970) and *K. cordiformis* (Fisher 1975) in their ichnogenus.

The most suitable name for the lunate marks is *Selenichnites* isp. Because of the close relation with the lunate marks, scratch mark pattern 2 may also be assigned to *Selenichnites*. Other marks are best left in open nomenclature.

## ENVIRONMENTAL SIGNIFICANCE

Triassic xiphosurid traces in the UK are known from Westbury on Severn and from the Needwood Basin of Staffordshire (Wright and Benton 1987). The author has also found scratch and lunate marks in the Westbury Formation at Patchway (ST 587815), near Bristol (Text-figs 1–2), also on the sole of the second sandstone above the base of the formation, though the scratches are finer. They may be expected to be present in the Westbury Formation at other localities. But considering their abundance, diversity and preservation, their occurrence at Westbury Garden Cliff is unique. *Kouphichnium* and *Rusophycus* of probably limulid origin from the Needwood Basin (Wright and Benton 1987) are rare and of small size (19–21 mm wide) compared with the lunate marks at Westbury Garden Cliff. No limulid body fossils have been recorded from the Rhaetic in the Bristol area. There are three possible interpretations for this unusual distribution: environmental factors, toponomic and preservational factors, or a combination of these.

Sedimentologically and ichnologically, the sections at Westbury on Severn, Patchway and the Needwood Basin, differ in several aspects. The sandstones from the Needlewood Basin are similar to those at Westbury, but thicker (more than 0·35 m thick) and rest directly on the mudstone of the Blue Anchor Formation (Wright and Benton 1987). Apart from the limulid trace fossils, other traces are similar to those found at Westbury on Severn. The rarity of limulid scratch and lunate marks in the Needwood Basin may be due to the thickness of the sandstone and lack of mud layers, though slabbing may reveal similar bioturbation. Indeed, in Wright and Benton's figure (1987, pl. 49, fig. 1), the asymmetrical area of the bioturbated sediment, lower left, is close to the area depicted in Text-figure 3.

At Westbury on Severn, it seems that only after periods of storm-event sedimentation is there evidence of limulid benthic activity, which only temporarily provided suitable conditions, including appreciable organic material and enough oxygen to the bottom waters. The underlying and overlying mud indicates a quiet and probably anoxic environment (indicated by the fine lamination, large amount of pyrite, absence of bioturbation) with sediments that would not readily preserve traces. The Lower Sandstone from which no limulid traces were recorded, however, was deposited in a relatively more stable, shallow, frequently reworked and well oxygenated environment as indicated by the U-shaped spreiten burrow *Diplocraterion* and the extensive bioturbation. Besides, compared with the sediments near Bristol, which contain more and larger *Diplocraterion* at the base of the formation and on the sole of the Lower Sandstone (which also exhibits common *Spongeliomorpha*), the salinity at Westbury on Severn could have been much reduced, possibly due to its location near the palaeocoast (Text-fig. 1). *Diplocraterion* is normally regarded as a marine trace fossil, though xiphosurid traces have been frequently reported from marginal brackish marine environments (Stormer 1952; Hardy 1970; Goldring and Seilacher 1971; Chisholm 1983, 1986; Eagar *et al.* 1985).

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# NEW ACTINOPTERYGIAN FISH FROM THE NAMURIAN MANSE BURN FORMATION OF BEARSDEN, SCOTLAND

*by* M. I. COATES

ABSTRACT. Four new species of actinopterygians are described from the Manse Burn Formation (Namurian) of Bearsden, Glasgow, Scotland. Two fusiform species are members of, and a third is questionably assigned to, *Mesopoma: M. carricki, M. ? smithsoni,* and *M. pancheni.* A new gibbose species is assigned to a new genus, *Frederichthys musadentatus. Mesopoma* is reviewed and rediagnosed, and its relationships to *Frederichthys* are examined with regard to a recent analysis of early actinopterygian (palaeoniscid) phylogeny; *Mesopoma* is a member of a probably paraphyletic group within a polytomous stem-group actinopteran radiation. An alternative phylogeny places *Mesopoma* on the common stem-group of the Haplolepidae, Aeduellidae, and Redfieldiformes. *Frederichthys* is closely related to the platysomids. Otoliths preserved within the mesopomid material are described and compared with those of other osteichthyans; the presence of three pairs of otoliths as a teleostome characteristic is questioned.

THE Bearsden site was discovered and excavated by Mr S. P. Wood (Wood 1982), with the assistance of the Hunterian Museum, University of Glasgow, and the Nature Conservancy Council, during the summers of 1981 and 1982. The fauna includes a diverse assemblage of early actinopterygians, from small, fusiform species of *Mesopoma* to large, rhombic-bodied species of *Amphicentrum* (Traquair 1879; Wood 1982; Coates 1988), a wide variety of crustaceans (Clark 1990, 1991), and remarkably well-preserved chondrichthyans (Dick *et al.* 1986). The closest comparable faunas are those of Bear Gulch, Montana (Lowney 1980, 1985; Lund and Melton 1982), which is also Lower Namurian, and Glencartholm (Dumfries and Galloway) of the Upper Viséan (Traquair 1881; Moy-Thomas and Bradley Dyne 1938). However, these three faunas have very little taxonomic overlap.

Early actinopterygian classification is currently undergoing a major review. Gardiner and Schaeffer (1989) produced a provisional scheme in which they incorporated a wide range of Palaeozoic taxa into groups regarded tentatively as monophyletic. The present paper is not intended to be an exhaustive review of their analysis, and no alternative hypothesis of interrelationships is provided. This problem will be addressed only after the publication of the Bearsden actinopterygians has been completed. The three new species of *Mesopoma*, and the species of *Frederichthys* gen. nov., are described and incorporated into Gardiner and Schaeffer's cladogram, with limited discussion of the relevant synapomorphies and resultant taxonomic positions.

Institutional abbreviations used in this work are: BM(NH), Natural History Museum, London; NMS, National Museum of Scotland, Edinburgh; GLAHM, Hunterian Museum, University of Glasgow; GN, University Museum of Zoology, Cambridge; SPW, the collection of Mr S. P. Wood, Edinburgh.

## LOCALITY AND HORIZON

The Bearsden site is located near Glasgow, Scotland. The type locality for the Manse Burn Formation is the Manse Burn, near Bearsden (Ordnance Survey Grid reference NS 529427329 – NS 53057325) (Clark 1989). The Manse Burn Formation has been dated as Pendleian (Namurian) $E_1$ Zone, based upon spore, conodont, and goniatite analysis. Clark defined the Formation as

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including the shales from the Top Hosie Limestone Marine Band to the base of the first thick sandstone. The Formation has been subdivided into six members on the basis of the fossil content and sedimentological characteristics of the shales: the Shrimp member, the Posidonia Member, the Nodular Shale Member, the Platey Shale Member, the Betwixt Member, and the Lingular Member. These Members correspond approximately to the 'beds' presented by Wood (1982). The fossil fish, and an abundance of crustaceans, are contained in finely laminated shales of the Shrimp Member, which has now been identified at several other localities in the western Midland Valley of Scotland (Clark 1989). The shales of the Manse Burn Formation are considered to have been deposited during conditions of varying salinity and oxygenation. The Shrimp Member bears evidence of a sequentially marine and non-marine environment, subject to seasonal fluctuations.

## SYSTEMATIC PALAEONTOLOGY

### Class ACTINOPTERYGII Woodward, 1891
### Infraclass ACTINOPTERI Cope, 1871
### Genus MESOPOMA Traquair, 1890

*Type species. Canobius pulchellus* Traquair, 1881, from the Glencartholm Volcanic Beds ($C_2$/5, Zone, Viséan) of Glencartholm, Dumfries District, Scotland.

*Emended diagnosis.* Scales arranged in 30–40 vertically oriented sigmoid rows; all fins bearing fringing fulcra; pelvic fin insertion narrow; pectoral fin rays proximally unjointed; anteroposteriorly narrow post-temporal; branchiostegal series reduced; surangular present; postorbital region of maxilla reduced, jaw articulation sited anteriorly relative to parietal-extrascapular suture; marginal dentition consisting of short uniformly sized conical teeth; dermohyal short; preopercular with short anterodorsal limb; posterior infraorbital narrow; parietals short and almost equilateral; frontals long, projecting into embayed rear of median rostral; nasals narrow; dermopterotic short; dermosphenotic triradiate and contacts nasal; hyomandibula with opercular process; ceratohyal bar consisting of two ossifications.

*Included species. M. pulchellum, M. politum, M. macrocephalum, M. crassum, M. ardrossense, M. becketense, M. carricki, M. pancheni,* and *M. ? smithsoni.*

*Remarks. Mesopoma* was erected by Traquair (1890) to separate from *Canobius* Traquair, the species *pulchellus* and *politus*, and from *Rhadinichthys* Traquair, the species *macrocephalus*. These three species were considered to have a configuration of dermal skull bones which placed them between the apparently advanced form of *Canobius* and the more 'typically palaeoniscid' (Traquair 1890) pattern of *Rhadinichthys*. However, Woodward (1891) placed all three species in *Canobius*, considering the erection of a new genus for these species to be premature, because they were insufficiently known. Traquair (1912) withdrew *Mesopoma*, because of difficulty in constructing an

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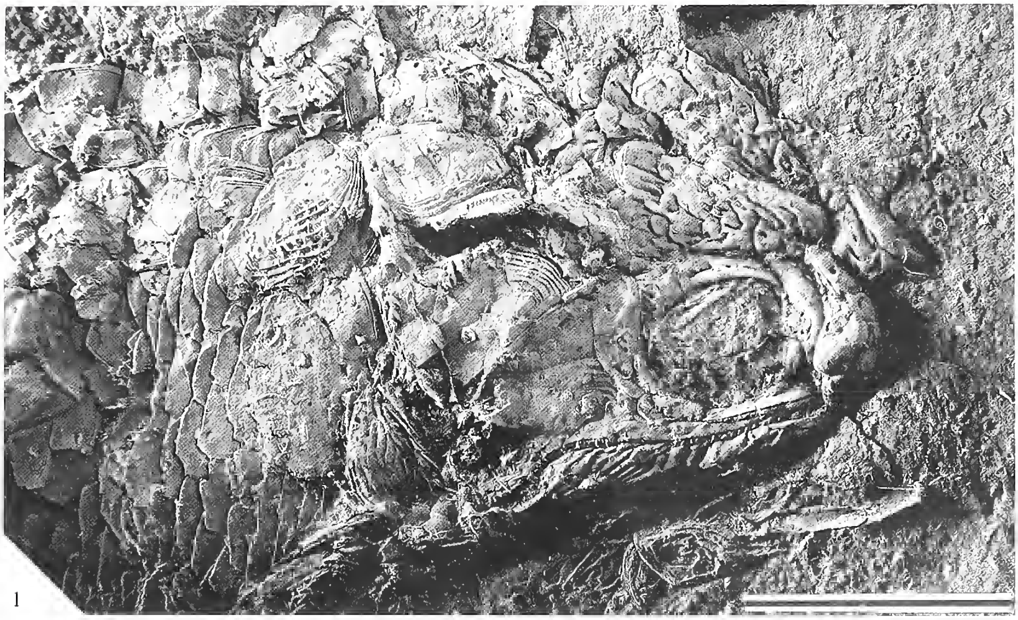
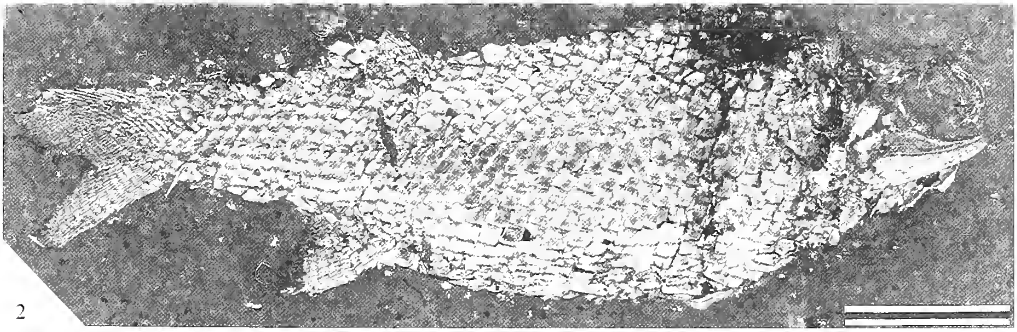
EXPLANATION OF PLATE 1

Fig. 1. *Mesopoma carricki* sp. nov.; NMS 1981.63.54*b*; latex peel of specimen, showing dermal ornament and isolated pores in (split) rostral region. Scale bar = 5 mm.

Fig. 2. *Mesopoma carricki* sp. nov.; GLAHM V8254; sealed with cellulose and photographed under toluene; note apparent patterning of squamation. Scale bar = 10 mm.

Fig. 3. *Frederichthys musadentatus* gen. and sp. nov.; composite photograph of specimens GLAHM V8286*a–b* immersed in toluene; for line drawing of specimen, see Text-fig. 9. Scale bar = 10 mm. Photographs for figs 2–3 taken by Dr J. K. Ingham; reprinted with permission of the Hunterian Museum, University of Glasgow.





COATES, *Mesopoma*, *Frederichthys*

adequate diagnosis. All three species were again placed in *Canobius*, with the addition of a new species, *Canobius crassus* Traquair, 1914. *Mesopoma* was resurrected by Moy-Thomas and Bradley Dyne (1938) in their description of the Glencartholm actinopterygian fauna. They provided a new generic diagnosis, and new descriptions of *M. pulchellum*, *M. politum*, and *M. crassum*. Moy-Thomas (1938) published a further diagnosis of *Mesopoma*, together with a redescription of *M. macrocephalum*, and a description of another new species, *M. ardrossense*. Lowney (1980) has also rediagnosed *Mesopoma*, and described another new species, '*M. becketense*', from Bear Gulch, Montana. Most recently, Gardiner and Schaeffer (1989) have characterized a '*Mesopoma* group', which is incorporated within their reclassification of lower actinopterygian fishes.

No type species for *Mesopoma* has been formally proposed; this role must therefore be assigned to *M. pulchellum* under the 'first species rule' (article 69, recommendations 69B (9) & (10), International Code of Zoological Nomenclature 1985).

### *Mesopoma carricki* sp. nov.

Plate 1, figs 1–2; Text-figs 1–3

*Derivation of name*. The species is named after the late James A. Carrick, formerly of the Hunterian Museum, University of Glasgow, who helped significantly at the Bearsden excavation in 1982.

*Holotype*. GLAHM V8289*a–b*.

*Referred specimens*. The above mentioned holotype, together with NMS 1981.63.44; NMS 1981.63.46; NMS 1981.63.47; NMS 1981.63.53; NMS 1981.63.54*a–b*; NMS 1981.63.55*a–b*; NMS 1987.7.131; GLAMH V8254; BM (NH) P62370; BM (NH) P62372*a–e*; SPW 2294*a–b*; SPW 2282; SPW 2285*a–c*.

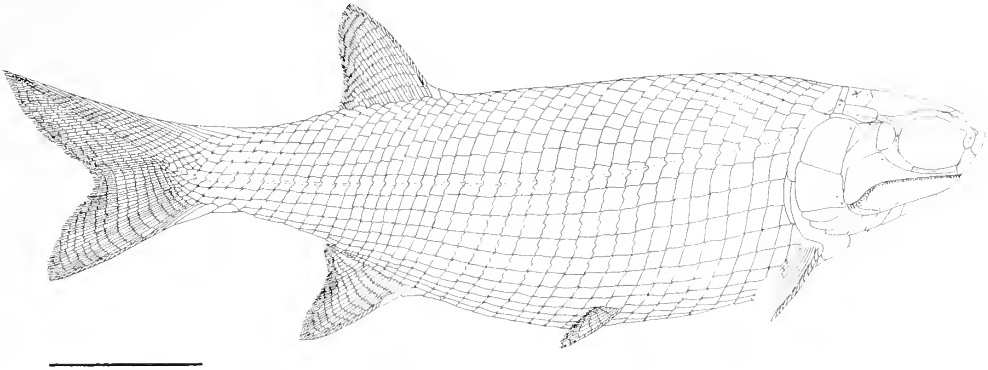
*Horizon and locality*. Shrimp member, Manse Burn Formation, Pendleian (Namurian) $E_1$ Zone, Lower Carboniferous, Bearsden, Glasgow, Scotland.

*Diagnosis*. Bulbous rostral and other dermal skull bones pierced occasionally by large pores not associated directly with the sensory canal system; single ovoid suborbital; dermohyal short and triangular; opercular five-sided; six branchiostegal rays; all median fins preceded by three basal fulcra; posterior basal fulcral scale preceding anal fin with narrow mid-region; squamation arranged in thirty eight rows; largest scales in flank region with serrated posterior edge; scales devoid of ornament except for two or three grooves parallel to anterior edge; maximum of seven scales above and ten below lateral line.

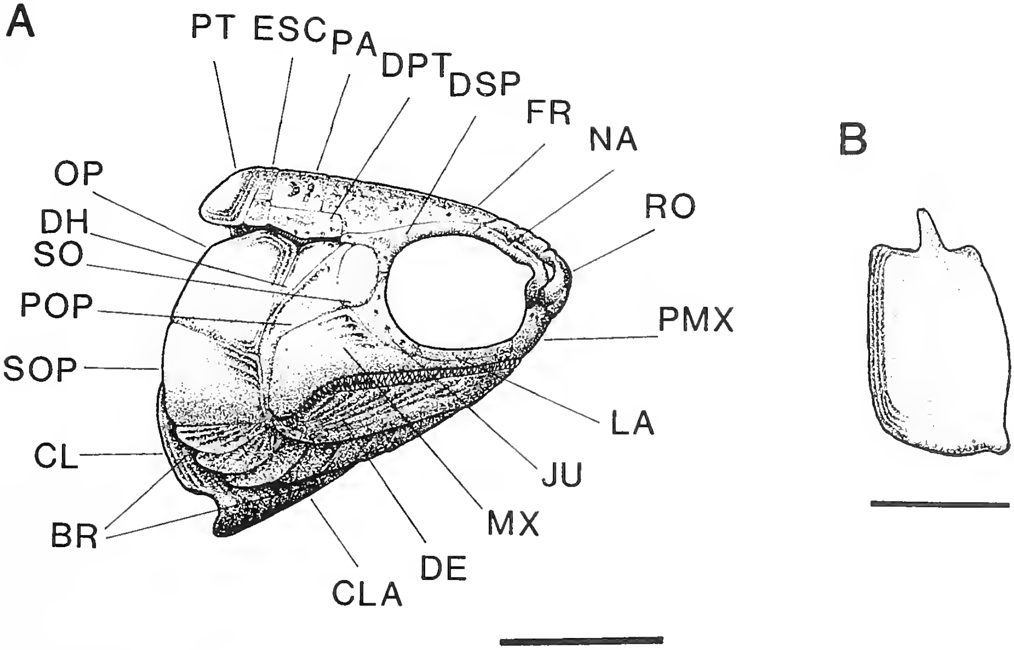
*Discussion*. *M. carricki* may be distinguished from *M. pancheni* on the basis of the following characters: a V-shaped rostronasal: frontal suture; isolated pores piercing dermal skull bones; the pattern of rostral ornament; the lack of highly ornamented scales behind the post-temporals; scales with mostly smooth surface, fewer anterior grooves, and scale proportions (compare Text-figs 2 and 6).

*Description*. This is one of the most frequently found actinopterygian species at the Bearsden site. *M. carricki* has been restored as a compressed fusiform fish (Keast and Webb 1966) because most articulated specimens are preserved lying on one side. The head is short relative to most other Palaeozoic fusiform actinopterygians, with a large orbit and near vertical jaw suspension. The skull, measured from the rostral apex to the rear of the operculogular series, is *c*. 12·5 mm long; the total body may reach 70 mm in length (Text-fig. 1).

*Skull and lower jaw*. Details of the skull are most clearly preserved in specimens GLAHM V8289 (Text-fig. 3) and NMS 1981·63·54*b* (Pl. 1, fig. 1). The maxilla is short, with a subrectangular posterior expansion (Text-figs 1, 2A, 3). A series of two or more small pits lies adjacent to the jugal border; the dermal ornament is restricted to the anterodorsal region. The maxilla bears a single row of uniformly sized small conical teeth. The preopercular has a slender vertical stem and a short anterodorsal limb; the sensory canal lies next to the posterodorsal edge. The short, triangular dermohyal is pierced by a single pit (Text-figs 1, 2A). An ovoid

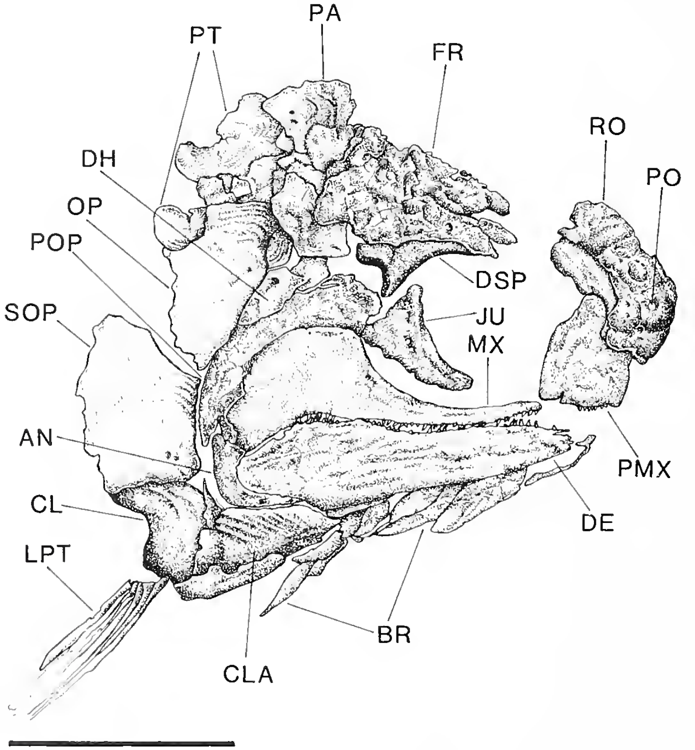


TEXT-FIG. 1. *Mesopoma carricki* sp. nov., restoration. Scale bar = 10 mm.



TEXT-FIG. 2. *Mesopoma carricki* sp. nov. A, restoration of dermal skull showing ornament. Scale bar = 5 mm. B, anterior flank scale. Scale bar = 1 mm. Abbreviations: AN, angular; AR, articular; ASP, ascending process of parasphenoid; BH, site of buccohypophyseal foramen; BPT, basipterygoid process; BR, branchiostegal ray(s); CL, cleithrum; CLA, clavicle; DE, dentary; DH, dermohyal; DSP, dermosphenotic; ESC, extrascapular; FMC, foramen for mandibular sensory canal; FR, frontal; GF, glenoid fossa; GL, lateral gular; HLPA, horizontal lamina of prearticular; JU, posterior infraorbital; LA, anterior infraorbital; LPT, lepidotrichia; MX, maxilla; NA, nasal; OP, opercular; PA, parietal; PAR, prearticular; PCL, postcleithrum; PMX, premaxilla; PO, pore not associated with sensory canal; POP, preopercular; PT, post-temporal; RO, rostral; SCL, supracleithrum; SO, suborbital; SOP, subopercular; ST, supratemporal; TS, tooth sockets.

suborbital lies between the preopercular and the infraorbital series (Text-fig. 2A). The triradiate dermosphenotic carries the otic portion of the infraorbital canal through posterior and ventral rami into the crescentic posterior infraorbital. Four pores overlie the sensory canal, which passes into a slender, tubular anterior infraorbital; neither bone is ornamented. The skull table bears anastomosing flattened tubercles and ridges (Plate 1, fig. 1). Four extrascapulars carry the occipital commissure. A short dermopterotic with a convex lateral edge encloses the otic portion of the infraorbital canal. The anterodorsal angle of the dermopterotic fits into the embayed posterolateral corner of the frontal. The subequilateral parietals have strongly convex anterior edges. The frontals are more than twice the length of the parietals; the supraorbital canal exits anterolaterally to join the nasal. The united anterior frontal apices project into the embayed posterodorsal rostral edge. Large crystalline otoliths are preserved occasionally beneath the dermopterotic. All examined specimens are in poor condition (surface detail has been lost); each is pear-shaped with the longest axis almost equal to the length of the dermopterotic (2·6 mm). The lateral surface is flat and the mesial surface slightly convex. Only one otolith has been found on each side of the skull. The large, characteristically bulbous, rostral resembles those of *Rhadinichthys canobiensis*, var. *elegantulus* Traquair, *Rhadinichthys planti* Traquair, and *Mesopoma pancheni* sp. nov. (Text-figs 2A,3). The bilaterally symmetrical ornament of broad ridges and tubercles is illustrated in Text-figure 3 and Plate 1, figure 1. Pores pock-mark the posterodorsal region (NMS 1981.63.54*b*) resembling those described in the snout of *Mimia toombsi* Gardiner (1984; interpreted as containing twigs of the upper branch of the profundus nerve (V)). The convex ventral edge overlaps the dorsomedial region of the premaxillae; whether it contains the ethmoid commissure is unclear. Long, narrow nasals flank the rostral; a groove next to the anterior edge marks the course of the supraorbital canal. Tall, smooth, subrectangular premaxillae contribute to the anteroventral orbital rim, and bear small conical teeth. The ethmoid commissure passes towards the ventral region of the rostral. The ethmoidal osteological pattern resembles closely that of the Gogo actinopterygians (Gardiner 1984), in which the commissure enters the rostral. The correspondent identification of the derm-ethmoidal shield of *Mesopoma* as consisting of a rostral and premaxillae, rather than a post-rostral and rostro(antorbito-)premaxillae (with implicit hypotheses of bone fusion) appears to be the most parsimonious interpretation. The palate is known from fragments of pterygoidal material, covered with small granular teeth. The lower jaw consists of a large dentary, a slender angular, and a surangular. The dentary is ornamented with bifurcating grooves, which radiate from the posteroventral corner. The dentition consists of numerous small conical teeth, all of approximately uniform size and lying in a single row. The irregularly pentagonal opercular is taller and narrower than the subopercular. Two or three shallow grooves



TEXT-FIG. 3. *Mesopoma carricki* sp. nov., GLAHM V8289*a*, holotype. Abbreviations: see Text-figure 2. Scale bar = 5 mm.

ornament the surface adjacent to the anterodorsal corner, occasionally pierced by an isolated pit (obscured by the right parietal in Text-figure 3). The subopercular is trapezoid, with a slightly convex posterior edge; four or more shallow grooves score the anterodorsal quarter of the surface, and two further pits lie in the anteroventral corner. The branchiostegal series consists of six rays which become narrower anteriorly, and an elongate triangular gular.

*Pectoral girdle.* The post-temporal is anteroposteriorly narrow, with an expanded posteroventral region (Text-figs 1–3). The lateral line canal passes through the anteroventral corner. The posterior edge of the ovoid supracleithrum bears four or more widely spaced serrations. The sensory canal traverses the dorsal, broadest, region. The cleithrum has a robust vertical blade, with an acute median angle dividing the post-branchial lamina from the posterolateral region. Apices of the ridged dermal ornament appear to be slightly denticulated. The elongate postcleithrum has a gently convex posterior edge. Fragments of the clavicle appear to be ornamented similarly to the clicthrum. The interclavicle is unknown.

*Fins.* All fins bear fringing fulcra. The dorsal and anal fins are situated opposite each other in the rear half of the body (Text-fig. 1). The subtriangular dorsal fin has a convex leading edge. The fin consists of twenty five or more lepidotrichia which articulate at even intervals throughout their length, and bifurcate distally before reaching the slightly emarginated trailing edge. The anal fin is similar to the dorsal fin, although more acuminate. The caudal fin consists of sixty or more lepidotrichia which are articulated throughout their length and bifurcate distally. The heterocercal tail has a deeply cleft, almost symmetrical profile. The incomplete pectoral fins consist of eight or more proximally unjointed lepidotrichia. The leading edge includes at least one primary, unbifurcated lepidotrich. The pelvic fin is small, subtriangular, and narrow based; situated about halfway between the anal fin and the pectoral girdle. It consists of ten or more articulated, distally bifurcated lepidotrichia.

*Squamation.* The most complete squamation is preserved in specimen GLAHM V8283; Plate 1, figure 2, shows dark bands within the scales, visible when the specimen is immersed in a solvent. The emergent pattern may be specifically diagnostic, but whether it preserves the patterning of the fish when alive, or merely the distribution of some other feature (e.g. ganoine density), remains uncertain. The large, rhomboidal scales have a clearly defined anterodorsal process (Text-fig. 2B). The trunk, from the origin of the tail to the rear of the pectoral girdle, bears thirty eight almost vertically oriented rows (Text-fig. 1). Mid-flank scales have a gently serrated posterior edge. The caudal lobe is not steeply up-turned; intercalaric scale rows are inserted ventrally at the base of the tail. A maximum of seven scales lie above, and ten below, the lateral line. A pair of fine grooves run parallel to the anterior and dorsal scale edges which may represent growth lines or restricted dermal ornament. A cut-water of fulcral scales lies along the dorsal mid-line of the caudal lobe. The insertions of the caudal, dorsal, and anal fins are each preceded by three basal fulcra. Specimen NMS 1981.63.53 has an unusual, waisted fulcral scale preceding the anal fin.

## *Mesopoma? smithsoni* sp. nov.

Text-figs 4–5

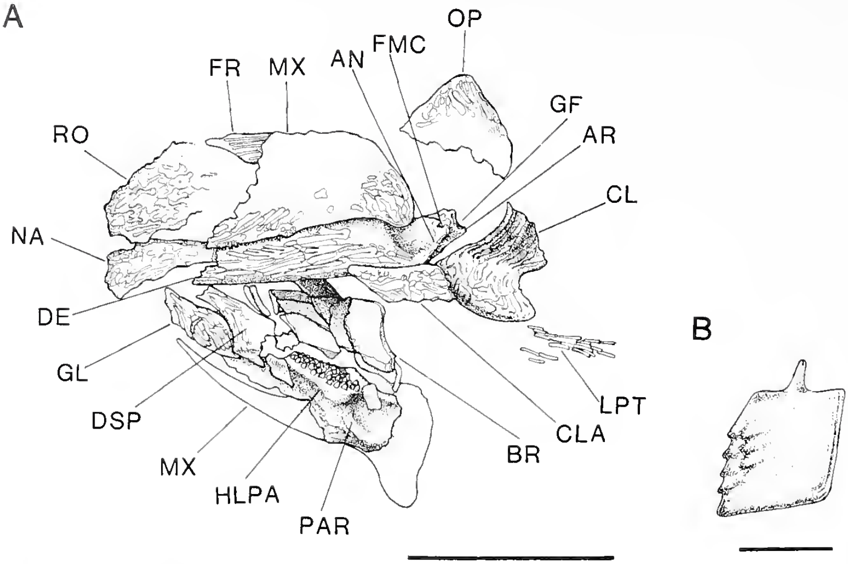
*Derivation of name.* Named after Dr T. R. Smithson, who provided valuable discussion and advice throughout the course of research on the Bearsden actinopterygian material.

*Holotype.* NMS 1981.63.43*a–b*.

*Referred specimens.* NMS 1981.63.31; NMS 1981.63.40*a–b*; NMS 1987.7.129*a–b*; GLAHM V8290*a–b*; GN 1022*a–b*; GN 1064; BM (NH) P62373*a–b*; SPW 2001*a–b*; SPW 2003*a–b*; SPW 2004; SPW 2007; SPW 2288; SPW 2292*a–b*; SPW 2295*a–b*.

*Horizon and locality.* Shrimp member, Manse Burn Formation, Pendleian (Namurian) $E_1$ Zone, Lower Carboniferous, Bearsden, Glasgow, Scotland.

*Diagnosis.* Postorbital region of maxilla accounts for less than half of its total length; lower jaw with greatly thickened prearticular bearing numerous large, rounded, flattened teeth; opercular rectangular with rounded posterodorsal corner; subopercular with extended anteroventral corner; gulars large with single curved pit-line; squamation arranged in thirty two or more rows; scales in flank region with faint, oblique, ridged dermal ornament; squamation approaching post-temporals



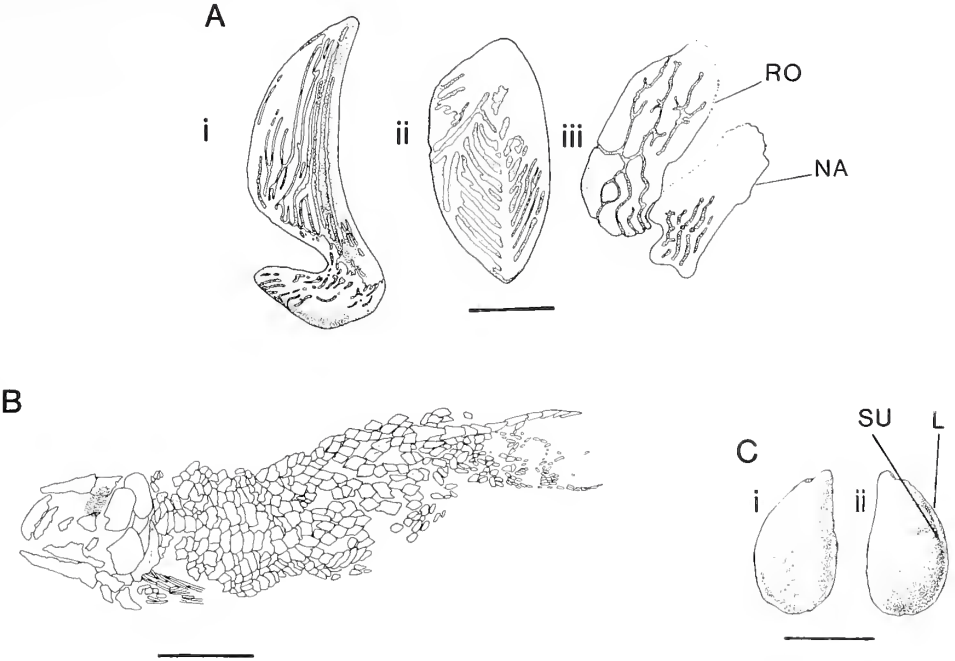
TEXT-FIG. 4. *Mesopoma? smithsoni* sp. nov. A, GN 1064. Disarticulated skull and pectoral girdle showing incomplete jaws with thickened prearticular. Scale bar = 10 mm. B, anterior flank scale. Scale bar = 1 mm. Abbreviations: see Text-figure 2.

has most pronounced ornament and convex posterior edges; eight or more scales above and eight or more below lateral line.

*Discussion. M.? smithsoni* is questionably assigned to *Mesopoma* on the basis of the following characters: the short postorbital region of the maxilla; uniformly sized, small marginal teeth; short parietals and long frontals; post-temporal anteroposteriorly narrow; squamation arranged in thirty two or more, vertically oriented sigmoid rows. *M.? smithsoni* most closely resembles *M. crassum*, sharing similar gross proportions, dermal ornament, and maxillae, but can be distinguished from the latter by the presence of specialized buccal dentition, a much broader opercular and the absence of a continuous line of ridge scales from the post-temporals to the dorsal fin insertion.

*Description.* This is the largest and most robustly constructed of the three species of *Mesopoma* found in the Bearsden fauna. Individual fish may be up to 80 mm long, an estimate based upon the most complete specimens of an incompletely known species.

*Skull and lower jaw.* The subrectangular postorbital region of the maxilla is more angular than that of *M. carricki*, accounts for less than half of the total length, and bears uniformly small teeth (Text-fig. 4A). Dermal ornament is limited to patches of broad tubercles and ridges originating at the ventral margin. The preopercular, quadratojugal, dermohyal, suborbital and infraorbitals appear to be similar to those of the larger members of this genus (cf. *M. crassum* Traquair, Moy-Thomas and Bradley Dyne 1938; Text-fig. 12G). The anteriorly slender dermosphenotic expands posteriorly, towards what may have been a T-junction as found in *M. carricki*. This and a slender anterior infraorbital are ornamented with discontinuous ganoine ridges and tubercles. Anteriorly convex, equilateral parietals project into the embayed posterior edge of the long frontals. The skull table bears irregularly shaped, flattened ganoine ridges. A single otolith is preserved on each side of the skull in several specimens (Text-fig. 5Ci and 5Cii depict the left otolith of GN 1022). The laterally compressed, pear-shaped otoliths consist of a crystalline material which reacts vigorously with a 10 per cent solution of acetic acid; therefore thought to be calcitic rather than phosphatic. An elongate, narrow sulcus borders the mesial surface of the convex posterior edge. The sulcus may extend around the posteroventral region, contributing to the delineation of a narrow crest along the posteroventral and anteroventral edge. The mesial surface is strongly convex; the less convex lateral surface has a shallow central depression from which



TEXT-FIG. 5. *Mesopoma? smithsoni* sp. nov. Ai, cleithrum; Aii, supracleithrum; Aiii, incomplete rostral and nasal; all from specimen NMS 1981·63·43*a*. Scale bar = 2 mm. B, almost complete squamation of specimen GN 1022*a* in lateral view; stippled area indicates site occupied by otolith. Scale bar = 10 mm. C, left otolith from specimen GN 1022*a*: i, lateral surface; ii, mesial surface. Scale bar = 2 mm. Abbreviations: L, lip; SU, sulcus; for others, see Text-figure 2.

faint grooves radiate posteroventrally. No growth-lines are apparent. The skull table and broad rostral are ornamentally similar (Text-figs 4A, 5Aiii). The nasal ornament resolves into more longitudinally oriented ridges; there is no distinct notch for the posterior nostril. The edges of the lower jaw bones are indiscernible. A smooth surangular area is surrounded by a thick ornament of ganoine ridges. The slender angular is pierced dorsally by a foramen for the mandibular sensory canal (FMC, Text-fig. 4A). The articular (AR) and glenoid fossa (GF) are visible in specimen GN 1064 (Text-fig. 4A). It is unclear whether the glenoid consists of more than a single articulatory depression. The thickened prearticular (PAR, Text-fig. 4A) has a pronounced angle dividing the smooth ventromesial surface from a broad dorsal lamina (HLPA, Text-fig. 4A), which bears large, rounded and flattened subconical teeth. The prearticular cannot be distinguished from coronoidal material. The subrectangular opercular is ornamented with a few broad flattened ganoine ridges which arise from the rounded anterodorsal corner; most of the external surface is smooth (OP, Text-fig. 4A). The similarly patterned subopercular is slightly smaller with an extended anteroventral corner. Fragmented remains of the branchiostegal plates resemble those of *M. carricki*. A pair of gular plates is incompletely preserved in a few specimens, including GN 1064 (GL, Text-fig. 4A). A crescentic pit line lies in the central; the dermal ornament consists of further closely packed short ganoine ridges.

*Pectoral girdle*. The post-temporals, notably from NMS 1981.63.43*a–b*, appear to be narrow anteroposteriorly. The short, elliptical, supracleithrum is ornamented with thick enamel ridges (Text-fig. 5Aii). The lateral line canal traverses the broadest span, and exits in front of the dorsal apex. The robust cleithrum has a tall, bipartite vertical blade (Text-fig. 5Ai) with a denticular-crested dormal ornament (cf. *Amia* Jarvik 1980). The moderately-sized clavicle has a smooth anterolateral margin. The scale-like postcleithrum bears a few shallow groves posteriorly.

*Fins*. All fins bear fringing fulcra. The incompletely preserved dorsal and anal fins are situated opposite each other within the rear half of the body. The lepidotrichia are articulated frequently throughout their length. The anal fin is slightly longer based than the dorsal. The caudal fin is preserved as isolated patches of lepidotrichia and fringing fulcra; all three resemble those of *Mesopoma carricki*. The pectoral fin consists of nine or more fin rays which are articulated distally, and bifurcate at least once before reaching the trailing edge. The pelvic fin has a broader insertion than that of *M. carricki*. It consists of ten or more fin rays which are articulated throughout their length and bifurcate once, distally.

*Squamation*. The large, rhomboidal scales have a clearly defined anterodorsal process (Text-fig. 4B) and a serrated posterior edge. Two or more parallel grooves flank the anterior and ventral edges. Occasionally, faint diagonal, posteroventrally oriented ridges may be observed in the centre of the external surface, which originate from the serrated posterior edge. Scales adjacent to the post-temporals bear the most prominent ornament, lack an anterodorsal process, and acquire a convex posterior edge. The squamation is arranged in approximately thirty two, almost vertically oriented rows. Each has eight or more scales above and eight or more below the lateral line. The median fins are preceded by basal fulcra, and a series of caudal lies along the dorsal mid-line of the tail.

### *Mesopoma pancheni* sp. nov.

Text-figs 6–7

*Derivation of name*. Named after Dr Alec L. Panchen, who supervised the original research on this material.

*Holotype*. NMS 1983.33.7.

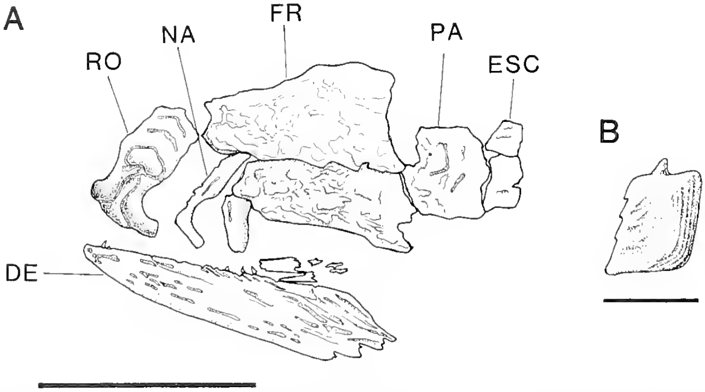
*Referred specimens*. The above-mentioned holotype, together with GLAHM V8283*a–b*; SPW 1941.

*Horizon and locality*. Shrimp member, Manse Burn Formation, Pendleian (Namurian) $E_1$ Zone, Lower Carboniferous, Bearsden, Glasgow, Scotland.

*Diagnosis*. Frontals forming W-shaped suture with rostronasal complex; rostral ornamented with three broad, posteriorly directed chevrons on posterodorsal surface; two or more basal fulcra preceding dorsal fin; three basal fulcra preceding anal fin; squamation arranged into thirty-five or more rows; scales have convex denticulated posterior edge in region behind post-temporals; dermal ornament consisting of distinct posteriorly directed chevrons, most prominent on scales surrounding dorsal mid-line, and four or more grooves parallel to anterior edge.

*Discussion*. *M. pancheni* may be distinguished from *M. carricki* on the basis of the following characters: a W-shaped rostronasal; frontal suture; incised posteriorly directed chevrons on rostral; denticulated scales bordering post-temporals; chevron-ornament on scales. None of these characters can be demonstrated to be ontogenetically precursive to the morphology of *M. carricki*.

*Description*. This is the rarest and least well known of three species of *Mesopoma* from Bearsden. *M. pancheni* appears to have been a slender, fusiform, species, not much more than 55 mm long. The length of the head, measured from the rostral apex to the rear of the operculogular series, is about 10 mm (Text-fig. 7).

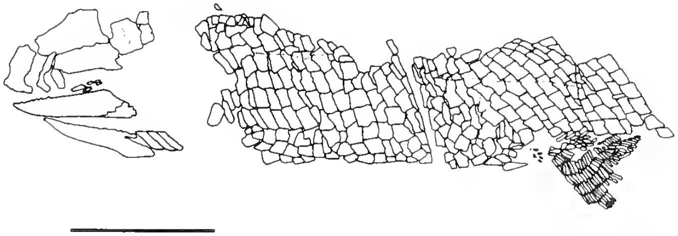


TEXT-FIG. 6. *Mesopoma pancheni* sp. nov. A, incomplete dermal skull of holotype, NMS 1983.33.7. Scale bar = 5 mm. B, anterior flank scale. Scale bar = 1 mm. Abbreviations: see Text-figure 2.

*Skull and lower jaw.* The maxilla, represented solely by a single median portion situated on specimen GLAHM V8283*a*, displays a few posteriorly directed ornamental grooves (these grooves are more vertically oriented than those of *M. carricki*). The marginal teeth are small and conical. The triradiate dermosphenotic passes the infraorbital canal from the dermopterotic to the dorsal apex of the posterior infraorbital. The dermosphenotic resembles closely that of *M. carricki.* The crescentic posterior infraorbital has an embayed posterodorsal region, indicating that one or more suborbitals may have been present. The extrascapular region of the skull table is unclear (ESC, Text-fig. 6A). A subrectangular dermopterotic with a convex ventral edge occupies the temporal region. Each subrectangular parietal has a convex anterior edge which projects into the embayed posterior edge of the frontal. The anteriorly narrow frontals combine to form a W-shaped suture with the posterior edge of the rostral and nasals.

Fronto-parietal dermal ornament consists of flattened ridges and tubercles, similar to those of *M. carricki.* The prominent rostral resembles that of *M. carricki.* The dermal ornament consists of a symmetrical arrangement of large ganoine tubercles which cap the apex of the snout. The dorsal portion bears a series of three broad, posteriorly directed chevron-shaped ridges. The nasal is smooth, with a discontinuous groove adjacent to the anterior edge overlying the sensory canal. Only the external surface of the lower jaw is known. The dentary is ornamented with a series of long grooves which radiate from the posteroventral corner. The dentition consists of uniformly sized, small conical teeth. A slender angular passes around the rear of the dentary. The surangular is unknown. Isolated narrow, subtriangular branchiostegal rays have faint shallow grooves radiating from the point of submandibular insertion.

*Pectoral girdle.* The subelliptical post-temporal has a posterior edge with a series of widely spaced denticulations. The supracelithrum is slightly more rhomboidal than that of *M. carricki*, but is otherwise similar. The dermal ornament consists of four parallel grooves which run parallel to the anterior and ventral edges. The cleithrum has a robust bipartite vertical blade with a ridged dermal ornament.



TEXT-FIG. 7. *Mesopoma pancheni* sp. nov., squamation of holotype, NMS 1983.33.7. Scale bar = 10 mm.

*Fins.* All fins bear fringing fulcra. The dorsal and anal fins are situated opposite each other in the rear half of the body. The dorsal fin is incompletely known, but appears to be similar to that of *M. carricki.* The lepidotrichia are articulated at frequent, even intervals throughout their length. The anal fin consists of about twenty five lepidotrichia; it is acuminate with an embayed trailing edge. The lepidotrichia resemble those of the dorsal fin. The pattern of bifurcation is unknown. The caudal fin is known only from isolated patches of lepidotrichia. The pectoral fin consists of an undetermined number of proximally unarticulated lepidotrichia. The posterior lepidotrichia display greater distal articulation. The pelvic fins are known only from isolated, incomplete lepidotrichia.

*Squamation.* The scales are large and rhomboidal, with a prominent anterodorsal angle (Text-fig. 6B). They are arranged into at least thirty-five vertically oriented rows. Next to the dorsal mid-line they develop a convex posterior edge. The dermal ornament is specifically characteristic: four or five sharply defined parallel grooves lie adjacent to the anterior edge, turning to follow the dorsal and ventral edges and occasionally bifurcating before fading posteriorly. The remainder of the surface is smooth if located on or near to the lateral line, but otherwise bears a series of posteriorly directed chevrons. The scales near to the post-temporals have a denticulated posterior edge. Only the proximal portion of the caudal lobe is known. The dorsal mid-line bears a series of caudal fulcra. The area preceding the origin of the hypochordal lobe shows fragments of a number of basal fulcra. A series of two or more basal fulcra precedes the insertion of the dorsal fin, and three basal fulcra precede the anal fin.

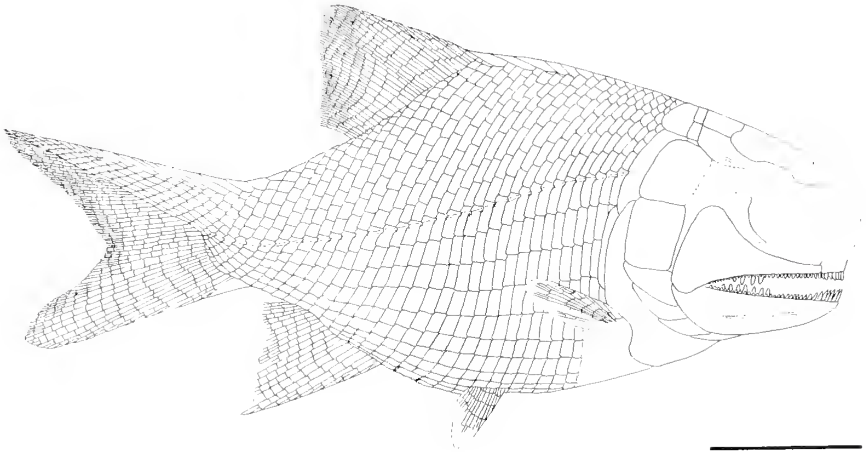
## Infraclass ACTINOPTERI

### Genus FREDERICHTHYS gen. nov.

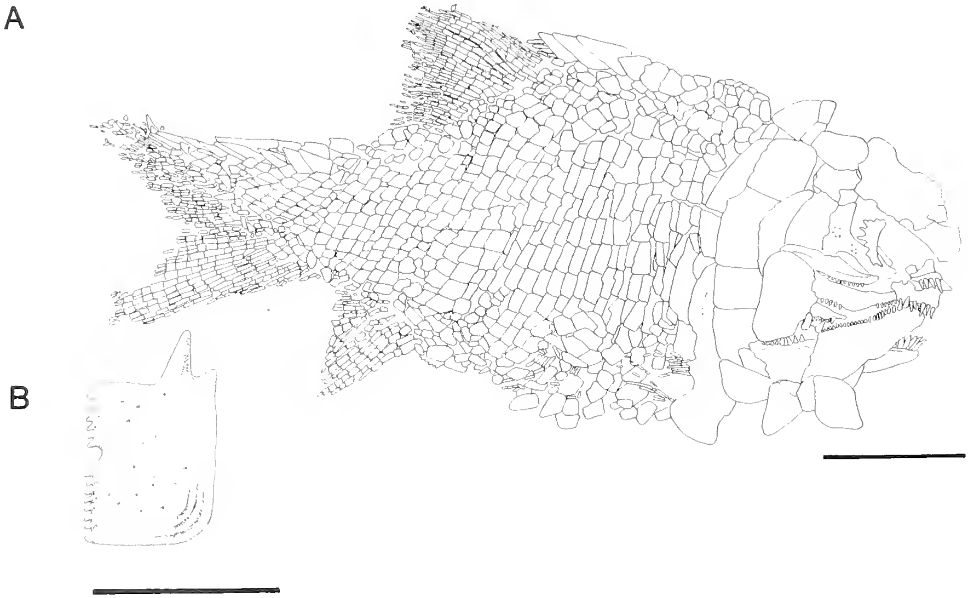
*Type species. Frederichthys musadentatus* sp. nov.

*Derivation of name.* After the nickname 'Fred fish' (+'ichthys', Greek, a fish) applied to the single known specimen of this genus whilst it was undergoing preparation and reconstruction.

*Diagnosis.* As that of the species.



TEXT-FIG. 8. *Frederichthys musadentatus* gen. et sp. nov., restoration. Scale bar = 10 mm.



TEXT-FIG. 9. *Frederichthys musadentatus* gen. et sp. nov. A, composite line drawing of holotype, GLAHM V8286*a*–*b*. Scale bar = 10 mm. B, anterior flank lateral line scale. Scale bar = 2 mm.

### *Frederichthys musadentatus*. sp. nov.

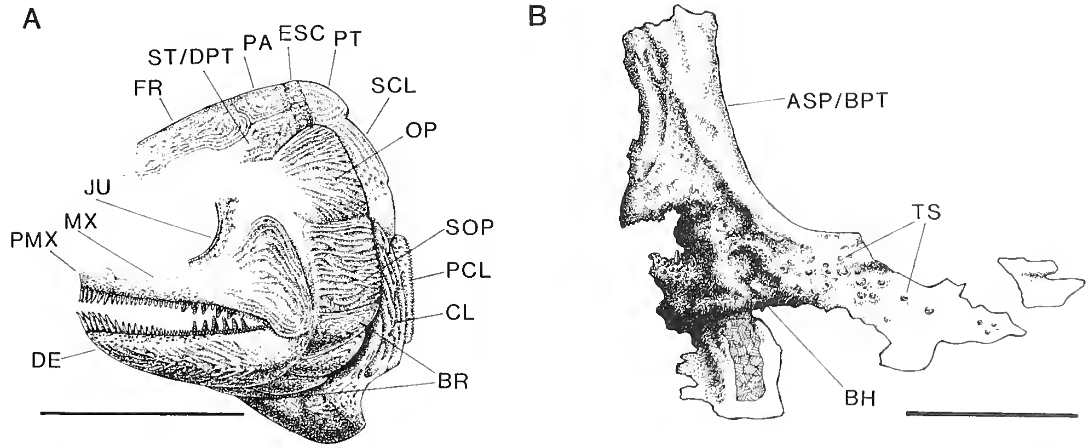
Plate 1, fig. 3; Text-figs 8–10

*Derivation of name*. New Latin *musa*, derived from the Arabic *muze* meaning banana or plantain, and late Latin *dentatus* meaning toothed, alluding to the shape of the anteriormost teeth.

*Holotype*. GLAHM V8286*a–b*, the only known specimen.

*Horizon and locality*. Not identified *in situ*, but probably from the Shrimp member, Manse Burn Formation, Pendleian (Namurian) $E_1$ Zone, Lower Carboniferous, Bearsden, Glasgow, Scotland.

*Diagnosis*. Maxilla with rounded triangular posterior expansion; mandible deep posteriorly; moderately enlarged premaxillae; mandible and palate thickly ossified; large conical teeth present on palate and medial surface of lower jaw; marginal dentition consisting of small conical teeth increasing in size and externally oriented curvature towards anterior of gape; jaw suspension near-vertical; parasphenoid well ossified with robust lateral processes; frontals with rounded, expanded anterolateral and posterolateral corners; opercular almost equal in size to subopercular; branchiostegal series reduced to four large plates; postcleithrum present; dorsal fin insertion longer than anal fin insertion; no fringing fulcra; ganoine scales with anterodorsal process, arranged in almost thirty three near-vertical sigmoid rows; body gibbose with deep scales in flank region; six or more fulcral scales preceding dorsal fin; one fulcral scale preceding caudal fin; pair of denticulated anal scales preceding anal fin; basal fulcra on dorsal margin of tail.



TEXT-FIG. 10. *Frederichthys musadentatus* gen. et sp. nov. A, restoration of skull and pectoral girdle, showing dermal ornament. Scale bar = 10 mm. B, GLAHM V8286*b*, incomplete parasphenoid (cross-hatch indicates adhering matrix). Scale bar = 2 mm. Abbreviations: see Text-figure 2.

*Discussion*. This unusual, gibbose (moderately deep-bodied) fish, like most Bearsden actinopterygians, has little preserved of its internal structure. The snout, circumorbital, cheek, and temporal regions of the dermal skull are also missing.

*Description*. The total length of *Frederichthys* is 57 mm. The length of the head accounts for 14 mm (measured from the anterior of the gape to the rear of the opercular series), and the maximum depth of the body is 23 mm.

*Skull and lower jaw*. The dermal ornament of the skull, lower jaw, and pectoral girdle is illustrated in Text-figure 10A. The maxilla has a large, triangular postorbital region, indicating that the jaw suspension was near-vertical. The marginal dentition increases in size anteriorly, mirroring the mandibular tooth distribution; the trend of increased tooth size passes forwards to the premaxillae. The insertion of the larger, tusk-like teeth is uncertain: they may have been born on the dermopalatines or a mesial ridge on the maxilla. An incompletely preserved posterior infraorbital has a ragged posterior edge, and appears to have been large and crescent-shaped. Four anteroposteriorly narrow, rectangular extrascapulars overlap the anterior margins of the post-temporals. Each of the subrectangular parietals has a notched anterolateral corner; neither appears to have a pit line. An incomplete, broad dermopterotic (DPT, Text-fig. 10A), carries the otic section of the infraorbital canal. The impression of a large otolith lies within the temporal region; the diameter appears to be about half the length of the restored dermopterotic. The frontals are about twice the length of the parietals; each has greatly expanded posterolateral and anterolateral corners. The anterolateral corner extends as an elongate process flanking an embayment for the derm-ethmoidal bones. Each incomplete premaxilla is rectangular, robust and ornamented with numerous small pits on the external surface; the dorsal edges are incomplete. Large curved teeth, identical to the anteriormost mandibular teeth, are borne on a mesial ridge adjacent to the ventral margin. A T-shaped parasphenoid (Text-fig. 10B) with an anteriorly expanded median ramus lies beneath the orbital region. The buccal surface bears numerous sockets for peg-like teeth. Mid-posteriorly, a circular depression may mark a closed buccohypophyseal foramen, flanked laterally by robust semicylindrical ascending or basipterygoid processes (ASP/BPT, Text-fig. 10B). These bear a complex system of grooves posteriorly. The greatly thickened palatoquadrate is preserved in cross-section above the maxilla, bearing further peg-like teeth. The lower jaw is well ossified and moderately deep. The full extent of the individual ossifications cannot be determined. The dentition is arranged into at least two series, one marginal, and the other born on a robust dorsomedial ridge. The marginal dentition consists of sharp conical teeth which increase in size anteriorly, accompanied by reorientation of the crowns of the largest to face anterolaterally. The constricted bases of the anteriormost teeth resemble closely those of *Mesolepis* Young, which were described by Rankin (*in* Traquair 1879) as 'Minié bullet-shaped'. Tusk-like teeth borne on the dorsomedial surface of the mandible lie towards the rear of the jaw. The broad subrectangular opercular is incomplete anteriorly. The dotted line on the reconstruction indicates its probable full extent. The slightly taller and narrower subopercular has a denticulated posterior edge. There are only four large plates within the branchiostegal series. The most posterodorsal of these is triangular; the central pair are of sub-parallelogram form; the anterior plate is more acutely triangular and extends to a point approximately half-way along the ventral surface of the lower jaw.

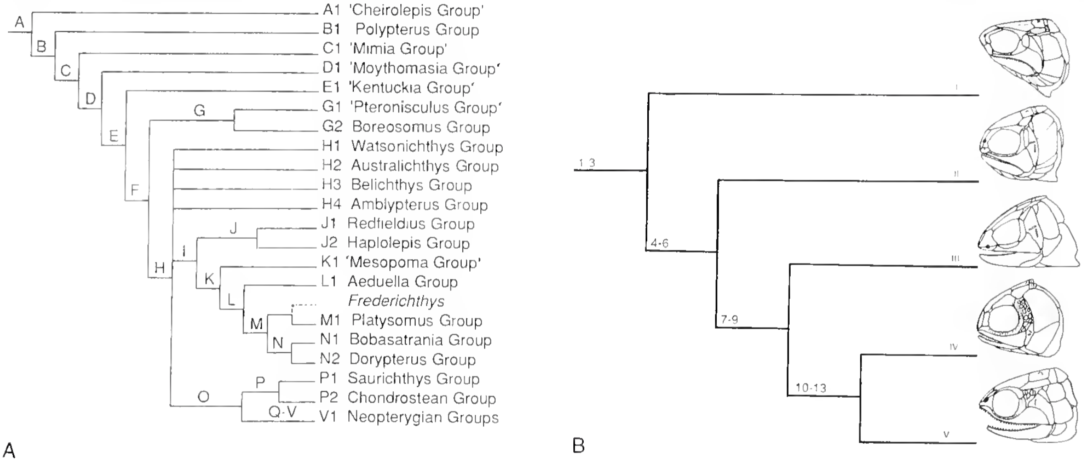
*Pectoral girdle.*The semi-elliptical post-temporal has a denticulated posterior border and a smooth anterior margin overlapped by the extrascapulars. The supracleithrum has a smooth posterior edge; the dorsal region contains the lateral line canal. The cleithrum has an exceptionally tall bipartite vertical blade, and a largely mesially curved ventral lamina. The postcleithrum is large, rectangular with a serrated posterior edge, and approximately double the size of the flank scales.

*Fins.* The leading edges of all fins consist of terminal lepidotrichia; no fringing fulcra have been found. The dorsal and anal fins are trapezoidal, broad-based, and situated in the rear half of the body (Text-fig. 8). The dorsal fin consists of thirty one or more lepidotrichia which articulate throughout their length and bifurcate at least once before the trailing edge. Neither of the fins appears to have been emarginated posteriorly. The anal fin is more acuminate than the dorsal fin; the insertion is shorter, and it is composed of fewer lepidotrichia (twenty or more). The principal lepidotrichia of the anal fin are broader and bifurcate less often than those of the dorsal. The caudal fin consists of forty or more frequently articulated lepidotrichia which bifurcate at least once distally, most commonly twice. The tail is equilobate with a moderately emarginating posterior edge. The pectoral fins appear to be small, consisting of only nine or more lepidotrichia which articulate up to four or five times, and bifurcate once, distally. The pelvic fins are situated half-way between the pectoral girdle and the anal fin. Each is moderately broad-based, consisting of ten or more frequently articulated lepidotrichia.

*Squamation.* The rhomboidal scales have a well-developed anterodorsal angle, of the type found in fusiform species. Dermal ornament consists of shallow grooves which originate from the denticulated posterior edge; three or more parallel grooves lie next to the anteroventral corner. The trunk bears about thirty three near-vertical scale rows. The number of scales per row increases in the central flank region and below the insertion of the dorsal fin. The caudal prolongation is moderately up-turned. Scales with a convex posterior edge and prominent dermal ornament lie adjacent to the rear of the skull table. Basal fulcra lie on the dorsal mid-line of the tail, and the hypochordal lobe is preceded by a single, elongate ventral caudal scale. The dorsal fin is preceded by a series of six or more fulcra. A pair of elongated, rhomboidal anal scales precede the insertion of the anal fin. These have a denticulated posterior edge, and lie across the fourteenth and fifteenth scale rows.

## DISCUSSION

Members of *Mesopoma* are generally described as palaeoniscids, although it is now widely agreed that these constitute a paraphyletic group of mostly Palaeozoic actinopterygians (Cladistia + Actinopteri). The revised classification was established principally by Patterson (1982) and Gardiner (1984), and elaborated upon by Lauder and Liem (1983), Long (1988), and Gardiner and Schaeffer (1989). Gardiner (1984), in particular, demonstrated that the majority of the palaeoniscids should be treated as 'plesion' (Patterson and Rosen 1977) members of the neopterygian stem-group, and that *Mesopoma* lay within this assemblage. However, Gardiner and Schaeffer (1989) have reassessed this pattern of relationships (their cladogram is depicted in Text-fig. 11A). In contrast to Gardiner (1984), the extant Chondrostei were found to share more characters with the Neopterygii (*sensu* Patterson 1982) than with most palaeoniscids. Consequently, genera such as *Mesopoma* are now considered to be 'lower', taxonomically, and, together with other taxa, form an unresolved polytomy within the stem-group of the Actinopteri (Chondrostei + Neopterygii).



TEXT-FIG. 11. A, cladogram of major groups of early actinopterygians showing taxonomic positions of species considered in this paper (cladogram adapted from Gardiner and Schaeffer 1989, fig. 12; for definitions of all terminal groups and complete character list see this reference). Selected characters of lettered nodes discussed in text; taxa within quotation marks may be paraphyletic. B, alternative cladogram of selected taxa rooted at node I in Gardiner and Schaeffer's cladogram. Characters 1–13 discussed in text. Taxa illustrated: i, *Mesopoma carricki* (exemplifying the genus *Mesopoma*); ii, *Canobius ramsayi*, after Moy-Thomas and Bradley Dyne 1938 (exemplifying the genus *Canobius*); iii, *Protohaplolepis scoticus*, after Lowney 1983 (exemplifying the family Haplolepidae); iv, *Aeduella blainvillei* after Heyler 1969 (exemplifying the family Aeduellidae); v, *Phlyctaenichthys pectinatus* after Hutchinson 1973 (exemplifying the infraorder Redfieldiformes).

In agreement with Gardiner and Schaeffer (1989), *Mesopoma* shares the following characters (as listed in the generic diagnosis) with the Actinopterygii: ganoine scales; scales with anterodorsal process; dentary includes mandibular sensory canal; dermohyal; basal fulcra on dorsal margin of tail; peg and socket scale articulation; postcleithrum.

This paper is not intended to be an exhaustive examination of Gardiner and Schaeffer's cladistic analysis. Therefore not all of their character list will be discussed. However, this revision has identified certain unsatisfactory choices or positions of characters. The following basal actinopterygian characters are taken from Node A, table 1 and figure 12, of Gardiner and Schaeffer's paper (Text-fig. 11A):

1. Otoliths in part composed of vaterite.
6. Dermosphenotic T-shaped, in contact with nasal bone.
18. Tail with hinge line (caudal inversion).

The first autapomorphy (1) of Gardiner and Schaeffer's list, that actinopterygian otoliths are *in part* (my italics) composed of vaterite, is a subtle restatement of character 10 of Gardiner's (1984) earlier list: otoliths formed of vaterite. This statement derives from Carlstrom (1963) via Lovtrup (1977) and Patterson (1982).

Almost all gnathostome otoliths consist of calcium carbonate, which occurs in three crystalline forms: calcite, aragonite, and vaterite (the least stable); the vast majority consist of aragonite (Carlstrom 1963). Otoliths occur as statoliths (large 'ear stones') or statoconia (minute 'ear dust'). The otic labyrinth of *Polypterus* contains both aragonite statoliths and vaterite statoconia. *Acipenser guldenstadti* and *A. sturio*, the Russian and Atlantic sturgeons, have vaterite statoliths and statoconia. *Lepisosteus* and *Amia* have aragonite statoliths and vaterite statoconia, and Carlstrom considered teleost otoliths to consist solely of aragonite statoliths. The distribution of vaterite within the Actinopterygii appeared to be restricted to the statoconia of non-teleosteans, and the statoliths of certain chondrosteans. However, Gauldie *et al.* (1986*b*) recorded the presence of statoconia in four neoteleostean taxa. Furthermore, Gauldie (1986) described experimentally induced vateritic statoliths in the chinook salmon (*Onchorhynchus tshawytscha*) and noted occurrences in other taxa (e.g. the dab, *Limanda limanda*), including the replacement of calcite by vaterite in certain diseases of the human ear. The erratic distribution of vateritic otoliths indicates that Gardiner and Schaeffer's character (1) is insufficiently precise. Maisey (1987) suggested an alternative characterization of the Actinopterygii: the presence of 'smaller statoconia of vaterite (absent in teleosts); separate lagenar and saccular otoliths', the first part of which appears tenable.

The second part of Maisey's characterization of the Actinopterygii (separate lagenar and saccular otoliths) is inconsistent with the presence of only a single, large statolith in each otic capsule of *Mesopoma? smithsoni*. Single otoliths are found in several other Bearsden actinopterygians (Coates 1988), *Mimia toombsi* (Gardiner 1984), and *Rhadinichthys canobiensis* (Moy-Thomas and Bradley Dyne 1938, pl. I fig. A, showing natural cast of statolith), whereas extant actinopyterygian otic capsules each contain three statoliths. Talimaa (*in* Nolf 1985) interpreted the oldest known otoliths, from the Lower and Middle Devonian, as actinopterygian because they, too, consist of three distinct types: saccular, lagenar, and utricular, resembling the sagitta, asteriscus, and lapillus of teleosts. Schultze (1988, 1990) accepted Talima's interpretation, although these otoliths are phosphatic and isolated from skeletal remains. Phosphatic otoliths are extremely rare within the gnathostomes (Maisey 1987 cited apatite statoconia as an autapomorphy of cyclostomes). Although diagenetic processes may alter fossil otolithic composition (Tucker 1990), 'metasomatic mineralisation' (Maisey 1988) from calcite to apatite is extraordinarily unlikely (Schultze 1990). Furthermore, although both Devonian and teleost statoliths have central sulci, statoliths preserved within early actinopterygians have a rim-located sulcus, resembling closely the lapillus and (single) saccular statolith of the dipnoan *Neoceratodus forsteri* (Gauldie *et al.* 1986*a*). The sacculus of *Latimeria* (Millot and Anthony 1965) similarly contains only a single statolith with an apparently rim-located sulcus. These single saccular statoliths should not necessarily be homologized with the sagitta. Extant non-teleostean actinopterygian sacculae contain both the sagitta and asteriscus, of which the asteriscus is usually the larger (Nolf 1985 misinterpreted the small cladistian sagitta for the lapillus (Coates 1988)).

In conclusion, Talimaa's interpretation of the Devonian otoliths is rejected. They are unlike actinopterygian statoliths in chemical composition; they differ morphologically from stem-group actinopterygian statoliths; they are not associated with actinopterygian skeletal remains. Out-group comparison suggests that the actinopterygian plesiomorphic condition is to have a single saccular calcitic statolith with a rim-located sulcus. This suggests that paired statoliths (sagitta + asteriscus) within the sacculus have been derived independently within the Cladistia and the Actinopteri. Because of this, Maisey's supplementary actinopterygian apomorphy (separate lagenar and saccular otoliths) is rejected. Maisey also failed to distinguish between the otic recesses and their contents, and to recognize that in extant actinopterygians, a distinct lagena is present only within the Teleostei. Schultze's (1990) hypothesis that three pairs of otoliths are a basic feature of teleostomes (uniting acanthodians with osteichthyans) is also rejected. Available data suggests that the basic osteichthyan saccular recess contains a single statolith.

The hypothesis that dermosphenotic:nasal contact (6) is primitive for actinopterygians is accepted, but not the linkage of this pattern to the 'T' or tau form of the bone. This refinement of an otherwise plesiomorphic character loses potential taxonomic value if applied loosely to a variety of sub-triangular forms of dermosphenotic, as found in most stem-group actinopterygians (see Gardiner and Schaeffer 1989, fig. 2). In contrast, the dermosphenotic of *Mesopoma*, where known, has three distinct rami (Text-fig. 2A). This form of dermosphenotic is considered to be more precisely T-shaped; it aids the characterization of the genus.

A caudal scale row inversion is accepted as plesiomorphic for actinopterygians (18), but not the concomitant appearance of a distinct hinge-line between trunk and tail squamation. *Cheirolepis* (Pearson and Westoll 1979), *Howqualepis* and other early actinopterygians described by Long (1988), and many of the Bearsden (Coates 1988) and Bear Gulch (Lowney 1980) taxa, including *Mesopoma*, show no distinct hinge-line.

At node B, *Mesopoma* shares the presence of a postcleithrum.

At node C, *Mesopoma* shares the presence of fringing fulcra on all fins.

At node D, *Mesopoma* shares the presence of supra-angular on the mandible.

At node E, *Mesopoma* shares the presence of suborbital bones.

At node F, *Mesopoma* shares the presence of a ceratohyal bar composed of two cartilages or ossifications (Lowney 1980; Text-fig. 11A).

At node G, *Mesopoma* shares the presence of a robust opercular process on the hyomandibula (Lowney 1980).

The presence of an opercular process was not anticipated by Gardiner and Schaeffer: node G defines the small monophyletic radiation of pteronisculids and boreosomids, fishes which share no other clear synapomorphies with *Mesopoma*. Opercular processes are probably more widely distributed amongst early actinopterygians than is suggested by Gardiner and Schaeffer. For a more detailed discussion of the hyoid arch in early actinopterygians, see Kazantseva 1974; Patterson 1982 and Veran 1988.

At node H, *Mesopoma* shares the presence of a dermopterotic.

At node I, *Mesopoma* shares a reduction in the number of branchiostegal rays below the primitive 12 or 13 (except '*M. becketense*' (attrib. Lowney, Text-fig. 12I)), and a dermopterotic which never normally overlaps more than one third of the dermosphenotic.

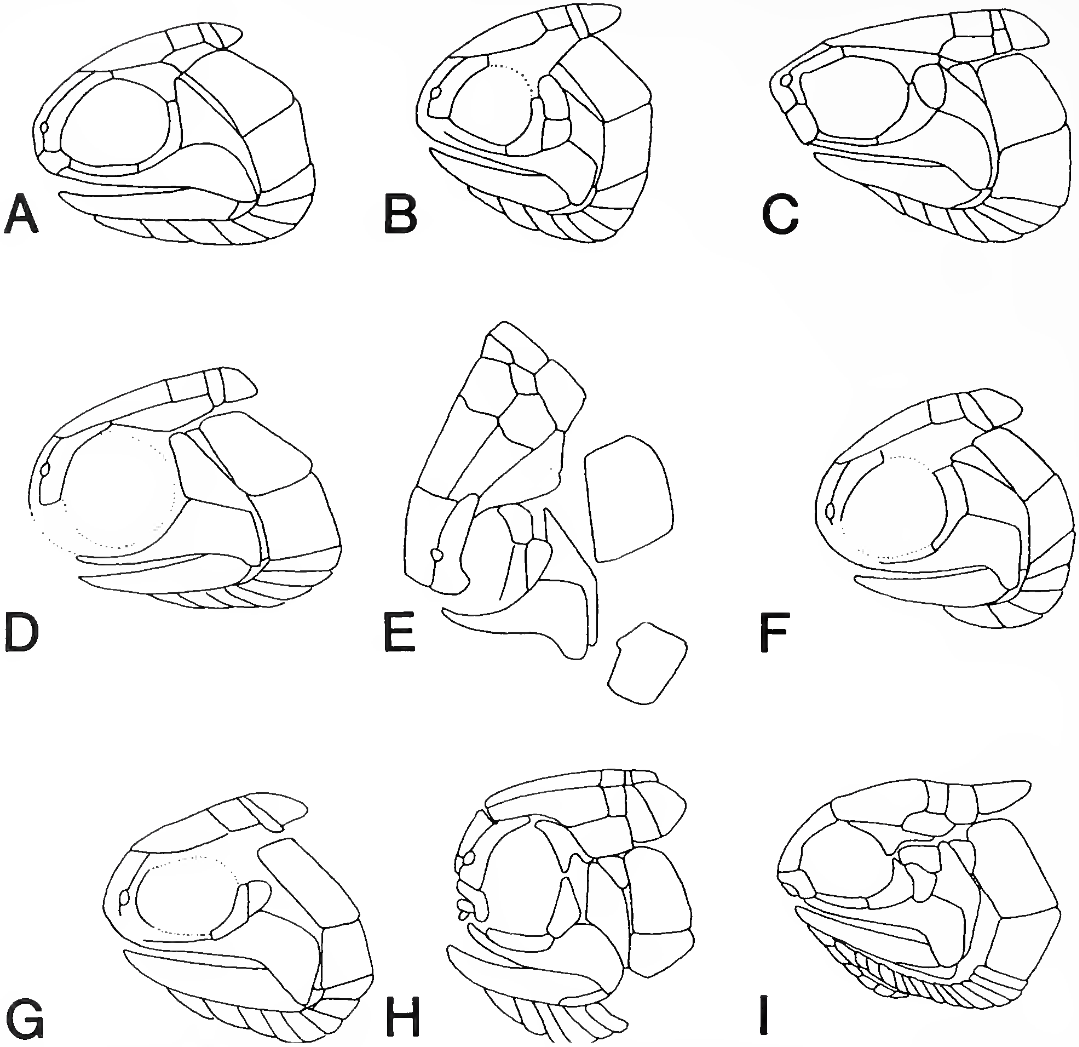
Gardiner and Schaeffer's cladistic analysis therefore places *Mesopoma* within the polychotomous radiation of stem-group actinopterans.

At node J, no characters are shared.

The absence of shared characters at node J corroborates Lowney's (1983), and Gardiner and Schaeffer's (1989) independent refutations of Westoll's (1944) influential evolutionary sequence (e.g. Moy-Thomas and Miles 1971), which led from *Mesopoma*, via *Canobius* to a hypothetical ancestor of the haplolepids. However, this transformational series recurs within an alternative phylogeny (Text-fig. 11B) discussed below.

At node K, *Mesopoma* should display three characters which unite it with its own and four further groups of Carboniferous to Permian actinopteran genera: the presence of a more vertical suspensorium; a reduced preopercular; the absence of suborbital bones in the cheek region.

Gardiner and Schaeffer's *Mesopoma*-group includes *Mesopoma*, *Canobius* Traquair, 1881 *sensu* Moy-Thomas and Bradley Dyne 1938, and *Styracopterus* Traquair, 1895 *sensu* Gardiner 1985. The description of the type species, *Mesopoma pulchellum*, is central to the diagnosis of the entire group and its interrelationships within the actinopteran stem-group radiation. Gardiner and Schaeffer's restoration of the dermal skull of *M. pulchellum* is reproduced as Text-figure 12A. However, the proportions and complement of dermal skull bones differ from those of Moy-Thomas and Bradley Dyne's (1938) reconstruction (Text-fig. 12B). Most obviously, the suborbital bones depicted by Moy-Thomas and Bradley Dyne have been removed. The figure legend of Gardiner and Schaeffer's illustration (1989, p. 174, fig. 18) states that their new reconstruction of *M. pulchellum* is based



TEXT-FIG. 12. *Mesopoma* species, skulls in lateral view. A, *M. pulchellum* (after Gardiner and Schaeffer 1989). B, *M. pulchellum* (after Moy-Thomas and Bradley Dyne 1938). C, *M. carricki* sp. nov. D, *M. macrocephalum* (after Moy-Thomas 1938). E, *M. ardrossense* (after Moy-Thomas 1938). F, *M. politum* (after Moy-Thomas and Bradley Dyne 1938). G, *M. crassum* (after Moy-Thomas and Bradley Dyne 1938). H, *M. macrocephalum* (after Lowney 1980). I, '*M. becketense*' (after Lowney 1980).

upon Moy-Thomas and Bradley Dyne's (1938) illustration, and specimen BM(NH) P14310. Significantly, no reference is made to the type specimen (m611d in the Geological Survey, Murchison House, Edinburgh).

The new reconstruction of *M. pulchellum* resembles closely *M. macrocephalum* as restored by Moy-Thomas (1938) (Text-fig. 12D), rather than Lowney (1980) (Text-fig. 12H). Both reconstructions of *M. macrocephalum* showed that it lacked suborbitals, a character which it formerly shared uniquely with *M. politum* (Text-fig. 12F) within this genus. Therefore, out of seven species of *Mesopoma* in which the cheek region is known, four must now be excluded, because they possess suborbitals. The misidentification of specimen BM(NH) P14310 (the source of Gardiner and Schaeffer's redescription of *M. pulchellum*) is probably the cause of this unexpected taxonomic revision. In fact, this specimen is catalogued and labelled clearly as *M. macrocephalum*. The specimen is in good condition, and is sufficiently similar to the type, NMS 1901-227-2, to leave this diagnosis in no doubt.

If the new reconstruction of *M. pulchellum* is based upon a misidentified specimen, then the specific diagnosis can revert to Moy-Thomas and Bradley Dyne's (1938), and the generic diagnosis may be revised to the form proposed earlier in this paper. The presence or absence of suborbital bones can be rejected as a diagnostic character at the generic level. Jain (1985) demonstrated surprisingly variable dermal bone patterns in the cheek region of the extant halecomorph *Amia calva*. In this single species the number of canal-bearing infraorbito-suborbitals varies from one to three or more between and even within (bilaterally asymmetric) individuals. This suggests that the arrangement of anamestic suborbitals in a fossil genus which displays a variety of cheek patterns may be unreliable as a taxonomic indicator.

The removal of the 'suborbital' synapomorphy from node K of Gardiner and Schaeffer's cladogram (Text-fig. 11A) does not affect their characterization of the *Mesopoma* group. Autapomorphies of mesopomids at node K1 are listed as:

i, a near-vertical suspensorium;
ii, a reduced preoperculum;
iii, a postorbitally reduced maxilla;
iv, a subopercular subequal to or larger than the opercular;
v, a T-shaped dermosphenotic.

Characters i–iii of this list are discussed below, because they are effectively identical to the remaining synapomorphies at node K. Character iv is probably valueless, and character v is recycled from node A (see above). The *Mesopoma* group therefore appears to be paraphyletic, and if retained in Gardiner and Schaeffer's scheme, should be placed within quotation marks (cf. '*Cheirolepis* Group', Text-fig. 11A).

If the 'absence of suborbitals' character is removed, then the aeduellids, platysomoids, bobasatraniids, and dorypterids (Text-fig. 11A) are united solely on the basis of having a 'more or less' (Gardiner and Schaeffer 1989) vertical suspensorium, and a reduced, sickle-shaped preopercular. These two closely linked synapomorphies provide little basis for the construction of a major phylogenetic hypothesis incorporating seventeen morphologically diverse genera. An alternative hypothesis of the interrelationships of the *Mesopoma*, *Aeduella*, *Haplolepis*, and *Redfieldius* group constituents (Text-fig. 11B), also rooted at node I of Gardiner and Schaeffer's cladogram, may be constructed using the following characters:

1, reduced branchiostegal series;
2, dermopterotic normally never overlaps more than one-third of dermosphenotic;
3, jaw articulation sited anteriorly relative to the parieto-extrascapular suture;
4, vertical jaw suspension;
5, reduced rostral projection ( = terminal gape);
6, triangular preopercular bearing one or more pit-lines;
7, two or fewer branchiostegals;
8, uninterrupted naso-rostral suture ( = loss of anterior nares: Schaeffer 1984);
9, dentition reduced or absent from premaxillae;
10, premaxillae excluded from gape;
11, supraorbital canal enters dermopterotic;
12, numerous suborbitals at head of preopercular;
13, ramose infraorbital canal.

The data upon which these characters are based were obtained from recent descriptions and reviews which provided alternatives to Gardiner and Schaeffer's reinterpretations of many of the selected taxa. In Moy-Thomas and Bradley Dyne (1938), *Canobius ramsayi* (Text-fig. 11Bii) possesses preopercular pit-lines and suborbitals. The sensory canal system penetrates the base of the median derm-ethmoidal shield, which corroborates the interpretation of this bone (and that of *Mesopoma*, see description) as a rostral rather than post-rostral. A vertical suspensorium and the lack of a rostrum unite *Canobius* with numerous other genera, illustrating the paraphyletic nature of the *Mesopoma* group. Haplolepids are exemplified by the earliest and least-derived genus known, *Protohaplolepis* (Lowney 1983) (Text-fig. 11Biii). Heyler's (1969) description of *Aeduella* (Text-fig. 11Biv), exemplifying the Aeduellidae, lacks an anterior nostril, the supraorbital canal enters the dermopterotic rather than the dermosphenotic, numerous suborbitals lie above a short triangular, pit-lined, preopercular, and the infraorbital canal bears an unusually profuse array of sub-branches. Many of these characters are shared with *Phlyctaenichthys* (Hutchinson 1973) (Text-fig. 11Bv), an early brookvaliid, exemplifying the Redfieldiformes (*sensu* Schaeffer 1984). Although unknown in this genus, other brookvaliids have a pit-lined preopercular. The haplolepid: aeduellid: redfieldiform relationship is more robust than the haplolepid: redfieldiform sister-grouping proposed by Gardiner and Schaeffer (node J, Text-fig. 11A, characterized by the presence of a single ventral nostril, a single branchiostegal ray, and an enlarged postcleithrum).

In the alternative cladogram (Text-fig. 11B), *Mesopoma* and *Canobius* are plesion taxa, contributing to the stem-group of three major early actinopteran radiations: the haplolepids, aeduellids, and redfieldiforms. This arrangement provides an alternative to Blot's (1966) and Heyler's (1969) unsatisfactory proposals of *Paramblypterus* as a sister group to the redfieldiforms (a problem most comprehensively discussed in Schaeffer 1984). Morphological trends include increased suspensorial angle, fragmentation of the dermal cheek-cover, exclusion of the premaxillae from the gape, and reduction of the gular-branchiostegal apparatus. The sequence of cladogenic events is consistent with the earliest known occurrences of each taxon: *Mesopoma* and *Canobius* from the Viséan (Moy-Thomas and Bradley Dyne 1938); *Protohaplolepis* from the Namurian (Lowney 1983); aeduellids, cf. *Bourbonella*, from the Upper Pennsylvanian (Gottfried 1987); redfieldiids from the Upper Permian (Hutchinson 1973).

A detailed discussion of the incorporation of deep-bodied early actinopterans into the revised cladogram is beyond the scope of this paper. However, characters 1–6 are present in the amphicentrids, and characters 9–10 suggest a separate origin for *Platysomus* and closely related taxa. This is consistent with subsequent discussion of the potentially diphyletic origin of the Platysomoidei (see below).

The geographical and stratigraphical distribution of the genus *Mesopoma* is relatively restricted. *M. pulchellum*, *M. politum*, and *M. crassum* are all known from the Viséan Calciferous Sandstone Measures of Glencartholm, Dumfriesshire. *M. macrocephalum* originates from the Pumpherstone Oil Shales of West Lothian, and *M. ardrossense* from the *Crangopsis* bed at Ardross, Fifeshire. Both the latter localities also lie within the Viséan Calciferous Sandstone Measures. The remaining four species all date from the Basal Namurian. *M. carricki*, *M.? smithsoni*, and *M. pancheni* are known from Bearsden, Glasgow, whilst '*M. becketense*' (the only non-Scottish species) is known from Bear Gulch, Montana, USA.

In contrast to the new species of *Mesopoma*, *Frederichthys* bears only a limited resemblance to any other group of early actinopterans, including those that are either gibbose or rhombic-bodied. Its taxonomic position can be established only in so far as it shares the following synapomorphies with node A of Gardiner and Schaeffer's (1989) cladogram (Text-fig. 11A): two pairs of extrascapulars; dentary with enclosed sensory canal; single dorsal fin; basal fulcra bordering upper lobe of caudal fin.

At node B, *Frederichthys* shares the presence of a postcleithrum.

At node C, *Frederichthys* lacks the presence of fringing fulcra on the leading rays of all fins: the only anatomical feature which can be compared usefully with Gardiner and Schaeffer's scheme.

*Frederichthys* displays no clear synapomorphies with nodes D to G.

At node H, *Frederichthys* is considered to share the presence of a dermopterotic. This provides the most parsimonious interpretation of the incomplete temporal bone in the skull table (ST/DPT, Text-fig. 10A) with regard to subsequent synapomorphies.

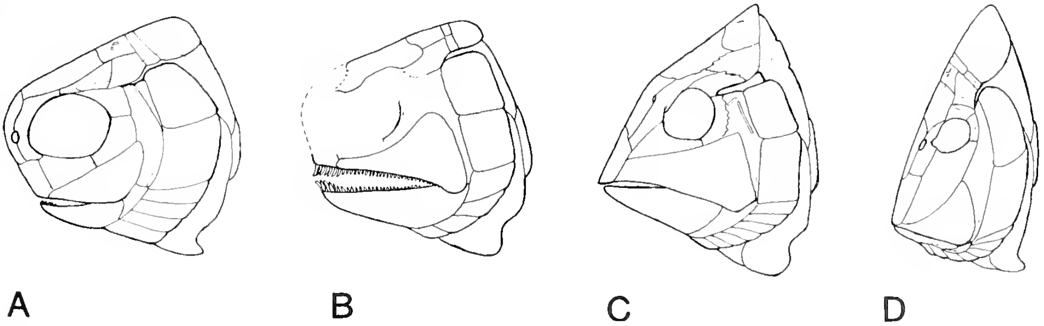
At node I, *Frederichthys* shares a reduced number of branchiostegal rays.

At node K, *Frederichthys* shares a 'more or less' vertical suspensorium.

At node L, *Frederichthys* probably shares a blunt and rounded snout. This character is implied solely by the distribution of fossil material.

At node M, *Frederichthys* shares (vaguely) peg-like teeth; a thickened palate rather than crushing toothplates; a deep, laterally compressed body.

Node M lies at the base of the radiation of deep-bodied early actinopterans, which have been subdivided by Gardiner and Schaeffer into three groups: platysomids, bobasatraniids, and dorypterids. This effectively reconstitutes the sub-order Platysomoidei (Romer 1966; Moy-Thomas and Miles 1971; Carroll 1988). The platysomoids have a long historical tradition which dates back to Young's (1866) Lepidopleuridae. Similarly, the monophyly of this group has been in doubt for over half a century, because the characters used to assign actinopterans to the Platysomoidei are essentially modifications caused by differential growth; therefore common to all actinopterans with a deep body (Moy-Thomas 1939). Gardiner and Schaeffer's platysomid group contains members of the two families formerly included in the Platysomoidei: the Platysomidae and the Amphicentridae. The amphicentrids (synonymous with the chirodontids) consist of forms with a crushing dentition of broad toothplates, and the platysomids of forms with more conventional teeth. The most extremely modified, and most completely described members of each family are the genera *Amphicentrum* Young, 1866 (Traquair 1875; = *Cheirodus* Traquair, 1879; Bradley Dyne 1939; Coates 1988) (Text-fig. 13C) and *Platysomus* Agassiz, 1833 (Traquair 1879; Moy-Thomas and Bradley Dyne 1938; Campbell and Phuoc 1983) (Text-fig. 13D). Gardiner and Schaeffer diagnosed their *Platysomus* group on the basis of the maxilla approaching a rounded, right-angled triangle; the premaxillo-antorbital enlarged and elongated dorsally; the mandible deep posteriorly, tapering anteriorly. *Frederichthys*, despite the incompleteness of the material, exhibits the first and third of these criteria, and the dorsal extent of the premaxilla is unknown.



TEXT-FIG. 13. Platysomid skulls in lateral view. A, *Paramesolepis tuberculata* (after Moy-Thomas and Bradley Dyne 1938). B, *Frederichthys musadentatus* gen. et sp. nov. C, *Amphicentrum crassum* (after Coates 1988). D, *Platysomus superbus* (after Moy-Thomas and Bradley Dyne 1938).

Clustered around *Amphicentrum* and *Platysomus* are a number of less specialized and more poorly known forms. From amongst these, the most likely candidate for a sister-group relationship with *Frederichthys* is *Paramesolepis* Moy-Thomas and Bradley Dyne 1938 (Text-fig. 13A). *Paramesolepis* is the least-derived member of the *Platysomus* group. Like *Frederichthys*, its most striking features (the pattern of the dermal skull, the elongated dorsal and anal fins) are products of differential growth associated with its gibbose shape. They are insufficient to commit it to a closer relationship with either of the amphicentrids or platysomids.

*Frederichthys* and *Paramesolepis* both have a branchiostegal series which consists of four broad plates located at the rear of the mandible. The marginal dentition of *Paramesolepis* is restricted to the anterior end of the jaws, and consists of a short series of small sharp pointed teeth. The marginal dentition of *Frederichthys* is reduced posteriorly, and anteriorly consists of outwardly oriented, curved, sharp pointed teeth. Differentiation along the tooth row is extremely unusual in early actinopterans. It is therefore suggested that these two genera display different expressions of the same character. Although it was noted in the systematic description that the teeth of *Frederichthys* individually resemble those of *Mesolepis*, there is no further evidence to indicate a close relationship between these genera. *Mesolepis* (Traquair, 1907) appears to resemble *Amphicentrum* or *Eurynotus* more closely than *Frederichthys*.

The platysomid, bobasatraniid, and dorypterid groups (Text-fig. 11A) require a major revision. Gardiner and Schaeffer's analysis neglected Campbell and Phuoc's (1983) paper on *Ebenaqua* and *Platysomus gibbosus*, which suggests a close relationship between *Platysomus* and *Bobasatrania* White, 1932. Furthermore, the Bearsden site has yielded a considerable quantity of new anatomical data concerning *Amphicentrum* (Text-fig. 13C, after Coates 1988), which is currently being prepared for publication.

Finally, the unusual morphology of *Frederichthys* requires a short note on its probable function in life. The gross functional morphology of extant actinopterygians of various body forms has been described by Keast and Webb (1966). In summary, their comments on the swimming of gibbose fish are as follows: the large lateral area prevents rolling and thereby provides considerable stability; pitch is controlled by the pectoral and pelvic fins, and asymmetrical vertical forces generated by these fins can tilt the body to any required angle; enlarged dorsal and anal fins are necessary to control yaw when swimming forwards, which is often assisted by rowing movements by the pectoral fins.

The unusual dentition and reinforced palate indicate that *Frederichthys* was a specialized feeder. It is difficult to propose an extant analogue because of the radical changes that have occurred to the actinopterygian feeding mechanism. However, it is possible that it was similar in habit to the sheephead wrasse *Pimelometopon*. These gibbose fish also have robust jaws and anterior teeth which point forwards and outwards (although these are chisel-shaped). The sheepheads feed in kelp beds in rocky areas, and prey on slow-moving benthic echinoderms, molluscs, and crustaceans (Wheeler 1985). The fusiform *M.? smithsoni*, described earlier, also has a reinforced palate with a specialized dentition, suited for processing physically resilient prey. It is probably significant that two further members of the Bearsden fauna, the rhombic-bodied platysomid *Amphicentrum*, and the chimaeroid chondrichthyan *Deltoptychius* (Wood 1982; Dick *et al.* 1986) bear robust tooth-plates. However, we can only speculate, at present, upon the palaeoecological relationships between the specialized vertebrate predators and the diverse invertebrates (Wood 1982) of the Bearsden fauna.

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# A NEW ASTEROID GENUS FROM THE JURASSIC OF ENGLAND AND ITS FUNCTIONAL SIGNIFICANCE

*by* DANIEL B. BLAKE

ABSTRACT. The new asteroid (Echinodermata) genus *Brachisolaster* is based on *Solaster moretonis* Forbes (Solasteridae), described from Jurassic rocks of Gloucestershire. *Brachisolaster* (Order Velatida) demonstrates that characteristic solasteroid features were defined by the Bathonian (Middle Jurassic); other fossils belonging to different orders further demonstrate the presence of close relatives of the living fauna by this time. Arms are more numerous in *Brachisolaster moretonis* than in living solasteroids; the appearance is suggestive of that of living *Heliaster* (Asteriidae). *Heliaster* feeds largely on molluscs and barnacles, whereas the diet of living solasteroids stresses more active echinoderms. Solasteroids use their fewer but larger arms to subdue and manipulate prey. *Brachisolaster* is suggested to have had feeding habits more like those of *Heliaster* than like those of extant solasterids. The interpretation complements an earlier suggestion that Jurassic asteriid behaviour might have involved more active predation. A solasteroid with fewer arms is known from the Jurassic, therefore to the extent that the suggested functional significance of arm number is accurate, disappearance of species with supernumerary arms reflects a narrowing of the active solasteroid adaptive zone rather than a functional shift. Together, the fossil asteriids and solasterids suggest some narrowing of adaptive zones since the Jurassic.

THE oldest relatively complete asteroids assignable to living families are from the Hettangian (lowest Jurassic) of Switzerland and southern Germany (Blake 1984, 1990); they represent two taxonomically widely separated orders, the Forcipulatida and Notomyotida. Isolated Triassic ossicles described by Zardini (1973) also have been included within living families (Gale 1987), although affinities are difficult to verify from isolated ossicles. Representatives of three additional orders, the Paxillosida, Valvatida and Velatida (including the Solasteridae) have been recognized from somewhat younger strata (e.g. Hess 1972), and some Jurassic species are assignable to extant genera (Blake 1986). Only two surviving orders (*sensu* Blake 1987), the Spinulosida and the deep-water Brisingida, have not been documented from the Jurassic. Jurassic solasteroids have long been recognized, and both Forbes (1856) and Wright (1863) provided good descriptive information on *Brachisolaster moretonis* (under the name *Solaster*); but the holotype is in need of modern illustration and added comparison. In order to further delineate the emergence of the modern asteroid fauna, this paper compares *B. moretonis* with living species.

## SYSTEMATIC PALAEONTOLOGY

### Class ASTEROIDEA de Blainville, 1830
### Order VELATIDA Perrier, 1891
### Family SOLASTERIDAE Perrier, 1884
### Genus BRACHISOLASTER gen. nov.

*Type species*. *Solaster moretonis* Forbes, 1856.

*Derivation of name*. From '*brachium*' (Latin), arm; living members of the Solasteridae have between 5 and 15 arms; the presence of approximately 33 in *Brachisolaster* is noteworthy. Retention of 'solaster' in the name reflects familial affinities and historical usage.

**[Palaeontology, Vol. 36, Part 1, 1993, pp. 147–154, 2 pls.]**

*Diagnosis.* Solasteroid with approximately 33 arms and relatively narrow adambulacral ossicles; the dorsal skeleton is reticulated and ossicles are stout; spines are large, forming clusters at arm tips. Spines have bulbous bases and long, tapering shafts.

*Remarks. Brachisolaster* can be distinguished from other solasteroids based on arm number, presence of relatively narrow adambulacrals, and clusters of spines distally on the arms. Forbes (1856) recognized arm number as the most striking difference between *B. moretonis* and living species, but he judged this difference did not justify recognition of a new genus. The living fauna is much better known now than it was in 1856, and the unique nature of arm number, and its possible functional significance, can be more clearly recognized. Recognition of a new genus therefore is now warranted.

### *Brachisolaster moretonis* (Forbes, 1856)

Plate 1, figs 1–2, 5; Plate 2, figs 1–4

1856 *Solaster moretonis* Forbes, p. 1.
1863 *Solaster moretonis* Forbes; Wright, p. 104.
1966 *Solaster? moretonis* Forbes; Spencer and Wright, p. U67.

*Material.* The holotype, BM(NH) 40421, in The Natural History Museum, London, is from Windrush Quarry situated 400 m SE of Windrush Church, about 8 km east of Northleach, Gloucestershire, UK. Included at this locality are the top of the Taynton Limestone, overlain by the Hampen Marly Formation and the basal Shipton Member of the White Limestone. The rocks belong to the *progracilis* and *subcontractus* Zones of the Middle Bathonian. Geological information was provided by Richardson (1933, section on p. 43) and Cope *et al.* (1980).

The specimen is essentially complete, with the ventral surface exposed. The dorsal surface is covered by a well-sorted pelletoidal calcarenite whereas minor amounts of mudstone remain among the unusually well-preserved ossicles of the ventral surface; some spines are also present on this surface. The individual would appear to have been quickly buried by calcarenite while on a soft, terrigenous mud, which was squeezed in among the ossicles and protected them. Most spines of the ventral surface were lost (during preparation?), although many remain near the tips of the arms and at scattered sites elsewhere, especially near the mouth angle ossicles. In addition, there is some disruption of the arm tips and of some of the main body ossicles. The proximal tips of the mouth angle ossicles have been rotated upward into the disc.

Although ossicles are very well preserved, exposure is incomplete; the lower portions of ambulacrals, adambulacrals, mouth angle ossicles, and actinal interbrachials are visible, but not their upper surfaces. Only the lower portion of some dorsal disc ossicles are exposed through the mouth frame. Few probable marginals are visible, and their orientation is disrupted; actinal interbrachials are also partly disrupted. The madreporite is not exposed, although a gap in ossicular arrangement and shape (curvature) of dorsal ossicles suggests its location. Terminals are not exposed.

*Diagnosis.* As for the genus.

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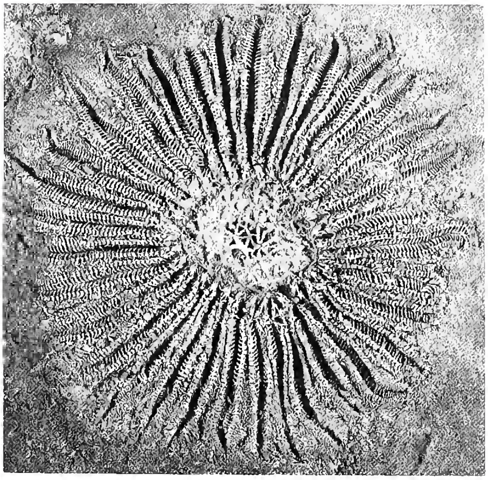
EXPLANATION OF PLATE 1

Figs 1–2, 5. *Brachisolaster moretonic* (Forbes). BM(NH) 40421; Windrush Quarry, Gloucestershire; Middle Bathonian. 1–2, views of ventral surface of specimen; compare overall proportions with that of modern solasterid (fig. 3); note enlarged mouth opening with dorsal ossicles exposed, robust mouth angle ossicles, and closely-spaced arms with comparatively large ambulacral ossicles; 1, ×0·5; 2, ×1. 5, ventral view of dorsal disc ossicles showing general arrangement, papular pores between ossicles; compare general arrangement with that of *Crossaster papposus*, ×6.

Figs 3–4. *Crossaster papposus* (Linné). USNM Div. Echinoderms 39942; Firth of Lorn, Scotland; Recent. 3, dorsal view showing general proportions of a modern solasterid, ×1. 4, dorsal view showing arrangement of dorsal ossicles, ×6.



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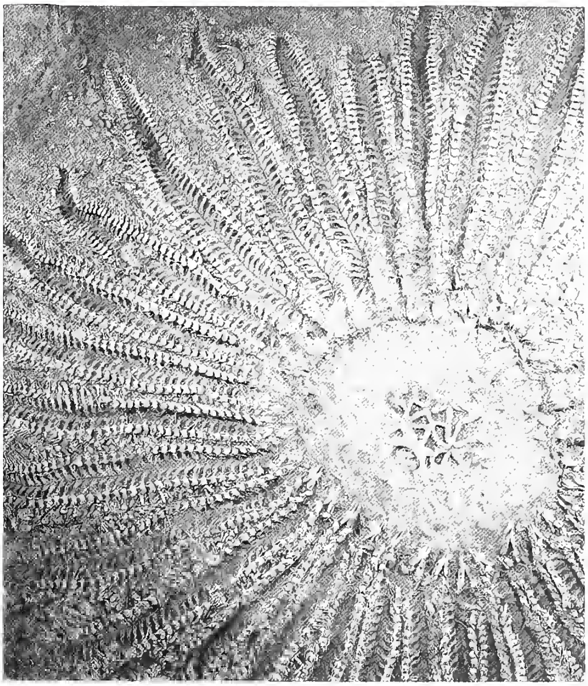

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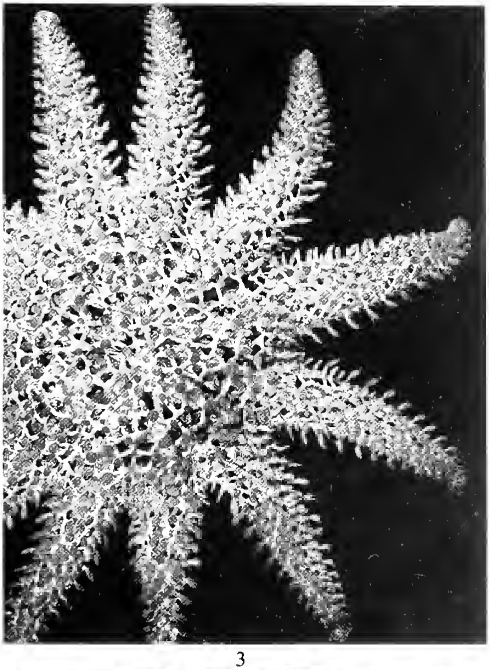

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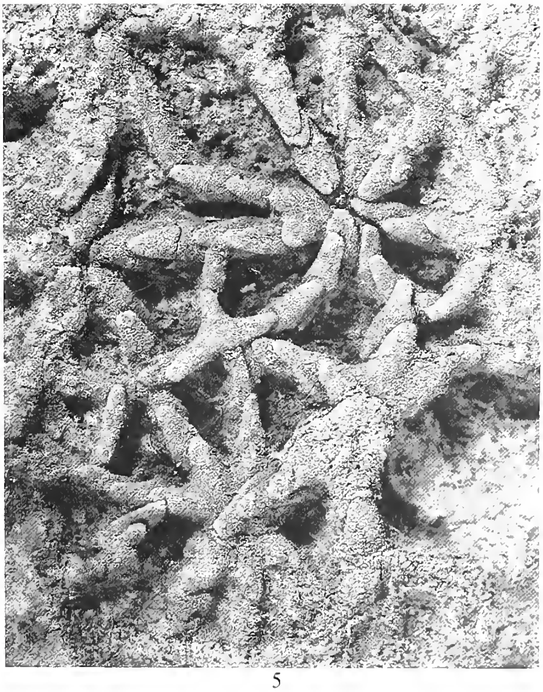

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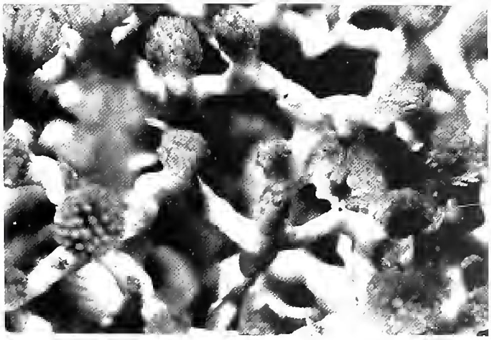


4

BLAKE, *Brachisolaster*, *Crossaster*

*Description.* Primary radius (from disc centre to arm tips) between 65 and 70 mm, interbrachial radius between 45 and 50 mm; the mouth opening is distorted and now roughly elliptical (Pl. 1, figs 1–2) with a greater axis of about 38 mm, the lesser about 28 mm; mouth opening size in life probably was intermediate. The dorsal surface is an open reticulum (Pl. 1, fig. 5), but popularia are not large (largest exposed example approximately 5 mm in length) and each probably could contain few papulae. Larger paxillate? dorsal ossicles bear multiple basal facets which overlap and are overlapped by one or more rod-like and Y-shaped connecting bars, or by other paxillate? ossicles; other than presence of the open reticulate pattern, no general dorsal ossicular arrangement is in evidence, and no dorsal spines are exposed.

Because of the partial collapse near arm tips, marginals are poorly exposed, but probable marginals appear laterally flattened (Pl. 2, fig. 4) and they probably were arranged in an upright orientation in life, with a crown of spine bases, similar to corresponding ossicles in living species; apparent marginals are about 1 mm in both height and width. Actinal interbrachials (Pl. 2, figs 3–4) are somewhat irregular; some are subpetalloidal but most are relatively elongate, tapering ossicles which appear to have formed a double column over much of the disc. Ventral areas near the oral frame are narrow so that proximal adambulacrals of some adjacent series now are abutted, but varied development and exposure from arm to arm show that actinal interbrachial areas reached the oral frame in life; some actinal interbrachials were taphonomically folded upward into the disc interior and are now obscured. Adambulacrals and probably ossicles lateral to the adambulacrals at the free tips of the arms bear distally-directed fans of slender conical spines 2–3 mm in length that apparently formed a closely arranged pavement between the arm tips in life (Pl. 2, fig. 4).

Ambulacrals near the disc are about 3 mm wide; the body of the ossicle is slender, and the proximal adradial tip strongly projects proximally (Pl. 2, fig. 1), overlapping the distal adradial margin of the next proximal ossicle and yielding an almost sinuous appearance; the ventral cross-furrow muscle depression, dentition, and ambulacral–adambulacral muscle articulation surfaces (Pl. 2, figs 1–4) are all well developed. Proximal ambulacrals are foreshortened, thus providing more tube feet per unit arm length near the mouth; midarm intervals have approximately 20 ambulacrals in 20 mm. Adambulacrals are strongly overlapping, and relatively narrow (proximally, 1 mm or slightly more in width) and elongate (nearly 2 mm in length). The distal (or ventral) muscle depression is large and deep. The outer face is relatively large and bears a transverse row of large spine bases; preserved spines are at least 2·5 mm in length. The characteristic (for solasteroids) palmate row of spine bases along the furrow margin does not remain on any ossicle, but spine base development suggests such a row was present; the furrow margin of the outer face is angular, providing a guide and separation between subsequent podia. Mouth angle ossicles (Pl. 2, figs 1–2) form a broad keel-like prominence on the ventral surface and have a row? of spine bases near the dorsal margins at the proximal ends of the ossicles. The few remaining enlarged spines appear typical of solasteroids although most of the lower portion of the ossicle lacked spines. The articular depression for the first adambulacral is deep and prominent.

## MORPHOLOGY AND BEHAVIOUR OF *BRACHISOLASTER*

Morphology of surviving representatives of most living asteroid orders converge on a single pattern suggested to reflect closely the ancestral appearance of these taxa (Blake 1987). In the Velatida, this morphology is best represented by the seven-armed genus *Rhipidiaster*, although *Lophaster*, with five arms, is primitive in this character.

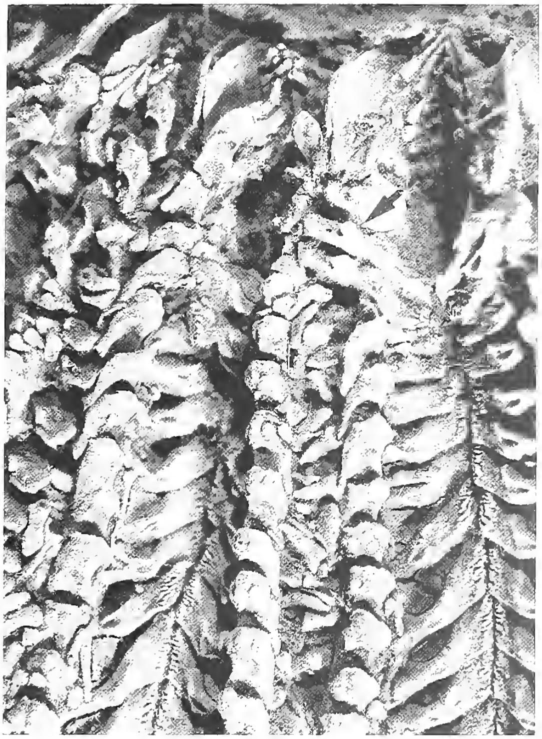
Hypothesizing a five-armed *Rhipidiaster*-like ancestry, arm number and disc size of *Brachisolaster* is derived. The dorsal surface of most living solasteroids is constructed of closely arranged, rather

EXPLANATION OF PLATE 2

Figs 1–4. *Brachisolaster moretonis* (Forbes). BM(NH) 40421; Windrush Quarry, Gloucestershire; Middle Bathonian; ventral views showing general ossicular form, which is essentially similar to that of Recent solasterids; ×6. 1–2, part of the mouth frame and proximal portions of ventral surface of the disc (distal to bottom of page); note well-developed articular structures, keel-like mouth angle ossicles in figure 2, with few spine bases and therefore few spines in life, and the sinuous ambulacrals; arrow in figure 2 shows typical solasterid articular structures linking ambulacrals to adambulacrals. 3, mid region of arms showing ossicular form, left side of ambulacral ossicular column is obscured, distal to top of page. 4, tips of two arms, distal to top of page, with spines extended to form a tight pavement; most of the area between adambulacrals is occupied by interbrachial ossicles but arrow points to probable marginal.

PLATE 2

1



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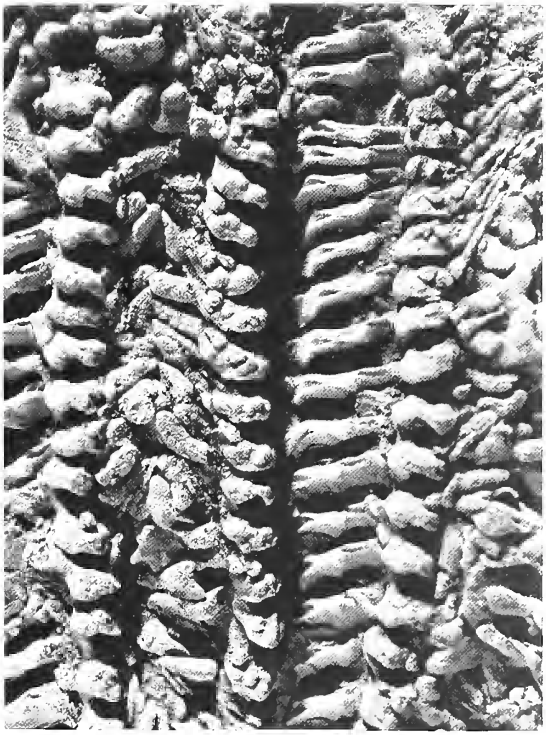

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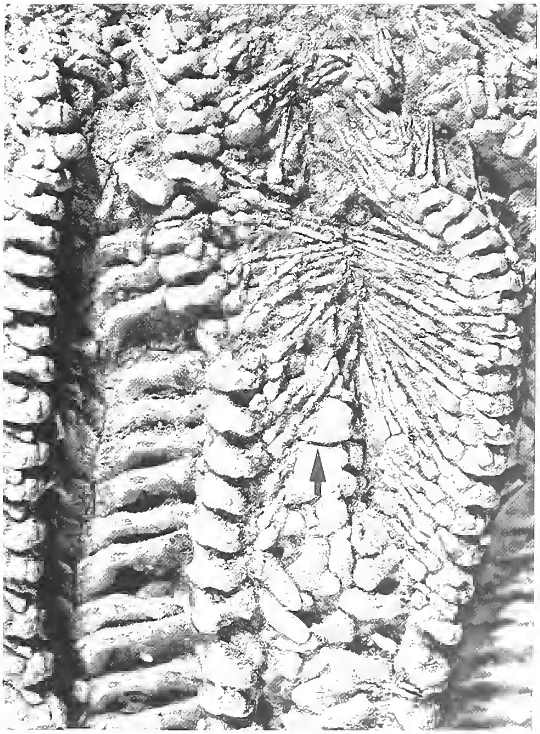

4

BLAKE, *Brachisolaster*

low paxilliform ossicles bearing tufts of spinelets. In a few species (e.g. *Crossaster papposus*, Pl. 1, figs 2, 4), the skeleton is in the form of an open reticulum with larger paxillae linked by smaller cross bars. *Brachisolaster* shares this derived pattern (Pl. 1, fig. 5), although its ossicles appear relatively stout and closely spaced. In *Brachisolaster*, marginals are difficult to identify with any certainty (Pl. 2, fig. 4), and they are no longer clearly aligned where exposed; nevertheless, probable marginals have a well-developed spine-bearing ridge, a state apparently derived relative to the condition in *Rhipidiaster* in which the ridge is less prominent. Adjacent marginals are abutted in *Rhipidiaster* but they do not appear abundant enough to have abutted in *Brachisolaster*; if so, this state is also derived. Ambulacral and adambulacral ossicular forms (Pl. 2, figs 1–4) in *Brachisolaster* are essentially similar to those of living solasteroids, although the adambulacrals are proportionately narrow. Development of mouth angle ossicles (Pl. 2, figs 1–2), including the absence of spines from much of the ossicular surface, is typical of that of living solasteroids.

*Brachisolaster moretonis* clearly is a solasteroid, in which many characters are derived relative to their state in *Rhipidiaster* and *Lophaster*, and suggestive of their state in *Crossaster*. Derived characters include presence of supernumerary arms (although more occur in the fossil than are known among living representatives), disc size, dorsal ossicular form and arrangement, ambulacral column arrangement (but adambulacral proportions are distinctive), and perhaps marginal development. Arm number, adambulacral breadth, and clusters of elongate distal spines are unlike arrangements in living solasteroids. Most living solasteroids have relatively wide adambulacrals whereas those of *Brachisolaster* are narrow; this seemingly primitive condition is a likely result of space constraints, in that the presence of many arms around the disc axis leaves only limited room for adambulacrals. Living solasteroids have between 5 and 15 arms (Clark and Courtman-Stock 1976) whereas the present specimen of *Brachisolaster* has 33; Lawrence and Komatsu (1990) noted that arm number is variable in asteroids with more than 12 arms, and therefore number likely was variable in *Brachisolaster* as well.

The functional significance of supernumerary arms seems important. Inferences for behavioural generalists such as asteroids are difficult, but comparisons of form suggest one explanation. *Brachisolaster* is superficially similar to the eastern tropical Pacific genus *Heliaster* (Forcipulatida: Heliasteridae) in terms of overall size, relative disc size (i.e. ratio of arm to disc radius) and arm number. Living solasteroids commonly feed on relatively large, mobile prey such as other echinoderms; *Solaster dawsoni*, for example, is a predator of other asteroids in the North Pacific. It searches the substrate with forward arms and a portion of the disc raised; when the extended tube feet contact the dorsal surface of a victim, *S. dawsoni* drops down and impedes retreat of the prey individual using rows of large transverse adambulacral spines (Van Veldhuizen and Oakes 1981). Comparison of ambulacra between certain Recent *Crossaster papposus* specimens in the collections of the National Museum of Natural History (Washington) and *Brachisolaster* suggests less robust construction in the fossil. The *Brachisolaster* specimen, with a primary radius of 60–70 mm, has approximately 20 ambulacral ossicles in 20 mm, whereas two *Crossaster* specimens with radii of approximately 80 and 90 mm have 12 or 13 ambulacral ossicles in 20 mm, and one specimen of radius approximately 45–50 mm has about 16–18 in 20 mm. The specimen of radius of about 80 mm has a proximal ambulacral breadth in excess of 9 mm, compared with about 3 mm in *Brachisolaster*. Deep muscle depressions and prominent articular facets suggest very strong articulation capabilities in the living species. All these traits suggest a robust construction well suited to manipulation of comparatively active prey in living solasteroids.

*Heliaster* is found along rocky shorelines where it commonly withstands high energy wave impact and feeds on molluscs and barnacles (Jangoux 1982). *Brachisolaster*, which lacked the ambulacral construction typical of many solasteroids, would seem to have been relatively inefficient in manipulating larger, more active prey. In addition, the open dorsal reticulum probably would have been less resistant to wave impact than apparently is the tightly interconnected skeleton of *Heliaster*. It is suggested that *Brachisolaster* was a predator on relatively small, passive prey individuals, much as *Heliaster* is today, but in quieter settings.

Arm number among the few known Jurassic solasteroids includes both those with supernumerary arms (Blake 1887) as well as one with an uncertain number, but apparently within the range of that of living solasteroids (Hess 1972). Feeding on more active echinoderm prey perhaps represents a behavioural complexity beyond that involved in feeding on relatively inactive molluscs, but if arm number is taken as indicative of this complexity, then predation on active prey had evolved by the Jurassic. Loss of a viable life mode (i.e. predation on molluscs) might have resulted from competition from asteriids.

As noted above, the pavement-like arrangement of the adambulacral spines toward the arm tips appears natural, but unlike patterns in living solasterids, if only because fewer arms means more widely separate arm tips for any given radius (Pl. 1, figs 1–3). Spines might have provided support on a soft substrate, they could have served to help smother prey, or perhaps other functions are possible.

Asteriids also might have suffered a narrowing of functional range since the Jurassic. It has been suggested (Blake 1990) that the prominent adambulacral spines of Jurassic asteriids, not known among living species, were similar to those of living solasterids, and might similarly have been used to impede prey retreat. Thus, limited evidence suggests a narrowing and specialization of adaptive zones of solasterids and asteriids since the Jurassic. This conjectural interpretation unfortunately can be only partly tested through studies of behaviour of living asteroids.

*Acknowledgements.* I am indebted to Andrew B. Smith and the authorities of The Natural History Museum, for the loan of the holotype of *Brachisolaster moretonis*, and to David L. Pawson and the authorities of the United States National Museum for the loan of modern solasterids. Paul D. Taylor kindly provided current information on stratigraphical terminology.

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# TERRESTRIAL PLANT MICROFOSSILS FROM SILURIAN INLIERS OF THE MIDLAND VALLEY OF SCOTLAND

*by* C. H. WELLMAN *and* J. B. RICHARDSON

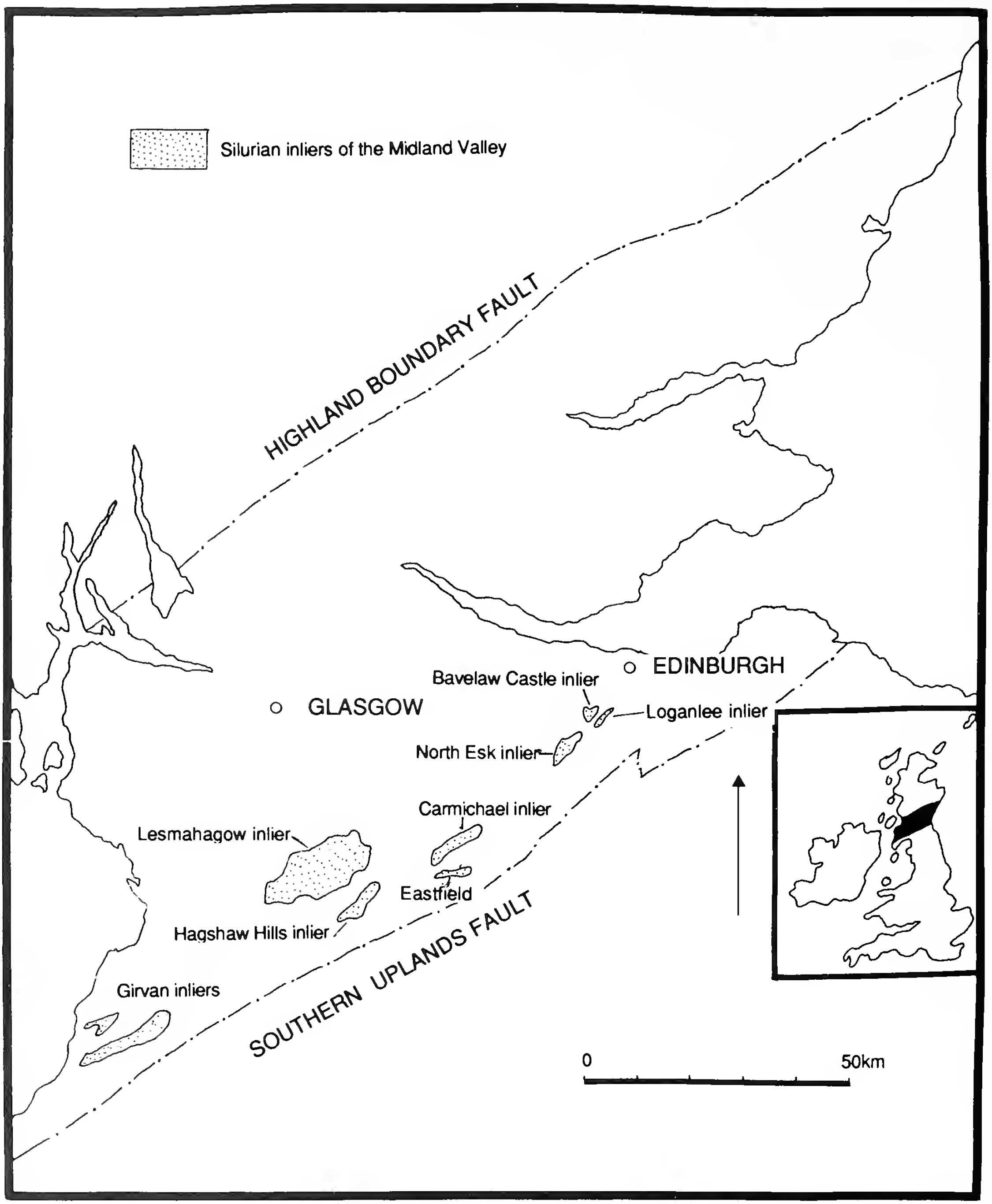
ABSTRACT. Palynomorph assemblages comprising sporomorphs (cryptospores and miospores) and plant fragments (cuticle-like sheets and tubular structures) were recovered from red-bed sequences in the Lesmahagow, Hagshaw Hills and North Esk inliers from the Midland Valley of Scotland. The assemblages all indicate an early Wenlock age and probably belong to the *chulus-nanus* Spore Assemblage Biozone. The cryptospore taxa *Cheilotetras caledonica* gen. et sp. nov. and *Pseudodyadospora petasus* sp. nov. are proposed, and *Tetrahedraletes* is emended. The palynomorph and plant microfossil assemblages consist of entirely land-derived forms except in the North Esk inlier where rare acanthomorph acritarchs were recovered from a single horizon. Palynology thus provides additional evidence that the deposits in the Lesmahagow and Hagshaw Hills inliers accumulated in a non-marine environment, whereas a brief marine incursion interrupted terrestrial fluviatile deposition in the North Esk inlier. This report describes rare examples of Silurian palynomorph assemblages of entirely land-derived forms.

THE red-bed sequences in the Silurian inliers situated along the southern margin of the Midland Valley of Scotland have hitherto been poorly age constrained. This was unfortunate as they contain important faunas associated with fish beds and herald the onset of 'Old Red Sandstone facies' sedimentation in this part of Scotland (Walton and Oliver 1991). The recovery of palynomorph assemblages from these deposits provided an ideal opportunity to initiate a biostratigraphical investigation. The assemblages were recovered from horizons in the purported continental sequences of several of the inliers and are all similar, essentially comprising an identical suite of taxa, except for the presence of rare acanthomorph acritarchs in a single preparation. The assemblages contain cryptospores, miospores, the enigmatic palynomorph '*Moyeria*', and phytoclasts such as cuticle-like sheets and tubular structures.

Recently the distribution of miospores and cryptospores has been described in sequences from the Llandovery and Wenlock type areas (Burgess 1991; Burgess and Richardson 1991). This work complements the miospore zonation scheme for the Silurian which was established by Richardson and McGregor (1986) and expanded by Richardson (*in* Richardson and Edwards 1989). Hence there now exists a working sporomorph zonation scheme for the Silurian with which the Midland Valley assemblages can be correlated. The sporomorph assemblages are systematically described, compared with similar, previously described assemblages, and correlated with sporomorph zonation schemes. Additionally, the plant microfossil assemblages occur in a sequence of strata which has been interpreted as non-marine, and palynofacies analysis provides useful supplementary evidence compatible with the previously published sedimentological and palaeontological data.

Plant macrofossils are rare in strata of this age and consequently the form and evolution of early terrestrial vegetation is not well understood (Edwards and Fanning 1985; Gray 1985; Edwards and Burgess 1990). The sporomorphs and phytoclasts provide an insight into the abundance, distribution and, to a certain extent, morphology of the land plants from which some of the microfossils may have derived. Additionally, certain palynomorphs which occur in the assemblages may have belonged to organisms inhabiting continental water bodies and hence contribute information concerning life in these environments.

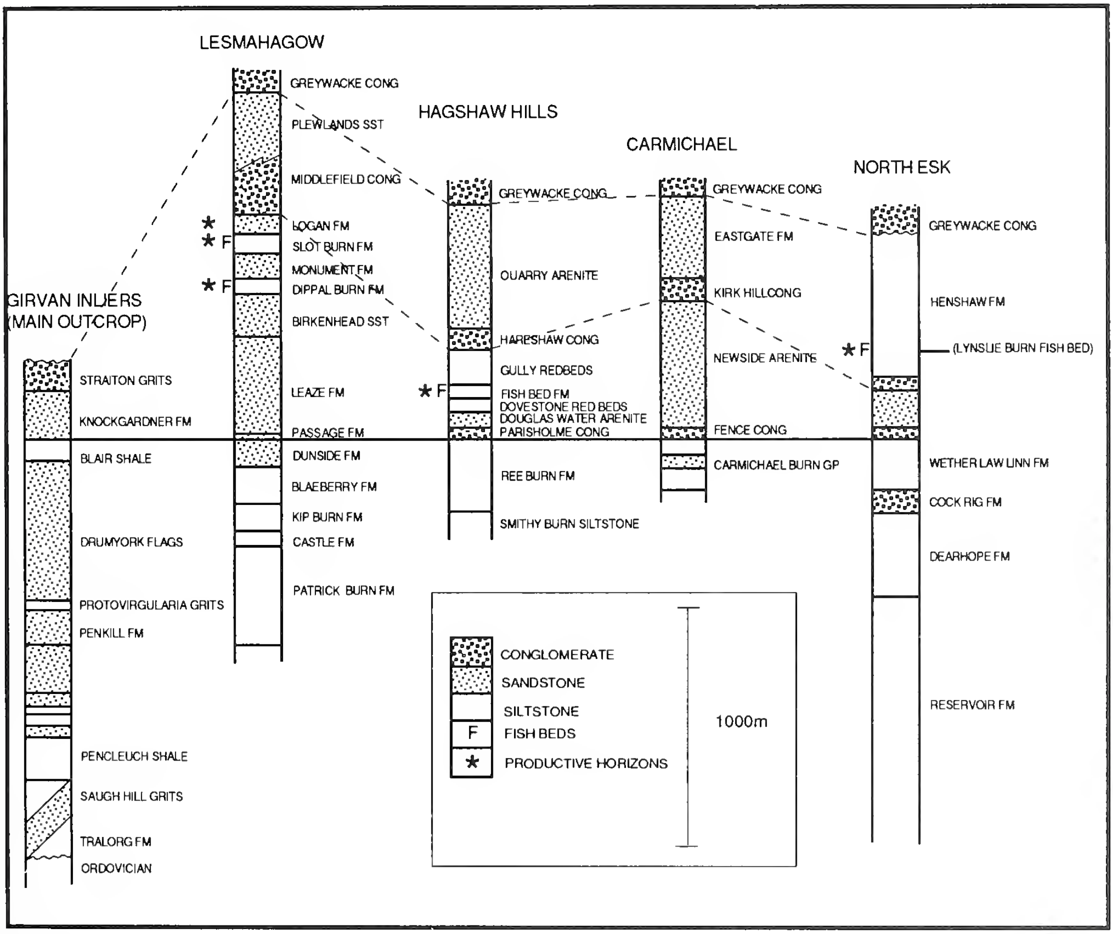
**[Palaeontology, Vol. 36, Part 1, 1993, pp. 155–193, 6 pls.]**



TEXT-FIG. 1. Location map of the Silurian inliers of the Midland Valley of Scotland (after Walton and Oliver 1991).

## GEOLOGICAL SETTING

A series of Silurian inliers occurs along the southern margin of the Midland Valley of Scotland (Text-fig. 1). These inliers show marine Llandovery and Lower Wenlock successions which pass up into non-marine sediments that are poorly age constrained, despite the presence of the faunas recovered from the fish beds (Rolfe 1973*a*, 1973*b*; Walton and Oliver 1991) (Text-fig. 2). Graptolites and shelly faunas have been used to date the marine successions (Lamont 1947; Rolfe 1961, 1973*a*, 1973*b*; Rolfe and Fritz 1966; Cocks and Toghill 1973; Bull 1987). The deposits are believed to have accumulated in an elongate basin with landmasses situated to the north and south. The tectonic scenario is contentious, but is clearly intimately related to the complex tectonic events associated with the southern margin of the Laurasian continent which was destructive throughout the Silurian (Bluck 1985; McKerrow 1988*a*, 1988*b*). Leggett (1980) suggested that the basin was an upper slope basin with a landmass to the north and an emergent accretionary prism, represented by the Southern Uplands, to the south. The descending oceanic plate would have been situated to the south beyond the accretionary prism. Alternatively, Bluck (1983) envisaged an interarc basin separated from the accretionary prism by an arc. This model requires that the accretionary prism was at some point thrust northwards into its



TEXT-FIG. 2. Stratigraphical successions with positions of productive samples in the Silurian inliers of the Midland Valley (after Walton 1991): stratigraphical nomenclature after Cocks and Toghill (1973) for the Girvan inliers, Jennings (1961) summarized in Walton and Oliver (1991) for the Lesmahagow inlier, Rolfe (1961) for the Hagshaw Hills inlier, Rolfe (1960) for the Carmichael inlier and Robertson (1989) for the North Esk inlier.

current position where it conceals the arc and fore-arc basin deposits. More recently, it has been suggested that large-scale strike-slip fault movement along the Southern Uplands Fault and Highland Boundary Fault may have been important (McKerrow 1988*a*, 1988*b*; Pickering *et al.* 1988; McKerrow *et al.* 1991).

At Girvan, deposits of Rhuddanian age (*cyphus* Biozone) rest with angular unconformity on Ordovician rocks, and over 1800 m of marine Llandovery strata is developed (Cocks and Toghill 1973). Towards the top of the sequence there is a regression and deep water turbiditic sediments of latest Llandovery age (*crenulata* Biozone) are succeeded by shallow water marine deposits which have been dated using acritarchs as early Wenlock age (Dorning 1982). These beds give way to unfossiliferous strata of red-bed facies presumed to have accumulated in a terrestrial–fluviatile environment. In the other inliers the base of the successions is not seen and the oldest strata are marine and of latest Llandovery and early Wenlock age (Lamont 1947; Rolfe 1961, 1973*a*, 1973*b*; Robertson 1989). Towards the top of the marine strata a regression is developed (Walton and Oliver 1991), which is apparently contemporaneous with the one present in the Girvan area. The deep basinal sediments are succeeded by strata which are believed to have accumulated in a shallowing marine environment, and eventually deposits of red-bed facies are developed.

The red-bed sequences in the inliers comprise a combination of conglomerates, sandstones and siltstones with over 1500 m of red-beds developed in the Lesmahagow inlier. They exhibit sedimentological characteristics indicative of accumulation in terrestrial–fluviatile and lacustrine environments (McGiven 1968; Rolfe 1973*a*). The conglomerates are typical of alluvial fan deposits and many of the siltstones show desiccation cracks and other features characteristic of floodplain deposits. Also, possible channel deposits are developed in the Logan Formation of the Lesmahagow inlier. However, it has recently been suggested that the fish recovered from the fish-beds are marine forms brought in by marine incursions (Blieck and Janvier 1991).

The red-bed sequences are generally unfossiliferous, except for the faunas of the fish beds. The fish beds are present in the Dippal Burn Formation and Slot Burn Formation of the Lesmahagow inlier, the Fish Bed Formation of the Hagshaw Hills inlier and the Henshaw Formation of the North Esk inlier. The fish beds of the Lesmahagow and Hagshaw Hills inliers comprise finely laminated siltstones which occur in a sequence of massive, dark greenish-grey sandstones and siltstones. The paucity of desiccation cracks and the lateral and vertical uniformity suggests that the formations in which these fish beds are located accumulated in permanent bodies of water such as lakes or possibly lagoons. The fish beds have yielded the anaspids *Birkenia elegans*, *Lasanius problematicus* and *L. armatus*, the thelodonts *Logania* (*Thelodus*) *taiti*, *Lanarkia horrida* and *L. spinosa*, the cephalaspid *Ateleaspis tessellata*, eurypterids and rare plant fragments (Ritchie 1963, summarized in Rolfe 1973*a*). The fish beds are laminated and the fossils are usually articulated which suggests an absence of bioturbating organisms. This may indicate that the bottom waters were not oxygenated (Rolfe 1973*a*). However, the fish bed in the North Esk inlier is different in that it comprises massive olive green siltstones and contains a fauna of disarticulated fragments. The fish *B. elegans*, *A. tesselata* and *Lasanius problematicus* are present, in addition to the crinoid *Pisocrinus campana*. This horizon has been interpreted as being due to a minor marine incursion (Robertson 1989).

The fauna of the fish beds is probably strongly facies controlled and therefore of little value biostratigraphically. However, Heintz (1939) tentatively suggested that the fish faunas were of mid to late Ludlow age after comparing them with other faunas, particularly the Oesal fish fauna of the Baltic. Later, Westoll re-evaluated the evidence and suggested that a 'late Wenlock or early to middle Ludlow age would seem reasonable' (Westoll 1951, p. 6).

Other indices which are of value in correlation between the inliers are the distinctive alluvial fan conglomerates. There are three major conglomerates which can be traced between the inliers; these are named the Igneous Conglomerate, the Quartzite Conglomerate and the Greywacke Conglomerate (Text-fig. 2). Each conglomerate is characterized by a distinct clast lithology. The variation in composition probably reflects differences in the lithology of the source area. It is possible that the conglomerates are strongly diachronous but they still provide useful reference points.

In the Pentland Hills the red-bed sequence of the Silurian inliers is overlain with angular unconformity by the Greywacke Conglomerate which is taken as the local base of the Devonian. However, at Lesmahagow the Greywacke Conglomerate succeeds the Silurian red-beds without apparent discordance, although there is almost certainly disconformity. The 'Lower Old Red Sandstone' deposits which overlie the Greywacke Conglomerate have yielded the Early Devonian fish *Cephalaspis* (Mykura 1991).

## PREVIOUS PALYNOLOGICAL INVESTIGATIONS

Little has been published concerning the palynology of the Silurian inliers of the Midland Valley. Richardson (1967) reported on assemblages from the Lesmahagow inlier which contained poorly preserved simple, smooth, azonate spores and apiculate bodies which lacked triradiate marks. Later, Jancis Ford investigated the Silurian inliers in more detail in her unpublished Ph.D. studies (Ford 1971). Richardson (*in* Aldridge *et al.* 1979) summarized Ford's findings noting that she had recorded sculptured miospores belonging to *Apiculiretusispora* and *Emphanisporites* from seemingly anomalous levels in the Hagshaw Hills and Lesmahagow inliers. After re-examining Ford's slides and verifying the presence of such spores, Ford's localities were recollected. Assemblages with only smooth-walled trilete spores, similar to those recovered from above and below her sample horizon, were recorded. The only other relevant publication from Girvan (Dorning 1982) described acritarchs and suggested an early Wenlock age for the Knockgardner Formation. He noted the presence of trilete spores referable to *Ambitisporites*. Samples from the Knockgardner Formation were recollected but trilete spores were not found, although permanent tetrads referable to *Tetrahedraletes medinensis* (Strother and Traverse) emend. were present.

## SAMPLING AND TECHNIQUES

Samples were collected from throughout the red-bed sequences of the Silurian inliers. Productive samples were confined to the Dippal Burn, Slot Burn and Logan Formations of the Lesmahagow inlier, the Fish Bed Formation of the Hagshaw Hills inlier and the Lynslie Burn fish bed in the Henshaw Formation of the North Esk inlier. Recovery was variable from within these formations, but some well-preserved assemblages were obtained. Thermal maturation was fairly high (Thermal Alteration Index scale 3–4) and the spores are dark brown. Sample details are given in Appendix 1. The stratigraphical terminology utilized throughout this paper is from Robertson (1989) for the North Esk inlier, Rolfe (1961) for the Hagshaw Hills inlier and Jennings (1961), summarized in Walton and Oliver (1991), for the Lesmahagow inlier.

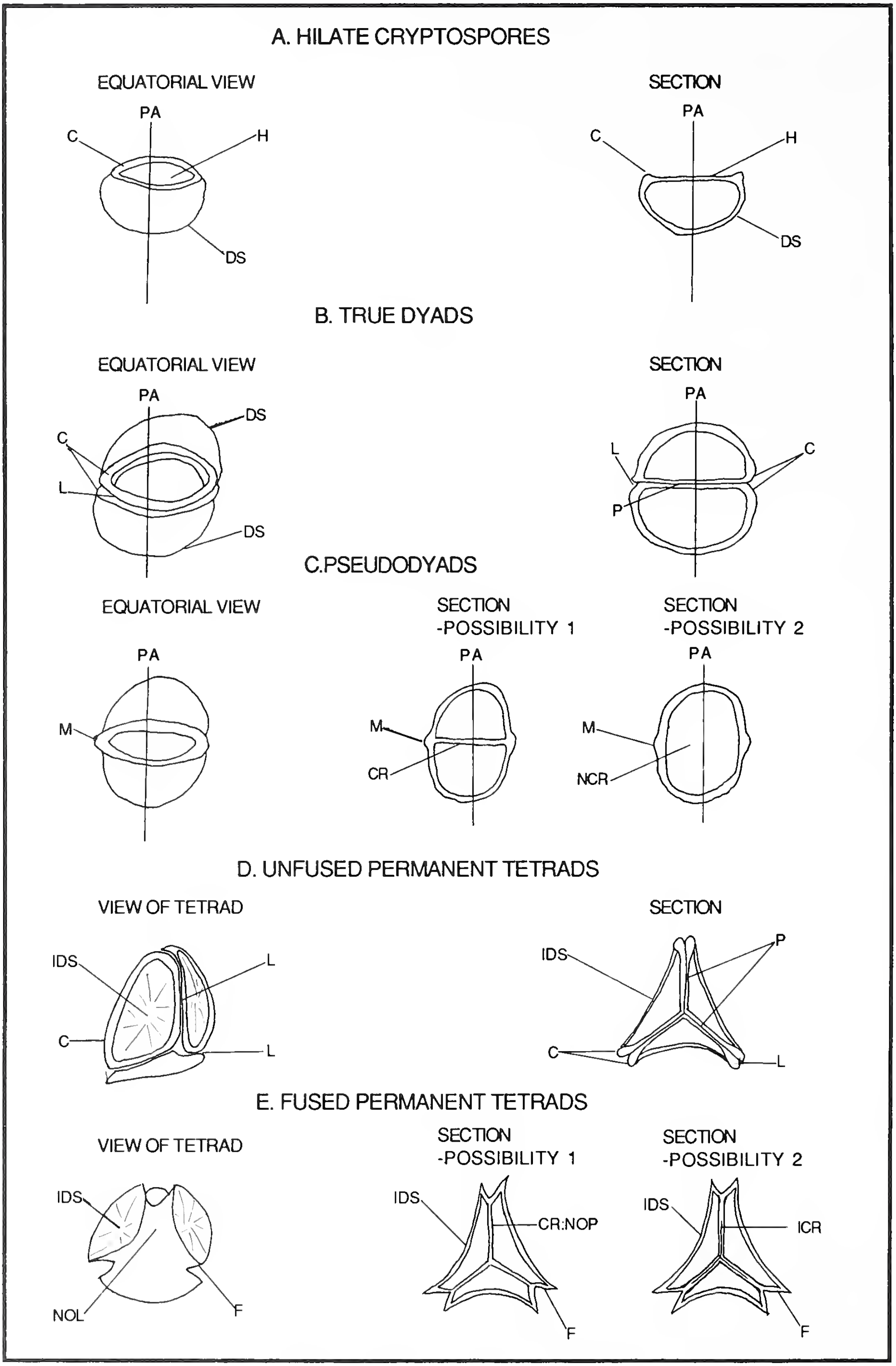
Samples were prepared for palynological investigation using standard HCl–HF–HCl acid maceration techniques followed by zinc bromide heavy mineral separation. The organic residue was sieved through a 10 $\mu$m mesh. The residue was strew-mounted using 'Elvacite' mounting medium. Some samples were oxidized for between 10 and 60 minutes in concentrated nitric acid in order to clear them for light microscope observation. Transmitted light investigation with the use of Nomarski interference contrast was carried out on a Zeiss Photomicroscope 111 (no. 2562). Additionally, stubs were strew-mounted and gold coated for scanning electron microscopy using an Hitachi 800 scanning electron microscope.

## SYSTEMATIC PALAEONTOLOGY

*Discussion.* In the twenty years following the first report of permanent tetrads by Gray and Boucot (1971) there has been an increasing awareness of the presence in Lower Palaeozoic deposits of palynomorphs which possess characteristics of subaerially dispersed land plant spores, but are in many respects atypical (Strother and Traverse 1979; Vavrdova 1982, 1984, 1988, 1989; Miller and Eames 1982; Gray, Massa and Boucot 1982; Gray *et al.* 1985; Gray 1985, 1988; Johnson 1985; Gray, Theron and Boucot 1986; Richardson 1988; Burgess 1991; Burgess and Richardson 1991). These spore-like microfossils have been termed cryptospores and the anteturma Cryptosporites erected for their inclusion (Richardson *et al.* 1984; Richardson 1988; Richardson and Edwards 1989). There are several major categories of cryptospore which are morphologically distinct. They include fused permanent tetrads, unfused permanent tetrads, fused permanent dyads (pseudodyads), unfused permanent dyads (true dyads), alete monads and hilate cryptospores. The hilate cryptospores are, in the main, believed to be spores liberated from true dyads which have dissociated (Burgess and Richardson 1991). Most of these cryptospore categories have been reported enclosed within a loose or tight fitting membranous envelope (Gray and Boucot 1971; Strother and Traverse 1979; Miller and Eames 1982; Gray 1985; Johnson 1985; Richardson 1988; Burgess 1991).

The oldest reported cryptospores are permanent tetrads from the Llanvirn (Vavrdova 1984). Abundant and diverse cryptospore assemblages have been described from geographically widespread localities of Caradoc, Ashgill and early Llandovery strata (Strother and Traverse 1979; Gray, Massa and Boucot 1982; Miller and Eames 1982; Vavrdova 1982, 1984, 1988, 1989; Gray 1985, 1988; Gray *et al.* 1985; Johnson 1985; Gray, Theron and Boucot 1986; Richardson 1988; Burgess 1991). Trilete miospores first appear in the Llandovery (Aeronian) (Richardson 1988) and co-exist with cryptospores until at least the Late Devonian, although the upper limit of cryptospore occurrence is not well documented.

*Terminology.* Suprageneric classification has not yet been proposed for the cryptospores, so the anteturma Cryptosporites is informally subdivided into general sections relating to the morphotypes outlined above.



TEXT-FIG. 3. For legend see opposite.

Wherever possible the terminology of Grèbe (1991) is utilized in the description of both miospores and cryptospores. However, because the morphology of cryptospores differs from that of miospores, the method of orientation of these sporomorphs requires explanation and is illustrated in Text-figure 3. The only new terminology introduced relates to the junctions between spores in cryptospores which comprise more than one spore. Those cryptospores composed of discrete spores and attached across a clear plane of separation are referred to as *unfused* and are united across a *plane of attachment*. The crack or suture which marks the junction between the spores is termed a *line of attachment*. Cryptospores which comprise more than one spore where there is not perceptible line of attachment marking the junction between the spores are termed *fused*. The fused state suggests that the spores probably share a single common wall and lack a plane of attachment. However, it is difficult to ascertain the structure of such cryptospores without the aid of thin sections. Text-figure 3 illustrates the main groups of cryptospore and demonstrates some possible alternatives where the structure is contentious.

*Repository of material.* Figured specimens are stored in the Palynology Section, Palaeontology Department, British Museum (Natural History), London. Specimen location refers to standard England Finder co-ordinates from the Zeiss Photomicroscope 111 (no. 2562) housed in the same department. Scanning electron micrograph print numbers refer to proof prints stored in the Electron Microscopy Unit of the British Museum (Natural History).

*Occurrence of sporomorph taxa.* All of the taxa reported were recorded in samples from the Dippal Burn, Slot Burn and Logan Formations of the Lesmahagow inlier, the Fish Bed Formation of the Hagshaw Hills inlier, and the Henshaw Formation of the North Esk inlier, apart from *Dyadospora murusdensa*, *Rimosotetras problematica* and '*Moyeria*' *cabottii* which were not recorded from the Henshaw Formation (see Text-fig. 4). Regarding data concerning figured specimens, FBF = Fish Bed Formation of the Hagshaw Hills inlier, DBF = Dippal Burn, SBF = Slot Burn; LF = Logan Formations of the Lesmahagow inlier; HF = Henshaw Formation of the North Esk inlier.

## Anteturma CRYPTOSPORITES (Richardson, Ford and Parker, 1984) Richardson, 1988

1. *Fused cryptospore tetrads.* This group comprises permanent tetrads in which the spores are fused together. There are no lines of attachment on the tetrad surface which mark the position of planes of attachment between the spores.

### Genus CHEILOTETRAS gen. nov.

*Type species. Cheilotetras caledonica* gen. et sp. nov.

*Derivation of name.* Greek *cheilos*, lip; *tetras*, four.

*Diagnosis.* Laevigate permanent tetrahedral tetrads composed of subtriangular to subcircular spore-like units. The spores are fused together, there are no visible lines of attachment, and each spore possesses an invaginated distal wall.

*Generic comparison.* The genus *Tetrahedraletes* (Strother and Traverse) emend. comprises discrete spores with a clear plane of attachment between them.

*Discussion.* The genus *Cheilotetras* has been proposed for spore tetrads united across entirely fused junctions, with no visible lines of attachment. Such sporomorphs are distinguished from other

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TEXT-FIG. 3. Orientation and morphological nomenclature of cryptospores: PA, polar axis; C, crassitude; H, hilum; DS, distal surface; IDS, invaginated distal surface; L, line of attachment; NOL, no line of attachment; P, plane of attachment; NOP, no plane of attachment; M, medial arcuate thickening; CR, crosswall; ICR, incomplete plane of attachment developed in crosswall; F, 'flange'.

| SPOROMORPHS / SAMPLES | HAGSHAW HILLS INLIER | | | | | | | | | LESMAHAGOW INLIER | | | | | | | | | | | | | | | | | | NORTH ESK INLIER | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | FISH BED FM | | | | | | | | | LOGAN FM | | | | | | | | | | SLOT BURN FM | | | DIPPAL BURN FM | | | | | LYNSLIE BURN FISH BED | | | |
| | AH5 | AH6 | AH10 | BH4 | BH8 | BH9 | BH13 | BH14 | BH15 | CL5 | CL6 | CL7 | CL8 | CL9 | CL10 | CL11 | CL12 | CL13 | CL14 | BL7 | CL16 | DL8 | BL13 | BL15 | BL16 | DL13 | DL14 | BP7 | CP6 | CP7 | CP9 |
| *Ambitisporites avitus* | X | X | X | 1 | 3 | 1 | X | X | X | 1 | 1 | 2 | 3 | 2 | X | X | X | X | X | 4 | X | 2 | 3 | X | X | 3 | 2 | - | X | X | X |
| *Ambitisporites dilutus* | X | X | X | 9 | 9 | 13 | X | X | X | 11 | 5 | 7 | 10 | 8 | X | X | X | X | X | 13 | X | 6 | 8 | X | X | 16 | 15 | X | X | X | X |
| *Laevolancis divellomedium* | X | X | X | 9 | 5 | 7 | X | X | X | 3 | 3 | 1 | 4 | 3 | X | X | X | X | X | 19 | X | 5 | 4 | X | X | 14 | 12 | X | X | X | X |
| *Laevolancis plicata* | - | X | X | 3 | 1 | 2 | X | X | X | 2 | 1 | P | 1 | 3 | X | X | X | X | X | 16 | X | 8 | 5 | X | X | 13 | 9 | X | X | X | X |
| *Dyadospora murusattenuata* | - | X | X | 3 | 1 | 2 | X | X | X | P | 2 | 2 | 2 | P | X | X | X | X | X | 1 | X | 1 | P | X | X | 1 | P | - | - | - | X |
| *Dyadospora murusdensa* | - | - | - | 2 | P | P | X | - | X | P | P | P | 1 | P | X | X | X | X | X | 1 | X | 1 | 2 | X | X | 1 | 1 | - | - | - | - |
| *Pseudodyadospora petasus* | - | X | X | 3 | 1 | 2 | - | X | X | 4 | 6 | 8 | 3 | 2 | X | X | X | X | X | 1 | X | 6 | 1 | X | X | 3 | 4 | X | - | X | X |
| *Tetrahedraletes medinensis* | X | X | X | 9 | 6 | 9 | X | X | X | 16 | 20 | 23 | 20 | 22 | X | X | X | X | X | 14 | X | 24 | 9 | X | X | 13 | 19 | X | X | X | X |
| *Rimosotetras problematica* | X | X | X | 1 | P | 1 | - | - | X | 1 | P | 1 | P | 1 | X | X | X | X | X | 1 | X | 3 | P | X | X | P | 1 | - | - | - | - |
| *Cheilotetras caledonica* | X | X | X | 4 | 2 | P | - | - | X | 5 | 6 | 15 | 5 | 4 | X | X | X | X | X | 4 | X | 7 | 5 | X | X | 2 | 4 | - | X | X | - |
| *'Moyena' cabottii* | X | - | X | 15 | 22 | 7 | - | X | X | 19 | 13 | 7 | 15 | 14 | X | X | X | X | X | 2 | - | - | 20 | X | X | 3 | 1 | - | - | - | - |
| Alete cryptospore monads | X | X | X | 35 | 47 | 51 | X | X | X | 38 | 43 | 35 | 36 | 41 | X | X | X | X | X | 24 | X | 37 | 43 | X | X | 31 | 32 | X | X | X | X |
| Acanthomorph acritarchs | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | X | - | - |
| PRESERVATION | P | P | P | G | G | G | P | P | P | G | G | G | G | G | G | G | G | G | G | G | G | G | G | P | P | G | G | P | P | P | P |

TEXT-FIG. 4. Occurrence of sporomorphs and results of frequency counts: ×, present; –, not recorded. Values refer to percentages recorded from frequency counts of 200 palynomorphs where P = present but not featured in counts. Regarding preservation: P, poor; G, good.

cryptospore permanent tetrads which comprise discrete spores with a clearly perceptible plane of attachment between the spores. There is an analogous situation in dyads, e.g. the true dyad genus *Dyadospora* (Strother and Traverse) Burgess and Richardson, 1991, is distinguished from pseudodyads (*sensu* Johnson 1985) because the spores are separated by a clear plane of attachment. However, the internal structure of such fused tetrads and pseudodyads is difficult to elucidate. Either the spores of the tetrad/dyad shares a common wall, or are discrete, where the plane of attachment is incompletely developed or the line of attachment is masked, perhaps by a tightly adherent membranous envelope.

### *Cheilotetras caledonica* gen. et sp. nov.

Plate 1, figs 1–7

*Derivation of name.* From the Latin '*Caledonia*', Scotland.

*Holotype and type locality.* FM 272, Pl. 1, figs 3, 6 (slide CL6/2, co-ord. 1120 109; E.F. no: K42/4), sample CL6, Logan Formation at Logan Water, Lesmahagow inlier.

*Paratypes.* Pl. 1, fig. 1, (stub CW36, Print P006225), sample CL7, LF. Pl. 1, fig. 2, (stub CW2, Print P004398), sample AH5, FBF. FM 273, Pl. 1, figs 4–5 (slide CL9/1, co-ord. 1319 107; E.F. no: K62/4), sample CL9, LF. FM 274, Pl. 1, fig. 7, (slide CL7/2, co-ord. 1333 062; E.F. no: F64/2), sample CL7, LF.

*Diagnosis.* A laevigate *Cheilotetras* where the exine of each spore is drawn out beyond the junction with adjacent spores into a distinct flange-like extension.

*Description.* Permanent tetrahedral tetrad composed of subcircular to subtriangular spore-like units. The individual spores have an invaginated distal surface. The crassitude of each spore is drawn out into a distinct rim 2–8 μm wide, which extends beyond the junction with the adjacent spores. The junction is entirely fused and no line of attachment is evident. The distal exine over the spores is laevigate, rigid and 1–2 μm in thickness.

*Dimensions.* 29(45)65 μm; 80 specimens measured.

*Comparison and remarks. Tetrahedraletes medinensis* (Strother and Traverse) emend. comprises discrete spores with distinct lines of attachment which mark the plane of attachment between adjacent spores. Additionally, the crassitudes associated with each spore in *Tetrahedraletes* is not extended into a 'flange'. *Rimosotetras problematica* Burgess, 1991 is composed of discrete spores which are loosely attached.

2. *Unfused cryptospore tetrads.* This group of permanent tetrads comprises discrete spores with planes of attachment between adjoining spores which form distinct cracks or sutures (lines of attachment) on the tetrad surface. The tetrads are not found dissociated and this suggests that they are dispersed intact, and remain permanently attached. Unfused tetrads have been reported naked and enclosed within laevigate or variously ornamented envelopes (Gray and Boucot 1971; Strother and Traverse 1979; Miller and Eames 1982; Gray 1985; Johnson 1985; Richardson 1988; Burgess 1991; Burgess and Richardson 1991).

### Genus RIMOSOTETRAS Burgess, 1991

*Type species. Rimosotetras problematica* Burgess, 1991, p. 586, pl. 1, figs 12, 14–15.

### *Rimosotetras problematica* Burgess, 1991

Plate 1, figs 8–10

?1979 'Spore tetrads, probably *Ambitisporites*', Holland and Smith, pl. 2, figs 5–6.
1985 'loose tetrads', Richardson *in* Hill *et al.*, pl. 15, figs 5–6.
?1987 'spore tetrad', Smelror, fig. 4*c*.

*Figured specimens* FM 275, Pl. 1, fig. 8 (slide CL7/2, co-ord. 1104 143; E.F. no: 040), sample CL7, DBF. FM 276, Pl. 1, fig. 9 (slide BH8/1, co-ord. 1222 099; E.F. no: K52/2), sample BH8, FBF. Pl. 1, fig. 10 (stub CW11, Print P004559), sample BL7, SBF.

*Description.* Permanent tetrads comprising subcircular to sub-triangular spore-like units. The individual spores usually have an inflated distal surface and are crassitate. The spores are discrete and a distinct line of attachment, in the form of a shallow cleft, is present at the junctions between adjacent spores. The tetrads are loosely attached but tend to remain bound together, although they are sometimes observed in a state of partial dissociation. The distal exine over the spores is laevigate, approximately 1 μm in thickness and frequently folded.

*Dimensions.* 32(48)70 μm; 27 specimens measured.

*Comparisons. Tetrahedraletes medinensis* (Strother and Traverse) emend. is always rigidly intact, and never in a state of partial dissociation, and comprises spores which are usually distally invaginated and have a more prominent equatorial crassitude. The spores of *Cheilotetras caledonica* gen. et sp. nov. are distally invaginated, fused to the adjacent spores of the tetrad and have flange-like extensions.

### Genus TETRAHEDRALETES (Strother and Traverse, 1979) emend.

*Type species. Tetrahedraletes medinensis* Strother and Traverse, 1979, Tuscarora Formation, Pennsylvania, USA.

*Emended diagnosis.* Permanent tetrahedral tetrads composed of subtriangular to subcircular spore-like units. The spores are crassitate and have a laevigate invaginated distal wall. The spores are discrete and the plane of attachment between adjoining spores forms a distinct line of attachment at the junction between the crassitudes.

*Generic comparison. Cheilotetras* gen. nov. has been erected for permanent tetrads with fused spores and *Tetrahedraletes* is retained only for those with discrete, unfused spores.

*Discussion.* Strother and Traverse (1979) proposed two genera of permanent tetrad, *Nodospora* and *Tetrahedraletes*, which were differentiated chiefly on the criteria that *Tetrahedraletes* has a tetrahedral configuration and *Nodospora* a cross-tetrad arrangement. Following intensive study of permanent tetrads, several authors concluded that the type specimens of *Tetrahedraletes* (*T. medinensis*) and *Nodospora* (*N. burnhamensis*) were synonymous as they represented different compressional morphologies of otherwise identical tetrads (Gray *et al.* 1983; Duffield 1985; Burgess 1991; Gray 1991). To account for this Burgess (1991) emended the diagnosis of *Tetrahedraletes* to accommodate naked, laevigate permanent tetrads and *Nodospora* was suppressed. Furthermore, *Velatitetras* Burgess, 1991 was erected to accommodate permanent tetrads that are enclosed within an envelope. Several forms of permanent tetrad with envelopes have previously been described and placed in *Nodospora* (Strother and Traverse 1979; Miller and Eames 1982; Johnson 1985). However, Burgess's emendation of *Tetrahedraletes* differs from the original definition of Strother and Traverse in one important aspect. Burgess stipulated that *Tetrahedraletes* comprised spores which could be either fused or unfused. We consider that the type species of *Tetrahedraletes* and *Nodospora* are synonymous but have emended the diagnosis of Strother and Traverse because we consider that the nature of the junction between the spores, i.e. fused or unfused, is an important character.

### *Tetrahedraletes medinensis* (Strother and Traverse, 1979) emend.

Plate 2, figs 8, 10–12

| | |
|---|---|
| 1971 | 'spore tetrads in tetrahedral configuration', Gray and Boucot, fig. 1*h*. |
| 1971 | tetrad of rather thick walled spore-like alete palynomorphs', Cramer, pl. 4, fig. 1. |

EXPLANATION OF PLATE 1

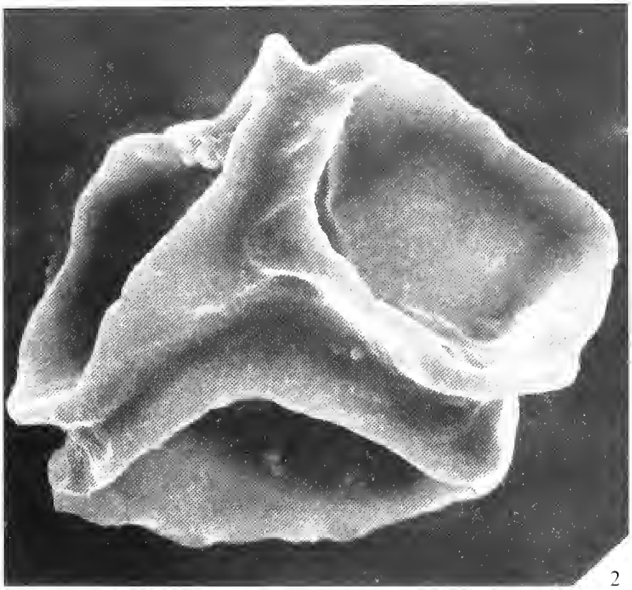
Figs 1–7. *Cheilotetras caledonica* gen. et sp. nov. 1, (stub CW36, Print P006225) sample CL7; Logan Formation; Logan Water, Lesmahagow inlier, × 1450. 2, (stub CW2, Print P004398) sample AH5; Fish Bed Formation; Glenbuck Loch, Hagshaw Hills inlier, × 1700. 3, 6, FM 272; holotype (slide CL6/2, co-ord. 1120 109; E.F. no. K42/4) sample CL6; Logan Formation; Logan Water, Lesmahagow inlier. 4–5, FM 273 (slide CL9/1, co-ord. 1319 107; E.F. no. K62/4) sample CL9; Logan Formation; Logan Water, Lesmahagow inlier. 7, FM 274 (slide CL7/2, co-ord. 1333 062; E.F. no. F64/2) sample CL7; Logan Formation; Logan Water, Lesmahagow inlier.

Figs 8–10. *Rimosotetras problematica* Burgess and Richardson, 1991. 8, FM 275 (slide CL7/2, co-ord. 1104 143; E.F. no. O40) sample BL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 9, FM 276 (slide BH8/1, co-ord. 1222 099; E.F. no. K52/2) sample BH8; Fish Bed Formation; Glenbuck Loch, Hagshaw Hills inlier. 10, (stub CW11, Print P004559) sample BL7; Slot Burn Formation, Slot Burn, Lesmahagow inlier. × 1530.

All figures × 1000, except where otherwise stated.

PLATE 1


1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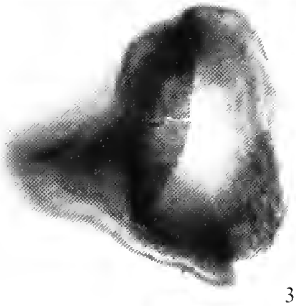
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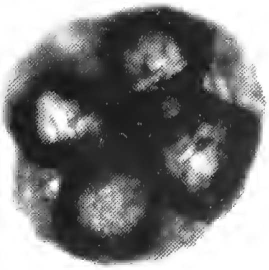
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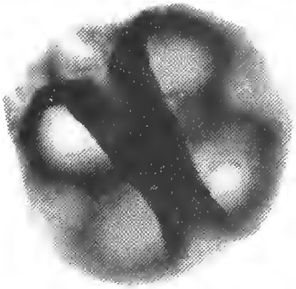
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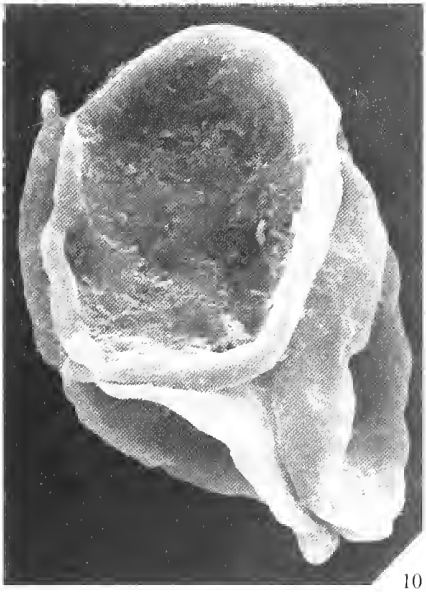
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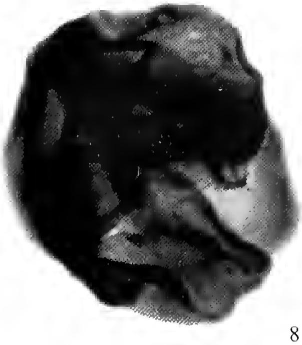
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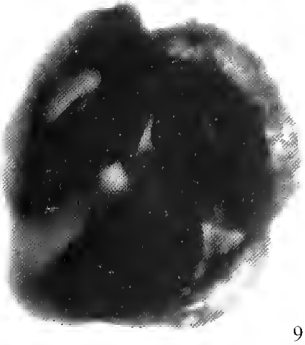
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WELLMAN and RICHARDSON, *Cheilotetras*, *Rimosotetras*

1972 'non-miospore tetradic palynomorph', Cramer and Diez del Cramer, p. 116, pl. 36, figs 79, 84.
1979 *Tetrahedraletes medinensis* Strother and Traverse, p. 8, pl. 1, figs 5, 14–17.
1979 *Nodospora burnhamensis* Strother and Traverse, p. 10, pl. 1, fig. 11; pl. 2, fig. 1.
1982 'tetrahedral tetrads', Gray *et al.*, figs 2A–B, 3, 4, 8, 9, 10A–B.
1982 *Tetrahedraletes medinensis* Strother and Traverse; Miller and Eames, p. 250, pl. 5, fig. 1; pl. 6, fig. 1.
1982 *Nodospora burnhamensis* Strother and Traverse; Miller and Eames, p. 248, pl. 5, fig. 5; pl. 6, fig. 3.
1985 *Tetrahedraletes* cf. *T. medinensis*, Gray *et al.*, fig. 5*f–h*.
1985 *Tetrahedraletes medinensis* Strother and Traverse; Johnson, p. 344, pl. 11, figs 1, 3.
1985 *Nodospora burnhamensis* Strother and Traverse; Johnson, p. 344, pl. 11, fig. 4.
1985 *cf. Tetrahedraletes medinensis* Strother and Traverse; Richardson *in* Hill *et al.*, pl. 15, fig. 1.
1985 'permanent tetrad', Richardson *in* Hill *et al.*, pl. 15, fig. 3.
1985 *Nodospora burnhamensis* Strother and Traverse; Duffield, fig. 1–6 (*non* fig. 8).
1986 *Tetrahedraletes* cf. *T. medinensis*, Gray *et al.*, fig. 6, items 1–7.
1987 *Tetrahedraletes medinensis* Strother and Traverse; Smelror, fig. 4J.
1989 *Tetrahedraletes medinensis* Strother and Traverse; Barron, fig. 6D.
1991 *Tetrahedraletes medinensis* var. *parvus* Burgess, p. 579, pl. 1, figs 1–4.
1991 *Tetrahedraletes medinensis* Strother and Traverse; Burgess and Richardson, p. 604, pl. 1, figs 12–13.

*Holotype and type locality*. As designated for *Tetrahedraletes medinensis* Strother and Traverse, 1979, Tuscarora Formation, Pennsylvania, USA.

*Figured specimens*. Pl. 2, fig. 8 (stub CW32, Print P007350), sample CL13, LF. FM 268, Pl. 2, fig. 10 (slide BL13/2, co-ord. 1280 159; E.F. no: Q59/1), sample BL13, DBF. FM 269, Pl. 2, fig. 11 (slide BL13/2, co-ord. 1069 060; E.F. no: F37/1), sample BL13, DBF. FM 270, Pl. 2, fig. 12 (slide BL7/4, co-ord 1153 100; E.F. no. K46/1) sample BL7, SBF.

*Emended diagnosis*. A *Tetrahedraletes* which is firmly bonded with prominent equatorial crassitudes on the individual spores and distinct lines of attachment at the junctions between adjacent spores. The distal walls of the spores are laevigate, rigid and invaginated.

*Description*. Permanent tetrahedral tetrads comprising subcircular to subtriangular spore-like units. Individual spores with a rounded crassitude, which is 1–4 $\mu$m wide, and an invaginated distal surface. The spores are discrete, and a plane of attachment is present between the junctions of adjacent spores forming distinct sutures (lines of attachment) on the surface of the tetrad between the crassitudes of adjacent spores. The tetrads are

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EXPLANATION OF PLATE 2

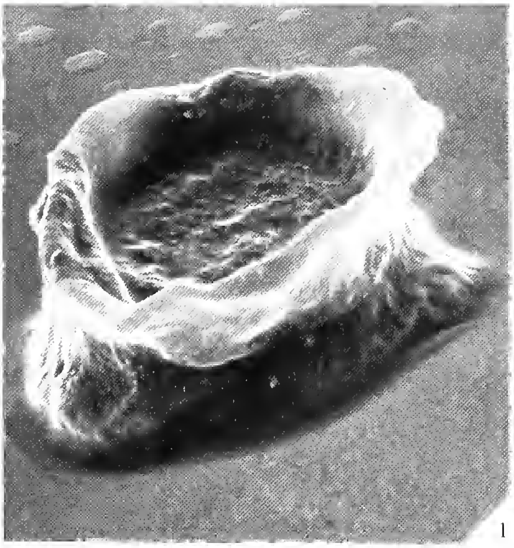
Figs 1–7. *Pseudodyadospora petasus* sp. nov. 1, 4, (stub CW17, Print P004937 and P004938) sample BH4; Fish Bed Formation; Glenbuck Loch, Hagshaw Hills inlier; 1, ×2170; 2, ×5000. 2–3, FM 266; holotype (slide CL6/2, co-ord. 1158 064; E.F. no. F46) sample CL6; Logan Formation; Logan Water, Lesmahagow inlier. 5, FM 267 (slide BL13/2, co-ord. 1293 062; E.F. no. F60/1) sample BL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 6–7, FM 296 (slide CL7/2, co-ord. 1147 070; E.F. no. F45/3) sample CL7; Slot Burn Formation; Slot Burn, Lesmahagow inlier.

Figs 8, 10–12. *Tetrahedraletes medinensis* (Strother and Traverse) emend. 8, (stub CW32, Print P007350) sample CL13; Logan Formation; Logan Water, Lesmahagow inlier, ×2500. 10, FM 268 (slide BL13/2, co-ord. 1280 159; E.F. no. Q59/1) sample BL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 11, FM 269 (slide BL13/2, co-ord. 1069 060; E.F. no. F37/1) sample BL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 12, FM 270 (slide BL7/4, co-ord. 1153 100; E.F. no. K46/1) sample BL7; Slot Burn Formation; Slot Burn, Lesmahagow inlier.

Fig. 9. '*Moyeria*' *cabottii* (Cramer) Miller and Eames, 1982. FM 271 (slide CL5/2, co-ord. 1155 182; E.F. no. S46) sample CL5; Logan Formation; Logan Water, Lesmahagow inlier.

All figures ×1000, except where otherwise stated.

PLATE 2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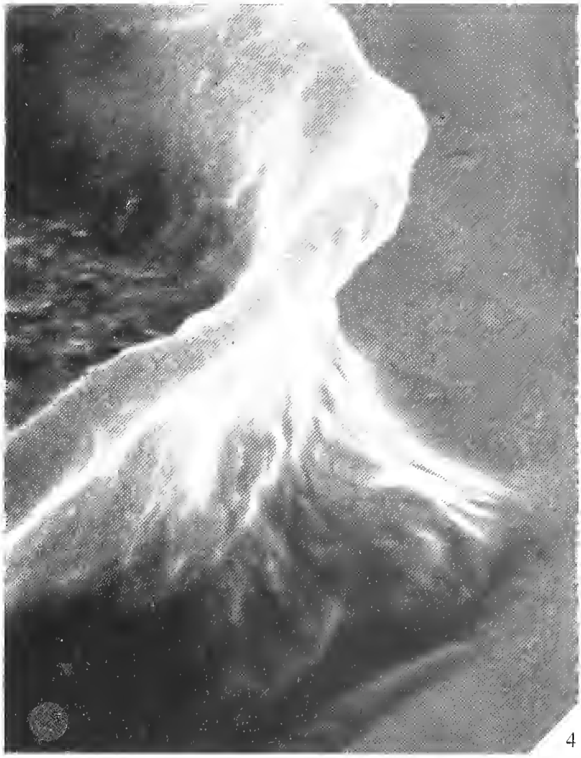
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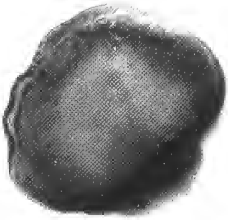
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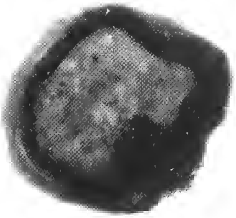
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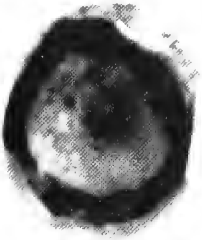
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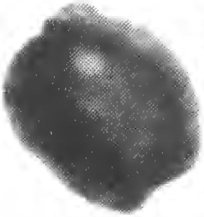
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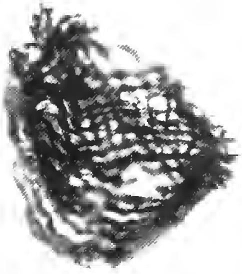
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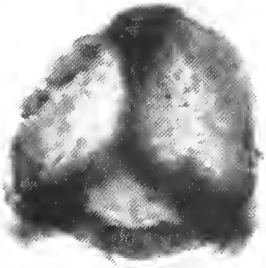
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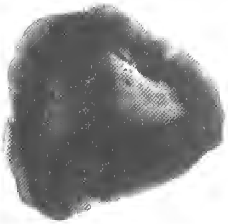
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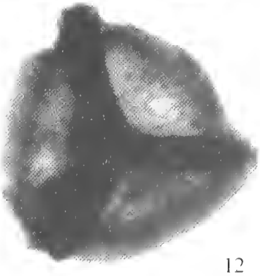
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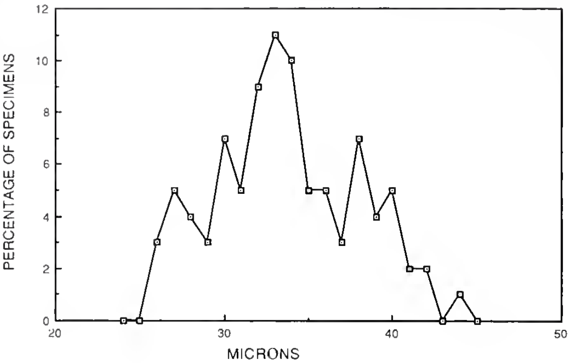
WELLMAN and RICHARDSON, *Pseudodyadospora*, *Tetrahedraletes*, '*Moyeria*'



TEXT-FIG. 5. Size frequency distribution of 100 *Tetrahedraletes medinensis* (Strother and Traverse) emend. from sample CL7, Logan Formation, Logan Water, Lesmahagow inlier.

securely bonded and none was observed in a state of dissociation. The distal exine is laevigate and 1–2 μm in thickness.

*Dimensions*. 24(34)50 μm; 100 specimens measured (Text-fig. 5).

*Comparison*. *Cheilotetras caledonica* gen. et sp. nov. comprises fused spores with their distal exines with flange-like extensions. The spores of *Rimosotetras problematica* Burgess, 1991 are loosely attached and usually comprises distally inflated spores.

3. *Fused cryptospore dyads* (*pseudodyads*). Permanent dyads of this type were first recognized by Johnson (1985) from strata of Llandovery age from Pennsylvania and are almost certainly equivalent to the 'diacrodoid acritarchs' described by Strother and Traverse (1979) (Gensel *et al.* 1991). Pseudodyads comprise two permanently fused spores joined by an encircling thickened band which may, or may not, be attached to a single crosswall (Text-fig. 3c). If a crosswall is present there is no noticeable plane of attachment between the spores of the pseudodyad and no line of attachment is seen on the exterior of the sporomorphs. Pseudodyads occur naked or enclosed within an envelope (Johnson 1985; Richardson 1988; Burgess 1991).

### Genus PSEUDODYADOSPORA Johnson, 1985

*Type species*. *Pseudodyadospora laevigata* Johnson, 1985

### *Pseudodyadospora petasus* sp. nov.

Plate 2, figs 1–7

*Derivation of name*. From the Latin '*petasus*', meaning hat, referring to the shape of each unit.

*Holotype and type locality*. FM 266, Pl. 2, figs 2–3 (slide CL6/2, co-ord. 1158 064; E.F. no: F46), sample CL6, Logan Formation at Logan Water, Lesmahagow inlier.

*Paratypes*. Pl. 2, figs 1, 4 (stub CW17, Print P004937 and P004938), sample BH4, FBF. FM 267, Pl. 2, fig. 5 (slide BL13/2, co-ord. 1293 062; E.F. no: F60/1), sample BL13, DBF. FM 296, Pl. 2, figs 6–7 (slide CL7/2, co-ord. 1147 070; E.F. no: F45/3), sample CL7, SBF.

*Diagnosis*. A *Pseudodyadospora* with an equatorial constriction at the place of attachment. Exine laevigate. Spores have a distinctly invaginated distal wall, and a shorter polar axis than equatorial axis.

*Description.* Pseudodyads circular in polar view and distally invaginated. In equatorial view the sporomorph has the profile of two shallow bowls attached by their undersides. The junction between the two spores is entirely fused and no line of attachment is present on the pseudodyad surface. The pseudodyads are generally isomorphic and usually preserved in polar compression. The exine is laevigate, 1–2 $\mu$m in thickness, and is rigid or occasionally folded.

*Dimensions.* 26(32)44 $\mu$m; 55 specimens measured.

*Comparison. Pseudodyadospora laevigata* Johnson, 1985 is distally inflated rather than invaginated and the spores are generally not joined across a marked constriction.

*Comments. Pseudodyadospora petasus* sp. nov. has a shape which distinguishes it from all other species of pseudodyad that have been described. In many respects the morphology is reminiscent of the cryptospore permanent tetrad *Cheilotetras caledonica* gen. et sp. nov. and it may be that the two are in some way related. However, like *Cheilotetras caledonica*, the internal structure of *Pseudodyadospora petasus* is unclear. It seems likely that the spores share a common crosswall, but the possibility exists that it comprises discrete spores where the plane of attachment is incompletely developed or the line of attachment is masked. Sporomorphs that can be assigned to *P. petasus* have been reported over a wide stratigraphical range including records from the Stonehaven Group at Stonehaven, Scotland which is of late Wenlock age (Wellman 1991) and the Downton and Ditton Groups of southern Britain, of Přídolí and Gedinnian age respectively (Richardson unpublished data).

4. *Unfused cryptospore dyads* (*true dyads*). These dyads comprise two distinct spores with a clear plane of attachment between them forming a line of attachment on the surface of the dyad. The dyads exhibit different degrees of dissociation across the contact area between the spores. Separated spores appear to be identical to hilate cryptospores, which generally co-occur with the dyads, and it is likely that the dyads are the source of most, if not all, of these sporomorphs (Burgess and Richardson 1991). True dyads are usually naked but there are reports of some enclosed in envelopes (Johnson 1985; Richardson 1988; Wellman 1991).

### Genus DYADOSPORA (Strother and Traverse, 1979) Burgess and Richardson, 1991

*Type species. Dyadospora murusattenuata* (Strother and Traverse) Burgess and Richardson, 1991.

### *Dyadospora murusattenuata* (Strother and Traverse) Burgess and Richardson, 1991

Plate 3, figs 9, 12

| | |
|---|---|
| 1979 | *Dyadospora murusattenuata* Strother and Traverse, p. 15, pl. 3, figs 9–10. |
| 1982 | *Dyadospora murusattenuata* Strother and Traverse; Miller and Eames, p. 247, pl. 6, fig. 8. |
| 1985 | *Dyadospora murusattenuata* Strother and Traverse; Johnson, p. 334. |
| 1991 | *Dyadospora* cf. *murusattenuata* Strother and Traverse; Burgess, p. 592, pl. 2, fig. 10. |
| 1991 | *Dyadospora murusattenuata* (Strother and Traverse) Burgess and Richardson, p. 614, pl. 2, figs 7, 9. |

*Figured specimens.* FM 262, Pl. 3, fig. 9 (slide DL13/2, co-ord. 1227 224; E.F. no: W53/4), sample DL13, DBF. FM 263, Pl. 3, fig. 12 (slide DL13/2, co-ord. 1274 133; E.F. no: N58), sample DL13, DBF.

*Description.* The dyads are circular to sub-circular in polar and equatorial view and generally isomorphic. They consist of two distally inflated spores which are normally slightly shorter than they are wide in equatorial view. Dyads usually preserved in oblique compression. The spores are joined at contact areas which are surrounded by an equatorial crassitude. There is a distinct plane of attachment between the spores identified by a line of attachment between the two crassitudes. The two spores are often partly separated. Distal exine laevigate, 1 $\mu$m or less in thickness, and almost invariably folded.

*Dimensions.* Total dyad length 30(37)48 μm, equatorial width 27(32)40 μm; 40 specimens measured.

*Comparisons. Dyadospora murusdensa* (Strother and Traverse) Burgess and Richardson, 1991 comprises spores with a thicker, more rigid exine which is not normally folded.

*Comments.* This true dyad species is believed to comprise two hilate cryptospores of the species *Laevolancis plicata* Burgess and Richardson, 1991. It is possible that many, if not all, of the specimens of *L. plicata* which co-occur with *D. murusattenuata* in the assemblages are derived from dissociation of such dyads. Because specimens of *L. plicata* are more abundant than *D. murusattenuata* in most preparations (Text-fig. 4), it seems likely that these sporomorphs are habitually dispersed in the dissociated form.

### *Dyadospora murusdensa* (Strother and Traverse, 1979) Burgess and Richardson, 1991

Plate 3, figs 10, 13

| | |
|---|---|
| 1979 | *Dyadospora murusdensa* Strother and Traverse, p. 15, pl. 3, figs 6–7 |
| 1982 | *Dyadospora murusdensa* Strother and Traverse; Miller and Eames, p. 247, pl. 6, fig. 7. |
| 1985 | *Dyadospora murusdensa* Strother and Traverse; Johnson, p. 334, pl. 7, fig. 9. |
| 1985 | *Dyadospora murusdensa* Strother and Traverse; Richardson *in* Hill *et al.*, pl. 15, figs 8–9. |
| 1988 | *Dyadospora murusdensa* Strother and Traverse; Richardson, p. 94, pl. 16, fig. 2. |
| 1989 | *Dyadospora murusdensa* Strother and Traverse; Barron, p. 84, fig. 6F. |

*Figured specimens.* FM 264, Pl. 3, fig. 10 (slide DL14/2, co-ord. 1161 156; E.F. no. P46/4), sample DL14, DBF. FM 265, Pl. 3, fig. 13 (slide DL13/2, co-ord. 1350 203; E.F. no. U66/3), sample DL13, DBF.

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## EXPLANATION OF PLATE 3

Figs 1–3. *Ambitisporites avitus* Hoffmeister, 1959. 1, (stub CW17, Print P004939) sample BH4; Fish Bed Formation; Glenbuck Loch, Hagshaw Hills inlier, × 2000. 2, FM 256 (slide BL7/4, co-ord. 1295 139; E.F. no. 060/1/2) sample BL7; Slot Burn Formation; Slot Burn, Lesmahagow inlier. 3, FM 257 (slide BL13/2, co-ord. 1093 189; E.F. no. T39/2) sample BL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier.

Figs 4–6. *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969. 4, FM 258 (slide CL9/4, co-ord. 1275 071; E.F. no. G58/1) sample CL9; Logan Formation; Logan Water, Lesmahagow inlier. 5, FM 259 (slide BL13/2, co-ord. 1095 190; E.F. no. T40/1) sample BL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 6, (stub CW11, Print P005069) sample BL7; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 2000.

Fig. 7. *Laevolancis plicata* Burgess and Richardson, 1991. FM 260 (slide BL7/5, co-ord. 1119 123; E.F. no. M42) sample BL7; Slot Burn Formation; Slot Burn, Lesmahagow inlier.

Figs 8, 11. *Laevolancis* (*Archaeozonotriletes*) *divellomedium* (Chibrikova) Burgess and Richardson, 1991. 8, FM 261 (slide DL14/2, co-ord. 1095 206; E.F. no. U39/4) sample DL14; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 11, (stub CW26, Print P005115) sample BH9; Fish Bed Formation; Glenbuck Loch, Hagshaw Hills inlier, × 2000.

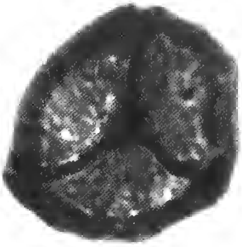
Figs 9, 12. *Dyadospora murusattenuata* (Strother and Traverse) Burgess and Richardson, 1991. 9, FM 262 (slide DL13/2, co-ord. 1227 224; E.F. no. W53/4) sample DL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 12, FM 263 (slide DL13/2, co-ord. 1274 133; E.F. no. N58) sample DL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier.

Figs 10, 13. *Dyadospora murusdensa* (Strother and Traverse) Burgess and Richardson, 1991. 10, FM 264 (slide DL14/2, co-ord. 1161 156; E.F. no. P46/4) sample DL14; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier. 13, FM 265 (slide DL13/2, co-ord. 1350 203; E.F. no. U66/3) sample DL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier.

All figures × 1000, except where otherwise stated.

PLATE 3


1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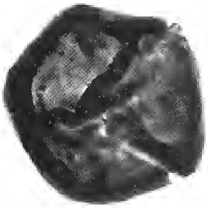
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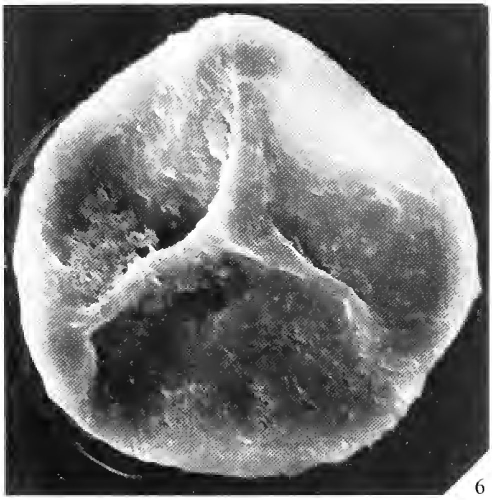
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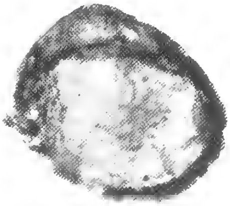
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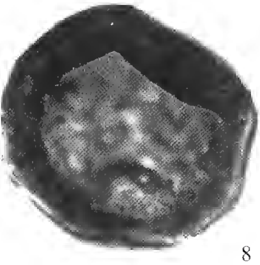
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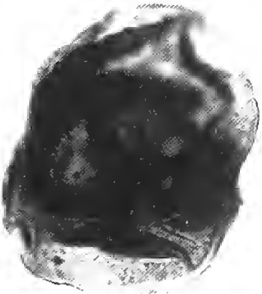
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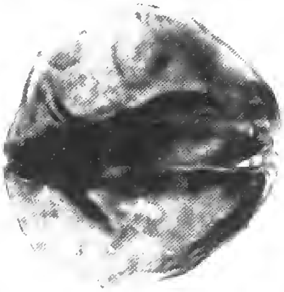
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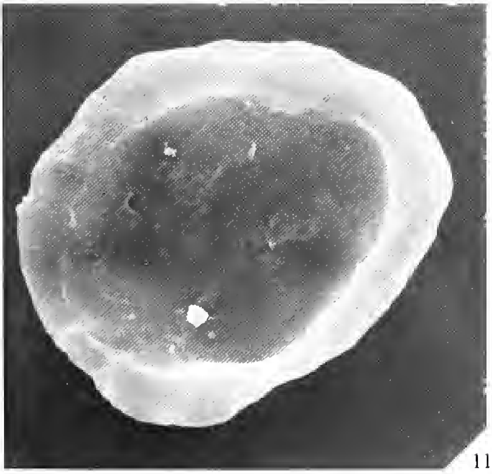
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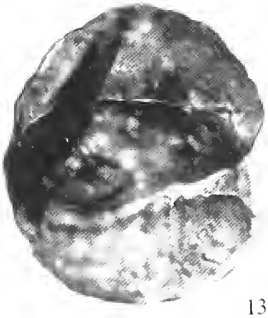
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WELLMAN and RICHARDSON, *Ambitisporites*, *Laevolancis*, *Dyadospora*

*Description.* Dyads consist of two spores which are distally inflated and, in equatorial view, are usually slightly shorter than they are wide. Dyads usually preserved in oblique compression and are circular to subcircular in polar and equatorial view and generally isomorphic. The spores are joined at contact areas which are surrounded by a prominent equatorial crassitude, and a distinct plane of attachment forms of a line of attachment, usually in the form of a cleft, between the two crassitudes. Spores frequently partly separated. Exine distally laevigate, rigid, *c.* 2 μm in thickness, and usually without folds.

*Dimensions.* Total dyad length 30(39)56 μm, equatorial width 32(35)48 μm; 26 specimens measured.

*Comparisons.* The exine of *Dyadospora murusattenuata* (Strother and Traverse) Burgess and Richardson, 1991 is thinner, less rigid, and usually folded.

*Comments.* Burgess and Richardson (1991) suggested that *Dyadospora murusdensa* comprises two hilate cryptospores of the species *Laevolancis* (*Archaeozonotriletes*) *divellomedium* (Chibrikova) Burgess and Richardson, 1991. It is possible that many, if not all, of these hilate cryptospores are derived from dissociated specimens of *D. murusdensa*. As is the case with *L. plicata* and *D. murusattenuata*, *L. divellomedium* is more abundant than *D. murusdensa* in most preparations (Text-fig. 4), and it seems likely that these sporomorphs are habitually dispersed in the dissociated form.

5. *Hilate cryptospores.* These cryptospores consist of a solitary spore (monad) which possesses a roughly circular contact area (hilum) often defined by an equatorial, or subequatorial, crassitude or a change in ornament. The contact area is usually thinner than the distal exine. The exine, including the contact area, may be laevigate or variously ornamented. Closely similar monads have been observed partly united at the contact area as a loose dyad.

### Genus LAEVOLANCIS Burgess and Richardson, 1991

*Type species. Laevolancis* (*Archaeozonotriletes*) *divellomedium* (Chibrikova) Burgess and Richardson, 1991, p. 607, pl. 2, figs 4, 6.

### *Laevolanics* (*Archaeozonotriletes*) *divellomedium* (Chibrikova) Burgess and Richardson, 1991

Plate 3, figs 8, 11

| | |
|---|---|
| 1959 | *Archaeozonotriletes divellomedium* Chibrikova, p. 65, pl. 9, fig. 4. |
| 1966 | *Hispanaediscus bernesgae* Cramer, p. 82, pl. 2, fig. 4. |
| 1969 | ?*Archaeozonotriletes* cf. *divellomedium* Chibrikova; Richardson and Lister, p. 238, pl. 43, fig. 12. |
| 1973 | ?*Archaeozonotriletes* cf. *divellomedium* Chibrikova; Richardson and Ioannides, p. 280, pl. 8, figs 10–11. |
| 1979 | *Archaeozonotriletes* cf. *chulus nanus* Richardson and Lister; Holland and Smith, pl. 2, figs 7–9. |
| 1979 | 'smooth-walled inaperturate spore', Strother and Traverse, p. 14, pl. 3, fig. 5. |
| 1984 | ?*Stenozonotriletes irregularis* Schultz; McGregor, p. 37, pl. 1, fig. 26. |

*Figured specimens.* FM 261, Pl. 3, fig. 8 (slide DL14/2, co-ord. 1095 206; E.F. no. U39/4), sample DL14, DBF., Pl. 3, fig. 11 (stub CW26, Print P005115), sample BH9, FBF.

*Description.* Amb circular to subcircular in polar compression. Equatorial to subequatorial crassitude 1–2 μm wide delimits a circular to subcircular contact area (hilum). Exine laevigate over contact area, appears thinner than the distal exine, and is sometimes folded, ruptured or collapsed. Distal exine laevigate, rigid and usually unfolded, *c.* 2 μm in thickness.

*Dimensions.* 28(36)46 μm; 100 specimens measured.

*Comparison and remarks. Laevolancis plicata* Richardson and Burgess, 1991 has a thinner, less rigid wall and a less prominent crassitude. *L. divellomedium* is probably derived from thick-walled true dyads, similar, if not identical to, *Dyadspora murusdensa* (Strother and Traverse) Burgess and Richardson, 1991.

### *Laevolancis plicata* Burgess and Richardson, 1991

Plate 3, fig. 7

1991 *Laevolancis plicata* Burgess and Richardson, p. 607, pl. 2, fig. 8.

*Figured specimen.* FM 260, Pl. 3, fig. 7 (slide BL7/5, co-ord. 1119 123; E.F. no. M42), sample BL7, SBF.

*Description.* Amb circular to subcircular. Equatorial to subequatorial crassitude *c.* 1 μm wide delimits a more or less circular contact area (hilum). Exine over contact area laevigate, thin, less than 1 μm in thickness, and often collapsed or absent. Distal exine laevigate, thin, *c.* 1 μm in thickness, and usually folded.

*Dimensions.* 30(34)40 μm; 40 specimens measured.

*Comparison and remarks. Laevolancis* (*Archaeozonotriletes*) *divellomedium* (Chibrikova) Burgess and Richardson, 1991, has a more prominent crassitude and a thicker, more rigid distal exine. Specimens of *L. plicata* are closely similar to spores to *Dyadospora murusattenuata* (Strother and Traverse) Burgess and Richardson, 1991

### Anteturma SPORITES Potonié, 1893
### Turma TRILETES Reinsch, 1891
### Subturma ZONOTRILETES Waltz, 1935, *in* Luber and Waltz 1938
### Infraturma CRASSITI Bharadwaj and Venkatachala, 1961
### Genus AMBITISPORITES Hoffmeister, 1959

*Type species. Ambitisporites avitus* Hoffmeister, 1959.

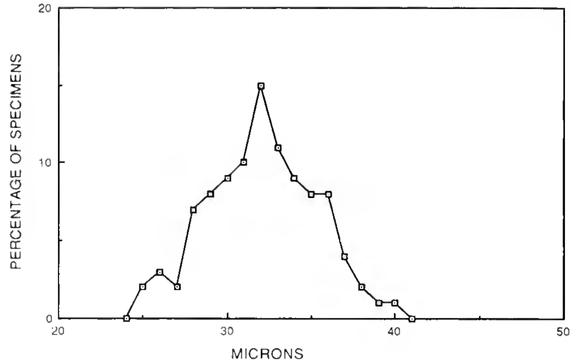
### *Ambitisporites avitus* Hoffmeister, 1959

Plate 3, figs 1–3

1959 *Ambitisporites avitus* Hoffmeister, p. 332, pl. 1, figs 1–8.
1969 *Ambitisporites* cf. *avitus* Hoffmeister; Richardson and Lister, p. 228, pl. 40, fig. 2.
1973 *Ambitisporites avitus* Hoffmeister; Richardson and Ioannides, p. 277, pl. 5, figs 1–8.
?1975 'single spore showing equatorial thickening', Smith, pl. 1*e*.
1977 *Ambitisporites avitus* Hoffmeister; Colthurst and Smith, pl. 2, fig. 15.
1978 *Ambitisporites avitus* Hoffmeister; Emo and Smith, pl. 1, fig. 4.
1978 *Ambitisporites avitus* Hoffmeister; Rodriguez, p. 412, pl. 1, fig. 4.
1983 *Ambitisporites avitus* Hoffmeister; Rodriguez, p. 28, pl. 1, fig. 1.
1987 *Ambitisporites avitus* Hoffmeister; Smelror, fig. 4A–B.
1989 *Ambitisporites avitus* Hoffmeister; Barron, fig. 6A.

*Figured specimens.* Pl. 3, fig. 1 (stub CW17, Print P004939), sample BH4, FBF. FM 256, Pl. 3, fig. 2 (slide BL7/4, co-ord. 1295 139; E.F. no. 060/1/2), sample BL7, SBF. FM 257, Pl. 3, fig. 3 (slide BL13/2, co-ord. 1093 189; E.F. no. T39/2), sample BL13, DBF.

*Description.* Amb subcircular to subtriangular. Trilete mark distinct and simple with straight laesurae which usually extend to the equator of the spore. Laesurae diverge into curvaturae which are coincident with the equator of the spore and form a distinct and prominent equatorial crassitude which is 1·5–2·5 μm wide. In



TEXT-FIG. 6. Size frequency distribution of 100 *Ambitisporites avitus* Hoffmeister, 1959 from sample CL7, Logan Formation; Logan Water, Lesmahagow inlier.

obliquely compressed specimens the curvaturae can sometimes be seen to invaginate. Exine laevigate, distally 1–2 μm in thickness.

*Dimensions*. 25(32)39 μm; 100 specimens measured (Text-fig. 6).

*Comparison*. *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969 is similar but has a less prominent equatorial crassitude. However, there is probably intergradation between the two species (see Richardson and Ioannides 1973, p. 277). In this investigation, the size range of the two species proved to be virtually identical (Text-figs 6–7).

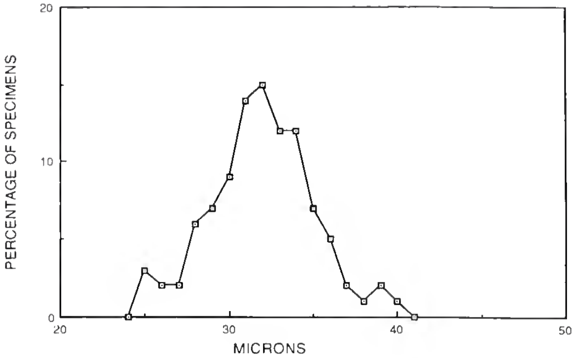
### *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969

Plate 3, figs 4–6

| | |
|---|---|
| 1959 | *Punctatisporites dilutus* Hoffmeister, p. 334, pl. 1, figs 9–13. |
| 1969 | *Ambitisporites* cf. *dilutus* (Hoffmeister) Richardson and Lister, p. 229, pl. 40, fig. 3. |
| 1973 | *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Richardson and Ioannides, p. 277, pl. 6, figs 1–5. |
| 1977 | *Ambitisporites avitus* Hoffmeister; Colthurst and Smith, pl. 2, fig. 17. |
| ?1978 | *Ambitisporites*, Pratt *et al.*, pl. 3, figs 7–10. |
| 1978 | *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Rodriguez, p. 412, pl. 1, fig. 5. |
| 1979 | *Ambitisporites* sp. Strother and Traverse, pl. 3, figs 1–4. |
| 1979 | *Ambitisporites avitus* Hoffmeister; Holland and Smith, pl. 2, figs 1–4. |
| 1983 | *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Rodriguez, p. 29, pl. 1, figs 3, 7. |
| 1984 | *Punctatisporites*? *dilutus* Hoffmeister; McGregor, p. 33, pl. 1, fig. 14. |
| 1985 | *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Richardson *in* Hill *et al.*, pl. 16, figs 3, 5–6. |
| 1987 | *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Smelror, fig. 4D, 4K. |
| 1989 | *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Barron, fig. 6B. |
| 1991 | *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Burgess and Richardson, p. 615, text-fig. 3D–H. |
| 1991 | *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; Burgess, p. 594, pl. 2, fig. 15. |

*Figured specimens*. FM 258, Pl. 3, fig. 4 (slide CL9/4, co-ord. 1275 071; E.F. no. G58/1), sample CL9 LF. FM 259, Pl. 3, fig. 5 (slide BL13/2, co-ord. 1095 190; E.F. no. T40/1), sample BL13, DBF., Pl. 3, fig. 6 (stub CW11, Print P005069), sample BL7, SBF.

*Description*. Amb circular to subtriangular. Triradiate mark distinct and simple with straight sutures which extend to the spore equator. The laesurae diverge into curvaturae which are coincident with the equator of the spore and form an equatorial crassitude. The crassitude varies from 0·5 to 1·5 μm in width. The curvaturae can be seen to invaginate in obliquely preserved specimens. The spores are smooth walled. Distal exine 1–2 μm in thickness.



TEXT-FIG. 7. Size frequency distribution of 100 *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969 from sample CL7, Logan Formation; Logan Water, Lesmahagow inlier.

*Dimensions.* 25(32)40 μm; 100 specimens measured (Text-fig. 7).

*Comparison. Ambitisporites avitus* Hoffmeister, 1959, has a more prominent crassitude.

6. *Indeterminate.* According to Fensome *et al.* (1991) the genus '*Moyeria*' is a junior synonym of *Dactylofusa*. However, we provisionally retain the genus '*Moyeria*' to accommodate atypical palynomorphs like '*Moyeria*' *cabottii* pending further detailed taxonomic work. '*Moyeria*' differs from typical acritarchs and alete cryptospore monads, e.g. *Strophomorpha ovata* Miller and Eames, 1982. *Strophomorpha* is of similar general morphology to '*Moyeria*' but has a thicker, more rigid, wall which resembles that of cryptospore tetrads and dyads and appears to differ from that of '*Moyeria*' (see also Miller and Eames 1982). Thus, in order to highlight the differences between '*Moyeria*' *cabottii*, acritarchs, and cryptospores we prefer to categorize '*Moyeria*' as indeterminate. In a comprehensive review, Gray and Boucot (1989) proposed that '*Moyeria*' inhabited freshwater environments and may have euglenoid affinities. Whilst we regard the latter as unproven, our paper also reports '*Moyeria*' *cabottii* from deposits interpreted as non-marine.

### Genus 'MOYERIA' Thusu, 1973

*Type species. Moyeria uticaensis* Thusu, 1973.

### *Moyeria cabottii* (Cramer) Miller and Eames, 1982

Plate 2, fig. 9

1970 *Eupoikilofusa cabottii* Cramer, p. 87, pl. 4, figs 66–67.
1974 *Schizaeoisporites* sp. 1, Martin, p. 32, pl. 4, figs 115–116, 123; pl. 7, figs 233, 236.
1978 *Moyeria uticaensis* Thusu; McGregor and Narbonne, pl. 1, figs 29–31.
?1979 *Moyeria* sp. Holland and Smith, pl. 2, fig. 10.
1982 *Moyeria cabotti* (Cramer) Miller and Eames, p. 242, pl. 3, fig. 3.
1983 *Eupoikilofusa cabottii* Cramer; Rodriguez, p. 63, pl. 10, figs 5–6.
1984 *Eupoikilofusa cabottii* Cramer; Turner, p. 109, pl. 12, figs 3, 6.
1985 *Moyeria cabottii* (Cramer) Miller and Eames; Johnson, p. 330, pl. 3, fig. 5.
1989 *Moyeria cabottii* Cramer; Gray and Boucot, figs 1A–E, 2A–B.

*Figured specimen.* FM 271, Pl. 2, fig. 9 (slide CL5/2, co-ord. 1155 182, E.F. no. S46), sample CL5, LF.

*Description.* Body ellipsoidal to ovoidal and hollow. Externally ornamented with muri arranged in a bihelical pattern, that is, the muri originate at one pole of the body from where they spiral in the same direction until they reach the pole at the opposite end of the body. The muri are less than 0·5–1·0 μm high, less than 0·75 μm wide and 0·5–1·0 μm apart. The body wall is relatively thin.

*Dimensions.* 29(45)73 μm; 85 specimens measured.

*Comparison. Qualisaspora fragilis* Richardson, Ford and Parker, 1984 has a similar ornament but comprises two layers: a laevigate, thick-walled inner body enclosed within an ornamented, thin-walled outer layer. *Strophomorpha ovata* Miller and Eames, 1982 is thick walled and is ornamented with broader and more closely space muri than those in '*Moyeria*' *cabottii.*

*Remarks.* As '*Moyeria*' *cabottii* occurs in non-marine deposits it seems reasonable to suppose that it either represents subaerially dispersed reproductive propagules derived from a terrestrial plant or the remains of an organism which inhabited non-marine water bodies. The dissimilarity of '*Moyeria*' *cabottii* to other sporomorphs, mainly because of its thin wall, may indicate that it was not subaerially dispersed. Therefore it seems likely that '*Moyeria*' *cabottii* represents the remains of some form of organism which inhabited continental water bodies. The possibility that the specimens of '*Moyeria*' *cabottii* are reworked from older marine strata is ruled out because no typical marine palynomorphs, such as chitinozoans and acritarchs, which would also be expected to be reworked are present.

## COMPOSITION OF THE PALYNOMORPH ASSEMBLAGE

Palynomorph assemblages consisting entirely of land-derived forms were recovered from the Fish Bed Formation (Hagshaw Hills inlier) and the Dippal Burn, Slot Burn and Logan Formations (Lesmahagow inlier). In the Henshaw Formation (North Esk inlier) rare marine acritarchs are also present (Pl. 4, fig. 6). The assemblages contain cryptospores, miospores, cuticle-like sheets, tubular structures and the enigmatic palynomorph '*Moyeria*'. The suite of palynomorphs is almost identical in each of the formations, except for the presence of acritarchs in the Henshaw Formation. Among the microfossils, cryptospores are dominant in variety and relative abundance but miospores are present in all of the samples. The relative abundances of the palynomorphs and a species list is presented in Text-figure 4. In the following synopsis, results of frequency counts are expressed in the form of three figures, for example 2(6)11 per cent, where the first and last numbers refer, respectively, to the minimum and maximum percentage frequency encountered in the counts, and the number in parentheses refers to the mean of all of the counts.

The cryptospores included permanent tetrads, pseudodyads, true dyads, hilate cryptospores and alete cryptospore monads. The permanent tetrads consist of forms with discrete spores (*Tetrahedraletes medinensis* and *Rimosotetras problematica*) and fused spores (*Cheilotetras caledonica*). None of the tetrads was observed enclosed within an envelope. Permanent tetrads comprise between 8 and 34 per cent of the total palynomorph content with *Tetrahedraletes medinensis* constituting 6(16)24 per cent, *Cheilotetras caledonica* 0(5)15 per cent and *Rimosotetras problematica* always less than 3 per cent.

True dyads comprise 0(2)5 per cent of the total palynomorphs and are represented by the smooth-walled forms *Dyadospora murusattenuata* and *Dyadospora murusdensa*. None has an envelope. They are occasionally seen separated into two laevigate hilate cryptospores and many, if not all, the hilate cryptospores are probably derived from them. The only pseudodyad recognized was the rather atypical form *Pseudodyadospora petasus* which is fused and has extended 'flanges' protruding from each spore. It comprises 0(3)8 per cent of the palynomorph assemblages.

All the hilate cryptospores are laevigate, crassitate forms referable to the species *Laevolancis divellomedium* and *Laevolancis plicata*. These two species constitute 1(13)35 per cent of the assemblage.

Alete cryptospore monads comprise a group of palynomorphs which consist of a discrete body which may, or may not, be enclosed within a membranous envelope. They are often thick walled and possess ornament comparable to that of cryptospore tetrads and dyads. The origin of most cryptospore monads is unknown but the similarity to other cryptospores suggests that some are subaerially dispersed propagules of land plants, although others may be derived from aqueous organisms such as protists and algae. Laevigate, alete cryptospore monads (Pl. 4, fig. 1) are usually the most common palynomorph in the Midland Valley sporomorph assemblage and comprise 24(38)51 per cent of the total palynomorph content. This collection of palynomorphs is nondescript and no attempt was made to classify them formally. However, the alete cryptospore monads vary dramatically in size and probably originate from more than one source (Text-fig. 8). Many of the alete cryptospore monads in the Midland Valley assemblages are relatively thin walled, although not as thin walled as typical marine sphaeromorphs, which suggests that they may not be subaerially dispersed reproductive propagules but are possibly derived from freshwater protists or other organisms which inhabited the body of water in which the sediment accumulated.

Only two species of trilete spores are present, *Ambitisporites avitus* and *Ambitisporites dilutus*, the latter being more common. The size range of each species is similar and narrow and there seems to be complete intergradation between them (see p. 174). Both are crassitate and laevigate and they comprise 6(12)19 per cent of the total palynomorphs.

The enigmatic palynomorph '*Moyeria*' is present in most of the samples studied and constitutes 0(11)22 per cent of the palynomorphs.

## DESCRIPTION OF OTHER ORGANIC FRAGMENTS

All the productive samples contain abundant fragmentary organic remains in the form of tubular structures, cuticle-like sheets, and rare cuticle fragments probably of arthropod origin. The affinities of these structures have been intensely debated in recent years (Banks 1975; Gray and Boucot 1977; Pratt *et al.* 1978; Strother and Traverse 1979; Edwards 1982, 1986; Edwards and Rose 1984; Gray 1985; Johnson 1985; Strother 1988; Burgess and Edwards 1991; Gensel *et al.* 1991). Because the tubular structures and cuticle-like sheets have been recovered from unequivocal non-marine deposits and they show remarkable similarities to structures in extant and fossil land plants they are generally considered to be derived from land plants (Gray 1985; Strother 1988; Edwards and Burgess 1991; Gensel *et al.* 1991). In order to facilitate the study of these fragments, attempts have recently been made to classify them in an artificial morphological classification (Edwards 1982, 1986; Edwards and Rose 1984; Burgess and Edwards 1991). A brief description of these remains isolated from the Midland Valley Silurian inliers follows.

### *Tubular structures*

The tubular structures are dominated by straight, parallel-sided, smooth-walled, diaphanous forms which appear identical to tubes described as *Laevitubulus plicatus* Burgess and Edwards, 1991 (Pl. 4, figs 3, 7). These tubes are 18–50 μm wide and up to 200 μm long, are always preserved flattened and have smooth walls with a corroded appearance. Constrictions, septae and branching are not observed, but rare specimens with a tapering termination have been recorded (Pl. 4, fig. 3). Other smooth-walled forms include those with thick, smooth, opaque walls which can be equated with *L. crassus* Burgess and Edwards, 1991 (Pl. 5, fig. 3). They are parallel-sided, 7–14 μm wide, up to 100 μm long and usually have a curved or helical organization. Terminations, branching, constrictions and septae were not recorded. Rare monospecific wefts of loosely aggregated and randomly orientated smooth tubes that can be assigned to *L. laxus* Burgess and Edwards, 1991 were also recorded (Pl. 5, fig. 1). The individual tubes have thin diaphanous walls, are straight with parallel sides and are 2–9 μm wide, up to 96 μm long and usually branch at acute angles. Constrictions are sometimes present but septae and terminations were not observed. *L. tenuis* Burgess and Edwards, 1991 is also present (Pl. 4, fig. 8). They comprise straight, parallel sided, flattened, smooth, opaque tubes. Specimens are 12(18)36 μm wide and up to 320 μm long. Terminations, septae or branching were not observed.

Less common are tubes which are externally smooth but have an internal ornament of annular, or less commonly spiral, thickenings (Pl. 4, figs 4–5; Pl. 6, fig. 2). Scanning electron microscope studies have illustrated that the internal thickenings are homogeneous with the walls. The tubes are straight with parallel sides, 15–45 $\mu$m wide and up to 146 $\mu$m long, and have not been observed branching or with septae or terminations. The internal thickenings are 0·5–1·5 $\mu$m wide, 0·5–1·0 $\mu$m high and 1·0–5·0 $\mu$m apart. The thickenings sometimes diminish in size and eventually disappear or may dichotomize at an acute angle (Pl. 6, fig. 2). The thickenings are most commonly arranged in an annular manner with rare dichotomies and can be assigned to *Porcatitubulus annulatus* Burgess and Edwards, 1991. Forms with spiral thickenings are less common and are assigned to *P. spiralis* Burgess and Edwards, 1991. Usually there is one helix, but occasionally more than one helix is present. Tubes with a pattern of very fine, closely packed striations which are arranged in an annular or spiral pattern were also recorded (Pl. 4, figs 9–10). This pattern is either formed by an internal ornament of closely packed minute thickenings or represents fibres within the wall of the tube. Burgess and Edwards (1991) illustrated similar tubes and included them in the taxon *P. spiralis* Burgess and Edwards, 1991, thereby implying that the tubes possess internal thickenings. However, the internal thickenings are much smaller than the size range Burgess and Edwards stipulated for this species. Similar tubes have also been illustrated by Pratt *et al.* (1978, pl. 2, fig. 9) from the Lower Massanutten Sandstone of Llandovery age from Virginia, and by Strother and Traverse (1979, pl. 3, fig. 14) from ?Wenlock age strata of Pennsylvania. Both Pratt *et al.* and Strother and Traverse suggest that the walls of these tubes possessed an internal fibrillar structure giving the impression of spiral striations when the light passed through the tubes. It is difficult to interpret the structure using light microscopy, although SEM observation of similar tubes from Lochkovian material suggests that the tubes may possess an internal ornament of thickenings (Wellman 1991). Similar tubes with an internal ornament of closely spaced, low thickenings which are up to 2 $\mu$m wide were also recovered (Pl. 5, fig. 2).

In addition to isolated tubular structures, rare associations of tubes were recorded (Pl. 4, fig. 6). These comprised straight, unbranched, wide tubes with a mesh of narrow, branched tubes adhering to their surface. The wide tubes are smooth-walled, 20–30 $\mu$m wide and up to 230 $\mu$m long, and are preserved flattened. The narrow tubes generally run more-or-less parallel to the wide tubes and are regularly branched with offshoots at 90 degrees. The branches are usually 4–12 $\mu$m long and frequently terminate in closed ends. The narrow tubes are unornamented and 1·5–2·5 $\mu$m wide.

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### EXPLANATION OF PLATE 4

Fig. 1. Alete cryptospore monad. FM 277 (slide BL7/4, co-ord. 1167 214; E.F. no. V47/3) sample BL7; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 1000.

Fig. 2. Acanthomorph acritarch. FM 278 (slide CP6/1, co-ord. 1221 085; E.F. no. H52/4) sample CP6; Lynslie Burn Fish Bed; Henshaw Formation, North Esk inlier, × 1000.

Figs 3, 7. *Laevitubulus plicatus* Burgess and Edwards, 1991. FM 279 (slide CL8/1, co-ord. 1165 172; E.F. no. R47) sample CL8; Logan Formation; Logan Water, Lesmahagow inlier, × 500. 7, FM 280 (slide BH8/1, co-ord. 1275 160; E.F. no. Q58) sample BH8; Fish Bed Formation; Glenbuck Loch, Hagshaw Hills inlier, × 315.

Fig. 4. *Porcatitubulus spiralis* Burgess and Edwards, 1991. FM 281 (slide BL13/2, co-ord. 1253 128; E.F. no. M56/3) sample BL13; Dippal Burn Formation; Dippal Burn, Lesmahagow inlier, × 500.

Fig. 5. *Porcatitubulus annulatus* Burgess and Edwards, 1991. FM 282 (slide BH8/1, co-ord. 1237 169; E.F. no. R54/2) sample BH8; Fish Bed Formation; Glenbuck Loch, Hagshaw Hills inlier, × 500.

Fig. 6. Fragment of ?*Prototaxites* sp. FM 283 (slide BL7/4, co-ord. 1116 125; E.F. no. M41/3) sample BL7; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 1000.

Fig. 8. *Laevitubulus tenuis* Burgess and Edwards, 1991. FM 284 (slide CL8/1 co-ord. 1277 136; E.F. no. N58) sample CL8; Logan Formation; Logan Water, Lesmahagow inlier, × 500.

Fig. 9. Tube with annular internal microthickenings. FM 285 (slide DL8/2, co-ord. 1290 090; E.F. no. J60) sample DL8; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 540.

Fig. 10. Tube with spiral internal microthickenings. FM 286 (slide DL8/2 co-ord. 1280 070; E.F. no. F58/4) sample DL8; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 500.

PLATE 4


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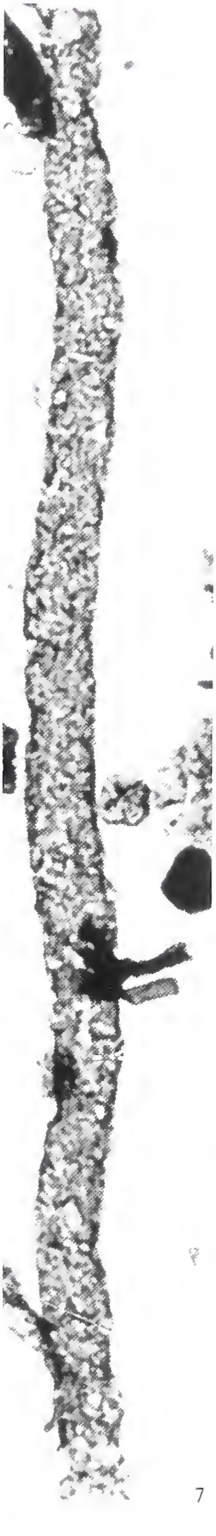
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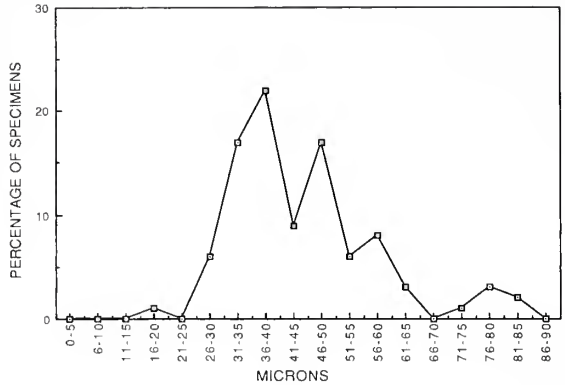
WELLMAN and RICHARDSON, palynomorphs and tubes



TEXT-FIG. 8. Size frequency distribution of 200 alete cryptospore monads from sample CL7, Logan Formation, Logan Water, Lesmahagow inlier.

Similar associations of tubes have been illustrated by Edwards (1982) from deposits of Ludlow age from Wales. Edwards noted the similarity between the organization of the fragmented tube associations and structures present in *Prototaxites*, a nematophyte known from plant megafossils. We also find the similarity striking and refer the associations to ?*Prototaxites* sp.

### *Cuticle-like sheets*

The cuticle-like sheets show little diversity. They are smooth on one surface and have an irregular reticulate pattern of ridges (muri) on the other. The units are either predominantly circular (Pl. 5, fig. 6; Pl. 6, fig. 5), or polygonal (Pl. 5, figs 4–5, 7–8; Pl. 6, fig. 1), vary in size on an individual sheet and do not form any recognizable patterns. Maximum unit size varies from 2 to 25 μm, average 10 μm. The sheets are up to 350 μm in maximum diameter but margins have not been observed. Perforations in the sheets are usually a result of abrasion as the edges of the holes are irregular and show signs of tearing. Infrequently almost perfectly circular perforations with clear-cut margins puncture the cuticle between muri (Pl. 6, figs 4, 6). It seems that these perforations are not a result of abrasion and may be primary, in which case they perhaps mark the position of some type of aerating structure (see Edwards and Rose 1984, p. 52), or may be the result of some form of infection or wounding.

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## EXPLANATION OF PLATE 5

Fig. 1. *Laevitubulus laxus* Burgess and Edwards, 1991. FM 287 (slide CL9/1, co-ord. 1205 105; E.F. no. K51) sample CL9; Logan Formation; Logan Water, Lesmahagow inlier, × 850.

Fig. 2. Tube with wide 'strap-like' internal thickenings. FM 288 (slide DL8/2, co-ord. 1260 100; E.F. no. K57/1) sample DL8; Slot Burn Formation; Lesmahagow inlier, × 1200.

Fig. 3. *Laevitubulus crassus* Burgess and Edwards, 1991. FM 289 (slide DL8/2, co-ord. 1180 095; E.F. no. J48/4) sample DL8; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 625.

Figs 4–8. Cuticle-like sheets. 4, 8, FM 290 (slide CL6/3, co-ord. 1260 090; E.F. no. J56/2) sample CL6; with polygonal units; Logan Formation; Logan Water, Lesmahagow inlier; 4, × 270; 8, × 600. 5, FM 291 (slide CL6/3, co-ord. 1240 150; E.F. no. P54/2) sample CL6; with polygonal units; Logan Formation; Logan Water, Lesmahagow inlier, × 270. 6, FM 292 (slide CL5/2, co-ord. 1216 150; E.F. no. P52) sample CL5; with rounded units; Logan Formation; Logan Water, Lesmahagow inlier, × 350. 7, FM 293 (slide CL5/3, co-ord. 1274 127; E.F. no. M58/3/4) sample CL5; with polygonal units; Logan Formation; Logan Water, Lesmahagow inlier, × 250.


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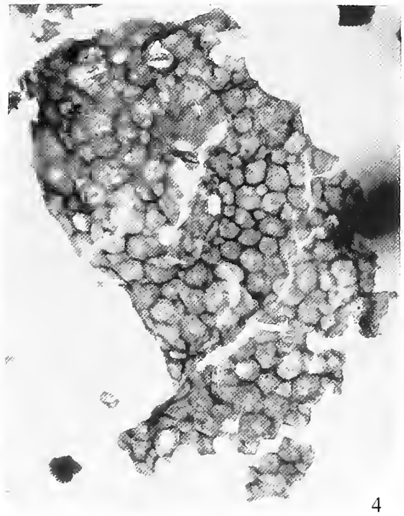
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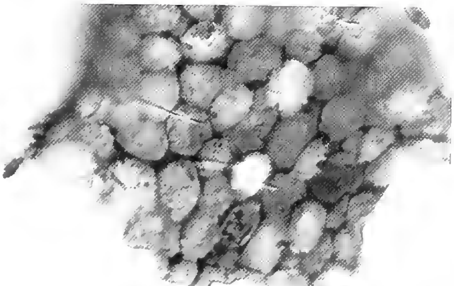
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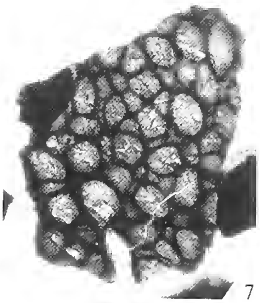
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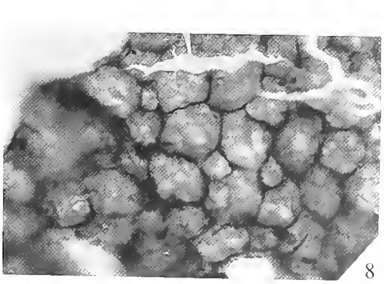
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WELLMAN and RICHARDSON, tubes and cuticles

## AGE OF THE ASSEMBLAGES

The salient features of the assemblages utilized in age dating are the presence of unsculptured trilete spores and hilate cryptospores, the absence of trilete spores and hilate cryptospores with ornament, and the general character of the assemblage.

In the type area of the Llandovery in South Wales, unequivocal laevigate trilete spores referable to *Ambitisporites* appear in the late Aeronian (upper *sedgwickii* Biozone) (Richardson 1988; Burgess 1991). However, Richardson (1988) noted that spore recovery is variable in this sequence and the first appearance of *Ambitisporites* may eventually prove to be slightly earlier. The earliest record of hilate cryptospores is a species of the laevigate genus *Laevolancis* from the early Wenlock (lower *centrifugus* Biozone) from the type area of the Wenlock (Burgess and Richardson 1991). The inception of sculptured miospores and hilate cryptospores is slightly later and the earliest reported examples are also from the type area of the Wenlock where they first appear in the Homerian (upper *lundgreni* Biozone) (Burgess and Richardson 1991). However, another occurrence of the same, or possibly earlier age, is cf. *Synorisporites verrucatus* from strata of *ellesae* to *lundgreni* Biozone ages from the Greyhound Law inlier in the Cheviot Hills of northern England which has been age constrained using graptolites (Barron 1989).

Thus the presence of laevigate hilate cryptospores suggests a lower age bracket of earliest Sheinwoodian (early *centrifugus* Biozone) and the absence of ornamented spores indicates an upper age bracket of Homerian (upper *lundgreni* Biozone) or possibly latest Sheinwoodian (*ellesae* Biozone) age. Therefore the assemblages are assigned an early Wenlock age. The spore-based age determination corresponds with biostratigraphical evidence derived from macrofaunas which indicates that strata which lie below the plant microfossil assemblages are of Telychian and possibly early Sheinwoodian age (Lamont 1947; Rolfe 1961, 1973*a*, 1973*b*; Rolfe and Fritz 1966; Bull 1987).

## COMPARISONS WITH SPOROMORPH ZONAL SCHEMES

In the scheme of Richardson and McGregor (1986) (see also Richardson 1988; Richardson and Edwards 1989) the Midland Valley assemblages can be accommodated in the *chulus-nanus* Assemblage Biozone which is of ?Telychian–early Homerian (upper *lundgreni* Biozone) age. This spore biozone is characterized by smooth-walled trilete spores, naked permanent tetrads and true dyads, and laeviage hilate cryptospores. The preceeding *avitus-dilutus* Assemblage Biozone contains the earliest laevigate trilete spores but hilate cryptospores have not been reported. Miospores and hilate cryptospores with sculpture appear at the base of the *protophanus-verrucatus* Assemblage Biozone which succeeds the *chulus-nanus* Assemblage Biozone.

The absence of laevigate patinate miospores from the Midland Valley assemblages, and hence the nominal species of the *chulus-nanus* Assemblage Biozone, may be a consequence of palaeo-

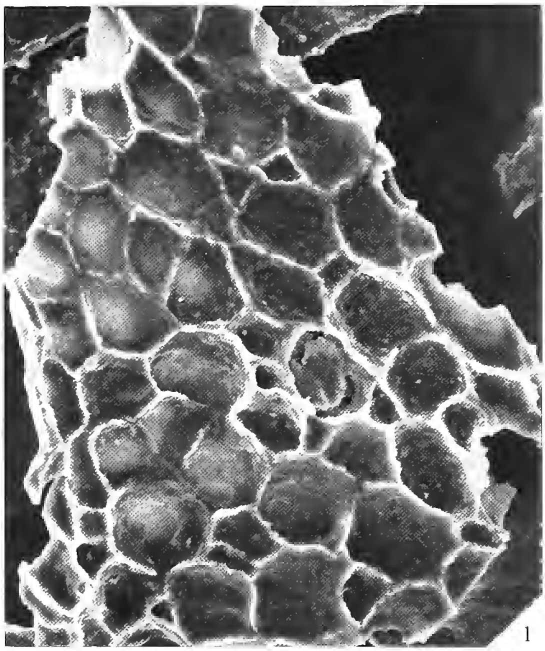
### EXPLANATION OF PLATE 6

Figs 1, 4–6. Cuticle-like sheets. 1, (stub CW6, Print P004401) sample BL7; with polygonal units; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 570. 4, (stub CW6, Print P004407) sample BL7; smooth external surface with perforations; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 580. 5, (stub CW48, Print P008556) sample DL8; with circular units; Slot Burn Formation; Slot Burn, Lesmahagow inlier, × 150. 6, FM 295 (slide CL6/3, co-ord. 1294 085; E.F. no. H60) sample CL6; with polygonal units, several of which are punctured by circular perforations; Logan Formation; Logan Water, Lesmahagow inlier, × 550.

Fig. 2. *Porcatitubulus* sp. Burgess and Edwards, 1991. (stub CW30, Print P007354) sample CL5; fractured specimen showing the internal thickenings; Logan Formation; Logan Water, Lesmahagow inlier, × 1670.

Fig. 3. ?Arthropod cuticle. FM 294 (slide CL5/2, co-ord. 1215 110; E.F. no. L52) sample CL5; Logan Formation; Logan Water, Lesmahagow inlier, × 250.

PLATE 6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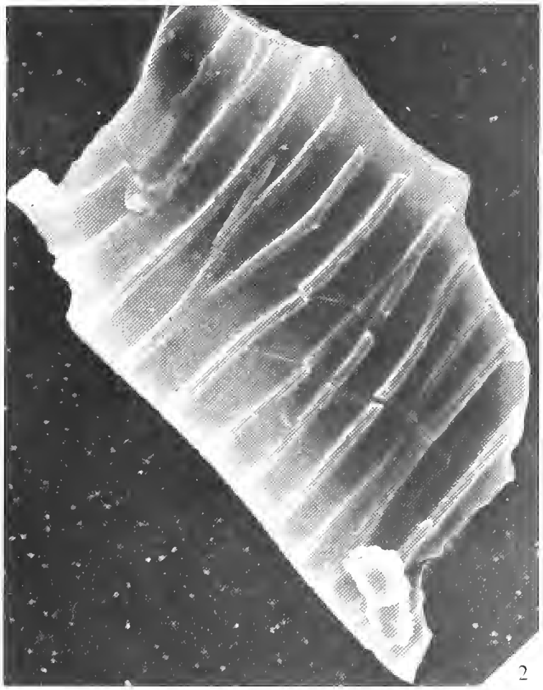
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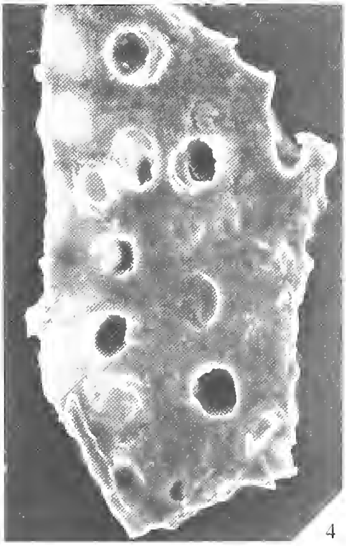
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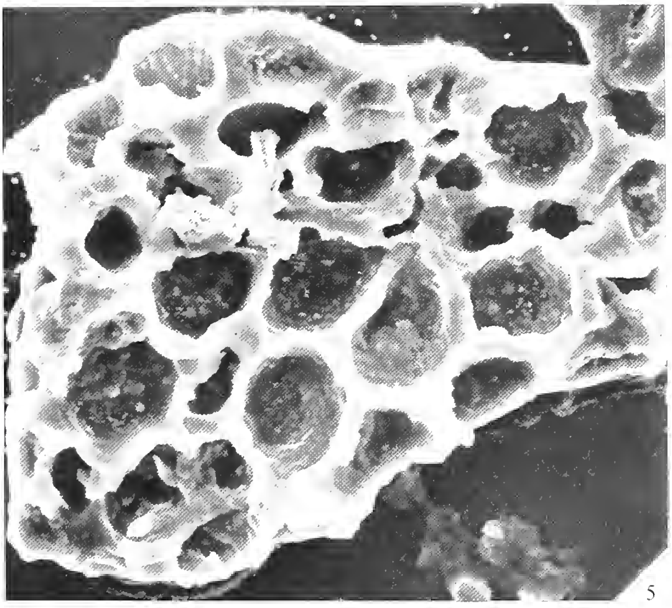
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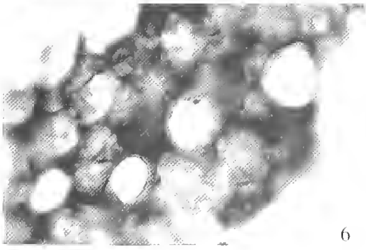
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WELLMAN and RICHARDSON, tubes and cuticles geographical or palaeoenvironmental factors. The *chulus-nanus* Assemblage Biozone is based largely on work in the marine and marginal marine deposits of southern Britain which are of different facies and palaeogeographical province from the Midland Valley deposits. Richardson and McGregor (1986) noted a similar situation in that the assemblage described by Smith (1975) from the Lettergesh Formation of Ireland is confidently dated as early Wenlock age, and therefore falls within the age range of the *chulus-nanus* Assemblage Biozone, but lacks patinate spores. However, it is noteworthy that there are remarkable similarities between the Midland Valley sporomorph assemblages and those described by Burgess and Richardson (1991) from early Wenlock strata of the type area (see below). Such observations support an early Wenlock age and inclusion in the *chulus-nanus* Assemblage Biozone.

## COMPARISON WITH PREVIOUSLY DESCRIBED SPOROMORPH ASSEMBLAGES OF LATE LLANDOVERY AND EARLY WENLOCK AGE

Sporomorph assemblages have been described from the type areas for the Llandovery and Wenlock in southern Britain and also from Llandovery and Wenlock strata in North Africa, North America, South America and various localities in Europe. The essence of these reports is outlined below.

In their preliminary investigation of the spores from the Silurian strata of the Anglo-Welsh basin, Richardson and Lister (1969) recorded *Ambitisporites* cf. *avitus* Hoffmeister, 1959, *A. dilutus* (Hoffmeister) Richardson and Lister, 1969, *Archaeozonotriletes chulus* Cramer var. *nanus* Richardson and Lister, 1969, *Retusotriletes* cf. *warringtonii* Richardson and Lister, 1969 and *Laevolancis divellomedium* Burgess and Richardson, 1991 (as ?*Archaeozonotriletes* cf. *divellomedium* Chibrikova, 1959) from the Coalbrookdale Formation of Sheinwoodian and early Homerian age. The earliest ornamented spores were recorded from the Much Wenlock Limestone Formation of Homerian age (*ludensis* Biozone). Following the recognition of cryptospores, the type Llandovery and type Wenlock were studied by Burgess (1991) and Burgess and Richardson (1991) respectively. Burgess recorded the inception of trilete spores, *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969, in the *sedgwickii* Biozone. It occurred in an impoverished assemblage with the cryptospores *Tetrahedraletes medinensis* Strother and Traverse, 1979, *Velatitetras reticulata* Burgess, 1991 and *Pseudodyadospora* cf. *laevigata* Johnson, 1985. Compared with older assemblages in the Llandovery, the younger assemblages exhibit a lack of variety of cryptospore species. In the type Wenlock strata, Burgess and Richardson (1991) recovered *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969, *A. avitus* Hoffmeister, 1959, *Archaeozonotriletes chulus* var. *chulus* and *nanus* Richardson and Lister, 1969, *Tetrahedraletes medinensis* Strother and Traverse, 1979, *Dyadospora murusdensa* (Strother and Traverse) Burgess and Richardson, 1991, *D. murusattenuata* (Strother and Traverse) Burgess and Richardson, 1991, *Laevolancis divellomedium* (Chibrikova) Burgess and Richardson, 1991 and *L. plicata* Burgess and Richardson, 1991 throughout the sequence. Higher assemblages in strata of early Homerian age (upper *lundgreni* Biozone) and younger contain ornamented hilate cryptospores and miospores in addition to these species. The Midland Valley assemblages are remarkably similar to the pre-upper *lundgreni* Biozone spore assemblages described by Burgess and Richardson from the type area of the Wenlock. All of the taxa reported by Burgess and Richardson were recovered in the Midland Valley, except for *Archaeozonotriletes chulus*. The only additional species recorded in the Midland Valley assemblage are *Cheilotetras caledonica* gen. et sp. nov. and *Pseudodyadospora petasus* sp. nov., and the latter has now been recognized in preparations of early Wenlock age (early *centrifugus* Biozone) from the Wenlock type area.

The first report of trilete spores from Llandovery strata was by Hoffmeister (1959) from possible early Aeronian deposits from Libya (Hoffmeister 1959; Gray and Boucot 1971; Richardson 1988). Richardson (1988) re-examined Hoffmeister's material and noted that the trilete spores co-occurred with cryptospores. He recorded naked permanent tetrads (probably mainly *Tetrahedraletes medinensis* (Strother and Traverse) emend.), permanent tetrads enclosed within a laevigate envelope, possible true dyads, naked pseudodyads and *Ambitisporites*? *vavrdovii* Richardson, 1988.

Other publications concerning Silurian sporomorphs from North Africa include Richardson and Ioannides (1973), Al-Ameri (1980), Richardson (*in* Hill *et al.* 1985), Richardson (1988) and Richardson and Edwards (1989). Richardson and Ioannides (1973) described a sequence of spore assemblages from two wells in Libya. At several positions in the sequence graptolite faunas have been recovered which suggest a Wenlock or early Ludlow age. Richardson (in Richardson and Edwards 1989) compared the spore associations with better age-constrained assemblages from southern Britain and suggested that the oldest assemblage, which lies beneath the graptolite-bearing horizons and comprises only smooth-walled miospores, belongs to the *chulus-nanus* Assemblage Biozone, which suggests a late Llandovery or early Wenlock age. Younger samples in the well are markedly different in that they contain ornamented spores. It is noteworthy that the Libyan succession of 'spore first appearances' is closely comparable to that observed in the southern British sequences.

Richardson (1988) expanded preliminary work in which he had investigated cryptospore and miospores distribution in Silurian strata from several wells in Libya (Richardson *in* Hill *et al.* 1985). In a sample which contained the miospores *Ambitisporites avitus* Hoffmeister, 1959 and *A. dilutus* (Hoffmeister) Richardson and Lister, 1969 he recorded cryptospores including naked permanent tetrads (probably mostly referable to *Tetrahedraletes medinensis* (Strother and Traverse) emend.), loose tetrads (probably *Rimosotetras problematica* Burgess, 1991), permanent tetrads enclosed in smooth and ornamented envelopes, the naked true dyads *Dyadospora murusattenuata* Strother and Traverse, 1979 and *D. murusdensa* Strother and Traverse, 1979, true dyads enclosed in a smooth envelope, pseudodyads enclosed within a rugose envelope and *Ambitisporites*? *vavrdovii* Richardson, 1988. On the basis of correlation with assemblages described from elsewhere he suggested a late Aeronian–early Telychian age. Like the Llandovery assemblages from the type area, these spore associations have much in common with the Midland Valley assemblage but again the major difference is the presence, in the Llandovery-age material, of rare cryptospores enclosed within envelopes.

From elsewhere in Europe, land-derived sporomorphs have been recovered from Silurian deposits in Ireland from both sides of the presumed Iapetus suture. Spores in strata which range from Telychian (*crispus* Biozone) to earliest Homerian (*lundgreni* Biozone) are composed exclusively of laevigate trilete spores, hilate cryptospores and tetrads (Doran 1974; Smith 1975, 1979; Colthurst and Smith 1977; Emo and Smith 1978; Holland and Smith 1979). The trilete spores are generally of the *Ambitisporites* complex, with rare *Retusotriletes* sp. and *Archaeozonotriletes* sp. The reported tetrads are almost certainly cryptospore permanent tetrads, and probable hilate cryptospores have been figured as species of smooth-walled, patinate miospores. In Scotland *Ambitisporites* sp. has been reported from the shallow-water marine Knockgardner Formation of the Girvan area which is of early Wenlock age (Dorning 1982) and in Norway, Smelror (1987) recorded *Tetrahedraletes medinensis* Strother and Traverse, 1979, *Ambitisporites avitus* Hoffmeister, 1959 and *A. dilutus* (Hoffmeister) Richardson and Lister, 1969 from the marine Steinsfjorden Formation of Sheinwoodian age from the Ringerike district.

From North America, Pratt *et al.* (1978) described an important sporomorph assemblage from the Lower Massanutten Sandstone in Virginia. They assigned a probable Llandovery age, based on field relations, and suggested a fluvial origin. They recorded rare *Ambitisporites* sp., 'tetrads of alete spores' (probably *Tetrahedraletes medinensis* (Strother and Traverse) emend.), alete spores (probably *Laevolancis* sp.) and sphaeromorphs. Also in North America, assemblages in which the trilete spores consist entirely of species of the *Ambitisporites* complex have been reported from deposits of Llandovery and Wenlock age by Cramer (1968, 1969, 1971). Additionally, assemblages dominated by a wide diversity of cryptospores, with possible trilete spores, have been described by Gray and Boucot (1971), Strother and Traverse (1979) and Johnson (1985) from deposits of Llandovery age. However, it appears that the rare trilete spores are probably *Ambitisporites*? *vavrdovii*, which mimics a miospore but is probably derived from a fragmented or loose permanent tetrad. These assemblages all contain cryptospores which are enclosed within envelopes.

Finally, from South America, McGregor (1984) noted the presence of rare, small, retusoid, equatorially thickened, unsculptured spores from the middle part of the Tarabuco Formation of Bolivia. Spores in the upper part of the formation suggested a Ludlow age and McGregor proposed a pre-Ludlow age for the older samples. It is probable that they are of late Llandovery or early Wenlock age. There are as yet no reports of late Llandovery or early Wenlock spore assemblages from Australia, Antarctica, Asia or Africa south of the Sahara Desert.

Other palynomorphs which co-occur with the sporomorphs in the Midland Valley assemblages are of less biostratigraphical value as they are long-ranging or their stratigraphical distribution is uncertain. The alete cryptospore monads which dominate the assemblages are long-ranging and can also be confused with marine forms such as prasinophycean cysts and sphaeromorph acritarchs, although the latter are usually thinner walled. Reports of the enigmatic palynomorph '*Moyeria*' *cabottii* so far extend to marine and continental strata of Caradoc to Ludlow age (Gray and Boucot 1989).

## COMPARISON WITH PREVIOUS REPORTS OF TUBULAR STRUCTURES AND CUTICLE-LIKE SHEETS FROM THE LOWER PALAEOZOIC

Burgess and Edwards (1991) outlined the stratigraphical distribution of tubular structures from latest Ordovician to earliest Devonian deposits from the Anglo-Welsh Basin. They identified two assemblages. The first ranges from the latest Ordovician to the latest Llandovery and consists almost exclusively of *Laevitubulus plicatus*. Filamentous types and internally thickened forms are absent. The second assemblage first occurs in the earliest Wenlock and persists into the Early Devonian. It is much more diverse and comprises the internally thickened forms *Porcatitubulus spiralis* and *P. annulatus*, the smooth forms *Laevitubulus plicatus*, *L. laxus*, *L. crassus* and the filament *Ornatifilum granulatum*. All of these species range from the early Wenlock to the Early Devonian. In the late Wenlock they are joined by the externally ornamented form *Constrictitubulus cristatus* and the smooth form *Laevitubulus tenuis* which persist until the Early Devonian. However, Burgess and Edwards suggested that the younger and more diverse assemblage of tubular structures might make its inception prior to the early Wenlock in the late Llandovery, but this is masked by sampling bias in the Anglo-Welsh Basin. The late Llandovery samples analysed by Burgess and Edwards were all from distal marine facies, an environment in which the land-derived tubes are very scarce. Pratt *et al.* (1978) reported internally thickened tubes from strata which are probably of late Llandovery age from North America.

The assemblage of tubular structures recovered from the Midland Valley inliers conforms closely with the distribution of tubular structures observed by Burgess and Edwards in the early Wenlock strata of the Anglo-Welsh Basin. However, filaments of the *Ornatifilum granulatum* type are not recorded in the Midland Valley assemblage, and the laevigate tube *Laevitubulus crassus*, which is not recorded in strata older than late Wenlock in southern Britain, is present.

There are few detailed descriptions of Silurian culticle-like sheets and hence their stratigraphical distribution is poorly understood. However, examples similar to those recorded from the Midland Valley are known to range from possibly the Caradoc to the Early Devonian (Gray *et al.* 1982; Edwards 1982, 1986; Edwards and Rose 1984; Edwards and Burgess 1991; Gensel *et al.* 1991).

## PALYNOFACIES

The red-bed sequences in the Silurian inliers of the Midland Valley have long been regarded as being entirely non-marine in origin, except for the Lynslie Burn Fish Bed in the North Esk inlier which contains crinoids and has been interpreted as being due to a brief marine incursion. Recently, however, certain fish workers have expressed doubts concerning this interpretation and have proposed that the fish are marine forms and that all the fish beds represents marine incursions (Blieck and Janvier 1991).

The strata have been interpreted as non-marine because the sedimentology of the deposits suggests that they accumulated in terrestrial–fluviatile and lacustrine environments and because unequivocal marine fossils are absent. The fish-bearing horizons are interspersed in red-bed sequences with sedimentological characteristics, e.g. desiccation cracks and alluvial fan conglomerates, typical of terrestrial–fluviatile deposition (McGiven 1968; Rolfe 1973*a*). Furthermore, the formations containing the fish beds exhibit certain characteristics typical of lacustrine deposits and although they contain well-preserved fossils, diagnostic marine forms are absent. Hence the fish beds, except for the Lynslie Burn Fish Bed, were generally accepted as being of lacustrine origin, although the possibility that they were rather atypical lagoonal or deltaic deposits was not completely dismissed (Rolfe 1973*a*).

Palynological preparations from the Slot Burn, Dippal Burn, Logan and Fish Bed Formations comprise palynomorphs presumed to be entirely of continental origin. Marine palynomorphs such as acritarchs or chitinozoans were not recorded. This is also true for samples collected from the fish-bearing horizons, which gives a strong indication that the deposits accumulated in an environment without marine influence. However, palaeoenvironmental interpretation based on palynofacies analysis is not infallible. It is possible for abnormal circumstances to result in the absence of marine palynomorphs from marine deposits. For example, freshwater wedges may profoundly affect marine environments. Gray (1988) discussed abnormal conditions which may result in confusion of both marine and non-marine environments. However, such possibilities rely on unusual conditions, and are probably remote. Considering all of the evidence, it seems most probable that the red-bed deposits accumulated in a terrestrial–fluviatile environment, and the fish-bearing horizons, represent accumulation in freshwater lacustrine environments, except for the Lynslie Burn Fish Bed.

The Lynslie Burn Fish Bed of the North Esk inlier is also situated in a red-bed sequence which is interpreted as accumulating in a terrestrial–fluviatile environment. However, preparations from this horizon contain rare acanthomorph acritarchs (Pl. 4, fig. 2). The possibility that the acritarchs have been reworked from older marine strata has been examined but is considered unlikely as acritarchs are absent from preparations from similar stratigraphical levels in the other inliers. Furthermore, the Lynslie Burn Fish Bed differs from the fish beds in the other inliers because it is unlaminated, the fish remains are disarticulated and crinoid ossicles are present. Therefore it seems likely that this horizon represents a minor and transitory marine incursion. The Lynslie Burn Fish Bed overlies the 'Quartzite Conglomerate' and it is noteworthy that evidence of marine influence has not been recognized at this level in the other inliers.

## GEOLOGICAL AND PALAEOBOTANICAL SIGNIFICANCE

The age constraint suggested by the Midland Valley sporomorph assemblages has several implications relating to the geology of the inliers. Firstly it gives a reliable age for the important faunas associated with the fish-beds. Sporomorph assemblages which indicate an early Wenlock age have been recovered from above, below and from the fish-bearing horizons. Secondly, palynofacies analysis provides further evidence that the red-bed sequence in the Hagshaw Hills and Lesmahagow inliers is entirely non-marine and that they are probably lacustrine and fluviatile rather than marginal marine deposits, but the Lynslie Burn Fish Bed may indeed represent a brief marine incursion. Thirdly, regarding tectonics and palaeogeography, the distribution of the samples which indicate an early Wenlock age clearly establishes that a large proportion of the red-bed sequences accumulated during early Wenlock times. At least 500 m of strata of red-bed facies in the Lesmahagow inlier is of early Wenlock age. Such evidence requires detailed consideration when formulating tectonic models for the Midland Valley during Silurian times.

The plant microfossil assemblages of the Midland Valley inliers have immense palaeobotanical significance. They are one of the few Llandovery or Wenlock palynomorph assemblages that has been interpreted as being of continental origin. Other examples are from the Lower Massanutten Sandstone in Virginia (Pratt *et al.* 1978), ?Clinton Strata, Pennsylvania (Strother and Traverse 1979) and possibly the Tuscarora Formation of Pennsylvania (Strother and Traverse 1979; Johnson 1985). Consequently, the Midland Valley palynomorph assemblages offer invaluable information concerning the nature of early Wenlock terrestrial plant microfossil associations and provide evidence pertinent to the study of early land plants.

Land-derived material in marine environments is obviously allochthonous and has probably undergone sorting during transportation. Therefore plant microfossils in marine palynomorph assemblages generally do not provide a true reflection of the composition and relative abundances of plant microfossils derived from continental vegetation. However, lacustrine and fluvial palynomorph assemblages are composed almost entirely of material which is derived exclusively from local vegetation and has generally not been transported far, and is consequently less likely to have been sorted. Therefore such assemblages provide a more accurate reflection of the composition of plant microfossil associations derived from local vegetation. The material can be compared with modern and fossil analogues and also with the record of similar microfloras described from elsewhere. This enables reasoned deductions regarding the nature and distribution of the vegetation and, to a certain extent, permits speculation concerning the physiology and evolution of the plants.

Text-figure 4 outlines the composition of the Midland Valley sporomorph assemblages and tabulates the results of frequency counts. The Midland Valley assemblages are remarkably constant in composition as the same species are present in nearly all of the samples and the frequency counts indicate little variation in abundance. This suggests that there was little or no variation in the composition of the local vegetation. Likewise but on an interregional scale, the Midland Valley assemblages are remarkably similar in composition to sporomorph assemblages described from strata of early Wenlock age from southern Britain, North America, North Africa and elsewhere. This indicates that the flora was not only well established, abundant and geographically widespread, but also cosmopolitan (see also Gray 1991). However, the lack of diversity shown by the sporomorph assemblages, only ten species, suggests that the vegetation comprised few forms. Recent *in situ* sporomorph studies may provide evidence concerning the nature of this simple flora. Fanning *et al.* (1991) have demonstrated that at least some late Silurian trilete spores are derived from rhyniophytoid plants, and certain cryptospores, namely true dyads and their related hilate cryptospores, are also derived from similar upright plants with terminal sporangia. This suggests that the early Wenlock flora from which the Midland Valley plant microfossils were derived may have contained similar rhyniophytoid plants. However, the derivation of other cryptospore morphotypes such as permanent tetrads and pseudodyads remains conjectural although their morphological similarities may be construed as reflecting similar relationships.

The cuticle-like sheets and tubular structures from the Midland Valley assemblages are remarkably similar to those described from other assemblages of early Wenlock age from elsewhere. This suggests that the ?land plants from which these enigmatic structures were derived were also geographically widespread and cosmopolitan. Furthermore, the abundance of such remains suggests that these ?land plants constituted an integral component of the vegetation. However, the precise affinities of the culticle-like sheets and tubular structures remain uncertain, although their overall form and facies relationships indicate that they are probably derived from some form of thalloid land plant (Edwards 1981; Strother 1988; Edwards and Burgess 1990; Burgess and Edwards 1991; Gensel *et al.* 1991). The nature of the reproductive propagules associated with these putative land plants remains unknown.

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*Note added in proof.* While this paper was in press a proposed supragenerric classification scheme for cryptospores was published (Strother 1991).

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## APPENDIX 1

| FORMATION | SAMPLE NUMBER | NATIONAL GRID REFERENCE | LOCATION |
|---|---|---|---|
| DBF | BL13 | 2691663138 | Section on north bank of Dippal Burn near derelict footbridge |
| DBF | BL15 | 2693063181 | North bank of Dippal Burn at the eastern end of the large gorge |
| DBF | BL16 | 2692763174 | North bank of Dippal Burn at the western end of the large gorge |
| DBF | DL13 | 2691663138 | Section on north bank of Dippal Burn near derelict footbridge |
| DBF | DL14 | 2691663138 | Section on north bank of Dippal Burn near derelict footbridge |
| SBF | BL7 | 2677263193 | Exposure in south bank of Slot Burn |
| SBF | CL16 | 2692763173 | Exposure in north bank of Logan Water |
| SBF | DL8 | 2680263206 | Exposure in north bank of Slot Burn west of the gulley |
| LF | CL5 | 2763363780 | Channel deposit on north bank of the hairpin bend in Logan Water |
| LF | CL6 | | |
| LF | CL7 | | |
| LF | CL8 | | |
| LF | CL9 | | |
| LF | CL10 | | |
| LF | CL11 | 276563778 | Channel deposit in north bank of Logan Water |
| LF | CL12 | 276563778 | Channel deposit in north bank of Logan Water |
| LF | CL13 | 2761663776 | South bank of Logan Water |
| LF | CL14 | 2761663776 | South bank of Logan Water |
| FBF | AH5 | 2761362838 | East shore of Glenbuck Loch (Rolfe 1973, locality 9) |
| FBF | BH4 | 2761462850 | East shore of Glenbuck Loch (Rolfe 1973, locality 9) |
| FBF | BH8 | 2761462840 | East shore of Glenbuck Loch (Rolfe 1973, locality 9) |
| FBF | BH9 | 2761462840 | East shore of Glenbuck Loch (Rolfe 1973, locality 9) |
| FBF | AH6 | 2777262905 | Headwaters of Sheil Burn (Rolfe 1973, locality 12) |
| FBF | AH10 | | |
| FBF | BH13 | | |
| FBF | BH14 | | |
| FBF | BH15 | | |
| HF(LBFB) | BP7 | 3131775746 | Exposure on south bank of Lynslie Burn (Robertson 1986, locality 29) |
| HF(LBFB) | CP6 | | |
| HF(LBFB) | CP7 | | |
| HF(LBFB) | CP9 | | |

*Key:*
DBF = Dippal Burn Formation, Lesmahagow inlier; SBF = Slot Burn Formation, Lesmahagow inlier; LF = Logan Formation, Lesmahagow inlier; FBF = Fish Bed Formation, Hagshaw Hills inlier; HF(LBFB) = Henshaw Formation (Lynslie Burn Fish Bed), North Esk inlier.

# THE BRACHIOPOD *STOLMORHYNCHIA STOLIDOTA* FROM THE BAJOCIAN OF DORSET, ENGLAND

*by* COLIN D. PROSSER

ABSTRACT. Numerous nominal species of the genus *Stolmorhynchia* have been recorded worldwide. These vary considerably in morphology and in reality are unlikely to belong to the same genus. The type species of *Stolmorhynchia* from the Bajocian of Dorset, *Stolmorhynchia stolidota* Buckman, 1918, is described in detail for the first time. This description provides a clear picture of the true nature of the genus *Stolmorhynchia*, and a sound foundation from which to redefine it. Species recorded from the Caucasus appear to be the only other forms which can definitely be attributed to *Stolmorhynchia*.

SPECIES of the Jurassic rhynchonellid genus *Stolmorhynchia* Buckman have been nominally recorded from around the world by a number of authors (see species lists given by Buckman 1918; Alméras 1964; Rousselle 1965, 1968, 1974; Kamyshan and Babanova 1973). Despite this, the genus is founded on a very poorly described type species, *Stolmorhynchia stolidota* Buckman, from the Bajocian Middle Inferior Oolite of Dorset, southwest England. As a result of being loosely defined, *Stolmorhynchia* has become something of a 'dustbin genus', with species being attributed to it because they do not appear to fit anywhere else (see Ager *et al.* 1972). The purpose of this paper, therefore, is to give a description of the type species in order to provide a better understanding of the nature of the genus and to facilitate future work in splitting-off nominal species groups which are found to vary significantly from the type species.

Buckman's (1918) initial description of this species consisted of only three lines and was accompanied by figures of a holotype and paratype. Unfortunately both specimens lack shells: a result of Buckman's technique of burning shells to produce internal moulds for examination of muscle scars and internal plates. In consequence, these types are difficult to relate to undamaged specimens.

Despite this rather poor description of *Stolmorhynchia stolidota*, the species has remained unstudied in Britain ever since. The only attempt to update knowledge of the taxon was made overseas by Kamyshan and Babanova (1973). Their study was not a detailed examination of *Stolmorhynchia stolidota*, as it was based solely on specimens from the Caucasus and no type material was examined.

The systematic descriptions provided below are based on re-examination of the type specimens, on topotype material examined in the Natural History Museum (BMNH) and on specimens collected by the author in the field. Previously unidentified topotype collections of 50 specimens (B. 71876) and 10 specimens (B. 71740) in the BMNH were particularly useful in demonstrating morphological variation within the species. Additional specimens were examined in the collections of the British Geological Survey (BGS GSM). The morphological terminology adopted here is widely accepted and is essentially that used in the *Treatise* (Moore 1965). The stratigraphical nomenclature adopted follows Parsons (1980).

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## SYSTEMATIC PALAEONTOLOGY

Class ARTICULATA Huxley, 1869
Order RHYNCHONELLIDA Khun, 1949
Superfamily RHYNCHONELLACEA Gray, 1848
Family ?BASILIOLIDEA Cooper, 1959
Subfamily LACUNOSELLINAE Smirnova *in* Ager, 1965
Genus STOLMORHYNCHIA Buckman, 1918

*Discussion.* The generic diagnosis given below is based almost entirely on the type species, although minor morphological variations seen in species recorded by Kamyshan and Babanova (1973) are taken into consideration.

*Diagnosis.* Medium- to large-sized rhynchonellids with a subtrigonal to subpentagonal outline. Dorsal fold usually well developed, often asymmetrical. Anterior commissure uniplicate. Costae strong and fairly angular, 12–16 in number. No posterior smooth area. Beak small, strong and suberect; beak-ridges poorly developed. Dental lamellae strong and subparallel. Hinge plates strong and slightly convergent ventrally. Median septum absent or barely detectable; no septalium. Crura of falcifer type.

### *Stolmorhynchia stolidota* Buckman, 1918

Text-figs 1–2

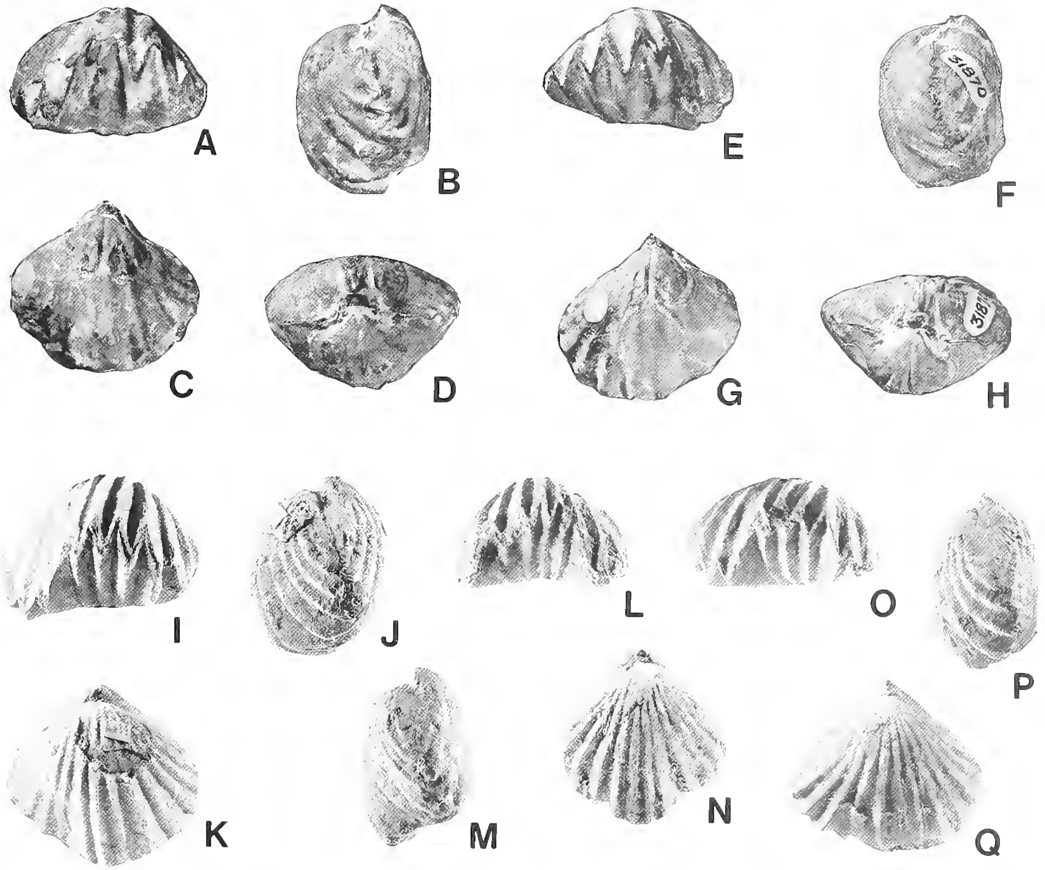
1918 *Stolmorhynchia stolidota* Buckman, p. 46, 228, pl. 13, figs 12–13.
1962 *Stolmorhynchia stolidota* Buckman; Ager, p. 132.
1965 *Stolmorhynchia stolidota* Buckman; Ager, p. H609, fig. 409, 3.
1967 *Stolmorhynchia stolidota* Buckman; Ager, p. 164.
1972 *Stolmorhynchia stolidota* Buckman; Ager *et al.*, p. 188.
1973 *Stolmorhynchia stolidota* Buckman; Kamyshan and Babanova, p. 37, pl. 2, figs 9–11.
1985 *Stolmorhynchia stolidota* Buckman; Prosorovskaya, p. 105, pl. 20, fig. 4.

*Diagnosis.* This is as given for the genus, with the addition that in this species the costae usually number 13–15.

*Type specimen.* Buckman (1918, pl. 13, figs 12–13) figured two specimens of this species from the Irony Bed, *blagdeni* Subzone of the *humphriesianum* Zone, of Louse Hill, Sherborne, Dorset. Buckman designated the original of figure 12 as the holotype and that of figure 13 as a paratype. These specimens are now located in the British Geological Survey, numbered BGS GSM 31869 and BGS GSM 31870 respectively. Their dimensions in mm are as follows: holotype: L = 21·9, W = 24·4, T = 16·7; paratype: L = 21·5, W = 23·8, T = 15·8. Both specimens are internal moulds.

*Description.* External characters: medium- to large-sized rhynchonellids with specimens measured being up to 22·6 mm long, 28 mm wide and 18·2 mm thick. Subtrigonal to subpentagonal in outline and biconvex in lateral view, with the brachial valve being the more convex of the two valves. The shell is often asymmetrical, with approximately equal numbers of left- and right-skewed specimens. The shell can be left-skewed, right-skewed or not skewed at all (see examples in Text-fig. 1). The anterior commissure is uniplicate. The dorsal fold starts to appear halfway down the valves, is usually well-developed, and is often skewed by the asymmetry. There are usually 13–15 strong, fairly angular costae. A widely spaced vascular system is clearly visible on many internal moulds, and is well demonstrated on Buckman's type specimens. The beak is small, strong and suberect, with beak ridges very poorly developed. The foramen is small, subcircular and submesothyrid, with small disjunct deltidial plates. In many specimens, however, the details of the foramen are obscured by sediment and are thus very difficult to examine.

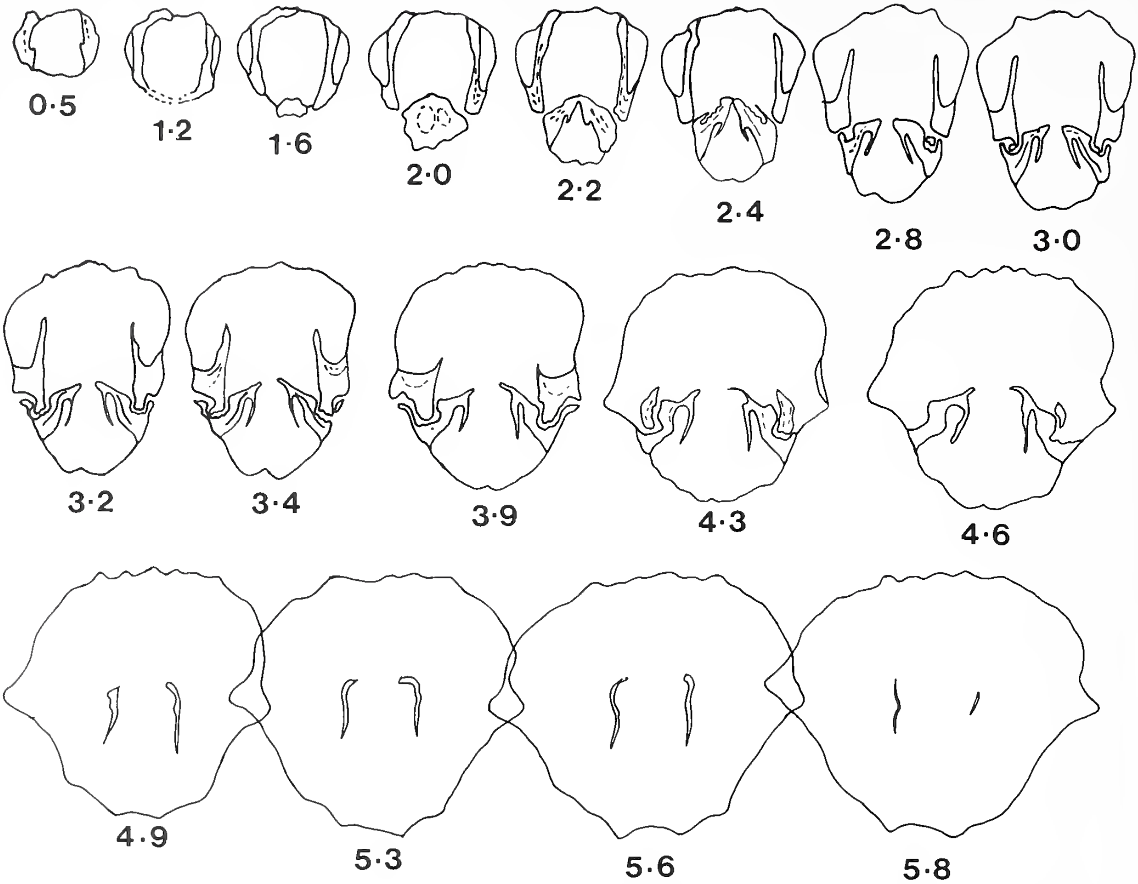
Internal characters. These are shown in Text-figure 2. Traces of a pedicle collar appear to be visible. The delthyrial cavity is rectangular. The dental lamellae are strong and virtually parallel. The lateral umbonal cavities are narrow and semi-elliptical. Ridges marking possible sites of muscle attachment are visible on the



TEXT-FIG. 1. *Stolmorhynchia stolidota* Buckman. Bajocian, *humphriesianum* Zone, Irony Bed; Louse Hill, Sherborne, Dorset. Specimens A–D and E–H are internal moulds and have been photographed uncoated to display internal plates and muscle scars. A–D, holotype GSM 31869; note asymmetry; figured Buckman 1918, pl. 13, fig. 12*a–d*. E–H, paratype GSM 31870. Internal mould showing vascular system; figured Buckman 1918, pl. 13, fig. 13*a–d*. I–Q, three topotypes; these specimens have shells and are coated with ammonium chloride. I–K, BMNH B.31890; Walker Collection; specimen with well-displayed asymmetry. L–N, BMNH. B.71740. Buckman Collection; specimen showing little asymmetry. O–Q, BMNH B.31609; specimen with strong asymmetry. All × 1.

inside of the pedicle valve. The teeth are crenulated and are inserted into their sockets in a slightly dorsally convergent manner. The hinge-plates are strong, straight and slightly convergent ventrally. The median septum is absent to barely detectable and there is no septalium. The crura are of the falcifer type.

*Occurrence and remarks.* The type material and virtually all the other specimens examined in the BMNH are recorded as coming from the *humphriesianum* Zone (*blagdeni* Subzone) of the Sherborne area in Dorset. In this area, Louse Hill is type locality of the species and has yielded most specimens. The few specimens of this species in the BMNH not from the Sherborne area are recorded as coming from the same biostratigraphical horizon at Burton Bradstock on the Dorset coast. Outside Dorset, the species has only been recorded from the *sauzei* Zone of the north-west Caucasus (Kamyshan and Babanova 1973) and from the *humphriesianum* Zone of the Transcaucasus (Prosorovskaya 1986).



TEXT-FIG. 2. *Stolmorhynchia stolidota* Buckman. Bajocian (*humphriesianum* Zone) Irony Bed; Louse Hill, Sherborne, Dorset. Topotype BMNH B.71933; Buckman Collection; internal mould. A series of 17 serial sections through the posterior part of the shell; note the well-defined falcifer crura, ×2·5.

*Stolmorhynchia stolidota* cannot easily be mistaken for its contemporaries in Britain. It is the only British Aalenian or Bajocian rhynchonellid with falcifer crura, and its often well-defined asymmetry is only matched in the Inferior Oolite by the larger and much more depressed Upper Bajocian *Rhactorhynchia*. Fürsich and Palmer (1984) investigated asymmetry in rhynchonellids, but concluded that it was not possible to prove whether or not asymmetry had an adaptive function. However, the relatively localized geographical and stratigraphical distribution of this species in the Inferior Oolite of England may suggest a degree of facies control.

*Other nominal species of* Stolmorhynchia. A full assessment of nominal species assigned to *Stolmorhynchia* would be a vast task, and this is not attempted here. However, the revision of the type species above suggests that considerable splitting-off of species from the genus is required. For example, the only other nominal species of *Stolmorhynchia* recorded from Britain, *Stolmorhynchia bouchardii* (Davidson) known from the Upper Lias of Ilminster, Somerset, has very little shell ornament (Ager 1962) and probably does not belong in this genus. This was in fact recognized by Ager in later papers (Ager 1967; Ager *et al.* 1972), where he expressed doubts as to whether his earlier assignment of this species to *Stolmorhynchia* was correct, and recognized the need for a revision of the type species to clarify matters. *Stolmorhynchia bouchardii* is still, however, entrenched in the literature and is consistently referred to in current research (Alméras *et al.* 1990). The same doubts apply to Upper Lias species of '*Stolmorhynchia*' described from Morocco by Rousselle (1974), which lack falcifer crura and which display a posterior smooth area, thus differing significantly from the type species. In fact, of all the nominal species investigated during the course of this study, it is only those described by Kamyshan and Babanova (1973) from the Caucasus which appear to be attributable with any degree of certainty to *Stolmorhynchia*. Whether or not the six new species (*S. inconspicua*, *S. karatschae*, *S. kusnetzovi*, *S. robinsoni*, *S. triplicata* and *S. urupensis*) from the *sauzei* and *humphriesianum* zones of the Bajocian, proposed by Kamyshan and Babanova (1973) are all valid species is debatable, as they vary little in morphology. They are all, however, very similar to *Stolmorhynchia stolidota*, which occurs with them, and are almost certainly attributable to the genus *Stolmorhynchia*.

## CONCLUSIONS

*Stolmorhynchia* is a poorly defined genus with a large number of nominal species attributed to it. The taxonomic revision of the type species undertaken here, supplemented by data from species of *Stolmorhynchia* from the Caucasus, enables the first detailed and well-defined diagnosis for the genus *Stolmorhynchia* to be given. Thus, for the first time, a solid basis has been provided from which the generic validity of nominal species of *Stolmorhynchia* can be assessed. In the light of this work, it appears that the splitting-off of nominal species of *Stolmorhynchia* will be required in due course.

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# REVISION OF THE ORDER STROMATOPORIDA

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ABSTRACT. The genus *Stromatopora* has been widely misinterpreted as characterized by vertical structural elements, but the type species, *Stromatopora concentrica*, has a structure, here called cassiculate, dominated by oblique elements like a chainlink fence. Only twenty-six species of the several hundred attributed to *Stromatopora* conform to a redefinition of the genus presented here. Cellular microstructure is distinct from microreticulate microstructure. As presently defined the Order Stromatoporida is polyphyletic. Genera that have cellular microstructure are placed in the redefined Order Stromatoporida and evolved from unknown ancestors in Llandovery time. Genera that have microreticulate microstructure are separated as the Order Syringostromatida (emended), that evolved from densastromatid ancestors about the same time. In a major episode of adaptive radiation starting in the Přídolí and culminating in Emsian time the ancestral syringostromatid, *Parallelostroma*, gave rise to *Coenostroma*, *Habrostroma*, *Syringostroma*, *Columnostroma* and *Parallelopora*. In late Early to Middle Devonian time *Stromatopora* radiated into *Lineastroma*, *Arctostroma*, *Pseudotrupetostroma*, *Glyptostromoides* and *Taleastroma*. The position of *Ferestromatopora* is problematic. *Syringostromella* coexisted with *Stromatopora* in Middle and Late Silurian time and gave rise to *Salairella* in late Early Devonian time. Concise definitions of all these genera are formulated, problems of distinguishing them are discussed, and representative species are listed.

THE genus *Stromatopora* Goldfuss, 1826, was originally described on the basis of external form and a crude vertical polished section of the type species by monotypy, *Stromatopora concentrica* Goldfuss, 1826. Before the internal structure of stromatoporoids was investigated using thin sections, the genus was used for nearly all stromatoporoids and for other laminated, cabbage-like structures, such as stromatolites.

In the first comprehensive review of stromatoporoids using their internal structure, H. Alleyne Nicholson (1886*a*) illustrated a specimen which according to him was 'absolutely identical with the original example of the species' from the Middle Devonian of the type locality, Gerolstein, Germany. Although the captions indicate that this specimen was shown only in external view and in tangential thin section (pl. 11, figs 15–16), labels on the thin sections indicate that the vertical section (pl. 11, fig. 18) is from the same specimen although it was identified as from another specimen (see Appendix for discussion of this plate). Nicholson's thin sections are difficult to match with the drawings.

Nicholson's vertical section (1886*a*, pl. 11, fig. 18; see Pl. 1, fig. 1) shows a skeleton dominated by vertical structural elements separated by dissepiments. Nicholson's concept of the genus in vertical section was used by palaeontologists for the next sixty-six years, during which sixty-nine species were established.

The type specimen of *Stromatopora concentrica* is in the Institut für Paläontologie, Bonn. The hand specimen illustrated by Goldfuss (1826) has been cut into a large vertical thin section and a small tangential thin section (both labelled 80) apparently at Nicholson's (1888*a*, p. 81) request, and three thin sections, one large (Pl. 1, fig. 3; Pl. 2, fig. 1) and one small vertical and a tangential apparently cut for Lecompte in about 1950. Lecompte (1952, pl. 53, fig. 1) illustrated the large vertical cut for Nicholson at low magnification, and Mistiaen (1985) illustrated the large vertical section cut for Lecompte. Lecompte (1952) also published illustrations of well-preserved specimens from the Devonian of Belgium that he believed better illustrated the structure of the type specimen (Pl. 2, fig. 2). These illustrations show that the type specimen is poorly preserved, latilaminate, and has a network structure like that of a chainlink fence with relatively insignificant continuous vertical structural elements. Neither the type nor the Belgian specimens assigned to *S. concentrica* by

[Palaeontology, Vol. 36, Part 1, 1993, pp. 201–229, 2 pls.]

Lecompte (Pl. 2, fig. 2) resemble Nicholson's (1886*a*) illustrations on which the widely accepted concept of *Stromatopora* had been based, and Lecompte (1952, p. 274) suggested that Nicholson's specimens were not conspecific with the type. Photographs of the Belgian specimens were also used by Lecompte (1956, fig. 91, 2) to illustrate the characteristics of *Stromatopora concentrica* in the *Treatise on Invertebrate Paleontology*. St. Jean (1957, p. 838) regarded these photographs as not representative of *Stromatopora concentrica* (whose type he incorrectly stated was illustrated by Nicholson 1886*a*, pl. 11, figs 16, 18), identifying them as *Ferestromatopora tyrganensis* Yavorsky, 1955. Galloway (1957, p. 447) endorsed this interpretation. Since then most stromatoporoid workers have continued to use Nicholson's concept of *Stromatopora* (see references under *Stromatopora* below), but described species under this generic umbrella that have included a wide range of internal morphologies. Up to 1990, two hundred and eight species have been first described as belonging to this genus, and many more have been referred to it subsequent to first description. V. I. Yavorsky alone (in many papers published between 1929 and 1956) has been responsible for describing fifty-four species of *Stromatopora*.

Mori (1970, p. 121) examined the sections of Goldfuss's types and agreed with Lecompte's (1952) interpretation.

Mistiaen (1985) re-examined Lecompte's and Goldfuss's specimens and reaffirmed Lecompte's view that *Stromatopora* is a genus with suppressed vertical elements and a tangled structure (*enchevêtrée*). Stearn (1990) suggested that a revision of the genus was long overdue as it had become useless as a taxon. This revision of *Stromatopora* and its relatives placed by Stearn (1980) in the Order Stromatoporida is attempted in this paper.

Many new genera have been proposed by authors in an effort to split useful taxa from the equivocally defined genus, *Stromatopora*. In this paper the diagnoses of these genera are reviewed and an attempt is made on the basis of a literature survey to divide species that have been assigned to *Stromatopora* in the broad sense between these new genera. Only those that closely resemble the type species as redescribed by Lecompte (1952) and Mistiaen (1985) are retained in *Stromatopora*. In this revision only twenty-six species are recognized as valid; *Stromatopora* and another eleven are doubtfully assigned to it. The genera previously placed by Stearn (1980) in the order Stromatoporida are divided between the redefined orders Stromatoporida and Syringostromatida, for which new concise definitions have been formulated. Lists of representative species of each genus are given in the text or, where extensive, deposited with the British Library, Boston Spa, Yorkshire, UK, as Supplementary Publication No. SUP 14042 (24 pages). The species have been revised on the basis of a survey of the literature and the writer's examination of all major stromatoporoid collections in museums outside the former Soviet Union and China.

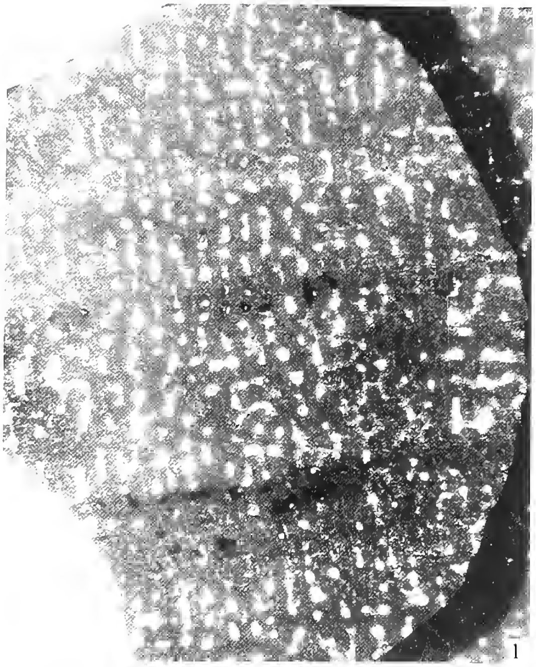
## STRUCTURAL ELEMENTS

Typical stromatoporids and syringostromatids have coenosteles (wall-like structures) as vertical elements, but some have pillars (post-like structures) or megapillars (complex vertical thickenings of the skeleton in mamelon columns). Coenosteles in tangential section are one, or commonly a combination of, the following: (1) separate, irregular, vermiform; (2) an open labyrinthine network enclosing galleries of labyrinthine outline; and (3) a closed network enclosing subcircular galleries. Tangential sections of the coenosteles are rarely diagnostic of genera (with exceptions, such as *Salairella*), as most show a wide range of forms including all three of the above conditions within a single thin section.

### EXPLANATION OF PLATE 1

Figs 1–3. *Stromatopora concentrica*. 1, vertical section; 2, tangential section illustrating Nicholson's concept of the species and genus; Sections 1a and 1 (Nicholson collection, P5869, Natural History Museum, London), × 10. 3, Goldfuss's (1836) type specimen, number 80, Institut für Paläontologie, Bonn, vertical section cut for Lecompte, No. Lecompte 32.2, × 10.

PLATE 1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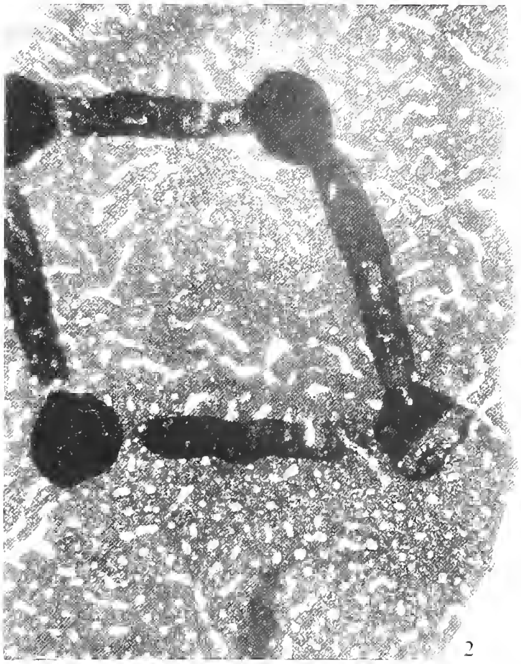
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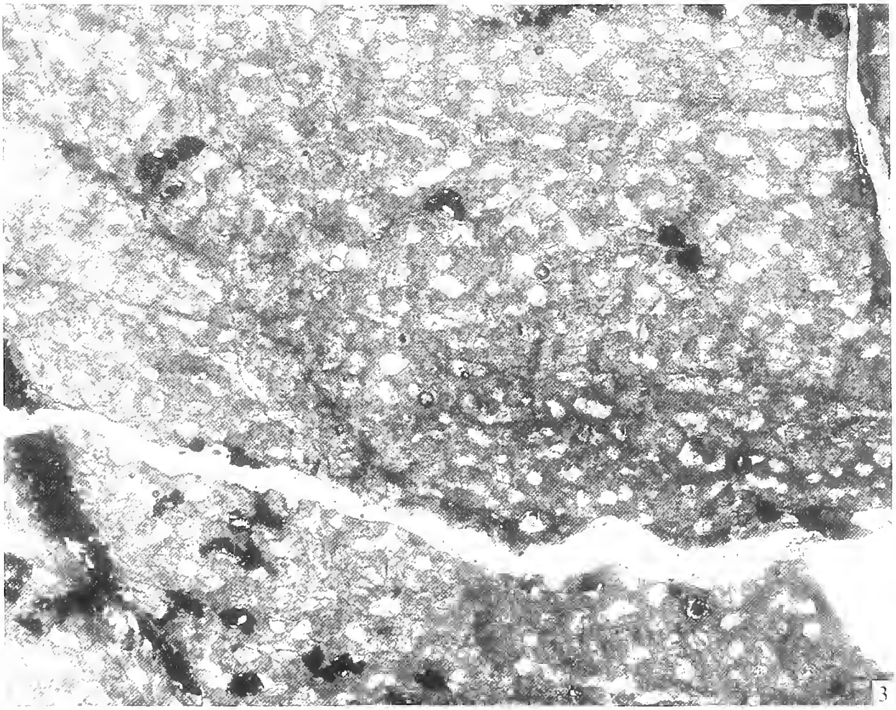
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STEARN, *Stromatopora*

Pillars are characteristic of certain genera such as *Columnostroma* and *Coenostroma* and commonly occur combined with coenosteles. The distinction between them is arbitrary.

In vertical section coenosteles are vertically elongate elements, irregular in form, joining and splitting. In species grouped in the same genus, large differences in the vertical extent of the coenosteles have been accepted by many workers. Stearn (1980) used the vertical persistence of coenosteles to separate the families Stromatoporoidae and Syringostromellidae.

Horizontal structural elements in the Stromatoporida are of three types: (1) horizontal coenostroms; (2) oblique coenostroms; and (3) microlaminae. The first are generally thick, horizontally continuous and are well-illustrated by *Parallelostroma* and *Lineastroma*. Thick laterally persistent coenostroms may enclose thin, dense microlaminae, as in *Parallelostroma*, or microlaminae may exist independently. In genera with structures dominated by coenosteles, coenostroms may be suppressed entirely and replaced by dissepiments or they may form short connections between two coenosteles.

Oblique coenostroms have been characterized as chevron-shaped or tangled elements united in a network. No term presently exists for the three-dimensional network formed by these oblique elements, which in vertical section is comparable to that of a chainlink fence whose 'wire' encloses diamond-shaped voids, or to that of a trellis. The term 'cassiculate' (Latin, *cassicula* = a small net) is proposed in this paper (Pl. 2, fig. 2) for this type of network. The adjective can be used to describe the network as a whole, or the coenostroms that form it. Such a network is particularly characteristic of genera such as *Ferestromatopora* and *Arctostroma* and, to a lesser extent, of *Stromatopora*.

The structures in vertical section of genera can be represented as fields distributed in two-dimensional space between three end-members (Text-fig. 1). The end-members represent genera dominated by: (1) long vertical elements (coenosteles or pillars); (2) persistent coenostroms; or (3) a cassiculate network. To carry the fence analogy further, these would be equivalent, in vertical section, to (1) picket; (2) rail or corral; and (3) chainlink fences, respectively. Near the three end-members are the fields of *Salairella*, *Lineastroma* and *Arctostroma*, respectively. The field of the genus *Stromatopora* in this morphological plane is near the centre but displaced toward the cassiculate end-member. Genera characterized by a grid of subequal coenostroms and vertical elements, such as *Coenostroma*, plot between poles 1 and 2. Those with strong coenosteles traversing a cassiculate network, for example *Glyptostromoides*, fall between poles 1 and 3.

If an axis along which pillars grade into coenosteles is added, the triangular morphological plane becomes a tetrahedron (Text-fig. 2). The pillar-dominant end-member is close to the field of *Columnostroma*. The field of *Taleastroma* separates from that of *Glyptostromoides* along the pillar-cassiculate axis. The imperfect integration of coenosteles into a network in *Syringostromella* places its field along the network–pillar axis. The fields of *Coenostroma* and *Pseudotrupetostroma* separate along the network–coenostrom axis.

These diagrams are an aid to visualizing morphological variation among the genera but do not include genera distinguished by features not easily plotted as end-members (e.g. megapillars). They do not imply close phylogenetic relationships between adjacent genera.

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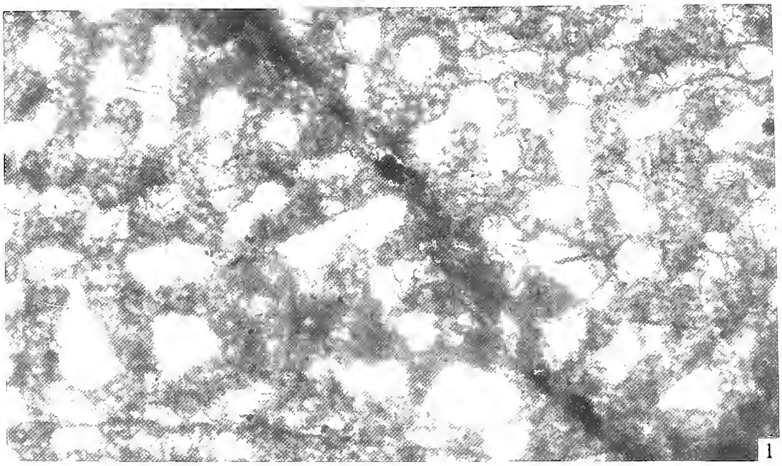
EXPLANATION OF PLATE 2

Figs 1–2. *Stromatopora concentrica*. 1. type specimen, number 80, Institut für Paläontologie, Bonn; vertical section cut for Lecompte, enlarged to show the cellular microstructure of a well-preserved part of the section, × 25. 2, vertical section of specimen from the Ardennes to illustrate Lecompte's concept of the genus; number 6224*a*, Institut Royal des Sciences Naturelles de Belgique, Brussels (Lecompte's pl. 53, fig. 2), × 10.

Fig. 3, *Coenostroma monticuliferum*. Vertical section to show microstructure of the type specimen, number 32409a University of Michigan; Galloway and Ehlers' (1960) thin section WI-1, × 25.

Fig. 4, *Pachystroma antiquum*. Vertical section of type specimen; Nicholson collection number 290*a* (P6003, Natural History Museum, London), × 10.



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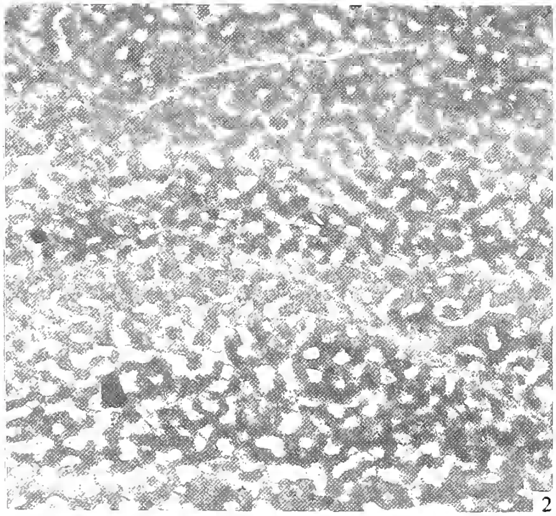

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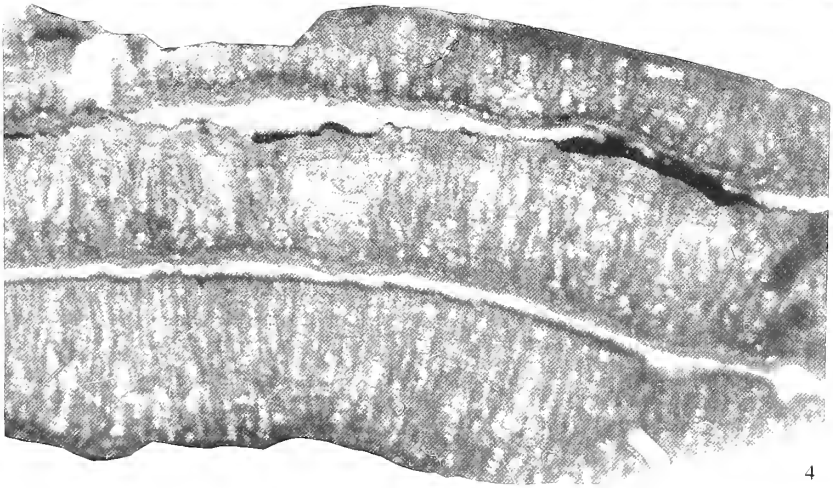

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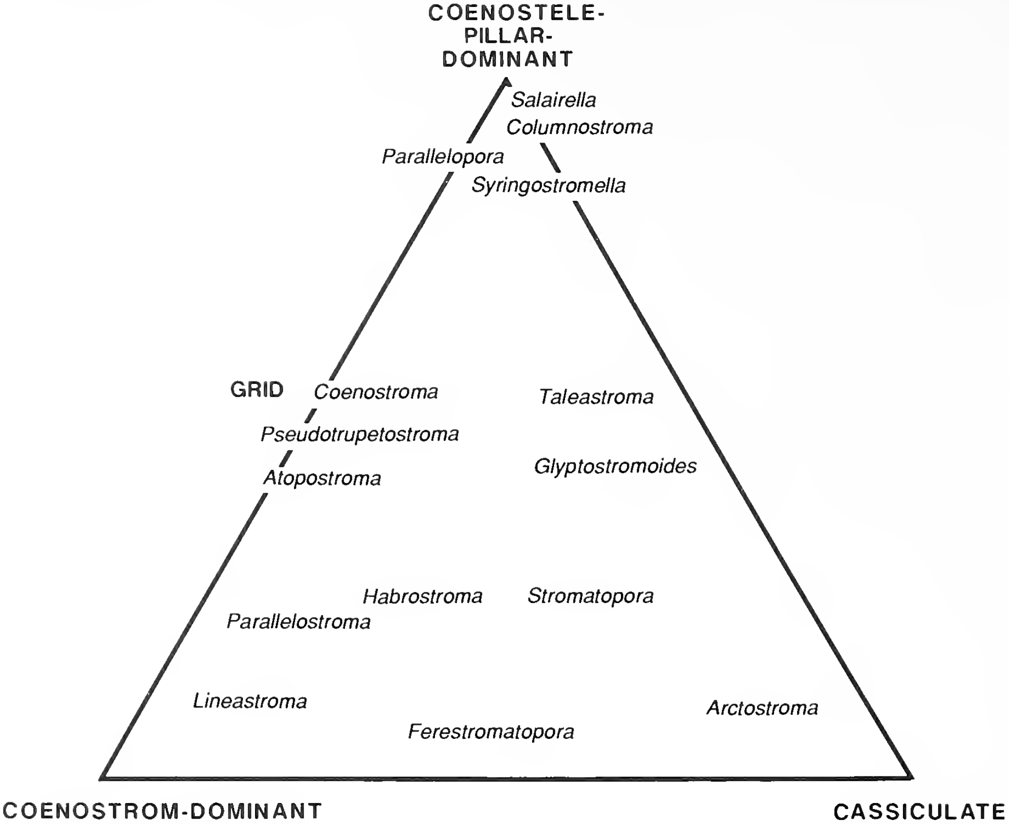
STEARN, *Stromatopora*, *Coenostroma*, *Pachystroma*



TEXT-FIG. 1. Genera of the Stromatoporida and Syringostromatida plotted on a two-dimensional field with cassiculate, vertical-dominant, and horizontal-dominant elements as end-members. Genera with vertical and horizontal elements of equal prominence intersecting at right angles plot at the GRID position.

## MICROSTRUCTURE

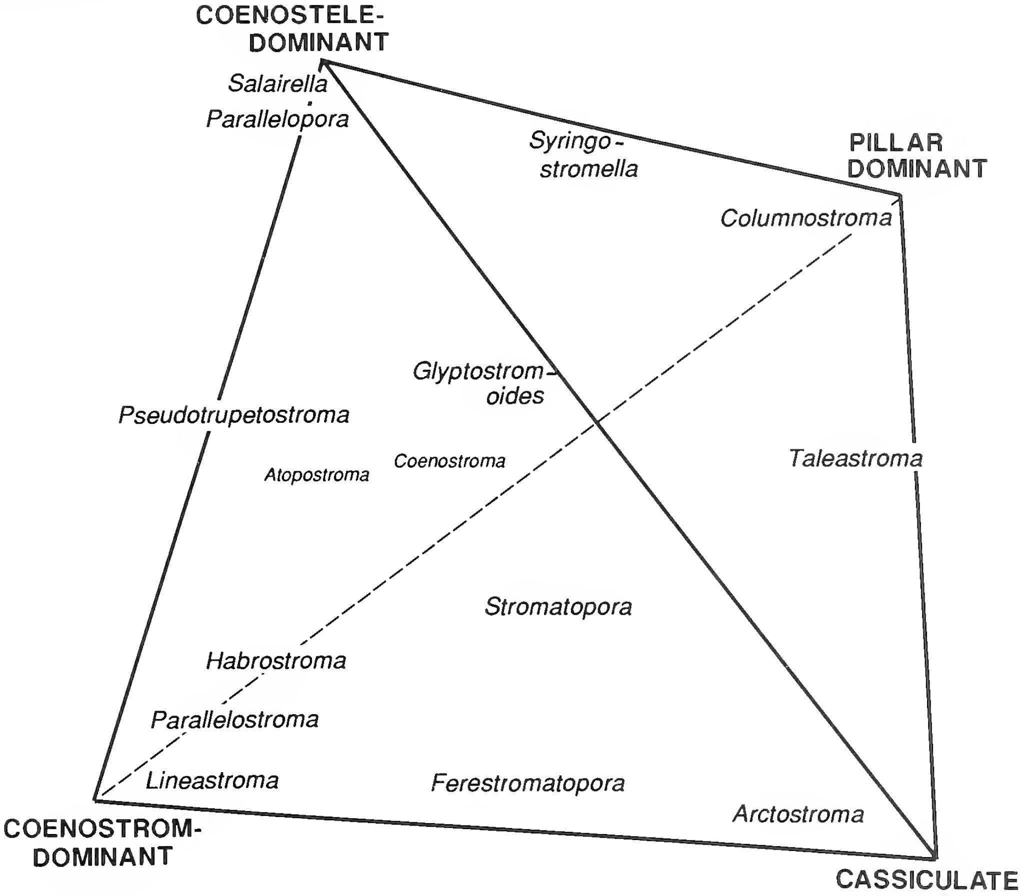
### *Cellular microstructure*

The microstructure of the type specimen of *Stromatopora concentrica* (Pl. 2, fig. 1) is locally coarsely cellular, that is, crowded with randomly arranged, subcircular parts that are less opaque than surrounding parts in both tangential and vertical section. These lighter parts have been interpreted by most workers as the remnants of subspherical voids (cellules), or of originally spherulitic texture.

In many genera of Stromatoporida this cellular microstructure is evident, but its expression is affected by diagenesis. In many specimens the microstructure can appropriately be described as consisting of dark (in transmitted light), subspherical masses in a lighter ground, a microstructure referred to as melanospheric. The origin and diagenesis of these microstructures have been discussed elsewhere (Stearn 1966*a*, 1977, 1980, 1989; St. Jean 1967; Wendt 1984; Stearn and Mah 1987). Melanospheric and cellular microstructure are not confined to the genera discussed here but are found in other orders and particularly in the Stromatoporellida.

### *Microreticulate microstructure*

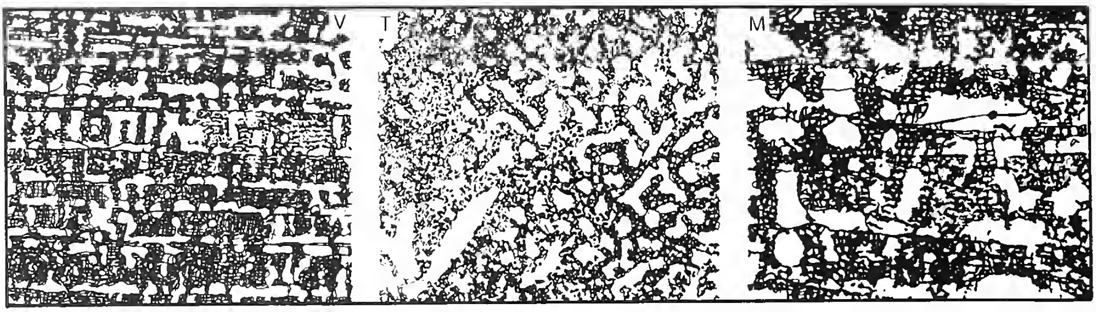
Not all stromatoporoid palaeontologists recognize that cellular microstructure is an expression of random voids in the skeletal material. A second concept of the origin and evolution of the



TEXT-FIG. 2. Genera of the Stromatoporida and Syringostromatida plotted on a three-dimensional solid (tetrahedron) with coenostrom-dominant, coenostele-dominant, pillar-dominant and cassiculate end-members. Genera in small type (*Coenostroma*, *Atopostroma*) are located on the back surface of the tetrahedron.

microstructure of the Stromatoporida emphasizes the origin of the more opaque skeletal material rather than that of the spaces that separate it. Parks (1909) appears to have originated the idea that the microstructure of *Stromatopora* and its relatives is defined by a fine, rectilinear, three-dimensional framework of posts and connecting beams (now called micropillars and microcolliculi) enclosing equidimensional voids (microgalleries). Parks (1936, p. 9) later explained this viewpoint of the microstructure of *Stromatopora* as 'reticulate' and as 'nothing more than the gross fibre of *Actinostroma* greatly reduced'. Unfortunately, he did not live to work out these ideas in a classification, but the idea that the skeletal material of *Stromatopora* and its allies evolved from 'very fine *Actinostroma*-like forms' (now called densastromatids) by the opening of cavities that became galleries is clearly stated in his work.

The 'reticulate' microstructure of Parks is now referred to as microreticulate, and some palaeontologists regard cellular microstructure as originating in microrcticulate skeletal material. Stock (1989) extended the idea of the origin of stromatoporid microstructure from micropillars and microcolliculi to explain cellular microstructure through the breakdown of the regularity of the microreticulum. He called such cellular microstructures 'akosmoreticulate' but the suffix -reticulate seems inappropriate for a microstructure that is not a regular framework. The concept has also been discussed by Kazmierczak (1971) and Nestor (1974).



TEXT-FIG. 3. Structure of *Parallelostroma* in vertical (V) and tangential (T) sections, × 10, and microstructure in vertical section (M), × 20 (based on photographs of Rosen's type specimen of *P. typica*, number Co009, Estonian Academy of Science, Tallinn).

The microreticulate microstructure of genera such as *Parallelostroma* can be attributed to the alignment of cellules in vertical and horizontal rows reducing the more opaque skeletal material to a rectilinear network or to a scaffold of minute posts and beams (Text-fig. 3). The preservation of most specimens does not allow an easy choice between these two models. However, in species in which the microreticulate microstructure is well-preserved, the microcolliculi (beam-like elements) tend in tangential section to protrude from the margins of structural elements, giving them poorly defined borders and margins with only partly enclosed cavities of the microgalleries. Cellular species are distinct in the smoother, more discrete borders of the structural elements and the cellules do not appear to open into galleries as do microgalleries. This evidence indicates that cellular skeletal material is not merely a variant of microreticulate but a distinct microstructural type.

Nestor (1974) called 'orthoreticulate' the microreticulate microstructure in which darker skeletal material forms a rectilinear framework; it is best shown in his genus *Parallelostroma*. He called stromatoporoids in which the micropillars diverge upward 'clinoreticulate'.

In advanced syringostromatids the increase in size of the microgalleries reduces the tissue between them to a fine, tenuous, lacy network.

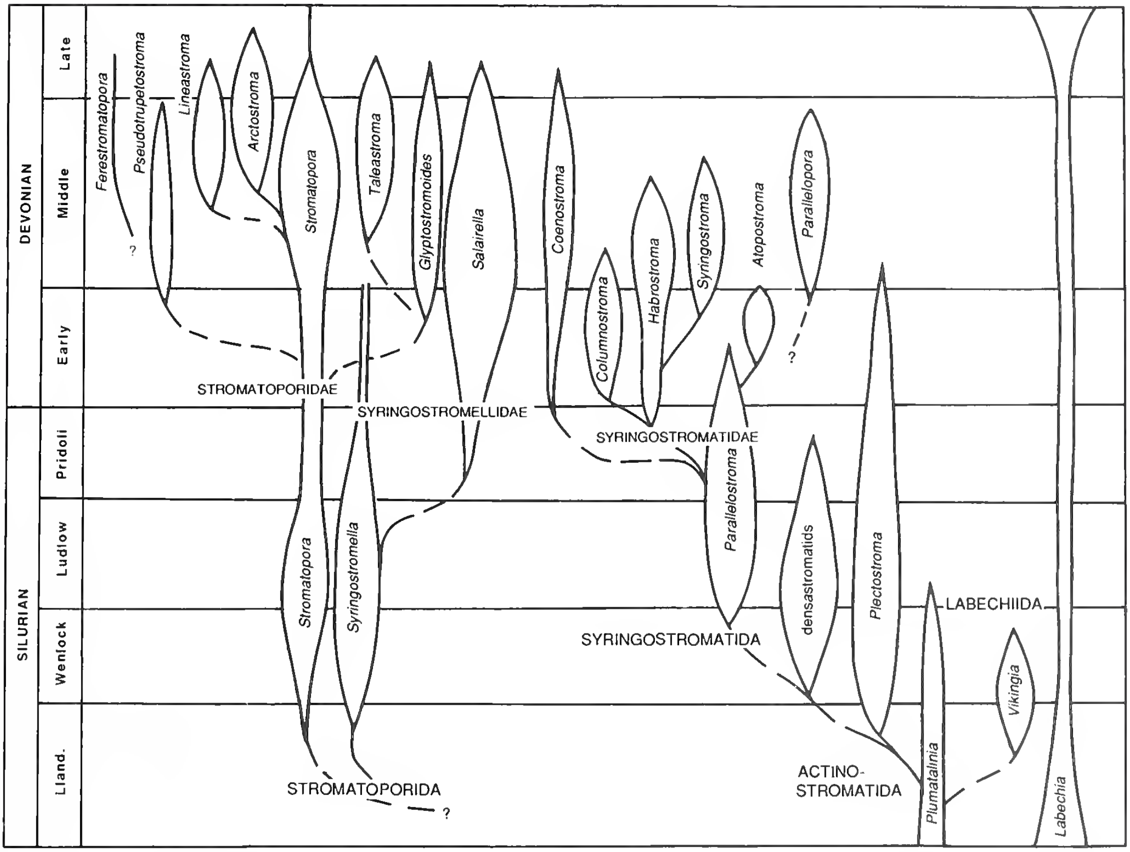
### *Microstructure evolution*

The following discussion is based on the premise that cellular and microreticulate microstructure are fundamentally different in origin. Orthoreticulate microstructure seems likely to have evolved from the densastromatids, through forms such as *Actinostromella*, and Nestor (1974) and Stock (1983) have traced phylogenies based on this premise. The tendency of the orthoreticulate laminae to break up into microlaminae in diagenesis is further proof that this microstructure is formed by a fine reticulum of posts and beams. Cellular microstructure is unlikely to have formed by the modification of this reticulum. Genera such as *Syringostromella* and *Stromatopora* have cellular microstructure fully developed by the late Llandovery before the densastromatids appear in the early Wenlock, and *Actinostromella* and *Parallelostroma* appear in late Wenlock time. Mori (1968, 1970) and Nestor (1982, 1990) documented the faunal succession in the Wenlock and Ludlow of the Baltic area; Llandovery faunas are less well known but have been described by Parks (1909), Nestor (1966), Bolton and Copeland (1972), and Bolton (1991). Nestor (1974) suggested the derivation of the cellular *Stromatopora* lineage from stromatoporoids of compact microstructure because there are only labechiids and clathrodictyids of compact skeletal material in early Llandovery rocks, but the ancestors of the lineage are still unclear. He also suggested an origin of the clinoreticulate group from labechiids like *Plumatalinia* (late Ordovician to mid-Silurian) and *Vikingia* (mid-Silurian) through actinostromatid genera such as *Pseudolabechia*.

If genera with cellular microstructure are not closely related to those of clinoreticulate and orthoreticulate microstructure, then the Order Stromatoporida as defined by Stearn (1980) is polyphyletic and contains at least two branches in Llandovery time. The microreticulate branch may include an early divergence of clinoreticulate from orthoreticulate genera as Stock (1989) believed, or genera with these two microstructures may have evolved independently as suggested by Nestor (1974).

## PHYLOGENY

Text-figure 4 is an attempt to arrange the stromatoporid genera in a phylogeny. Clearly the Stromatoporida had two periods of adaptive radiation: late Early Silurian and late Early Devonian times. These correspond to similar increases in diversity in other stromatoporoid orders and to episodes when seas were transgressing widely over continental platforms. Decreases in diversity took place at times of regression of the epeiric seas at the end of the Silurian and Devonian.



TEXT-FIG. 4. Phylogeny of the Stromatoporida and Syringostromatida (the range of *Lineastroma* is shown in the Devonian only, as the stratigraphical placement of the type species in the Silurian is uncertain).

Microstructure analysis suggests that the Order Stromatoporida is polyphyletic despite the similarity of the mid-Devonian members of the two lineages. The *Stromatopora* lineage was derived from unknown ancestors, either the clathrodictyids or labechiids, in early Llandovery time, and early on split into genera with dominantly vertical elements (*Syringostromella*) and those with cassiculate structure (*Stromatopora*). The second radiation of the *Stromatopora* group gave rise to such genera as *Arctostroma* and *Glyptostromoides*. The position of *Ferestromatopora* is problematic. *Syringostromella* survived into the Devonian and appears to have given rise to *Salairella*.

The Actinostromatida appear to have evolved from labechiid ancestors in late Llandovery time through transitional genera such as *Plumatalinia*. The rootstock of the Actinostromatidae, represented by *Plectostroma*, and of the Densastromatidae separated shortly afterwards. In Wenlock time *Parallelostroma* had evolved from densastromatid stock by the opening of dominantly horizontal galleries. The diversification of this lineage took place in Emsian time with the evolution of forms with dominant pillars of clinoreticulate microstructure such as *Syringostroma* and *Columnostroma*. *Atopostroma* arose from *Parallelostroma* in Early Devonian time by the superposition and thinning of the pillars, but apparently did not survive into the Eifelian. The possibility that clinoreticulate forms arose independently of *Parallelostroma* from advanced labechiids, like *Pseudolabechia*, suggested by Nestor (1974) cannot be discounted. The relationships between *Habrostroma*, *Coenostroma* and *Syringostroma* must be close, but their relationship to *Columnostroma* and *Parallelopora*, and of these two to each other, are less certain.

## CLASSIFICATION

The stromatoporids have been separated from other stromatoporoid orders by a combination of: (1) thick cellular or microreticulate skeletal material; and (2) vertical elements that are coenosteles. Nearly all members have coenosteles but a few genera have pillars in combination with coenosteles, and *Columnostroma* has only pillars joined in an incipient network. Both cellular microstructure and coenosteles appear in other orders and neither is diagnostic of the stromatoporids.

The genera of the Order Stromatoporida have been considered to be divided into three families, the Stromatoporidae, Syringostromellidae and Syringostromatidae (Stearn 1980) on the basis of the form of the structural elements. Because these genera did not have an immediate common ancestor, the Order Stromatoporida as recognized in Stearn's (1980) classification is polyphyletic and should be divided into two orders. The name Stromatoporida is retained and redefined for the branch including cellular genera; the branch including microreticulate genera is redefined as the order Syringostromatida. The Stromatoporida are divided into the redefined families Stromatoporidae and Syringostromellidae on the basis of the dominance of cassiculate–laminate structures in the former and of coenosteles in the latter. The only family recognized in the Syringostromatida is the redefined Syringostromatidae.

## SYSTEMATIC PALAEONTOLOGY

### Phylum PORIFERA Grant, 1836
### Class STROMATOPOROIDEA Nicholson and Murie, 1878
### Order STROMATOPORIDA Stearn, 1980 (emended)

*Diagnosis*. Stromatoporoids with cellular microstructure and structure dominated by coenosteles and coenostroms forming amalgamate networks.

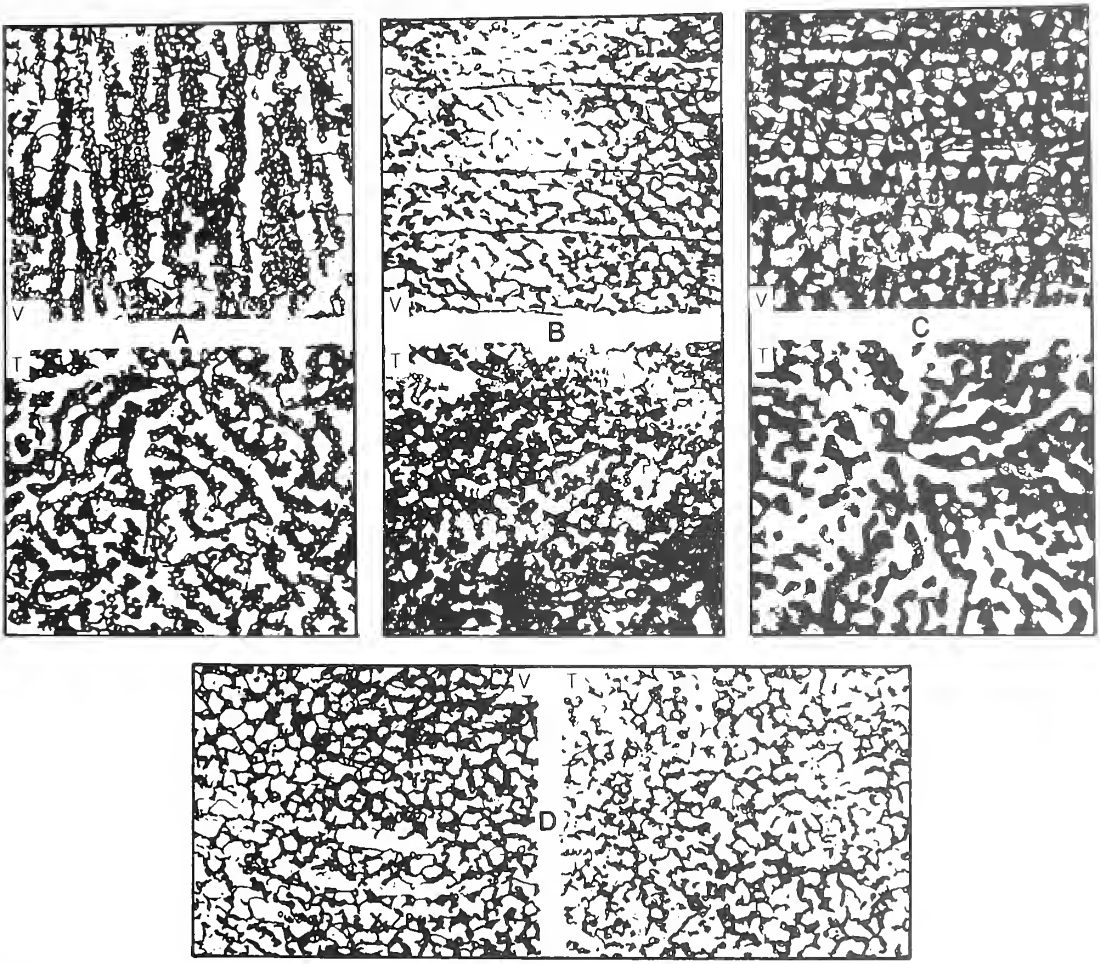
### Family STROMATOPORIDAE Winchell, 1867 (emended)

*Diagnosis*. Stromatoporids dominated by coenostroms, laminae, and cassiculate structures.

### Genus STROMATOPORA Goldfuss, 1826

Plate 1, figs 1–3; Plate 2, figs 1–2

[= *Stromatopora* Goldfuss, 1826, p. 21 (see Flügel and Flügel-Kahler (1968) for pre-1968 synonymy); Sleumer 1969, p. 46; Mori 1970, p. 121; Kazmierczak 1971, p. 88; Stock 1979, p. 336, 1984, p. 778; Mistiaen 1980, p. 208, 1985, p. 134; Bogoyavlenskaya and Khromych 1985, p. 84; Stearn 1990, p. 506. ?*Perplexostroma*



TEXT-FIG. 5. Sketches of Stromatoporida in vertical (V) and tangential (T) section, × 10. Microstructure somewhat stylized. A, *Syringostromella* (based on *S. borealis* in Mori 1970). B, *Ferestromatopora* (based on *F. kruppenikovi* in Yavorsky 1955). C, *Lineastroma* (based on *Stromatopora vorkutensis* in Yavorsky 1961. The original photograph is interpreted as inverted). D, *Arctostroma* (based on *Stromatopora contexta* in Stearn 1966*b*).

Bogoyavlenskaya 1981, p. 32; Bogoyavlenskaya and Khromych 1985; p. 84. *Ferestromatopora* Yavorsky; Galloway 1957, p. 446; Stearn 1966*a*, p. 111. *non Stromatopora* Goldfuss, Nicholson 1886*a*, p. 23; Galloway 1957, pp. 447; St. Jean 1957, p. 838; Zukalova 1971, p. 60.]

*Type species. Stromatopora concentrica* Goldfuss, 1826, p. 22, pl. 8, fig. 5*a–c*.

*Diagnosis.* Skeleton composed largely of cellular, cassiculate, oblique coenostroms and scattered dissepiments; in some successive phases in latilaminae containing short coenosteles; structural elements in tangential section labyrinthine network or discrete vermiform elements.

*Discussion.* Confusion concerning the internal structure of this genus has been reviewed in the introduction to this paper. Recognition of the dominantly cassiculate structure of the genus leaves twenty-six species definitely assigned to *Stromatopora*, and a further eight species placed in it provisionally. The list of these species has been deposited with the British Library as Supplementary Publication No. SUP 14042.

*Stromatopora* is close to *Arctostroma* Yavorsky, 1967 (see below) but does not have the prominently arched galleries of this genus, the tendency for the melanospheres to be aligned vertically, and the finer and more regular cassiculate network. Although these features might seem to have taxonomic value below the generic level, the species grouped below under *Arctostroma* do constitute a taxon readily separable from *Stromatopora*.

*Perplexostroma* Bogoyavlenskaya, 1981, based on *Stromatopora dzvenigorodensis* Riabinin, 1953, is monotypic. Riabinin's illustrations of the type species show prominent discrete pillars and large astrorhizal systems of the hidden type (Nestor 1966, p. 37). Bogoyavlenskaya's (1981) illustrations show a structure like that of *Arctostroma* with no discrete pillars or coenosteles and small simple astrorhizae. Khromych (1982) retained the species in *Stromatopora*. The diagnosis in Bogoyavlenskaya and Khromych (1985) is too brief to distinguish the genus from others.

*Stromatopora* is rare in the late Llandovery and Wenlock, increases in diversity during the Late Silurian and Early Devonian, and reaches its acme in Middle Devonian time. It is less abundant and diverse in Frasnian and rare in Famennian time.

### Genus FERESTROMATOPORA Yavorsky, 1955

Text-fig. 5B

*Type species. Ferestromatopora krupennikovi* Yavorsky, 1955, subsequently designated by Galloway (1957, p. 446).

*Discussions of the genus.* Yavorsky 1955, p. 109; St. Jean 1957, p. 838; Galloway 1957, p. 446; Stearn 1963, p. 665, 1966*a*, p. 111, 1966*b*, p. 57, 1980, p. 898, 1990, p. 506; Flügel and Flügel-Kahler 1968, p. 544; Sleumer 1969, p. 45; Mori 1968, p. 85; Kazmierczak 1971, p. 52; Khromych 1974, p. 52, 1976, p. 63; Bogoyavlenskaya and Khromych 1985, p. 76.

*Diagnosis.* Skeleton composed of elements that are largely oblique in vertical section and form a cassiculate network in which neither coenostroms nor coenosteles are easily distinguished. The network is traversed by thin, continuous, compact, widely spaced paralaminae. In tangential section the structural elements join in a labyrinthine network. Dissepiments are common but coenotubes are absent. The microstructure is obscurely cellular or, more commonly, melanospheric.

*Discussion.* Yavorsky's original definition stressed the net-like nature of the skeleton, its latilamination, the short vertical elements (columns), oblique horizontal elements (leaning on columns), and similarity of the galleries to those of *Clathrodictyon confertum* Nicholson, 1889. In his description of the type species the fibre is described as porous in contrast to the compact tissue of *C. confertum*. The microstructure of Nicholson's species is, unfortunately, obscure, for his specimens from Devon are completely recrystallized.

Flügel and Flügel-Kahler (1968, p. 544) discussed the microstructure of *Ferestromatopora* and recorded that Yavorsky indicated in a personal communication that the microstructure should be considered to be compact and the genus placed in synonymy with *Intexodictyon* Yavorsky, 1963. If the microstructure is compact, then *Ferestromatopora* is closer to *Plexodictyon* Nestor, 1966 than to *Intexodictyon* as pointed out by Nestor (personal communication).

The confusion between *Ferestromatopora* and *Stromatopora* begun by St. Jean's (1957, p. 838) and Galloway's (1957) assertions that the specimens used by Lecompte (1952, pl. 53, fig. 2, 1956, fig. 91) to illustrate *Stromatopora concentrica* Goldfuss is a *Ferestromatopora* is reviewed in the introduction to this paper. Sleumer (1969) considered *Ferestromatopora* to be an ecophenotypic variant of *Stromatopora*.

Since the genus was established, at least twenty species of *Ferestromatopora* have been proposed, but few of them closely resemble the typical species in its cassiculate structure and paralaminae.

Nearly all these species can be reassigned to genera such as *Lineastroma*, *Habrostroma*, *Parallelostroma*, *Clathrocoilona* and *Stromatopora*, in the revised sense, and these assignments are listed under the appropriate genera in this paper. As here reinterpreted, the following species (in addition to the type species) can be assigned to *Ferestromatopora*: *Ferestromatopora tyrganensis* Yavorsky, 1955; *Ferestromatopora formosa* Yang and Dong, 1979; *Ferestromatopora talovensis* Yavorsky, 1955 (established as a variety of *F. krupennikovi* but given species status here). Investigation of the type material of this last taxon may show that it is better placed in *Habrostroma* Fagerstrom, 1982. *Clathrodictyon confertum* Nicholson, 1889 may also prove to be a *Ferestromatopora* when topotype material of better preservation is collected to supplement the type specimen, which is very poorly preserved. Unfortunately the type locality, the Pit Park quarry near Dartington, Devon, UK, has been filled in. The stratigraphical range of *Ferestromatopora* as here restricted appears to be Givetian to Frasnian.

### Genus LINEASTROMA Khalfina and Yavorsky, 1973

Text-fig. 5c

[= *Lineastroma* Khalfina and Yavorsky, 1973, p. 31 (p. 150 of translation); Stearn 1980, p. 818; Bogoyavlenskaya and Khromych 1985, p. 80; Dong 1988, p. 35. In part, *Stromatopora* Goldfuss; Yavorsky 1951, p. 11, 1955, p. 81, 1961, p. 44; Yang and Dong 1979, p. 48. *Stromatopora* ? Yang and Dong 1979, p. 52. In part, *Parallelostroma* Nestor; Bol'shakova 1973, p. 86. In part, *Climacostroma* Yang and Dong 1979, p. 72. In part, *Ferestromatopora* Yavorsky; Wang 1978, p. 30; Yang and Dong 1979, p. 898.]

*Type species. Stromatopora vorkutensis* Yavorsky, 1961, p. 39, pl. 23, figs 1–3.

*Diagnosis*. Skeleton composed of prominent but interrupted coenostroms and short largely vertical, but locally oblique, coenosteles largely confined to an interval between coenostroms and only locally superposed or more continuous vertically. Dissepiments scattered. Microlaminae missing or inconspicuous. Coenosteles in tangential section isolated irregular masses or more or less joined in a labyrinthine pattern. Microstructure finely and inconspicuously cellular.

*Discussion*. Only a single species, the type, has been ascribed to this genus, but a group of species that are poorly accommodated in *Stromatopora*, *Parallelostroma* and *Ferestromatopora* can be grouped conveniently in *Lineastroma*. These are stromatoporoids whose skeletal structure is dominated by coenostroms but are not conspicuously microreticulate, or characterized by microlaminae like *Habrostroma* Fagerstrom, 1982, and *Parallelostroma* Nestor, 1966, or by oblique structural elements like *Arctostroma* Yavorsky, 1967, and *Ferestromatopora* Yavorsky, 1955. By this diagnosis, *Lineastroma* is a convenient receptacle for species that do not have the unique features of other coenostrom-dominated stromatoporoids. Future workers may find criteria by which to further clarify the relationships of species included here in *Lineastroma*.

In typical *Parallelostroma* the coenostroms are sharply bounded above by a microlamina and the microstructure is microreticulate, commonly breaking down in diagenesis into a set of closely spaced microlaminae. In *Habrostroma* the tissue has a diffuse, lacy appearance typical of the advanced syringostromatids.

*Climacostroma* Yang and Dong, 1979, is based on the type species *C. guangxiense* Yang and Dong, 1979. The distinctive features ascribed to the genus are largely microstructural and include microlaminae and pillars with small vertical tubules and vertical rods. These features are not clearly shown in the illustrations of *C. guangxiense*, which has the structure of *Lineastroma* and is considered here to belong in this genus. The other two species placed by Yang and Dong (1979) in *Climacostroma* show vertically aligned melanospheres and arched galleries that characterize species of *Arctostroma* and are now assigned to that genus. Fagerstrom (1982) has discussed the relationship of *Climacostroma* to *Habrostroma*.

In addition to the type species, the following species are assigned here to *Lineastroma*: *Stromatopora fortuita* Yavorsky, 1955 (referred to ?*Parallelostroma* by Bol'shakova 1973);

*Stromatopora pulchra* Yavorsky, 1955; *Stromatopora schelmonensis* Yavorsky, 1955 (referred to *Trupetostroma* by Yavorsky 1963 and to *Stromatopora* by Stearn 1966*a*); *Stromatopora karaensis* Yavorsky, 1961; *Ferestromatopora jacquesensis* Galloway, 1960; *Stromatopora? mammillaris* Yang and Dong, 1979; *Ferestromatopora compacta* Yang and Dong, 1979; *Climacostroma guangxiense* Yang and Dong, 1979.

Species that can probably be placed in *Lineastroma* but require further investigation include: *Stromatopora obrutchevi* Yavorsky, 1955 (referred by Bol'shakova 1973 to *Parallelostroma*); *Stromatopora czekanowskii* Yavorsky, 1955; *Stromatopora ylychensis* Riabinin, 1939; *Stromatopora sokolensis* Yavorsky, 1951; *Syringostroma minutitextum* Lecompte, 1951 (referred doubtfully to *Habrostroma* by Fagerstrom 1982); *Stromatopora praelonga* Bogoyavlenskaya, 1977; *Ferestromatopora tuqiaoziensis* Wang, 1978; *Stromatopora interrupta* Yang and Dong, 1979.

Species of *Lineastroma* have stratigraphical ranges within Silurian (stage unspecified for the type species by Yavorsky 1961) to Frasnian strata. All species definitely assigned to the genus, other than the type, are from the Eifelian to Frasnian interval.

### Genus ARCTOSTROMA Yavorsky, 1967

Text-fig. 5D

[= *Arctostroma* Yavorsky, 1967, p. 30; Bogoyavlenskaya and Khromych 1985, p. 69; Dong 1988, p. 35. *Angulatostroma* Khalfina, 1968*a*, p. 152; Bogoyavlenskaya and Khromych 1985, p. 68; Dong 1988, p. 35. In part, *Ferestromatopora* Yavorsky; Stearn 1963, p. 665, 1980, p. 898; Wang 1978, p. 30.]

*Type species*. *Ferestromatopora contexta* Stearn, 1963, p. 666, pl. 88, figs 3–5. [= *Arctostroma ignotum* Yavorsky, 1967; *Stromatopora mikkwaensis* Stearn, 1966*b* (Stearn and Shah 1990)].

*Diagnosis*. Skeleton composed of oblique structural elements forming a continuous cassiculate network in vertical section, enclosing galleries that are arched at the top. Neither coenosteles nor coenostroms prominent; structural elements and galleries typically labyrinthine in tangential section; microstructure coarsely cellular, commonly melanospheric, commonly with vertical alignment of melanospheres.

*Discussion*. Stearn (1980) placed *Arctostroma ignotum* Yavorsky, 1967 in synonymy with *Ferestromatopora contexta* Stearn, 1963, and concluded that *Arctostroma* should be considered a synonym of *Ferestromatopora*. However, the type species, *A. ignotum*, and other species considered to belong to the genus, do not have paralaminae that are characteristic of *Ferestromatopora*, and the two genera are now considered to be separate. The nominal type species should be *F. contexta*, as this name has precedence. Apart from the paralaminae, the skeletal structure of *Ferestromatopora* and *Arctostroma* are similar.

*Angulatostroma* Khalfina, 1968*a*, based on *Stromatopora angulata* Yavorsky, 1947, was described as having short laminae bent into chevron form, like those of *Ecclimadictyon* Nestor, 1964, but composed of porous tissue (Khalfina 1968*a*). Stearn (1980) suggested that the genus was synonymous with both *Ferestromatopora* and *Arctostroma*, but synonymy with the former now seems unlikely. The only species, other than two *nomina nuda* and the type species, ascribed to *Angulatostroma* by Khalfina (1968*a*) was *Stromatopora compacta* Yavorsky, 1955.

Species, other than the type which are included in this review in *Arctostroma* are: *Stromatopora angulata* Yavorsky, 1947; *Stromatopora compacta* Yavorsky, 1955; *Climacostroma microlaminata* Yang and Dong, 1979; *Climacostroma facetum* Yang and Dong, 1979; *Trupetostroma kennisoni* Birkhead, 1967; *Ferestromatopora fistulosum* Wang, 1978; *Stromatopora longitubulata* Riabinin, 1941; *Stromatopora maculata* Lecompte, 1952.

These species are recorded from Middle and Upper Devonian rocks, and the genus appears to be particularly characteristic of the Givetian–Frasnian interval. It has been described from Russia, western Canada, China and Australia.

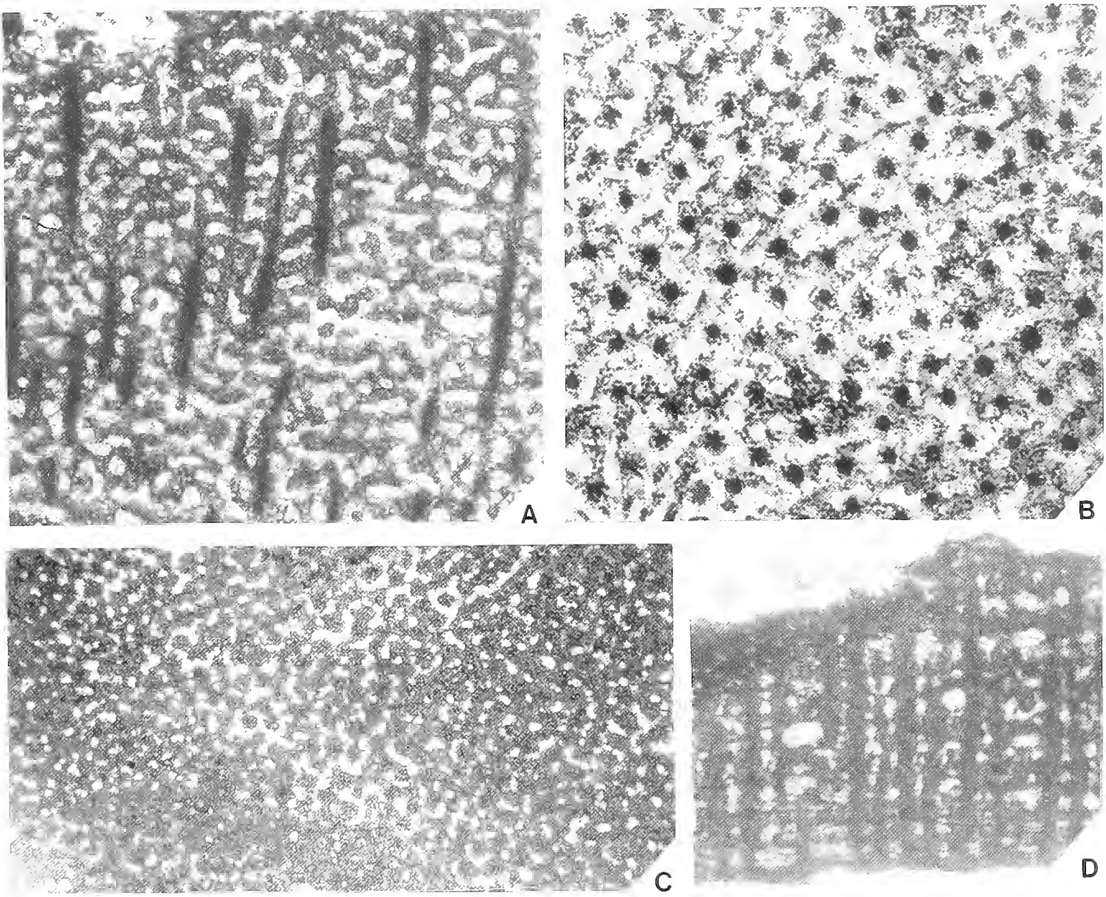
## Genus TALEASTROMA Galloway, 1957

Text-figs 6A–B, 7A

[= *Taleastroma* Galloway, 1957, p. 448; Stearn 1966*a*, p. 112; Flügel and Flügel-Kahler 1968, p. 578; Stearn 1980, p. 898; Bogoyavlenskaya and Khromych 1985, p. 91; Mistiaen 1985, p. 148. In part, *Neosyringostroma* Kazmierczak, 1971, p. 117. In part, *Glyptostroma* Yang and Dong, 1979, p. 65.]

*Type species. Stromatopora cunningsi* Galloway and St. Jean, 1957, p. 182, pl. 15, fig. 4*a–b*.

*Diagnosis.* Horizontal structure an irregular cassiculate network of cellular elements like that of *Stromatopora* penetrated by thick, persistent, columnar pillars that in well-preserved specimens are compact in axial regions and cellular or melanospheric peripherally. Pillars circular or annular, prominent and distinct in tangential section.



TEXT-FIG. 6. A–B *Taleastroma logansportense*. Vertical (A) and tangential (B) sections; Slave Point Limestone, N.E. British Columbia; Geological Survey of Canada, plesiotype 102,372, × 10. C–D, *Columnostroma ristigouchense*. Vertical (C) and tangential (D) sections of Spencer's type in the Nicholson collection 309 (P5591, Natural History Museum, London), × 10. The vertical section is too thick to show the microstructure clearly and only the thinner part is illustrated.

*Discussion.* Questions about the validity of this genus have centred on the microstructure of the pillars, which Galloway (1957) originally characterized as peripherally maculate and axially compact. Most later workers have ascribed the more opaque outlines of the typical species to diagenesis, yet this feature is consistently present in the group of species usually united under the generic name *Taleastroma*. The origin of the microstructure characteristic of the pillars is obscure, but they appear to be axially compact, possibly trabecular, and certainly different from the other structural elements. This microstructure is clearly shown by specimens from the Slave Point Limestone at Evie Lake, British Columbia (Text-fig. 6A–B).

*Taleastroma* is close to *Glyptostromoides*, but the long pillars that cross the cassiculate network are conspicuously round in cross-section, commonly dark with melanospheres on their edges giving them an annular appearance, and may have a dark axial spot. In *Glyptostromoides* the vertical elements are submerged in the labyrinthine network of tangential sections and their configuration in cross-section is uncertain.

*Neosyringostroma* Kazmierczak, 1971, is based on the type species *Hermatostroma logansportense* Galloway and St. Jean, 1957. Stearn (1980) placed this genus in the Ecclimadictyidae, but Mistiaen (1985) considered it a synonym of *Taleastroma* and this placement is endorsed here. Mistiaen (1985) discussed at length the relationship between *Taleastroma*, *Glyptostromoides* and *Neosyringostroma*, and placed the last two in synonymy. He showed that the species assigned by Kazmierczak (1971) to his genus cannot be recognized as forming a valid generic grouping. I have examined the types of the several species of *Syringostroma* of Fritz and Waines (1956) that Kazmierczak placed in *Neosyringostroma*. They are all poorly preserved specimens of a single species of *Syringostroma* and should not be referred to either *Taleastroma* or *Neosyringostroma*.

Representative species of *Taleastroma* (in addition to the type species) include the following: *Stromatopora boiarschinovi* Yavorsky, 1961; *Hermatostroma logansportense* Galloway and St. Jean, 1957; *Stromatopora magnimamillata* Galloway and St. Jean, 1957; *Stromatopora pachytextum* Lecompte, 1952; *Stromatopora sinopachytextum* Yang and Dong, 1963; *Glyptostroma sinense* Yang and Dong, 1979; *Glyptostroma yangdongi* Mistiaen, 1985 (new name for *G. pachytextum* Yang and Dong, 1979).

The assignment of several other species to *Taleastroma* is of doubtful validity. The generic assignment of *T. vitreum* Galloway, 1960, and *T. lenzi* Galloway, 1960, needs to be re-examined; they appear to be poorly preserved species of *Trupetostroma*. Both *T. steleforme* Stearn, 1975 and *T. condensum* Zukalova, 1971 are poorly preserved and do not have the cassiculate network of this genus.

All the species that can be assigned to *Taleastroma* with confidence occur in Middle Devonian rocks.

### Genus GLYPTOSTROMOIDES Stearn, 1983

Text-fig. 7B

[= *Glyptostromoides* Stearn, 1983, p. 553. In part, *Glyptostroma* Yang and Dong, 1979, p. 65; Stearn 1980, p. 553; Bogoyavlenskaya and Khromych 1985, p. 77. In part, *Taleastroma* Galloway; Mistiaen 1985, p. 148.]

*Type species. Glyptostroma simplex* Yang and Dong, 1979, p. 66, pl. 35, figs 5–6.

*Diagnosis.* Horizontal structure a cassiculate network of cellular elements like that of *Stromatopora* penetrated by thick, cellular, persistent coenosteles joined into a labyrinthine network in tangential section.

*Discussion.* Stearn (1980, 1983) and Mistiaen (1985) have reviewed the unfortunate choice of '*Stromatopora benthii*' of Yavorsky, 1955, as the type species of *Glyptostroma*, the change of the typical species to *Glyptostroma simplex* and the generic name to *Glyptostromoides*. The differences between *Glyptostromoides* and *Taleastroma* are discussed under the latter genus.

In addition to the type species, the following are representative of the genus: '*Stromatopora beuthii*' Yavorsky, 1955 (not Bargatzky, 1881); *Glyptostroma liujingensis* Yang and Dong, 1979; *Glyptostroma oblique* Yang and Dong, 1979; *Stromatopora pseudotyrganicum* Khalfina, 1960; *Stromatopora tyrganica* Yavorsky, 1947.

All these species are found in rocks of Early or Middle Devonian age.

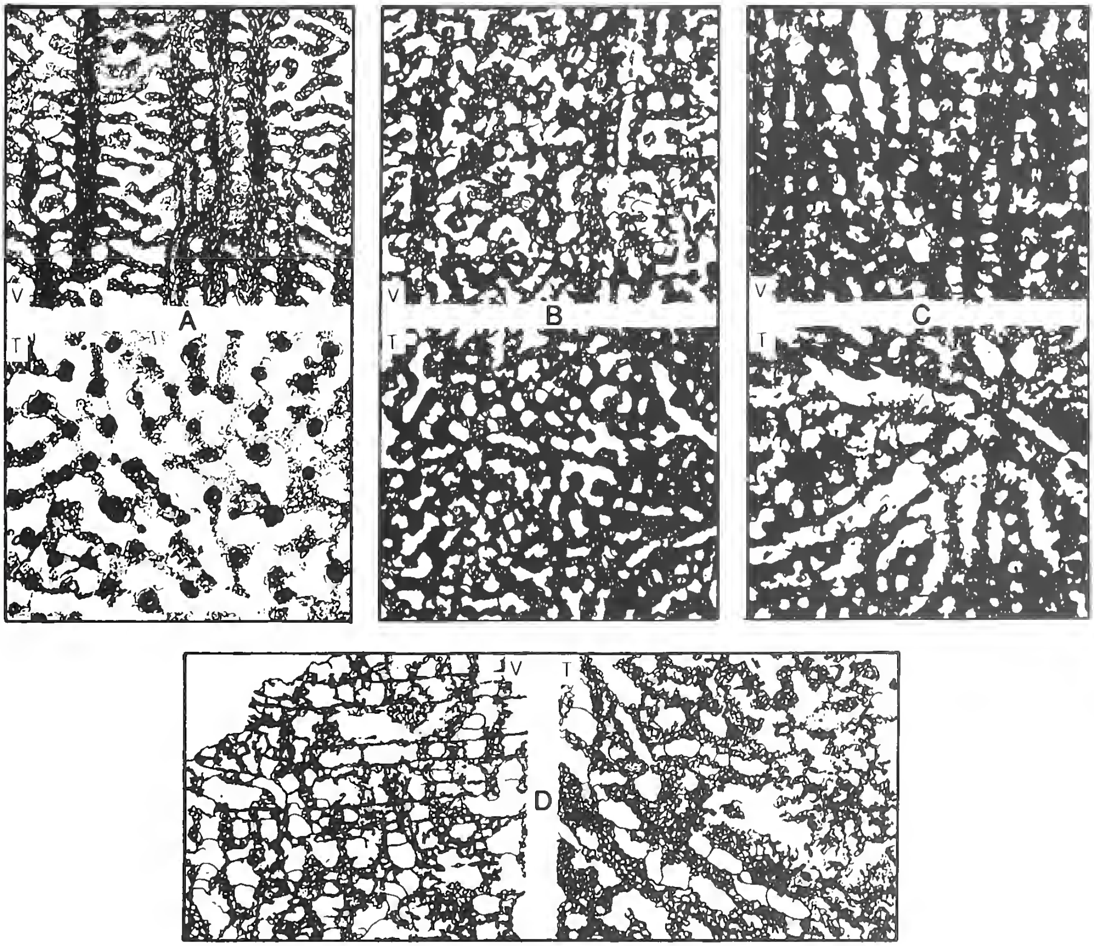
### Genus PSEUDOTRUPETOSTROMA Khalfina and Yavorsky, 1971

Text-fig. 7D

[= *Pseudotrupetostroma* Khalfina and Yavorsky, 1971, p. 120; Bogoyavlenskaya and Khromych 1985, p. 86; Dong 1988, p. 35.]

*Type species*. *Stromatopora pellucida* var. *artyschtensis* Yavorsky, 1955, p. 100, pl. 52, figs 1–2.

*Diagnosis*. Coenosteles short, interlaminar, commonly superposed in vertical section, in tangential



TEXT-FIG. 7. Sketches of Stromatoporida in vertical (V) and tangential (T) section. A, *Taleastroma* (based on *T. logansportense* in Kazmierczak 1971). B, *Glyptostromoides* (based on *G. simplex* in Yang and Dong 1979). C, *Salairella* (based on *Stromatopora nices* in Yavorsky 1955). D, *Pseudotrupetostroma* (based on *P. artyschtense* in Yavorsky 1955). All figures ×10.

section forming a closed network, vermicular or rarely isolated, coarsely cellular; horizontal elements fine microlaminae, locally coated with cellular tissue.

*Discussion.* Because the original diagnosis of Khalfina and Yavorsky (1971) is brief, a discussion of the genus is absent from the proposal, and the illustrations of the tangential section of the type species are obscure, this genus has been little used and is difficult to characterize. The original diagnosis, translated from Russian, is 'vertical plates and pillars most often combined, sporadically not combined; laminae irregular type with dark median line'. This diagnosis was repeated by Bogoyavlenskaya and Khromych (1985).

*Pseudotrupetostroma* is close to *Atopostroma* Yang and Dong, 1979, but in the latter the pillars are round in cross-section and finely clinoreticulate. It differs from *Trupetostroma* Parks, 1936 in its coarsely cellular tissue throughout the coenosteles and their union into a network in tangential section. This genus could be accommodated in either the Stromatoporidae or the Hermatostromatidae.

The following species closely resemble the type species and can be assigned to the genus: *Trupetostroma cincinnatum* Khalfina, 1960; *Stromatopora flexuosa* Yavorsky, 1955; *Parallelopora jucunda* Khalfina, 1953; *Syringostroma tschichatchevi* Yavorsky, 1931; *Trupetostroma virgulatum* Khalfina, 1960. The following species may belong in this genus but their placement deserves further study: ?*Parallelopora crassa* Yavorsky, 1963; *Trupetostroma lecomptei* Stearn, 1961; *Stromatopora pellucida* Yavorsky, 1955; ?*Parallelopora yangmeishanensis* Yang and Dong, 1963.

*Pseudotrupetostroma* is restricted to Middle Devonian strata.

### Family SYRINGOSTROMELLIDAE Stearn, 1980 (emended)

*Diagnosis.* Stromatoporids with structure dominated by coenosteles.

### Genus SYRINGOSTROMELLA Nestor, 1966

Text-fig. 5A

[= *Syringostromella* Nestor, 1966, p. 47; Mori 1968, p. 87, 88; Bogoyavlenskaya 1973, p. 53; Bol'shakova 1973, p. 96; Khromych 1974, p. 56, 1976, p. 102; Stearn 1980, p. 898; Bogoyavlenskaya and Khromych 1985, p. 91. *Yavorskiina* Khalfina, 1968*a*, p. 148 (*nomen nudum*); Nestor 1976; pp. 71, 90; Stearn 1980, p. 898; Bogoyavlenskaya and Khromych 1985, p. 94; Dong 1988, p. 36. ? *Pachystroma* Nicholson and Murie, 1878, pp. 214, 223; Nicholson 1886*a*, p. 91; Flügel and Flügel-Kahler 1968, p. 555.]

*Type series. Stromatopora borealis* Nicholson, 1891*a*, p. 175; 1891*b*, p. 315, pl. 9, figs 7–8.

*Diagnosis.* Coenosteles long, continuous, joining and dividing in vertical section; coenostroms rudimentary or absent; dissepiments common. In tangential section coenosteles vermiform or a loose labyrinthine network. Microstructure cellular.

*Discussion. Syringostromella* differs from *Parallelopora* Bargatzky in the fine cellular microstructure of its coenosteles and the lack of rectilinear micropillars within them. It differs from both *Parallelopora* and *Salairella* in the labyrinthine form of both the coenosteles, and the galleries between them, in tangential section. In *Salairella* the galleries are small, mostly circular in cross-section. *Syringostromella* is one of the most abundant and diverse of the Stromatoporida. It originated in Wenlock time and persisted into the beginning of the Middle Devonian when it was largely displaced by *Salairella*. Nestor (1974) suggested that it could have arisen from *Labechia*, but its cellular microstructure indicates that derivation from *Stromatopora* in late Llandovery time is more probable.

*Yavorskiina* Khalfina (1968*a*) was proposed in a parenthesis without an adequate definition to distinguish it from other genera and is therefore invalid according to Article 13*a* of the *International Code of Zoological Nomenclature* (1985). However, Nestor (1976), while recognizing that the proposal was invalid, used the genus and remarked on the clinoreticulate microstructure of the coenosteles and its relationship in this to *Vikingia*. There is little in the diagnosis of Bogoyavlenskaya and Khromych (1985) or in the original description of the type species *Stromatopora membrosa* Yavorsky, 1957, to justify distinguishing this taxon from *Syringostromella*.

*Pachystroma* Nicholson and Murie, 1878, is characterized by prominent latilaminae commonly separated by thin sediment layers and a structure dominated by coarsely cellular coenosteles and dissepiments (Pl. 2, fig. 4). The type species is *Pachystroma antiquum* Nicholson and Murie, 1878. Nicholson (1886*a*, p. 91) placed the genus in synonymy with *Stromatopora* soon after it was proposed, and since then few authors have used it. However, Nicholson (1891*b*, p. 311) recognized that *P. antiquum* strongly resembles *Syringostroma* in the prominence of the vertical structures and differs from *Stromatopora*, in which such elements are suppressed. *Pachystroma antiquum* is unlike *Stromatopora* in vertical section and resembles *Syringostromella*. It differs in its extreme latilamination and the round shape of many of the coenosteles (or pillars) in tangential section. Unfortunately, Nicholson's type tangential section is very thick and does not show the form of the pillars/coenosteles clearly. Other specimens of *P. antiquum* are poorly preserved (Parks 1908). Either *Pachystroma* is a valid taxon separate from *Stromatopora* and *Syringostromella*, or the latter is its junior synonym. This problem needs further consideration and resectioning of the type specimen.

A survey of species of *Syringostromella* in the literature has shown that twenty-five can be positively assigned to this genus and another eleven probably belong in it but require further investigation. The Supplementary Publication No. SUP 14042 deposited in the British Library lists species that have the structure and microstructure typical of the genus.

### Genus SALAIRELLA Khalfina, 1980

Text-fig. 7c

[= *Salairella* Khalfina, 1960, p. 330; Flügel and Flügel-Kahler 1968, p. 563; Stearn 1983, p. 555; Bogoyavlenskaya and Khromych 1985, p. 87. ?*Lecomptella* Khalfina, 1972, p. 151.]

*Type species*. *Salairella multicea* Khalfina, 1960, p. 331, pl. D5, fig. 3.

*Diagnosis*. Coenosteles long, continuous, joining and dividing in vertical section; in tangential section most are joined in a closed network enclosing coenotubes which are round in cross-section; coenostroms rudimentary or absent; dissepiments common. Microstructure finely cellular.

*Discussion*. *Salairella* is similar to *Syringostromella*, particularly in vertical section. It differs in the tangential section of the coenosteles. In *Salairella* they typically enclose round coenotubes but in *Syringostromella* these tubes are vermiform and open into each other forming a labyrinth. It also resembles *Parallelopora* Bargatzky, 1881, but does not have the coarse reticulate microstructure of this genus. *Salairella* first appeared in the Early Devonian, thrived in Middle Devonian time and at least two species survived into early Late Devonian time.

*Lecomptella* has been used only by Khalfina for the type species *Stromatopora racemifera* Khalfina, 1960. In this species coenostroms are more prominent and continuous than in typical *Salairella*, and this feature may justify retaining the taxon despite the close resemblance to *Salairella*.

Species considered representative of the genus *Salairella*, and those provisionally assigned to it are listed in Supplementary Publication No. SUP 14042 deposited in the British Library.

## Order SYRINGOSTROMATIDA Bogoyavlenskaya, 1969 (emended)

*Diagnosis*. Stromatoporoids of microreticulate microstructure and skeleton composed of discrete structural elements including commonly dominant coenostroms and microlaminae, coenosteles and pillars.

*Discussion.* Justification for the establishment of this new order has been given in the section on classification. The syringostromatids evolved from the family Densastromatidae of the order Actinostromatida by the introduction in the microreticulum of galleries which divided it into structural elements such as coenostroms and coenosteles. Not all microreticulate stromatoporoids belong to this order; only those in which discrete structural elements can be distinguished. The transition to syringostromid structure can be recognized in such advanced densastromatids as *Actinostromella.*

### Family SYRINGOSTROMATIDAE Lecompte, 1951

### Genus PARALLELOSTROMA Nestor, 1966

Text-fig. 3

[= *Parallelostroma* Nestor, 1966, p. 52; Mori 1970, p. 132; Bol'shakova 1973, p. 86; Nestor 1976, p. 69; Stock 1979, p. 342, 1988, p. 10; Guo 1980, p. 103; Dong 1984, p. 66; Stock and Holmes 1986, p. 562; Stearn 1990, p. 505.]

*Type species. Stromatopora typica* Rosen, 1867, p. 58, pl. 1, figs 1–3; pl. 2, fig. 1.

*Diagnosis.* Coenostroms thick, composed of orthoreticulate tissue enclosing multiple microlaminae and micropillars, at base separated by short coenotubes into coenosteles of same microstructure; coenosteles largely confined to intercoenostrom space, some superposed, labyrinthine or a closed network in tangential section.

*Discussion.* Nestor (1986) related this genus to the densastromatids and particularly to *Actinostromella* Boehnke. Mori (1970) placed the genus in the Stromatoporidae and decreased the emphasis on the microreticulation as a generic character. Bol'shakova (1973) listed many species ranging from Early Silurian to Middle Devonian that she assigned to *Parallelostroma.* Fagerstrom (1982) and Stock and Holmes (1986) discussed the relationship between *Parallelostroma* and *Habrostroma.* Stock (1989) reinforced previous conclusions about the origin of *Parallelostroma* from the densastromatids. *Habrostroma* is distinguished from *Parallelostroma* by the irregularity of its microreticulation, giving the tissue a diffuse, lacy appearance, but is similar in its structural elements. Some species with long coenosteles, such as *Stromatopora constellata* Hall, 1852, have been placed in *Parallelostroma* on the basis that *P. typica*, the type species, shows some superposed coenosteles, but these are not typical of the genus. Species considered by the writer to be representative of the genus *Parallelostroma* are listed in Supplementary Publication No. SUP 14042, deposited in the British Library.

Stratigraphical and microstructural evidence suggests that this genus is the rootstock of the Syringostromatida and arose from densastromatid ancestors in Wenlock time. Its acme was in Ludlow time and in Přídolí to Early Devonian time it gave rise to the more advanced members of the family such as *Habrostroma*, *Syringostroma*, *Atopostroma* and *Coenostroma.*

### Genus ATOPOSTROMA Yang and Dong, 1979

[= *Atopostroma* Yang and Dong, 1979, p. 74; Stearn, 1980, pp. 889, 895; Stearn, 1983, p. 548.]

*Type species. Atopostroma tuntouense* Yang and Dong, 1979.

*Diagnosis.* Laminae regular, persistent, formed of a single microlamina with skeletal material from pillars spread irregularly below; pillars confined to interlaminar spaces, typically superposed through many interlaminar spaces, narrow, subcircular in cross-section at base, spreading upward on to bottom of microlaminae forming an irregular network, composed of orthoreticulate to clinoreticulate skeletal material.

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*Discussion.* Owing to its resemblance to *Gerronostroma* this genus was placed in the Clathrodictyidae by Stearn (1980). Further examination has shown that the microstructure is microreticulate and much like that of *Parallelostroma*. Transitional forms between *Atopostroma* and *Parallelostroma* occur in the Martin Well Limestone of Pragian age in Queensland, Australia. *Atopostroma* differs from *Parallelostroma* in the consistent superposition of the pillar/coenosteles and the opening out of galleries by thinning of the vertical elements in *Atopostroma*. The genus is here transferred to the Syringostromatida.

In the grid formed by pillars and laminae and the microreticulate skeletal material, *Atopostroma* resembles *Coenostroma*. It differs in the upward spreading of the pillars as a network on to the nae. Apart from the network evident in tangential sections formed by the pillars below the e, the microreticulate skeletal material, and the upward-spreading (rather than spooled) shape of the pillars, *Atopostroma* resembles *Gerronostroma*.

The genus evolved from *Parallelostroma* early in Devonian time and became common in Emsian time in China, Australia and arctic Canada. In these areas it is a distinctive element of Early Devonian faunas.

## Genus COENOSTROMA Winchell, 1867

Plate 2, fig. 3; Text-fig. 8A

[= *Coenostroma* Winchell, 1867, p. 99; Nicholson 1886*b*, p. 11; Miller 1889, p. 157; Flügel and Flügel-Kahler 1968, p. 539. *Coenostoma* Winchell; Spencer 1884; p. 598 (*lapsus calami*)].

*Type species. Stromatopora monticulifera* Winchell, 1866, p. 91 (subsequently designated by Miller 1889, p. 157).

*Diagnosis.* Persistent, thick coenostroms, coenosteles and pillars forming an imperfect grid in vertical section; galleries small, irregular; microstructure of structural elements obscurely microreticulate, locally with microlaminae. In tangential section coenosteles an irregular network or, in some species, circular.

*Discussion.* Nicholson (1886*b*) placed Winchell's genus in synonymy with *Stromatopora* because it was defined only on the basis of external characteristics, and he did not investigate the internal structure of the type species. Miller (1889) distinguished it from *Stromatopora* on the number of astrorhizal tubes in the mamelon columns. Subsequently the name *Coenostroma* has only been used as a subgenus of *Stromatopora* by Grabau and Shimer (1909). Galloway and Ehlers (1960) described Winchell's specimens of the type species and continued to place the species in *Stromatopora*. My re-examination of these type specimens confirms what is evident from Galloway and Ehlers' illustrations: the internal structure is not close to that of *Stromatopora concentrica* Goldfuss and represents a structure that can be recognized in other species of stromatoporoids. Although the genus was established before internal structures were investigated by thin section, it is valid, as is the genus *Stromatopora* or as brachiopod genera described before serial sections were used.

The preservation of Winchell's suite of type specimens of *S. monticulifera* is not good, and in the lectotype (University of Michigan, 32409A, Galloway and Ehlers 1960, pl. 1, fig. 1*b*) the microstructure shows vague clusters of specks but is not clearly melanospheric. In places the lectotype shows traces of microreticulation (Pl. 2, fig. 3). Away from the mamelons the upper part of the laminae seems to be a darker microlamina like those typical of *Parallelostroma* Nestor. In the vertical section of the paralectotype (University of Michigan 32409B, section WI-1) microlaminae in the laminae are prominent. Galloway and Ehlers (1960) described as *Parallelopora winchelli* specimens from Winchell's type suite of *S. monticulifera* with well-preserved 'maculae' arranged in vertical rows in the pillars. The similarity in structure, external appearance and occurrence leaves little doubt that these specimens are *Coenostroma monticuliferum* with better preserved microreticulate microstructure. The prominent thick coenostroms in the specimens they called *P. winchelli* preclude their assignment to *Parallelopora*.

The similarity of *Coenostroma monticuliferum* to species of *Habrostroma* Fagerstrom, 1982, is striking. This is particularly true of *Habrostroma* species with prominent pillars, such as *H. beachvillense* Fagerstrom, 1982, which should be transferred to *Coenostroma*. *Habrostroma* should be restricted to species like the type species that do not have prominent pillars/coenosteles. *Coenostroma* differs from *Syringostroma* Nicholson, 1875, in its lack of diffuse megapillars associated with mamelon columns, but some species that have been referred to *Syringostroma* should be transferred to *Coenostroma* (see below). *Parallelostromella* Kosareva, 1968, may be a junior synonym of *Coenostroma* but is not valid as it was published without diagnosis (*International Code of Zoological Nomenclature* 1985, Article 13).

Representative species of *Coenostroma* (in addition to the type species) are listed in Supplementary Publication No. SUP 14042 deposited at the British Library. I have examined type specimens of *Coenostroma botryoideum* (Spencer, 1884), and *Coenostroma galtense* Dawson, 1879; both are dolomitized and indeterminate at the generic level.

Most of the species of *Coenostroma* come from Middle Devonian strata, but the range of the genus spans the Devonian and possibly the older Přídolí (Stock, personal communication, 1991).

## Genus HABROSTROMA Fagerstrom, 1982

Text-fig. 8B

[= *Habrostroma* Fagerstrom, 1982, p. 11; Dong 1984, p. 189; Stock and Holmes 1986, p. 562; Stearn 1990, p. 508].

*Type species*. *Stromatopora proxilaminata* Fagerstrom, 1961, p. 8, pl. 1, figs 4–6.

*Diagnosis*. Coenosteles short, irregular, largely confined between coenostroms, forming a diffuse irregular network in tangential section, of irregularly cellular tissue with diffuse boundaries; coenostroms prominent, of similar cellular tissue, containing one or more microlaminae. Structural elements may appear microreticulate in well-preserved specimens.

*Discussion*. Fagerstrom (1982) discussed the relationship of this genus to similar genera at length. Stock and Holmes (1986) suggested that it cannot be separated from *Parallelostroma* although Stock (1989) later used the genus. Stearn (1990) suggested that species assigned to *Habrostroma* by Fagerstrom that have persistent coenosteles should be referred to genera such as *Salairella* and *Columnostroma*. The similarity of *Habrostroma* and *Climacostroma* Yang and Dong, 1979 has been noted by Fagerstrom (1982). Differences between their microstructures must be investigated by comparison of the type specimens (see *Lineastroma* above).

*Habrostroma* has been recognized in rocks as old as Přídolí (Stock 1989), and ranges as high as Frasnian strata but is most diverse in the Eifelian.

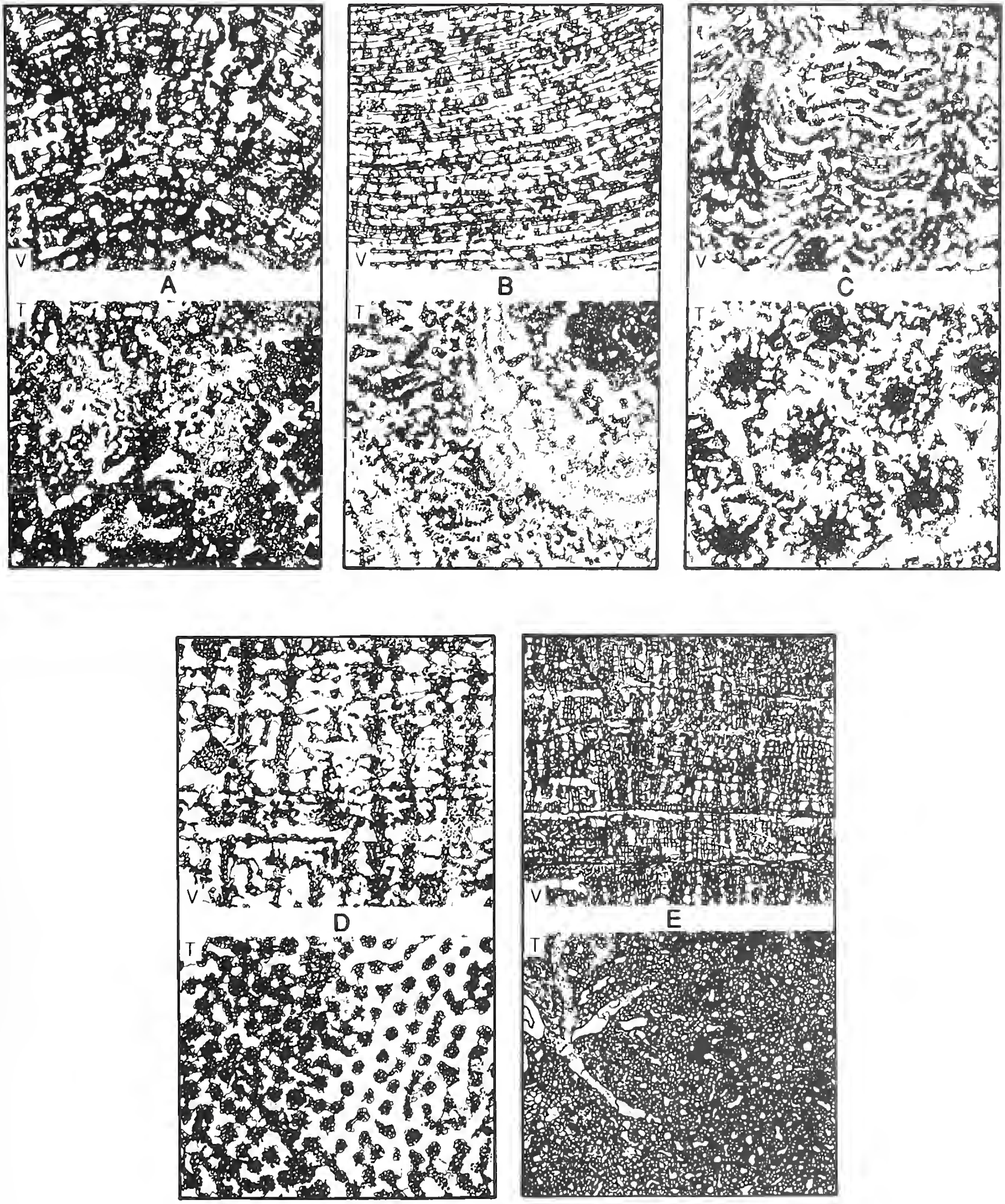
Species that are considered representative of this genus are listed in Supplementary Publication No. SUP 14042 deposited in the British Library.

## Genus SYRINGOSTROMA Nicholson, 1875

Text-fig. 8C

[= *Syringostroma* Nicholson. Fagerstrom (1982) has provided a complete synonymy. Discussion since 1982 has been provided by Bjerstedt and Feldmann 1985, p. 1049; Stearn and Shah 1990, p. 507. *Stylodictyon* Nicholson and Murie, 1878, p. 221.]

*Type species*. *Syringostroma densa* Nicholson, 1875, p. 251 (subsequently designated by Nicholson 1886*a*, p. 98).



TEXT-FIG. 8. Sketches of Syringostromatida in vertical (V) and tangential (T) section. A, *Coenostroma* (based on photographs of the type specimen of *C. monticuliferum*). B, *Habrostroma* (based on *H. proxilaminatum* in Fagerstrom 1982). C, *Syringostroma* (based on *S. scherzeri* in Fagerstrom 1982). D, *Columnostroma* (based on illustrations of Parks's topotype of *Coenostroma ristigouchense* in Fagerstrom 1982. E, *Parallelopora* (based on Bargatzky's type of *P. ostiolata* illustrated by Lecompte 1952). All figures × 10.

*Diagnosis*. Coenosteles short, irregular, coarsely cellular, without precise boundaries, irregular in tangential section; megapillars long, continuous, clinoreticulate, round in tangential section; coenostroms persistent, thick, cellular, containing one or more microlaminae; dissepiments rare.

*Discussion*. Fagerstrom (1982) discussed the relationship between *Syringostroma*, *Habrostroma*, *Parallelopora* and *Stylodictyon*. The characteristic features that distinguish *Syringostroma* are the clinoreticulate megapillars, the diffuse nature of the tissue of the structural elements and the prominent microlaminae. In the light of Fagerstrom's (1982) extensive review of the species assigned to this genus, no attempt is made to reassign the many species that have been incorrectly attributed to this genus.

The genus evolved from *Parallelostroma* in the mid-Early Devonian (Pragian) and reached its acme during the Eifelian. The genus did not survive into the Givetian.

### Genus COLUMNOSTROMA Bogoyavlenskaya, 1972

Text-figs 6C–D, 8D

[= *Columnostroma* Bogoyavlenskaya, 1972, p. 33; Stearn 1980, p. 899; Bogoyavlenskaya and Khromych 1985, p. 74.]

*Type species*. *Coenostroma ristigouchense* Spencer, 1884, p. 599, pl. 6, figs 12, 12*a* (*Coenostroma* is consistently misspelled *Coenostoma* in this paper).

*Diagnosis*. Pillars long, continuous, rarely joining or dividing, clinoreticulate, round in tangential section and joined by radial processes; coenostroms thick, only locally laterally persistent, interrupted by foramina; dissepiments common crossing coenotubes between pillars.

*Discussion*. Nicholson's (1886*a*, 1891*b*) illustrations of the type do not show the thick coenostroms that are present in parts of the slides in his collection (P5591, Natural History Museum, London, marked as from Spencer's original) (Text-fig. 6C–D). Fagerstrom (1982) illustrated Parks's (1909) topotype. The microstructure is not well preserved in the type specimen and Nicholson's sections are thick, but the pillars appear to be clinoreticulate and the coenostroms are vaguely orthoreticulate. Stearn (1966*a*) suggested it was better assigned to *Parallelopora*, but the tangential aspect of round pillars is distinctive and the microreticulate microstructure is not as coarse as that of typical *Parallelopora*. Fagerstrom (1982) retained Nicholson's (1891*b*) assignment of the species to *Syringostroma*. Features that distinguish *Columnostroma* appear to be the dominant, discrete, clinoreticulate pillars joined in tangential section, but not into a continuous network, and lack of the smaller secondary pillars and microlaminae typical of *Syringostroma*. It closely resembles *Coenostroma* but can be distinguished by the dominantly vertical structure of the clinoreticulate tissue and the lesser importance of the coenostroms. The 'arms' joining the pillars in tangential section appear near the laminae to be of microreticulate skeletal material and between the laminae to be dissepiments.

Only Bogoyavlenskaya (1972, 1977) has assigned species to the genus. The following are considered sufficiently similar to the type to justify assigning them to *Columnostroma*: *Actinostroma fenestratum* Nicholson, 1889; *Stromatopora gallowayi* Fritz and Waines, 1956; *Columnostroma grandisculum* Bogoyavlenskaya, 1977; *Syringostroma parallelum* Parks, 1908; *Actinostroma parksi* Fritz and Waines, 1956; *Parallelopora pulchra* Galloway and St. Jean, 1957; *Parallelopora snoufferensis* Galloway and St. Jean, 1957.

The type species comes from rocks of Early Devonian (?Gedinnian) age near Dalhousie, New Brunswick, Canada. The genus is most diverse in Eifelian rocks and there is no evidence that it extends above this stage.

### Genus PARALLELOPORA Bargatzky, 1881

Text-fig. 8E

[= *Parallelopora* Bargatzky, 1881, p. 63 (see Flügel and Flügel-Kahler for pre-1968 synonymy); Flügel and Flügel-Kahler 1968, p. 556; Mori 1970, p. 130; Zukalova 1971, p. 68; Kazmerczak 1971, p. 119.]

*Type species. Parallelopora ostiolata* Bargatzky, 1881, p. 64 (subsequently designated by Nicholson 1886*a*, p. 193).

*Diagnosis.* Coenosteles long, continuous, branching and joining in vertical section, in tangential section mostly joined in a closed network enclosing round coenotubes; coenostroms suppressed or absent, dissepiments abundant. Microstructure of coenosteles coarsely microreticulate, apparently formed of closely spaced opaque micropillars and more widely spaced short microlaminae.

*Discussion. Parallelopora* has been used as a repository for many species with prominent coenosteles and indifferent preservation. Most of the species tentatively assigned to the genus in Flügel and Flügel-Kahler (1968) should be referred to genera such as *Syringostromella* and *Salairella. Parallelopora* is distinguished from *Salairella* by the coarse microreticulate microstructure of the coenosteles. The microgalleries between the micropillars are large enough to be confused with galleries in the typical species. From *Columnostroma* it is distinguished by this microstructure and the fact that the coenosteles in tangential section join into a closed network enclosing coenotubes rather than being discrete.

As defined above, *Parallelopora* is restricted to Eifelian and Givetian rocks.

A review of the literature suggests that only the species listed in Supplementary Publication No. SUP 14042 deposited at the British Library have the features (above) which closely relate them to the type species.

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## APPENDIX

Nicholson's thin sections of *Stromatopora concentrica* in the Natural History Museum, London, are difficult to match with the drawings and the captions of his illustrations as the captions do not correspond with the notations on the thin sections. In plate 11 Nicholson (1886*a*) illustrated a whole specimen (fig. 15), two tangential sections (figs 16–17) and a vertical section (fig. 18). The vertical section and one of the tangentials (pl. 11, fig. 17) are identified in the caption as coming from a specimen in the Caunopora-state, one different from that of figures 15 and 16, which was identified as 'absolutely identical with the original example of the species' (Nicholson 1886*a*, pl. 11). (The term 'Caunopora-state' was used by early workers to indicate specimens intergrown with syringoporoid corals.) The relevant thin sections in the collection are labelled as from specimens 1 and 3. Only specimen 3 is in the 'Caunopora-state'. Labels on the thin sections indicate that figures 16 and 18 come from sections 1 and 1*a*, and figure 17 comes from 3*a*. The three thin sections cannot be matched precisely with the drawings in Nicholson's plate 11; however, the tangential section of figure 17 is in the 'Caunopora-state' and is likely to come from specimen 3, as the section label indicates. The label on thin section 1*a* and the fact that the drawing of the vertical section of figure 18 does not show the 'Caunopora-state' both indicate that the caption for figure 18 is incorrect, and both figures 18 and 16 are from the specimen Nicholson regarded as 'identical' with the type, that is specimen 1 (P5869). The thin sections 1 and 1*a* which I conclude are the basis of figures 16 and 18 respectively are illustrated above in Plate 1, figures 1–2.

# LATE CRETACEOUS SELACHIANS FROM INDIA AND THE AGE OF THE DECCAN TRAPS

*by* G. V. R. PRASAD *and* H. CAPPETTA

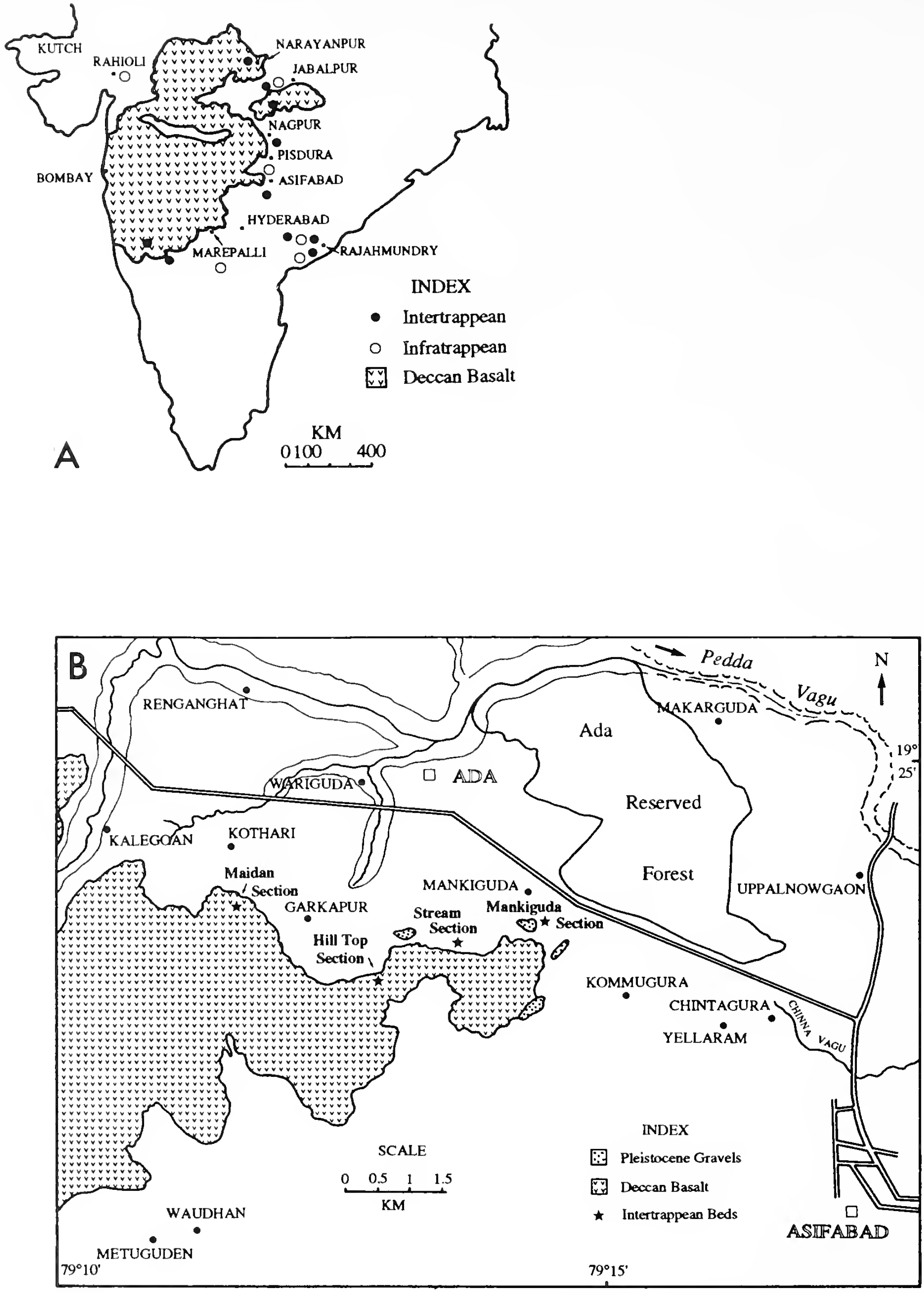
ABSTRACT. Thin sedimentary sequences associated with the Deccan Traps (infra- and intertrappean) of peninsular India have previously been dated as ranging in age from Late Cretaceous to Early Oligocene. Systematic work carried out in recent years on the fauna and flora of these sedimentary beds has led to the discovery of many previously unknown microvertebrate, invertebrate, and plant remains. The present paper deals with the systematics and stratigraphical significance of batoid fish remains from Asifabad and Marepalli, Andhra Pradesh state, India. The selachian fauna of these localities, represented by isolated teeth and dermal denticles, is identified with the genera *Raja*, *Rhombodus*, and *Igdabatis*. All the dental remains referred in earlier works to *Dasyatis* and *Rhinoptera* are now identified as lateral teeth of *Igdabatis*. The study reveals the presence of two new species: *Raja sudhakari* sp. nov. and *Igdabatis indicus* sp. nov. obtained from the infratrappean and intertrappean beds of Marepalli and Asifabad respectively. The new palaeontological data support a Late Cretaceous, Maastrichtian, age for the infra- and intertrappean beds of peninsular India.

THE volcanic rocks of peninsular India popularly known as 'Deccan Traps' cover over one third of the total area and have been a topic of discussion at many national and international symposia in the past. These rocks are interbedded at many places with fossiliferous sedimentary beds designated as 'infratrappean' (underlying the basal flow) and 'intertrappean' (enclosed between two flows). Over a period of more than a century, Deccan volcanic flows have been dated as ranging in between the Late Cretaceous and the Early Oligocene based on inconsistent K-Ar dates of the lava flows (Rama 1968; Kaneoka and Haramura 1973; Agarwal and Rama 1976; Alexander 1981) and biostratigraphically insignificant plant fossils and molluscs occurring within the intertrappean beds (Hislop 1860; Sahni 1934; Prakash 1960; Bhatia and Mannikeri 1976; Shivarudrappa 1978). In view of the longstanding disparities in the age determinations and the significance attached to Deccan Traps in some of the theoretical models to explain mass extinctions at the Cretaceous-Tertiary boundary, concerted efforts have been made to obtain a representative sample of infratrappean and intertrappean fauna and flora from widely separated localities in peninsular India.

The present paper is the result of a collaborative research project carried out by the Departments of Geology, Panjab and Jammu Universities, India and the Laboratoire de Paléontologie, Université des Sciences et Techniques du Languedoc, Montpellier, France in the last five years. As a consequence of this collective effort, a larger number of microvertebrate, invertebrate, and plant remains have been collected from the infratrappean as well as intertrappean sedimentary sequences.

The microvertebrate fauna comprises fish, anurans, lacertilians, snakes, turtles, crocodiles, dinosaurs, and mammals; the invertebrate fauna is composed of gastropods, bivalves, and ostracodes. Charophytes, pollen, and spores substantiate the floral component. A significant variation is, however, noticed in the biotic component at one of the investigated localities. The intertrappean beds of Naskal, occurring on the southeastern margin of Deccan Traps, yield predominantly freshwater and terrestrial elements whereas the infra- and intertrappean sequence of the eastern margin such as Jabalpur, Nagpur, Pisdura, and Asifabad produce a mixed assemblage of freshwater and marine elements. The selachian teeth described in this paper have been obtained from an infratrappean section exposed southwest of the village of Marepalli (lat. 17° 20′; long. 77° 42′), Rangareddi District and an intertrappean section located 2·5 km south of the village of

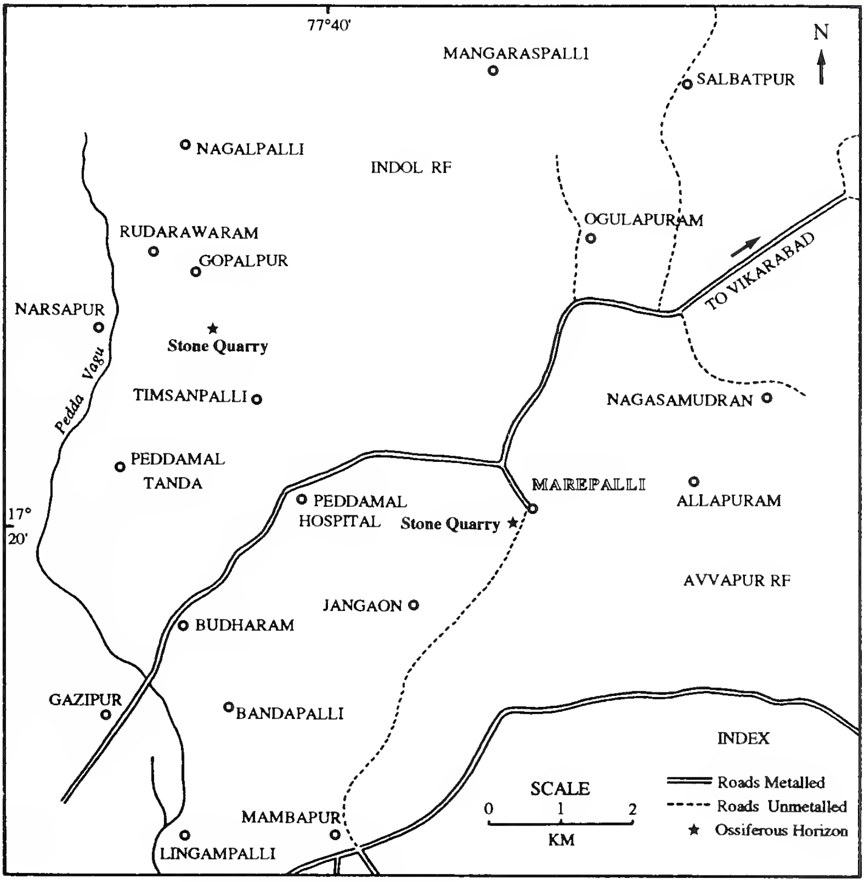
**[Palaeontology, Vol. 36, Part 1, 1993, pp. 231–248, 4 pls.]**



TEXT-FIG. 1. Location maps of the investigated localities. A, distribution of infra- and intertrappean beds in peninsular India. B, detailed locality map of Asifabad.

Ada (lat. 19° 25′; long. 79° 15′), Asifabad Taluq, Adilabad District, Andhra Pradesh (Text-fig. 1). The volcano-sedimentary sequence of Asifabad represents the eastern extension of the Deccan Traps in the Pranhita-Godavari Valley and is underlain by a succession of Precambrian and Gondwana Group rocks. Four intertrappean sections have been demarcated in this region out of which one, very close to the village of Ada and designated as 'stream section', proved to be rich in batoid fish remains (Text-fig. 2). The selachian teeth were recovered mainly from quartz arenite and lithic wacke units. Though a few lateral teeth of *Igdabatis* are known from the basal lithic arenite, it is the rajids which dominate the batoid component of this unit. Associated fauna and flora include freshwater fish, anurans, lacertilians, snakes, crocodiles, dinosaurs, molluscs, ostracodes, and charophytes. The infratrappean beds of Marepalli, on the other hand, constitute a part of the volcanic sequence on the southern margin of the main mass of Deccan Traps. The bone-bearing section is exposed in a quarry located southwest of the village of Marepalli. Here, mudstones of different hues yielded only the remains of fish, frogs, turtles, crocodiles, and dinosaurs and are devoid of invertebrate and plant remains (Text-fig. 2). The batoid collection of Marepalli includes dental remains of *Igdabatis* and *Rhombodus*, and a few dermal denticles. Dentition of *Raja* is not known from this locality and this seems to be characteristic of all infratrappean (Lameta) sequences such as Jabalpur and Pisdura.

Selachian fish are known to show considerable variation in their dental morphology, which is



TEXT-FIG. 2. Detailed locality map of Marepalli.

attributed to various factors such as their position on the jaw, maturity of the animal, and sexual dimorphism (Cappetta 1987). When complete dental plates of batoids are available, one can make the taxonomic assignment with greater confidence, but when there are only isolated teeth, such studies are susceptible to misinterpretations. In India, batoid fish of Cretaceous age have so far been recovered from the infratrappean beds of Jabalpur, Pisdura, and Marepalli, and the intertrappean beds of Nagpur and Asifabad. The Jabalpur collection includes a single broken median tooth and a few lateral teeth which have rightly been referred to the genus *Igdabatis* (Courtillot *et al.* 1986; Tripathi 1986). The fauna from Pisdura consists of a few median and lateral teeth (Jain and Sahni 1983), who compared the median teeth with *Igdabatis sigmodon* Cappetta, 1972 (but referred them to *I. sigmoides*; [*sic*, a misprint for *sigmodon*]). These authors also assigned the lateral teeth of *Igdabatis* affinity to *Rhinoptera*. The batoid collection from Nagpur includes only lateral teeth of *Igdabatis* but based on morphological differences, they were placed under different species of *Dasyatis* and *Rhinoptera* (Rana 1984). Similarly, the teeth from Asifabad have been related to various species of *Dasyatis*, *Rhinoptera*, *Rhombodus*, *Raja*, and *Igdabatis* (Prasad 1985; Prasad and Sahni 1987). In addition to the collections from the above-mentioned localities, a few lateral teeth referable to *Igdabatis* have recently been recovered from the intertrappean beds of Gurmatkal (Srinivasan, personal communication) and Naskal. Comparison of the Indian material with rich African selachian faunas, and dentition of many living forms available to one of us (H. C.) necessitated a revision of preexisting systematics of fossil selachians of India. All the lateral teeth which were earlier referred to different species of *Dasyatis* and *Rhinoptera* could now be compared by extrapolation to the lateral series of *Igdabatis*. It is further realized that the Indian teeth could not be assigned to any of the previously described species of *Raja*, *Rhombodus*, and *Igdabatis*. The terminology used in the description of the teeth follows Cappetta (1987). The specimens described in the present paper are stored in the Vertebrate Palaeontology Laboratory, University of Jammu, Jammu Tawi, India and referred to by their VPL/JU numbers.

## SYSTEMATIC PALAEONTOLOGY

Superorder BATOMORPHII Cappetta, 1980
Order RAJIFORMES Berg, 1940
Suborder RAJOIDEI Garman, 1913
Family RAJIDAE Bonaparte, 1931
Genus RAJA Linnaeus, 1758

*Type species*. *Raja batis* Linnaeus, 1758, Recent.

### *Raja sudhakari* sp. nov.

Plate 1, figs 1–7

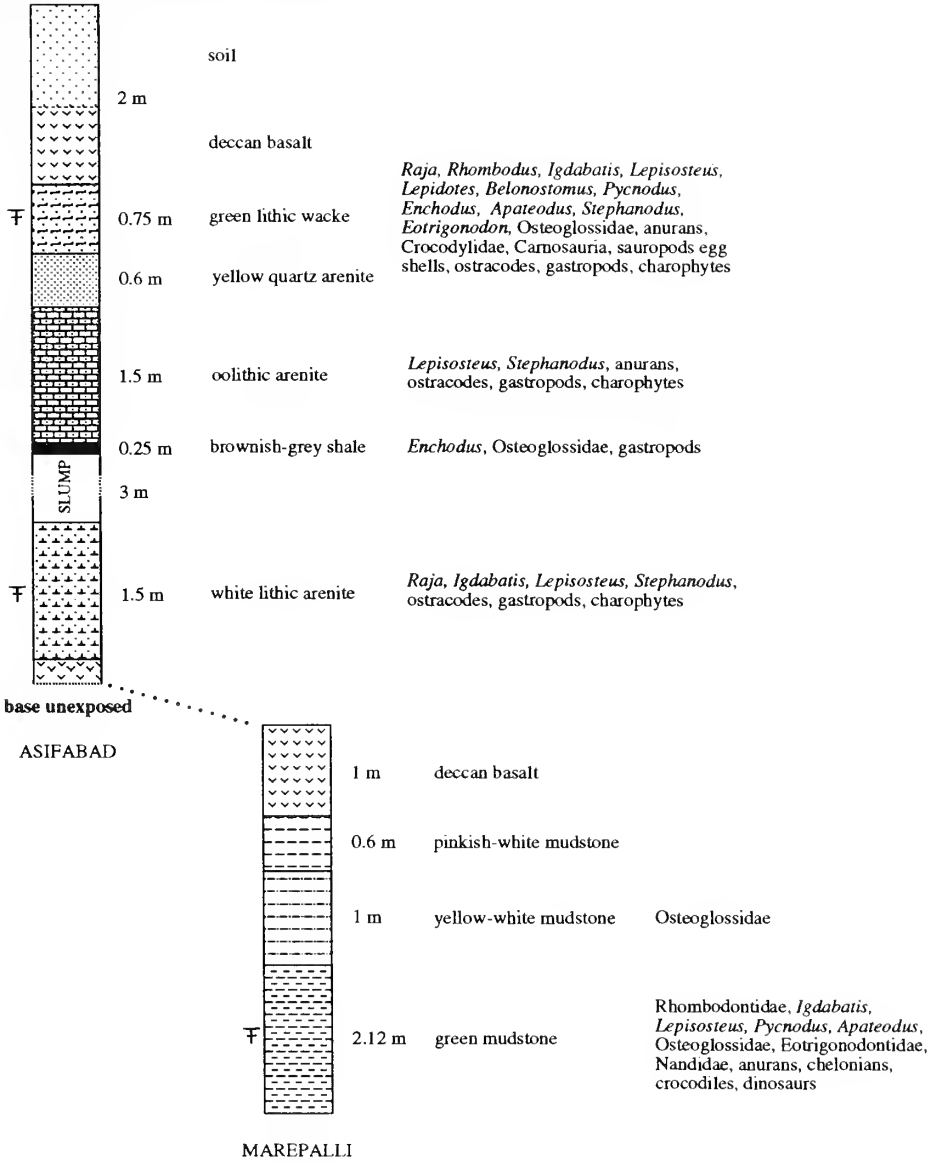
*Material*. Sixty-five isolated median and lateral teeth.

*Horizon and locality*. Intertrappean beds (green lithic wacke of Text-figure 3) of Asifabad, Andhra Pradesh, India.

*Holotype*. VPL/JU 101; Pl. 1, fig. 2*a–c*.

*Derivation of name*. The species is named in honour of Shri G. Sudhakar, Sarpanch (chief) of the village of Ada, Asifabad Taluq, Adilabad District, Andhra Pradesh, India for his generous and unfailing help during the field work.

*Diagnosis*. Teeth of small size (less than 1 mm width) with a crown longer than wide and showing a generally well-differentiated cusp. In occlusal view, the crown shows a rhombic outline, with a



TEXT-FIG. 3. Stratigraphical columns of the ossiferous sections.

lingual part more developed than the labial one. The marginal angles are distinct but not acute. There is a well marked medio-labial angle, often blunted and a distinct uvula partially overhanging the root groove. The cusp is high and bulky with a well-marked transverse keel joining the lateral angles. In profile view, the lingual outline of the cusp is almost vertical and the labial one oblique. The lower part of the visor is wide, gently rounded and oblique, well separated from the labial face of the crown by a distinct ridge.

Root much narrower than the crown in occlusal view, with labio-lingually elongated lobes separated by a deep groove; basal face of each lobe transversally convex and oblique in labial view; a large foramen opens in the labial part of the groove.

*Description.* Teeth with a rather low cusp in comparison to very long, elongated cusps found in recent and many fossil rajids. This is indicative of weak sexual dimorphism in the Indian species. The teeth, probably belonging to the parasymphyseal and anterior rows, have crowns with roughly rhombic outline with the long axis lying in the labio-lingual direction (Pl. 1, figs 2–3). The central part of the crown is projected into a conical cuspid which points lingually. In profile, the cuspid has nearly a vertical face on the lingual side with a slight concavity at the base and an inclined convex base on the labial face. The summit of the cuspid is connected to the lateral margins of the crown by transverse cutting ridges. The cuspid is more developed lingual to the transverse ridge. The labial and lingual margins of the crown are convex in outline but in a few teeth, the labial margin is truncated in its median part and exhibits a weakly concave outline (Pl. 1, fig. 1*a–b*). The crown margin all around the central cuspid is slightly raised with a shallow depression at the base of the cuspid. The median part of the crown on lingual margin is slightly bulged and in many teeth bears a central uvula. The crown is much higher than the root and almost completely covers the lingual face of the root. The labial face of the crown overhangs the root to such an extent that its length is nearly equal to the total length of the root. The teeth show various stages of wearing due to occlusion. In teeth with little wearing, only the summit of the cuspid is eroded (Pl. 1, fig. 6), while in teeth with maximum wearing, the cuspid is completely worn out to the base (Pl. 1, fig. 1). In some cases, even the basal crown is worn out to a flat surface. Many intermediate stages between the two extremes of wearing also exist. The root is very small (half the width of the crown or even less), inclined lingually, and is divided into two subtriangular or crescentic lobes labio-lingually elongated by a deep and wide groove.

*Discussion.* The lobes may or may not be equal in size and have generally convex basal faces. A foramen opens at the labial extremity of the root groove. No other foramina are visible on the lingual and labial faces of the root. Small teeth with reduced cuspids may belong to the females but they could also be compared to the lateral teeth of a male. As discussed earlier, the remarkable variation in the dentition of rajids does not allow a precise allocation of these teeth either to the females or males.

Ward (1984) suggested that the presence of a root directly below the crown may be considered as a diagnostic feature of females, but this rule does not apply to all species of *Raja*. If the present teeth are distinguished by the above criterion, then they should be identified with males as they have more lingually placed roots. The crown in these teeth is approaching an elliptical outline. In extreme lateral teeth, the cuspid is highly reduced and only in the form of a feeble transverse crest and the crown attains the elliptical outline. The labial face of the crown is flat and convex on the labial margin. There is a minor concavity on the lingual face below the transverse crest and the lingual margin of the crown is bulged. The root is inclined lingually but in some cases, it is nearly central in position. A wide and deep root canal divides the root into two crescentic and basally convex lobes.

The family Rajidae includes more than two hundred species distributed among about twenty subgenera or genera (McEachran and Miyake 1990). This family exhibits a broad range of dental morphological diversity according to the species; to the normal interspecific dental variations are added intraspecific variations which are often pronounced because of a very marked gynandric heterodonty. By their morphological features, the teeth of the Indian rajid can be assigned unequivocally to the genus *Raja*. The majority of the species of *Raja* are known from Tertiary deposits all over the world. Affinities of the only Cretaceous (Late Santonian) species *R. davisi* Fowler, 1958 are doubtful (Cappetta 1987). The Tertiary forms of *Raja* are represented by *R.*

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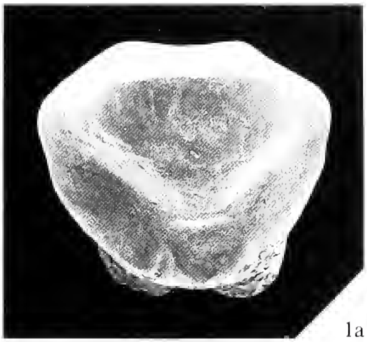
EXPLANATION OF PLATE 1

Figs 1–7. *Raja sudhakari* sp. nov.; Maastrichtian, intertrappean beds of Asifabad. 1, VPL/JU 100; lateral tooth; *a*, occlusal view; *b*, basal view; *c*, profile. 2, VPL/UK 101, holotype, anterior tooth; *a*, occlusal view; *b*, basal view; *c*, labial view. 3, VPL/JU 102; anterior tooth; *a*, occlusal view; *b*, lingual view. 4, VPL/JU 103; anterior tooth; *a*, occlusal view; *b*, labial view. 5, VPL/JU 104; anterior tooth, profile. 6, VPL/JU 105; anterior tooth; *a*, profile; *b*, labial view. 7, VPL/JU 106; anterior tooth; basal view. All figures ×43.

PLATE 1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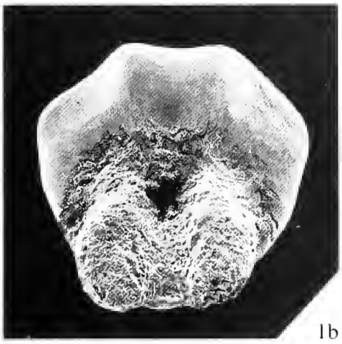
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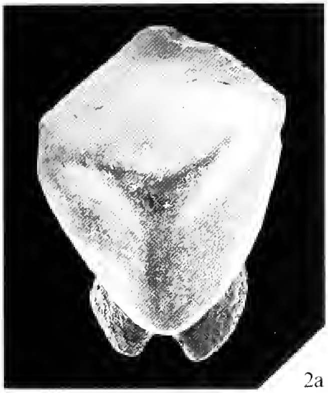
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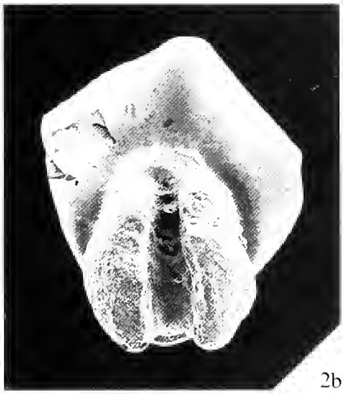
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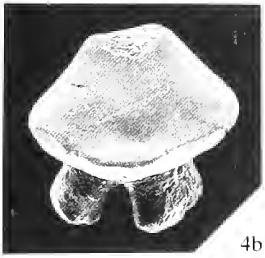
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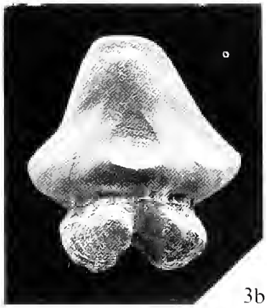
3a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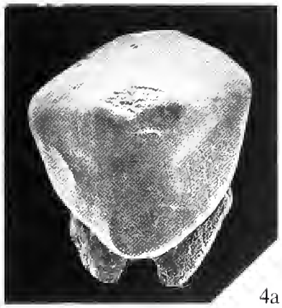
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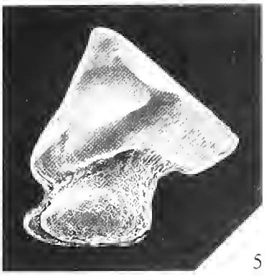
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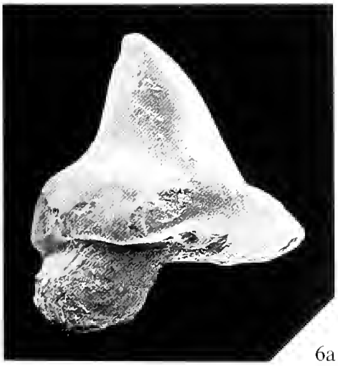
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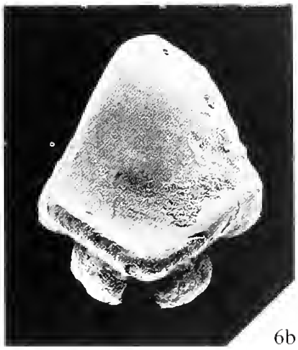
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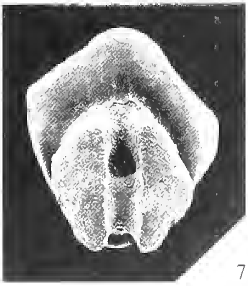
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PRASAD and CAPPETTA, *Raja*

*harrisae* (Lower Eocene of England, Ward 1984), *R. gentili* (Middle Miocene of France, Joleaud 1912; Cappetta 1970, 1975; Lower and Middle Miocene of Switzerland, Leriche 1927), *R. casieri*, *R. cecilae*, *R. heinzelini*, *R. terhangensis* (Early Oligocene of Belgium, Steurbaut and Herman 1978) and *R. louisi* (Late Palaeocene of Niger, Cappetta 1972). Comparison of the Indian specimens with these forms leads to the following observations. *R. sudhakari* differs from *R. louisi* in which the crown is wider than long, the lingual face of the crown is nearly straight without a wide lip, the labial face is concave, and the labial part of the crown has a short ridge at the summit which divides into two branches, each joining the lateral angles. *R. sudhakari* is distinguished from *R. harrisae* in which the male teeth are highly cuspidate, base of the crown is highly inflated, a transverse cutting ridge is absent but a labial cutting ridge is present, the cuspid is more lingually inclined and the teeth are larger in size. *R. sudhakari* does not show any affinities to *R. gentili* in which the lateral teeth are pyramidal in shape, lingual extension of the uvula does not reach the indentation of the root lobes, a small ridge is present on the lingual face and often a similar one on the labial face, the male teeth have elongated, lingually inclined cuspids with a distinct collar at the base, and the root is expanded, outflanking the crown basally and with two laterally diverging root lobes.

*R. sudhakari* exhibits the following differences from *R. cecilae*, *R. heinzelini*, *R. terhangensis*, and *R. casieri*: in *R. cecilae*, the cuspid is lanceolate in outline, acute and lingually inclined, root lobes are subquandrangular and outflank the crown on the symphyseal and commissural sides. Similarly, *R. heinzelini* has a tetragonal crown, whose labial face is flat and diamond-shaped, and a root completely masked by the crown in projection. *R. terhangensis* is represented by male teeth with very elongated cuspids bent lingually, a circular or elliptical crown base, laterally expanded root lobes, and a labially wide root canal. *R. casieri* has a massive, flattened crown, a feebly curved labial face, a high and robust root not too developed lingually and root lobes that outflank the crown from symphyseal and commissural sides.

It is clear from the above comparison that the Indian teeth are morphologically distinct from the known species of *Raja* and, therefore, justify their inclusion in a new species.

### Rajiforme indet.

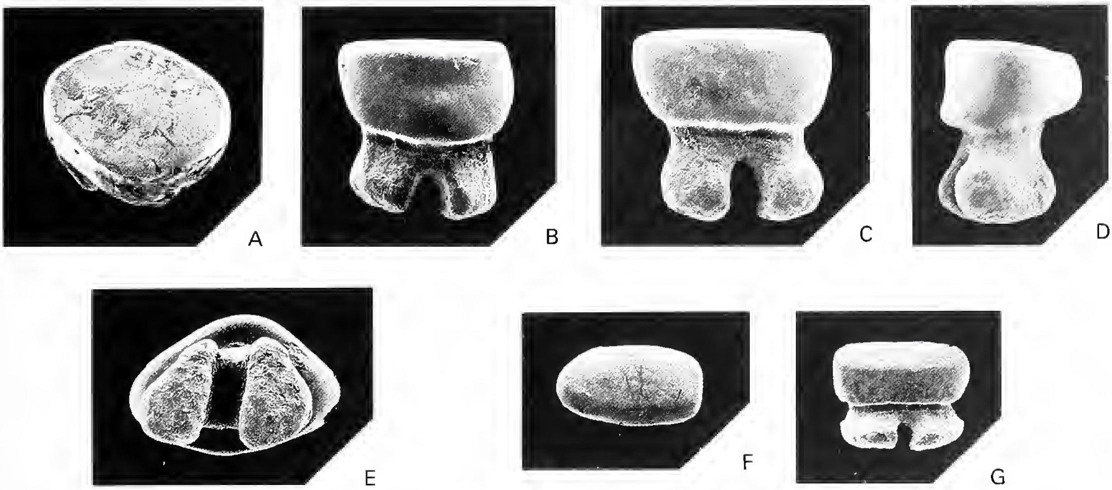
Text-fig. 4

*Material*. Three teeth, VPL/JU 128–130.

*Horizon and locality*. Intertrappean beds (green lithic wacke of Text-figure 3) of Asifabad, Andhra Pradesh, India.

*Description*. As well as the specimens described as *Raja sudhakari*, there are three more teeth in the collection of Asifabad which have a peculiar morphology slightly different from those of the lateral teeth of *R. sudhakari*. Of the three specimens, one is too small (Text-fig. 4F–G) and the other two are large for lateral teeth (Text-fig. 4A–E). In these teeth, the crown is wider than long. The larger specimen (Text-fig. 4C–E) has an ovoidal crown with flat occlusal surface, and is devoid of cuspid; labial and lingual faces of the crown are equally developed and the margins are almost vertical. The root is very large for a lateral tooth and is divided by a groove into two subtriangular or crescentic lobes. The labial margin of the crown is convex and projects medially over the root. The smaller tooth has an elliptical crown which is flat occlusally. The labial and lingual faces are equally developed. The labial face of the crown does not overhang the root like a roof as in the lateral teeth described before. The root is equally well developed, slightly outflanks the crown lingually, and is less wide than the crown. It is divided into a large triangular lobe and a smaller crescentic lobe by a wide groove.

*Discussion*. The three teeth are morphologically different from the lateral teeth of *R. sudhakari* sp. nov. and probably belong to a different genus. Since there are only three specimens in our collection, we have avoided creating a new taxon and prefer to place them as Rajiforme indet. until additional material is procured.



TEXT-FIG. 4. Rajiforme indet., Maastrichtian, intertrappean beds of Asifabad. A–B, VPL/JU 128; anterior tooth; occlusal and lingual views. C–E, VPL/JU 129; lateral tooth; lingual, profile and basal views. F–G, VPL/JU 130; very lateral tooth; occlusal and labial views. All figures ×43.

### Order MYLIOBATIFORMES Compagno, 1973
### Superfamily MYLIOBATOIDEA Compagno, 1973
### Family MYLIOBATIDAE Bonaparte, 1838
### Genus IGDABATIS Cappetta, 1972

*Type species. Igdabatis sigmodon* Cappetta, 1972

### *Igdabatis indicus* sp. nov.

Plate 2, figs 1–7; plate 3, figs 1–8

1983 *Igdabatis sigmoides* [*sic*] Cappetta; Jain and Sahni, pp. 68–69, fig. 2A–E; pl. 1, figs 1–4.
1986 *Igdabatis* cf. *sigmodon* Cappetta; Courtillot *et al.*, p. 365, fig. 3.

*Material.* Six median and 190 lateral teeth.

*Horizon and locality.* Infratrappean beds (green mudstone of Text-figure 3) of Marepalli and intertrappean beds (green lithic wacke and white lithic arenite of Text-figure 3) of Asifabad, Andhra Pradesh, India.

*Holotype.* VPL/JU 107; Pl. 2, fig. 1.

*Derivation of name.* After the country of its origin.

*Diagnosis.* Median teeth 2 to 3·5 times wider than long, transversely arcuated with a convex lingual border and a concave labial border, and acute lateral angles. Sigmoidal contour of the tooth is not a characteristic feature. Crown surface with rugose and pitted ornamentation. Middle part of the crown higher than the lateral ends, hexagonal occlusal outline with slanting labio-marginal facet. Root in polyaulacorhize with root lobes of variable width. Lateral teeth hexagonal or subtrapezoidal in outline, crown wider than long and rather higher; root less high than crown, and root lobes varying from two to four in number. Extreme lateral teeth elliptical or oval in shape and height of the crown reduced; root projects lingually and is divided into a larger triangular and smaller crescentic lobes.

*Description*. Median teeth are wider than long; the width/length ratio varies from specimen to specimen (2 to 3·5). All the median teeth are transversely arcuated with a concave labial border and a convex lingual (Pl. 2, figs 2–4). The lateral angles of these teeth are oriented labially. The sigmoidal contour of the teeth, a feature characteristic of *Igdabatis sigmodon* Cappetta, 1972 is not distinct except in one specimen (Pl. 2, fig. 3); but even in this specimen it is not profoundly developed. The occlusal surface of the crown is convex and ornamented with polygonal pits. In some small specimens, the surface of the crown is covered with vermiculate or rugose enameloid (Pl. 3, figs 6, 8). The crown is higher than the root and its thickness varies from the middle to the lateral parts. Generally, the middle part of the crown is higher than the lateral ends (Pl. 2, fig. 2*b*). The occlusal surface of the crown is hexagonal in shape, but some of the teeth do not show the lateral facets lingually and form a continuous, convex and arcuate outline. The labial margin of the crown is slightly sloping labially and is ornamented with very fine pits or vertical wrinkles. This is the labial articulating facet for the succeeding tooth. The lingual margin may be smooth or have wrinkles and is separated from the root by a lingual extension of the crown in the form of a rounded ridge. The root in the median teeth shows polyaulacorhize condition being divided into a number of lobes and grooves. In a complete specimen of large size (not figured), there are eight lobes and seven grooves. In a fragmentary tooth with half of the tooth intact, there are five lobes and four grooves, so one may expect about ten lobes and nine grooves in a full specimen. The two lateral lobes are triangular in shape whereas the remaining lobes are rectangular in outline. Width of the lobes and grooves is variable. The grooves bear foramina which may be central in position or may open laterally. Some teeth also bear foramina on the labial face of the root.

Lateral teeth exhibit varied morphology corresponding to their position on the dental plate. Teeth that are close to the median series (Pl. 2, fig. 6) are comparatively larger than those on the extreme lateral ends (Pl. 3, figs 3–5) and have a hexagonal or subtrapezoidal occlusal outline. In some of the worn teeth, the shape becomes fusiform or oval. The crown is wider than long and is ornamented with polygonal pits. As in the median teeth, the labial margin of the crown slopes labially forming an articulating facet for the following tooth row. Similarly, the lingual face of the crown is separated from the root by a rounded ridge-like lingual extension of the crown. Unlike the median teeth, the crown shows an increase in height at its lateral ends (Pl. 3, figs 2*b*, 3*b*, 4*b*). The lateral ends of the labial and lingual faces of the crown meet with an acute angle. The root in the lateral teeth is always less high than the crown. The number of root lobes and grooves probably varies according to their position on the dental plate. Those teeth presumed to be very close to the median series have three or four lobes separated by two or three grooves. Some of the teeth show a central foramen and many irregular foramina opening on the labial face of the root near the junction of crown and root. The extreme lateral lobes are triangular in shape, wider than the medium rectangular lobes. Teeth situated further from the median teeth probably have only two lobes separated by a single groove. The extreme lateral teeth have elliptical or oval crowns (Pl. 3, fig. 5). In these teeth, the height is reduced and the root projects lingually beyond the crown. The root is divided into two unequal lobes; the smaller one is crescentic in outline whereas the larger one is triangular in shape. There are a few teeth in which the crown has the form of a rectangle or parallelogram. In some living genera of batoids, the teeth of the lateral files get compressed transversely and acquire the shape of a rectangle or parallelogram. In addition to the teeth described above, there are ten isolated teeth, smaller in size (0·9 to 1·5 mm in width) with cuspidate crowns at various stages of development. A typical tooth of this kind (Pl. 3, figs 6–8) has a roughly triangular crown. A median transverse crest separates the labial face of the crown from the lingual face.

The part of the crown labial to the central crest is spindle-shaped with a median notch on the labial margin and is centrally depressed. The lingual part is triangular in shape, centrally depressed, and projects lingually over the root in the form of a cuspid. The occlusal surface of the crown exhibits pitted and interconnecting ridge ornamentation. In teeth slightly larger than the above (Pl. 3, fig. 7), the median concavity of the labial margin becomes reduced, the median crest is blunt and broader, the lateral ends of the spindle-shaped labial crown become more rounded, acutely pointed, and the lingually projecting cuspid has a straight linear face.

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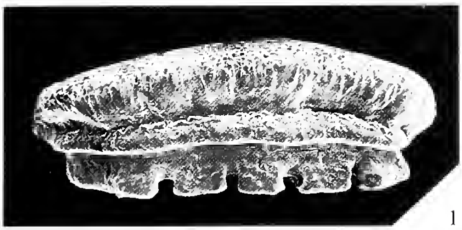
## EXPLANATION OF PLATE 2

Figs 1–7. *Igdabatis indicus* sp. nov. Maastrichtian; infratrappean beds of Marepalli. 1, VPL/JU 107; holotype; median tooth; lingual view, × 9·6. 2, VPL/JU 108; median tooth; *a*, occlusal view; *b*, lingual view; *c*, basal view, × 15·6. 3, VPL/JU 109; median tooth; *a*, occlusal view; *b*, basal view, × 15·6. 4, VPL/JU 110; median tooth; *a*, occlusal view; *b*, labial view, × 15·6. 5, VPL/JU 111; lateral tooth; *a*, occlusal view; *b*, basal view, × 15·6. 6, VPL/JU 112; lateral tooth; *a*, occlusal view; *b*, labial view, × 13·2. 7, VPL/JU 113; lateral tooth; *a*, occlusal view; *b*, basal view; *c*, profile, × 13·2.

PLATE 2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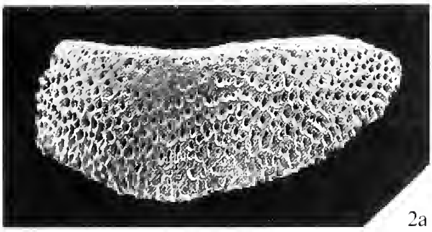
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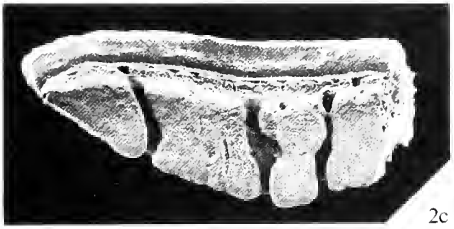
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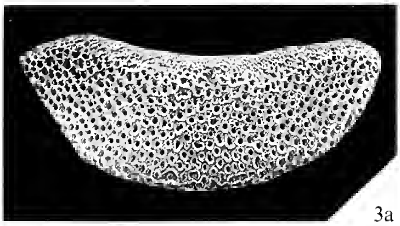
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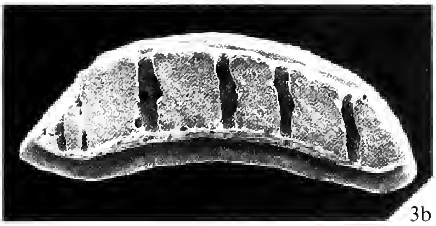
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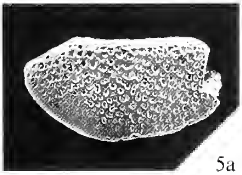
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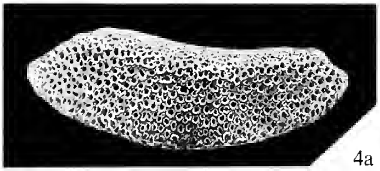
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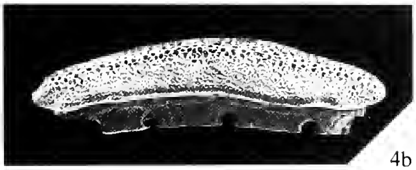
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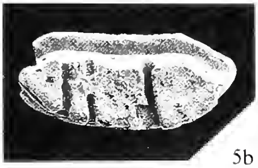
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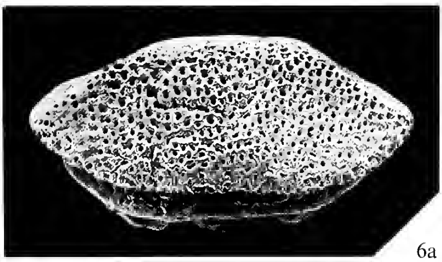
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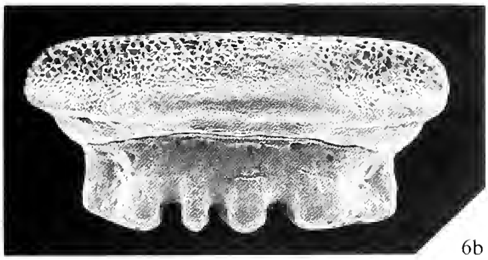
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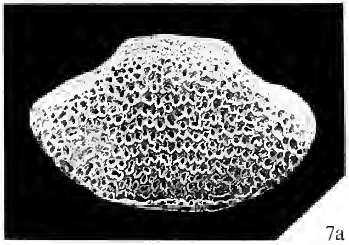
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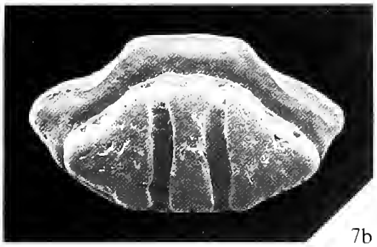
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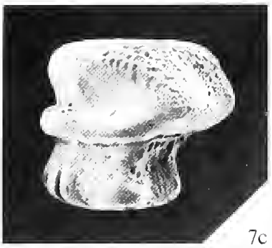
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PRASAD and CAPPETTA, *Igdabatis*

The root is divided into two triangular lobes by a central groove. The groove bears a central foramen and many irregular pits open also on the labio-lingual distal faces of the root. These teeth with their cuspidate crowns and smaller size are distinct from the median and lateral teeth described above. At first one gets an impression that the cuspidate teeth represent male individuals of the same species. But their small size and morphology of the crown do not favour such a conclusion. It is probable that this type of tooth belonged to young specimens, but absence of a complete dental plate of the genus *Igdabatis* for comparison and their occurrence in association with median and lateral teeth of *Igdabatis indicus* sp. nov. does not permit a definitive conclusion.

*Discussion.* At generic level, the present specimens exhibit close morphological similarities to *Igdabatis* reported from the Maastrichtian of Niger (Cappetta 1972). The median teeth, as in *Igdabatis*, are transversely arcuate, broader than long, have crowns with variable thickness, are hexagonal in outline, and have roots formed of alternating lobes and grooves maintaining more or less the same height throughout the breadth of the root. This genus has so far been represented by a single species *Igdabatis sigmodon* Cappetta, 1972, the specific name being derived from the sigmoidal contour of the teeth. As well as the present collection, *Igdabatis* has previously been reported from two other localities in peninsular India. One is from the Lameta sediments of Pisdura (Jain and Sahni 1983) and the other is from coeval beds at Jabalpur (Courtillot *et al.* 1986). The tooth from Jabalpur is fragmentary (0·4 mm in width) whereas the teeth from Pisdura are complete (13·2 mm in width). In the present collection also there is a fragmentary tooth which approaches the size of the teeth from Jabalpur and Pisdura (estimated width approximately 16 mm). In contrast to the Indian specimens, median and lateral teeth of *Igdabatis sigmodon* reach a maximum size of 26 mm and 10 mm in width respectively. On the other hand, the lateral teeth from Indian localities do not exceed 5 mm in width. Other than the differences in size, the Indian specimens also differ from the African species in the morphology of median and lateral teeth. The median teeth, though transversely arcuate, do not show the strong sigmoidal curvature characteristic of *I. sigmodon* or lack any such curvature. In most of the median teeth described in the present paper, the lateral angles point labially.

The contour of the median teeth is suggestive of the presence of more than one series of teeth (probably two series) in the middle of the dental plate. Similarly, lateral teeth do not show thickening of the crown at places as in *I. sigmodon* and, therefore, lack asymmetric crowns. Lateral teeth from Asifabad and Marepalli also exhibit widely varying morphology in comparison to those of *I. sigmodon*. Moreover, in *I. sigmodon*, the lingual bulge differentiates a sort of uvula above each root groove, a morphological feature that is not observed in *I. indicus*.

On the basis of the differences in size and morphology between the median and lateral teeth and those of *I. sigmodon*, the Indian teeth are assigned to a new species. Jain and Sahni (1983) described a lateral tooth as *Rhinoptera* sp. Since the morphology of the tooth is similar to that of lateral teeth from Asifabad and Marepalli, its transfer to *I. indicus* is suggested here. Lateral teeth with a morphology resembling those of *I. indicus* have also been reported from the Lameta beds of Jabalpur (Tripathi 1986), intertrappean beds of Nagpur (Rana 1984), Gurmatkal (Srinivasan, personal communication) and Naskal. As discussed earlier, lateral teeth from Nagpur were erroneously assigned to different species of *Dasyatis* and *Rhinoptera*.

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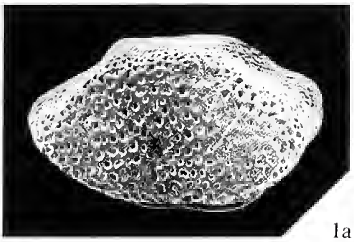
## EXPLANATION OF PLATE 3

Figs 1–8. *Igdabatis indicus* sp. nov. Maastrichtian; infratrappean beds of Marepalli. 1, VPL/JU 114; lateral tooth; *a*, occlusal view; *b*, basal view, × 13·2. 2, VPL/JU 115; lateral tooth; *a*, occlusal view; *b*, lingual view, × 13·2. 3, VPL/JU 116; lateral tooth; *a*, occlusal view; *b*, lingual view, × 13·2. 4, VPL/JU 117; very lateral tooth; *a*, occlusal view; *b*, lingual view, × 13·2. 5, VPL/JU 118; very lateral tooth; *a*, occlusal view; *b*, profile, × 13·2. 6, VPL/JU 119; tooth of a very young specimen; *a*, occlusal view; *b*, lingual view; *c*, profile, × 36. 7, VPL/JU 120; tooth of a very young specimen; *a*, occlusal view; *b*, basal views, × 36. 8, VPL/JU 121; tooth of a very young specimen; *a*, occlusal views; *b*, labial view, × 36.

PLATE 3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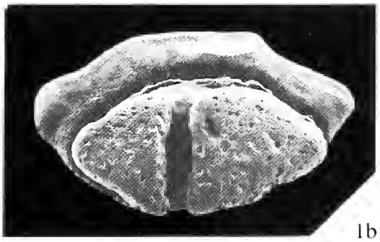
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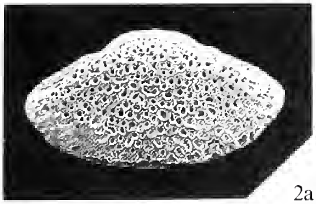
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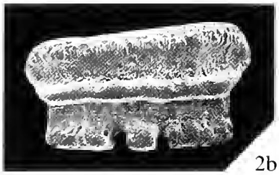
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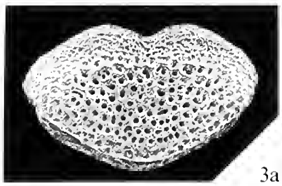
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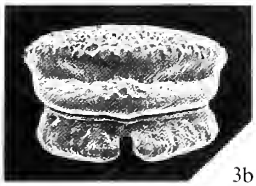
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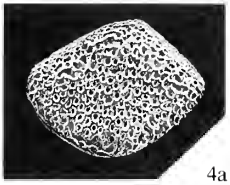
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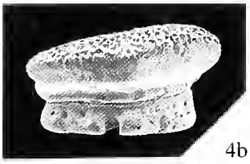
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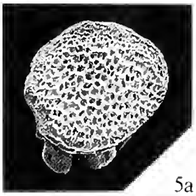
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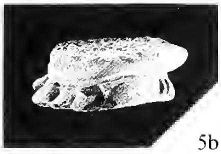
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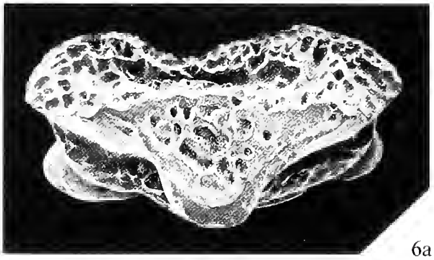
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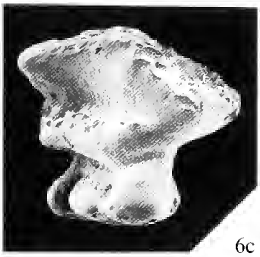
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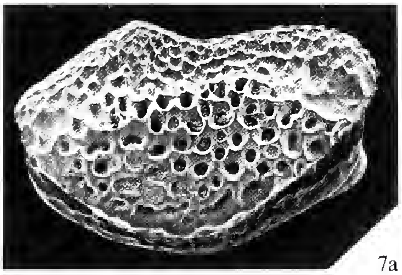
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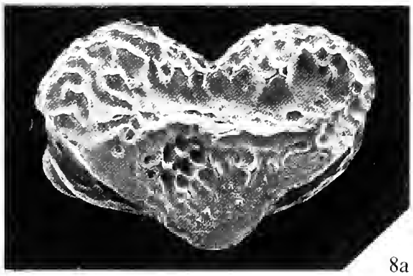
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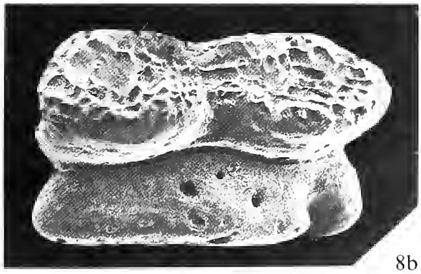
8b

PRASAD and CAPPETTA, *Igdabatis*

### Family RHOMBODONTIDAE Cappetta, 1987
### Genus RHOMBODUS Dames, 1881

*Type species. Rhombodus binkhorsti* Dames, 1881.

### *Rhombodus* sp. 1

Plate 4, figs 1–2

*Material.* Isolated lateral teeth.

*Horizon and locality.* Infratrappean beds of Marepalli and intertrappean beds of Asifabad, Andhra Pradesh, India.

*Description.* The teeth are elongated labio-lingually and hence, the length of the crown is much greater than the width. In occlusal view, the crown is in the form of a rectangle or parallelogram. The oral surface, strongly convex transversely and labio-lingually, is ornamented with interconnecting ridges and pits oriented labio-lingually (Pl. 4, fig. 1). Labially and laterally, the crown bears articulating facets. The root is much lower than the crown (Pl. 4, fig. 2), elongated labio-lingually, and divided into two elongated lobes by a wide central groove. One of the teeth from Marepalli (not figured), is subrectangular in outline, smaller than the specimens from Asifabad; the crown, ornamented with pits, is occlusally convex; the root is also rectangular in shape and is divided into two roughly triangular lobes by a deep obliquely oriented groove. At the bottom of the groove, four distinct foramina are visible. Similar foramina are also found on the labial face of the root below the crown.

*Discussion.* From their general morphology, these teeth correspond to lateral or peripheral lateral elements of the dentition. Because of their size and morphology, they are very different from the teeth of *Rhombodus* sp. 2 and represent a distinct species; but because of the scarcity of material, it is difficult to give a more precise species assignment.

### *Rhombodus* sp. 2

Plate 4, figs 3–6

*Material.* Nine isolated cuspidate teeth.

*Horizon and locality.* Intertrappean beds of Asifabad, Andhra Pradesh, India.

*Description.* The crown in these teeth is roughly rhombic in form, projected lingually with a sharp lingual margin practically cuspidate. The occlusal surface is convex and ornamented with polygonal pits and interconnecting ridges but can be practically flat and smooth because of functional wear (Pl. 4, fig. 4*b*). The crown is higher than the root and lingually the cuspid is connected to the lower limit of the crown by a sharp ridge. The articulating facets on either side of this ridge are deep. Lingual extension of the crown at the junction of crown and root is in the form of a rounded bulge of U-shape. The labial margin of the crown is ornamented with vertical wrinkles. The root has a roughly rhombic outline and is divided by a deep and wide groove oriented obliquely. In some cases (Pl. 4, fig 4), the groove is not fully developed.

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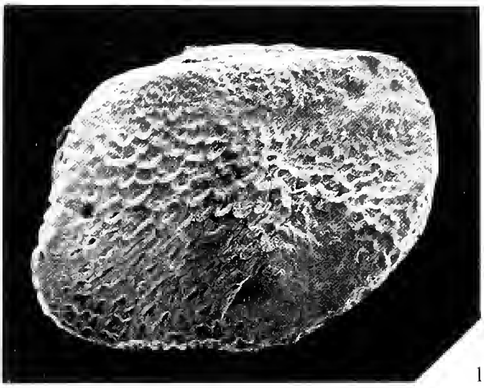
#### EXPLANATION OF PLATE 4

Figs 1–2. *Rhombodus* sp. 1. Maastrichtian; intertrappean beds of Asifabad. 1, VPL/JU 122; lateral tooth; occlusal view. 2, VPL/JU 123; lateral tooth; profile, × 12.

Figs 3–6. *Rhombodus* sp. 2. Maastrichtian; intertrappean beds of Asifabad. 3, VPL/JU 124; lateral tooth; *a*, occlusal view; *b*, lingual view. 4, VPL/JU 125; lateral tooth; *a*, lingual view; *b*, occlusal view. 5, VPL/JU 126; very lateral tooth; *a*, lingual view; *b*, occlusal view. 6, VPL/JU 127; tooth of the symphyseal region; *a*, labial view; *b*, occlusal view, × 14·4.

PLATE 4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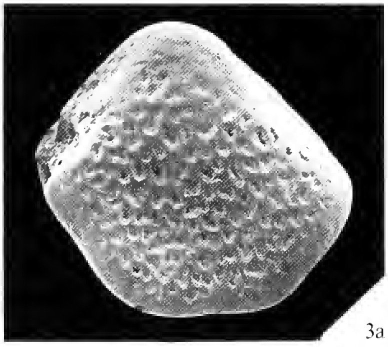
2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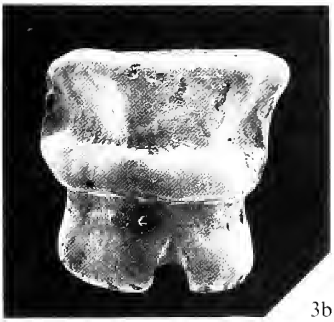
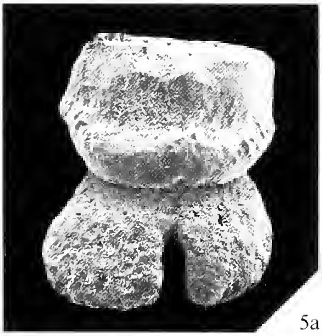
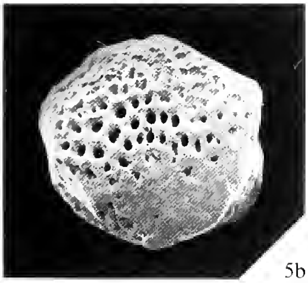

3b

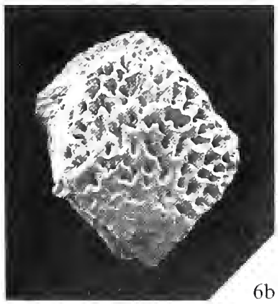

4a


4b


6a


5a


5b


6b

PRASAD and CAPPETTA, *Rhombodus*

One of these cuspidate teeth (Pl. 4, fig. 6) has a pointed lingual cuspid and a convex labial margin with a medium notch. The occlusal surface of the crown is a mosaic of interconnected ridges and pits. The crown is nearly twice as high as the root. The lingual bulge is smooth, broad and has a U-shape. The labial margin of the crown overhangs the root to a great extent. The root is compressed labio-lingually and, hence, elongated width-wise. It is divided into two roughly triangular lobes by a deep groove oriented labio-lingually. No foramina are visible on the bottom of the groove. This tooth is very small (1·4 mm in width).

*Discussion.* The teeth described here as *Rhombodus* sp. 2 are much smaller than all the known species of *Rhombodus* previously described. In comparison to Moroccan species, which show a trend towards increase in size from Middle Maastrichtian to Late Maastrichtian (nearly 20 mm), the Indian forms are only 4 mm in width. The median teeth are few in number, worn, and their morphology does not compare well with known species of *Rhombodus* such as *R. binkhorsti*, *R. meridionalis*, *R. bondoni*, *R. laevis*, and *R. microdon*. Furthermore, the lateral teeth are larger than, or nearly equal to, the median teeth in size, which is not the case in the dental plates of living batoids. Therefore, the affinity of these teeth is in doubt. Cuspidate teeth further complicate the problem because no cuspidate teeth are known in rhombodontids except in some teeth of *R. microdon*. Absence of a living representative or distantly related form does not allow any comparison with a recent dentition. Teeth of *Rhombodus* have a grinding-type dentition (Cappetta 1987); animals with this type of dentition generally lack cuspidate teeth. Nevertheless, the high, rhombic crown, robust root, and wrinkled crown faces favour their inclusion in *Rhombodus*.

## AGE OF THE SEDIMENTS

As discussed before, the age of the intertrappean beds has been the subject of speculation since 1860. Initially, many workers, influenced by the Rev. S. Hislop, the well-known British palaeontologist, and the Indian palaeobotanist Birbal Sahni, favoured a Tertiary (Early Eocene) age for the intertrappean beds. Suggests to the contrary (Cretaceous age) were few in number and were overwhelmed by the flood of reports on intertrappean plant fossils. A few had even proposed an Early Oligocene age for these beds (Shivarudrappa 1978). However, the systematic work carried out by us in recent years has revealed the widespread occurrence of microvertebrate remains along with molluscs, ostracodes, and charophytes in the infra- and intertrappean beds all along the eastern, western, southern, and southeastern margins of Deccan Traps. It is now well established that the fauna and flora from the infra- and intertrappean sedimentary sequences are more or less similar and contain dinosaurs, mammals, pollens and spores which unequivocally favour a Late Cretaceous age (Sahni *et al.* 1986, 1987; Prasad and Sahni 1988; Prasad 1989). The batoid fish fauna described here also lends support for the Late Cretaceous age. The genus *Igdabatis* is restricted to the Maastrichtian sediments of Niger and has not been reported from any other country, except India. In India, this genus occurs in the Lameta sediments of Jabalpur and Pisdura which have been dated as Maastrichtian on the basis of dinosaurs (Huene and Matley 1933; Tripathi 1986) and radiometric studies (Courtillot *et al.* 1988). Similarly, *Igdabatis* was found in association with limb bones and egg shell fragments of sauropod dinosaurs and dental remains of theropod dinosaurs at Asifabad. Therefore, a Late Cretaceous age of the upper range of this genus seems to be an acceptable limit. Likewise, *Rhombodus* is known so far from Cretaceous rocks of Europe, North America and Africa and is considered to have become extinct by the end of that period (Cappetta 1987). *Raja* is not significant biostratigraphically as it ranges from the Cretaceous to the present, but its association with *Rhombodus*, *Igdabatis*, and dinosaurs implies a similar age for the Indian species. It is important to emphasize that isolated teeth of the genus *Raja* are here reported for the first time in Cretaceous deposits. This palaeontological evidence is in agreement with the recent palaeomagnetic and radiometric investigations which had given compressed dates for Deccan Volcanism i.e. 1 to 3 Ma. duration for the volcanic activity across the Cretaceous–Tertiary boundary (Courtillot *et al.* 1986, 1988; Venkatesan *et al.* 1986; Duncan and Pyle 1988).

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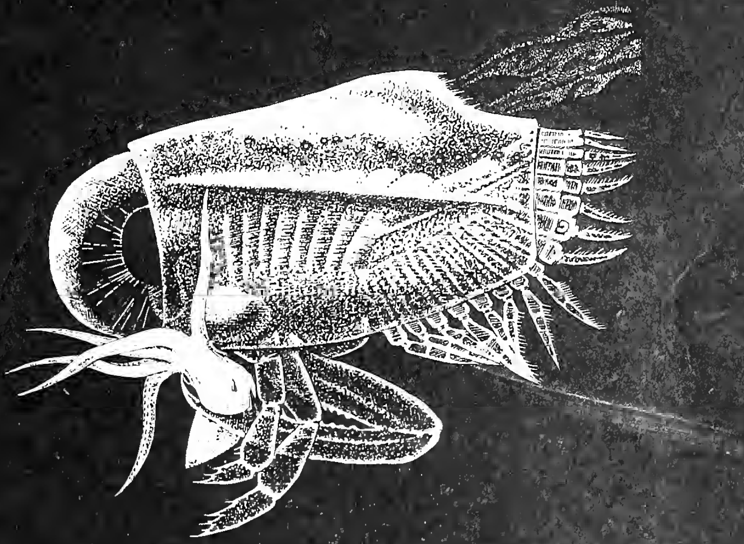

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Cover: Reconstruction of *Paraostenia voultensis* Secretan from the Middle Jurassic of the Ardèche, France, preying upon a coleoid. This is a typical thylacocephalan, a recently recognized arthropod group of uncertain, but probably crustacean, affinity, ranging from Silurian to Cretaceous, × 1.25. Reproduced by permission of the Royal Society of Edinburgh and Dr W. D. I. Rolfe from *Transactions of the Royal Society of Edinburgh*, **76**, 398, fig. 4.

# THE AMMONITES *CRIOCERATITES* (*PARACRIOCERAS*) AND *SHASTICRIOCERAS* FROM THE BARREMIAN OF SOUTHWEST JAPAN

*by* MASAKI MATSUKAWA *and* IKUWO OBATA

ABSTRACT. *Crioceratites* (*Paracrioceras*) *asiaticum*, *Shasticrioceras nipponicum*, *Shasticrioceras patricki* and *S. intermedium* sp. nov. are described from Barremian strata of southwest Japan. The occurrence of these ammonites in southern Japan provides important evidence for the existence of a cold water current originating in the Arctic and separating northeast Japan from the Asian continent. The lineage of crioceratids from Japan is discussed. *Crioceratites* (*C.*) *ishiwarai*, *C.* (*Emericiceras*) *emerici* and *C.* (*P.*) *asiaticum* from Japan are interpreted as immigrant species from the Tethyan Sea or their descendants.

THE heteromorph ammonites *Crioceratites* (*Paracrioceras*) and *Shasticrioceras* were distributed principally in the northwest European and north Pacific faunal provinces respectively during the Barremian, though two species of *Shasticrioceras* have been recorded from the Lower Hauterivian of Speeton and from the Barremian of Bulgaria (Koenen 1902; Anderson 1938; Doyle 1963; Dimitrova 1967; Jeletzky 1971; Rawson 1975; Murphy 1975; Immel 1978; Kemper *et al.* 1981). Both of these genera have been recognized in Barremian strata of Japan and two species of *Shasticrioceras* have either been listed or briefly described in Japanese (Matsumoto 1947; Obata and Ogawa 1976; Obata and Matsukawa 1984, 1988; Matsukawa and Eto 1987). Furthermore, the occurrence of these typical NW European and north Pacific genera in the Barremian has generated much discussion, because Barremian faunas in Japan are mostly of Tethyan affinity (Eto 1987; Matsukawa 1988; Obata and Matsukawa 1988). However, several problems still remain: (1) the need for full descriptions of the four Japanese species belonging to *Crioceratites* (*Paracrioceras*) and *Shasticrioceras*; (2) determination of the causal relationship between the occurrences of these ammonites and the Barremian palaeogeography of Japan; and (3) interpretation of the lineage of crioceratids from Japan. This paper provides a taxonomic description of the Japanese species and discusses these outstanding problems.

## LOCALITIES

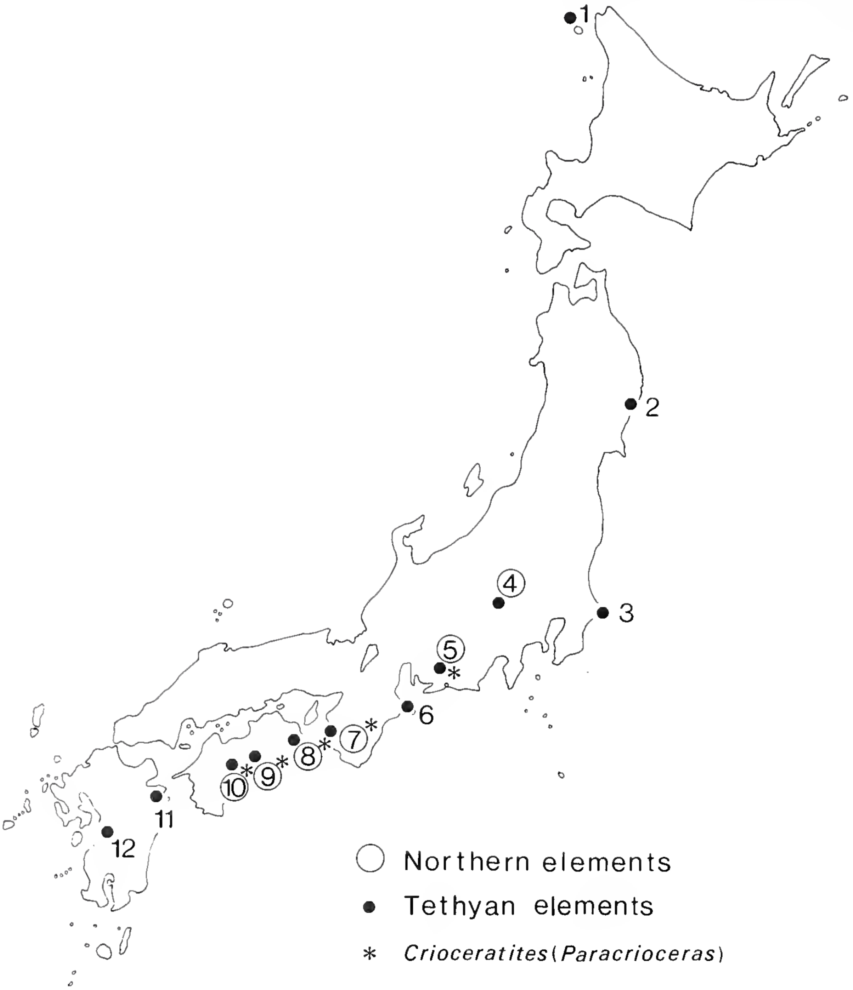
All localities mentioned in the text are shown in Text-figure 1. Below we give brief stratigraphical information on all those from which we have examined specimens.

*Idaira*: Akasaka, Inasa-cho, Inasa-county, Shizuoka Prefecture (locality 5 in Text-fig. 1). This locality was discovered by Hayashi *et al.* (1981), but ammonite species were not identified by them. Recent collecting from the brown mudstone in the lower part of the Idaira Formation has yielded the ammonites *Crioceratites* (*Paracrioceras*) *asiaticum* and *Shasticrioceras nipponicum*.

*Arida*: Yuasa, Yuasa-cho, Arida-county, Wakayama Prefecture (locality 7 in Text-fig. 1). This is the type area of the Arida Series in Japan (approximately corresponding to Barremian). The lithostratigraphy and biostratigraphy of this area were reviewed by Obata and Ogawa (1976), and ammonites from this area were figured by Matsumoto (1947) and Obata and Ogawa (1976).

*Katsuuragawa*: Nakagoya, Katsuura-cho, Katsuura-county, Tokushima Prefecture (locality 8 in Text-fig. 1). The littoral to shallow neritic facies of the Hanoura Formation consists of muddy sandstone which yielded the ammonites figured by Matsukawa and Eto (1987).

**[Palaeontology, Vol. 36, Part 2, 1993, pp. 249–266, 3 pls.]**



TEXT-FIG. 1. Occurrences of Barremian ammonites in Japan. Key to localities: 1, Rebun; 2, Kitakami; 3, Choshi; 4, Sanchu; 5, Idaira; 6, Shima; 7, Arida; 8, Katsuuragawa; 9, Monobe-Ryoseki; 10, Kochi; 11, Ohita; 12, Yatsushiro.

*Monobegawa*: Yunoki, Kahoku-cho, Kami-county, Kochi Prefecture (locality 9 in Text-fig. 1). The deltaic facies of the Ryoseki Formation consists of muddy sandstone containing the ammonite *Shasticrioceras patricki*.

For descriptions of the localities yielding these specimens see Matsumoto (1947), Obata and Ogawa (1976), Hayashi *et al.* (1981) and Matsukawa and Eto (1987).

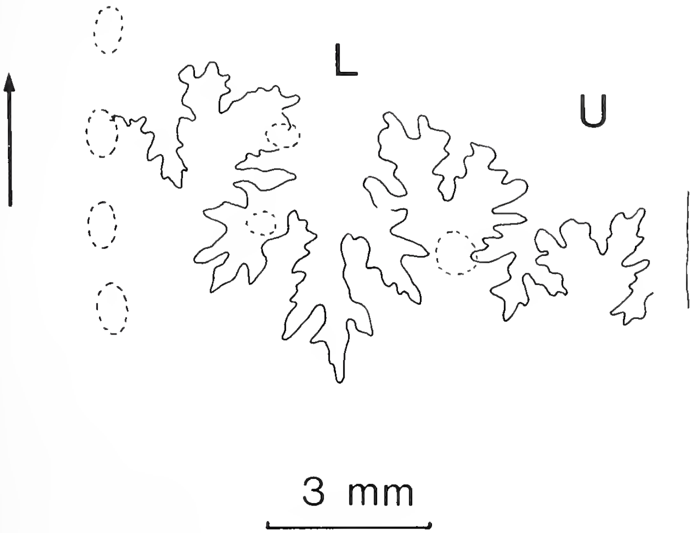
*Repositories*. Material has been examined from the following collections (abbreviations used in the text are shown in parenthesis): National Science Museum, Tokyo (NSM-PM); Department of Earth Sciences, Faculty of Science, Ehime University, Matsuyama (EE-AM); Collection of Mizuno Fossil Museum, Nagoya (YM).

## SYSTEMATIC PALAEONTOLOGY

Order AMMONOIDEA Zittel, 1884
Suborder ANCYLOCERATINA Wiedmann, 1966
Superfamily ANCYLOCERATACEA Gill, 1871
Family ANCYLOCERATIDAE Gill, 1871
Genus CRIOCERATITES Léveillé, 1837
Subgenus PARACRIOCERAS Spath, 1924

*Type species. Ammonites* (*Crioceras*) *occultum* Seeley, 1865, from the middle Barremian of England (subsequent designation by Rawson 1975).

*Remarks.* Differing opinions have been presented concerning the taxonomic status of *Paracrioceras*. Based on the arguments of Rawson (1975), who regarded *Emericiceras* as a junior subjective synonym of *Paracrioceras*, Kemper *et al.* (1981) proposed that *Paracrioceras* is a subgenus of *Crioceratites*. On the other hand, Immel (1978) concluded that *Paracrioceras* is better considered as a synonym of the subgenus *Crioceratites* (*Crioceratites*). This latter interpretation is based on the minor morphological differences which exist between the type species of *Paracrioceras*, *Emericiceras* and *Crioceratites*.



TEXT-FIG. 2. Suture line of *Crioceratites* (*Paracrioceras*) *asiaticum* (Matsumoto). External suture, the fifth last suture of TI-1; locality 2505, Kumaiguchi in the Yuasa area (see Pl. 1, fig. 1).

As far as the Japanese Barremian material is concerned, *Crioceratites* (*Paracrioceras*) *asiaticum* Matsumoto (described below) is characterized by trituberculate major ribs in the mature stage, whereas *Crioceratites* (*Emericiceras*) *emerici* Léveillé has minor ribs lacking tubercles. The characters of both species are considered to satisfy at least the generic definition of *Crioceratites*. Under such circumstances, the authors are inclined to follow the classification of Kemper *et al.* (1981).

### *Crioceratites* (*Paracrioceras*) *asiaticum* (Matsumoto, 1947)

Plate 1, figs 1–17; Plate 2, figs 3–5; Text-fig. 2

1947 *Australiceras asiaticum* Matsumoto, p. 13, pl. 1, fig. 1; text-fig. 1.
1976 *Paracrioceras* aff. *elegans* (Koenen); Obata and Ogawa, pl. 1, figs 2, 4; text-figs 6–2, 7.

*Material.* Lectotype: GK.H8301, chosen here, the original of Matsumoto (1947, pl. 1, fig. 1), from the Arida Formation at locality YU-103, Yuasa-Fujinami in the Yuasa area (T. Matsumoto Colln). Paralectotypes: GK.H8311 and GK.H8312 from the same formation and locality (T. Matsumoto Colln). GK.H8302 from the same formation at locality Ys-8, Yuasa-Suhara, in the Yuasa area (T. Matsumoto Colln). GK.H8303 from the same formation at locality Yu-5, Yuasa town, in the same area (Aiba, Kutsuna and Matsumoto Colln). NSM-PM 7447, a slightly deformed specimen from the same formation at locality 1703, Suhara in the Yuasa area (Y. Ogawa Colln). NSM-PM 7449 from the Arida Formation but probably derived from locality 2505, Kumaiguchi in the Yuasa area (T. Ishibashi Colln). NSM-PM 7629 (locality 1703), NSM-PM 7640 (locality 1703), NSM-PM 7632 (locality 1405), NSM-PM 7633 (locality 1703) and NSM-PM 7634 (locality 1403), all from the Arida Formation at Suhara in the Yuasa area (Y. Igawa Colln). NSM-PM 7638 and NSM-PM 7639, plaster casts of YM-1001 and YM-1002 respectively, from locality 2505 of the Arida Formation at Kumaiguchi in the Yuasa area (Y. Mizuno Colln). YM-1003 (locality 1507) of the Arida Formation at Suharazaka in the Yuasa area (Y. Mizuno Colln). EE-AM 1001, from the upper part of the Hanoura Formation at locality 4052, Nakagoya in the Katsuuragawa area (F. Eto Colln). NSM-PM 7641 from the lower part of the Idaira Formation at locality 03, Akasaka in the Idaira area (T. Komatsu Colln).

*Diagnosis.* Whorls compressed, subquadrangular to subhexagonal in section, with flattened dorsum and venter. Umbilical bullae, lateral and ventro-lateral spines present from middle stage on major ribs. Lateral spines are located at one-half to two-thirds the distance from umbilical shoulder to venter. A few minor and shorter ribs with weak tubercles or non-tubercles are intercalated between major ribs.

*Description.* The shell is of medium size, less than 60 mm in diameter in most specimens, but one specimen (YM-1003) is very large, about 340 mm in diameter. The whorl is crioceratid with tightly coiled early stage (e.g. in NSM-PM 7447 less than 17·1 mm in diameter, in NSM-PM 7449 less than 9·6 mm in diameter) and loosely coiled later stage. The whorl section is subquadrangular to subhexagonal and fastigate with narrow and flat venter, becoming high and more compressed with growth. Flanks are almost flat in the central region and gently convergent towards the ventro-lateral shoulder from a point at about one-half to two-thirds the distance from the umbilical margin. The ventro-lateral shoulder is rather subangular. The whorls are ornamented with tuberculate major ribs and generally non-tuberculate minor ones. The ribs number 55 per whorl on NSM-PM 7449 (43 mm in maximum diameter of loosely coiled whorls).

Four stages are recognized in the morphologic development of *C.* (*P.*) *asiaticum*:

1. *Early growth, less than 9·6 mm.* Whorls tightly coiled and almost completely covered with fine ribbing only.
2. *9·6–14·5 mm.* Whorls have only trituberculate major ribs. The tubercles are the site of ventro-lateral and lateral spines and umbilical bullae.
3. *Later growth, 14·5–270 mm.* Whorls consist of trituberculate major ribs characterized by ventro-lateral and lateral spines and umbilical bullae, with a few intercalated, non-tuberculate minor ribs.
4. *Latest growth, greater than 270 mm.* Whorls have only trituberculate major ribs, separated by narrow interspaces of the same width or half as wide as the ribs. The major ribs are radial, strong and broad, forming a triangle in section. They spring from the umbilical margin and continue over the venter where they decrease

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EXPLANATION OF PLATE 1

Figs 1–17. *Crioceratites* (*Paracrioceras*) *asiaticum* (Matsumoto). 1–16, Lower Barremian, upper part of the Arida Formation. 1, NSM-PM 7449; locality 2505; lateral view, × 1·3. 2, NSM-PM 7447; locality 1703; lateral view, × 1·3. 3, YM-1001; locality 2505; lateral view, × 1. 4, YM-1002; locality 2505; lateral view, × 1. 5, NSM-PM 7632; locality 1405; lateral view, × 1·0. 6, NSM-PM 7623; locality 1711; lateral view, × 1·2. 7, NSM-PM 7633; locality 1703; lateral view, × 1·0. 8–11, NSM-PM 7629; locality 1703; lateral (8, 10), ventral (9) and front (11) views, × 1·2. 12, NSM-PM 7624; locality 1403; lateral view, × 1·2. 13, NSM-PM 7634; locality 1403; lateral view, × 1·0. 14–16, YM-1003; locality 1507; front (14) and lateral (15, 16) views, × 0·5, × 0·3, × 0·2 respectively. 17, EE-AM 1001; Lower Barremian, upper part of the Hanoura Formation; locality 4052; lateral view, × 1·2.

PLATE 1


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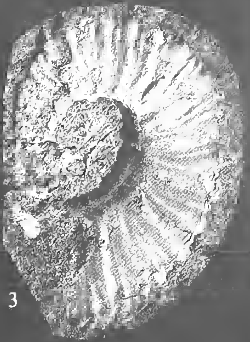
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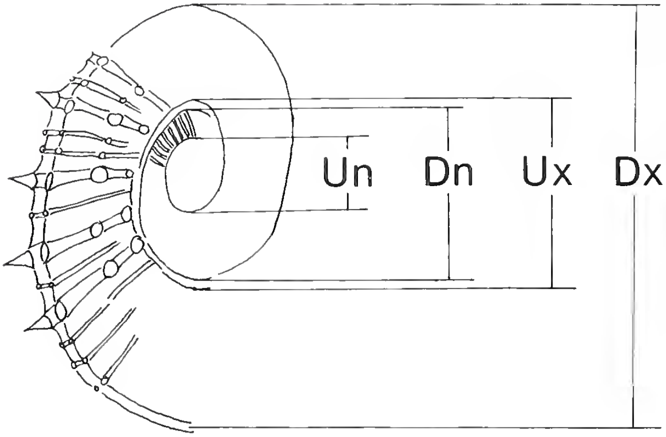
MATSUKAWA and OBATA, *Crioceratites*

in strength. The minor ribs are fine and narrow, originating at the umbilical margin or at mid-flank, and continuing over the venter where they decrease in strength. The tubercles are the sites of stout and cone-like ventro-lateral and lateral spines and umbilical bullae. Two rows of lateral spines are found, in the ventral and the umbilical regions, but change their position with growth; the lateral spines near the ventral side are located at one-half to two-thirds the distance from the umbilical shoulder, whereas the lateral spines near the umbilical side are at one-quarter to one-sixth the distance. The dorsum is flat and without ornamentation. The suture line consists of the elements of E, L, U, and I (see Text-fig. 2). The ventral saddle is bifid and slightly asymmetric. Lateral lobe (L) is deep, showing symmetrically trifid lobules. Umbilical lobe (U) is smaller than lateral ones. The first lateral saddle is as broad as the second lateral one, but the third one is rather narrow.



TEXT-FIG. 3. Dimensions measured on shells of *Crioceratites* (*Paracrioceras*) *asiaticum* (Matsumoto). Dx, diameter of loose spire; Ux, maximum umbilical gap; Dn, maximum diameter of tight spire; Un, umbilicus of tight spire.

*Measurements*. (in mm; see Text-fig. 3 for explanation of symbols used).

| | Dn | Dx | H | B | B/H | Un | Ux |
|---|---|---|---|---|---|---|---|
| Gk.H8301 (lectotype) | 15·9 | | 6·4 | 4·5 | 0·70 | 5·7 | |
| | | 26·5 | 11·6 | | | | 9·5 (0·36) |
| MSM-PM 7447 | 42·1 | | | | | 16·6 (0·39) | |
| | | 50·0 | 18·7 | | | | 21·3 (0·43) |
| NSM-PM 7449 | 32·8 | | 15·4 | | | 9·6 (0·29) | |
| | | 37·5 | 17·6 | | | | 12·5 (0·33) |
| NSM-PM 7638 | | | 39·3 | 15·0 | | | 13·5 (0·34) |
| NSM-PM 7640 | | | | 91·7 | 34·5 | 0·38 | |

*Comparisons*. The present species is closely similar to *Paracrioceras elegans* (Koenen 1902, p. 295, pl. 24, figs 1–3; pl. 29, fig. 3) from the Barremian of the Hoheneggelsen, near Hannover, Germany, in the nature of its coiling, its narrow flat venter and unornamented flat dorsum, and the alternating trituberculate major ribs and fine minor ones. The whorl section of the latter is, however, more rounded or oval at middle to late stage than *C.* (*P.*) *asiaticum*. Furthermore, the lateral spines near the ventral side are situated at one-half to two-thirds the distance from the umbilical shoulder on later growth stage of *C.* (*P.*) *asiaticum*, whereas in *C.* (*P.*) *asiaticum* they are located three-quarters the distance from the umbilical shoulder.

*C.* (*P.*) *asiaticum* is also distinct from *Paracrioceras occultum* (Seeley), the type species of the genus (Rawson 1975, p. 275. text-fig. 1; pl. 43, figs 1–6). In *P. occultum* the ribs are almost all equal in strength and the lateral tubercles disappear at the late growth stage, whereas in *C.* (*P.*) *asiaticum* the ribbing includes both major and minor ribs, with the major ribs exhibiting three tubercles through the middle to late growth stages.

The present species is readily distinguished from *Crioceratites* (*C.*) *ishiwarai* (Yabe and Shimizu), described as *Crioceras ishiwarai* by Yabe and Shimizu (1926, p. 85, text-figs 1–2; pl. 4) from the Oshima Formation of northeast Japan. In the latter species, the shell consists of tightly coiled whorls showing five to eight minor ribs intercalated between major ribs in the adult stage. In *C.* (*P.*) *asiaticum*, the shell exhibits loosely coiled whorls at later stages, and only a few minor, shorter ribs are intercalated between major ones.

*Crioceras yagii* Yabe and Shimizu (1926, p. 72, pl. 15, figs 16–19), from the Ishido Formation of central Japan, differs from the present species in having a subcircular whorl section, three to six minor ribs between major ribs, and three long spines on each major rib.

*Occurrence.* Lower Barremian. Upper Arida Formation, upper Hanoura Formation and lower Idaira Formation.

## Genus SHASTICRIOCERAS Anderson, 1938

*Type species. Shasticrioceras poniente* Anderson, 1938, from Barremian deposits of California (subsequent designation by Arkell *et al.*, 1957, p. L208).

### *Shasticrioceras nipponicum* Matsumoto, 1947

Plate 2, figs 1–2, 6–7; Plate 3, figs 1–14

1947 *Shasticrioceras nipponicum* Matsumoto, p. 19, pl. 1, fig. 3; text-fig. 2.
1976 *Shasticrioceras nipponicum* Matsumoto; Obata and Ogawa, pl. 1, fig. 1; pl. 4, fig. 6; text-fig. 6–1.

*Material.* Lectotype: GK.H8305, chosen here, the original of Matsumoto (1947, pl. 1, fig. 3), from the Arida Formation at Yu-103, Yuasa-Fujinami in the Yuasa area (T. Matsumoto Colln). Paralectotypes: GK.H8306, H8307 and H8313 from the same formation and locality (T. Matsumoto Colln). Other specimens include NSM-PM 7635, NSM-PM 7636 and YM-1004, all from the Arida Formation at locality 1711, Yada in the Yuasa area (NSM-PM 7635 was collected by Y. Ogawa, NSM-PM 7635 by Y. Kotake and YM-1004 by Y. Mizuno). NSM-PM 7637 and NSM-PM 7444, casts and moulds, from the Arida Formation at locality 2505, Kumaiguchi in the Yuasa area (Y. Ogawa and S. Higashiyama Colln). EE-AM 1002, casts and moulds, from the upper part of the Hanoura Formation at locality 4052, Nakagoya in the Katsuuragawa area (F. Eto and M. Matsukawa Colln). NSM-PM 7700, from the lower part of the Idaira Formation at locality 03, Akasaka in the Idaira area (T. Komatsu, T. Kitamura and M. Matsukawa Colln).

*Diganosis.* A compressed and loosely coiled species of *Shasticrioceras* with radial or slightly sinuous ribs, on which strongly pronounced clavate tubercules present. Ribs arise between umbilical margin and mid-flank, cross flank to ventral shoulder, but are interrupted on venter.

*Description.* The shell is of medium size, less than *c.* 140 mm in diameter, and the whorl is slightly uncoiled. The whorl section is compressed planulate, oblong and somewhat swollen at mid-flank and gradually convergent towards the venter. The venter is rather narrow in comparison with the dorsum and both are flat. Flanks are ornamented with radial to slightly sinuous major ribs and intercalated straight or branching minor ones. The ribs are sharpened near the venter, forming a nearly triangular ridge separated by narrow interspaces. Most ribs start at the umbilical margin but some of the minor ribs arise at mid-flank; all reach to the ventral shoulder and exhibit the ventro-lateral clavi, being interrupted on the venter. Umbilical bullae are found only on the major ribs. In the inner whorls of the early growth-stage (e.g. in NSM-PM 7635, about 30 mm in diameter) the ribs are rather rectiradiate and uniform in strength. In contrast, the outer volution of the middle to late growth-stage (e.g. in NSM-PM 7635, more than 30 mm in diameter, and in YM-1004, more than 35 mm in diameter) exhibits ribbing consisting of stout major and somewhat weaker minor ribs, often quite similar in appearance and often difficult to distinguish. The minor ribs, however, arise higher on the flanks than the major ones.

*Measurements*. (in mm; see Text-fig. 3 for explanation of the symbols used).

| | Dx | H | B | B/H | Ux | Ux/Dx |
|---|---|---|---|---|---|---|
| GK.H8305 (lectotype) | 22·7 | 10·6 | 5·6 | 0·53 | 8·3 | 0·37 |
| NSM-PM 7635 | 67·6 | 31·5 | | | 17·9 | 0·26 |
| NSM-PM 7444 | | 33·4 | | | | |
| NSM-PM 7636 | 45·7 | 20·2 | | | 13·8 | 0·30 |
| YM-1004 | 133·1 | 51·9 | | | 47·4 | 0·36 |

*Comparisons*. The present species is distinct from *Shasticrioceras* sp. aff. *S. patricki* Murphy (Obata and Matsukawa 1984, p. 18, pl. 5, fig. 2; pl. 6, fig. 2) from the Barremian of the Ishido Formation. In *S. nipponicum*, the venter is narrow, the clavate tubercles at the ventral shoulder are more strongly pronounced, and the ribs are coarser and more frequently branched at the umbilical margin. In contrast, *S.* sp. aff. *S. patricki* shows a broader venter, weaker clavi, and more numerous and crowded ribs.

*Shasticrioceras poniente*, the type species of the genus from the upper part of the Lower Barremian of California, described by Anderson (1938, p. 204, pl. 57, figs 1–3; pl. 67, figs 4–5) and Murphy (1975, p. 41, pl. 10, figs 1–2, 6; pl. 11, figs 5, 7), somewhat resembles the present species in its tightly coiled crioceratid whorl and in its branching or intercalated ribbing. *S. poniente* can be distinguished from *S. nipponicum*, however, by its continuous ribs which are sigmoidal and biconcave in adult stage, and rounded on the lower half of the flank.

*Occurrence*. Lower Barremian. Middle Arida Formation, upper Hanoura Formation and lower Idaira Formation.

### *Shasticrioceras patricki* Murphy, 1975

Plate 2, figs 8–9; Text-fig. 4

1975 *Shasticrioceras patricki* Murphy, p. 46, text-fig. 26; pl. 7, figs 1–2; pl. 10, figs 3–5; pl. 13, fig. 4.

*Material*. EE-AM 1003, from the Monobe Member of the Ryoseki Formation at locality R2, Yunoki in the Monobegawa area, Kochi Prefecture (T. Okada and M. Matsukawa Colln).

*Description*. The shell is large, about 110 mm in diameter. The whorl is crioceratid and loosely coiled below about 62 mm in diameter. The whorl-section is compressed, planulate and oblong with more-or-less swollen flanks which are gently convergent toward the venter from a point at about three-quarters of the distance from the umbilical margin. The ventro-lateral shoulder is rather subangular and the venter is narrow and flat. Flanks

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### EXPLANATION OF PLATE 2

Figs 1–2, 6–7. *Shasticrioceras nipponicum* Matsumoto. 1–2, NSM-PM 7700; Lower Barremian, lower part of the Idaira Formation; locality 03; internal mould (1) and external mould (2); lateral views, × 1·2. 6–7, GK H8305, lectotype; Lower Barremian, upper part of the Arida Formation; locality Yu-103; ventral (6) and lateral (7) views, × 1·2.

Figs 3–5. *Crioceratites* (*Paracrioceras*) *asiaticum* (Matsumoto). 3, NSM-PM 7449; Lower Barremian, lower part of the Idaira Formation; locality 03; lateral view, × 0·8. 4–5, GK H8301; lectotype; Lower Barremian, upper part of the Arida Formation; locality Yu-103; ventral (4) and lateral (5) views, × 1·2.

Figs 8–9. *Shasticrioceras patricki* Murphy. EE-AM 1003; Lower Barremian, Monobe Member of the Ryoseki Formation; locality R2; ventral (8) and lateral (9) views, × 0·8.

PLATE 2


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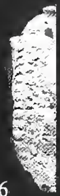
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MATSUKAWA and OBATA, *Shasticrioceras*, *Crioceratites* are ornamented with straight and coarse ribs in early growth-stages (less than *c.* 27·6 mm in diameter), which become biconcave and finer in later stages (more than *c.* 34·8 mm in diameter). Most of the ribs originate at the umbilical margin and cross the venter in a straight line; some of them arise on the flank or bifurcate at about three-quarters of the distance from the umbilical margin. Ribs are sharpened at the top, forming a nearly triangular ridge in cross-section, and are separated by interspaces of equal width. A small pointed clavus is found on each rib at the periphery of the venter. The suture line is not completely preserved but shows trifid lobes (see Text-fig. 4). The saddles are broader than the lobes and show an asymmetrically divided top. Ventral lobe (E) is shallow. Lateral lobe (L) is narrow and deep, showing subsymmetrically trifid lobules. The umbilical lobe (U) is broadest, but is rather shallow.

*Measurements.* (in mm; see Text-fig. 3 for explanation of the symbols used).

| | Dx | Dn | H | Ux | Un |
|---|---|---|---|---|---|
| EE-AM 1003 | *c.* 110·0 | | 40·0 | *c.* 64·0 | |
| | | *c.* 27·6 | 7·4 | | *c.* 20·2 |

*Remarks.* The shell is considered to be discoidal with successive whorls just in contact with each other. The present specimen is closely similar to the illustrated specimens of *Shasticrioceras patricki* Murphy, 1975 (pl. 7, figs 1–2; pl. 10, figs 3–5), from the upper part of the Lower Barremian of California. Japanese and Californian specimens show a similar shell form with fine, biconcave ribs most of which traverse the entire flank, rarely arising or branching on the flank, and possessing a small clavus at the ventral shoulder.

The present specimen is different from the specimen of *S.* sp. aff. *S. patricki* Murphy (Obata and Matsukawa 1984, pl. 5, fig. 2; pl. 6, fig. 2) from the Lower Barremian of the Sanchu area, Japan. The latter specimen exhibits nearly radial, straight ribs which are rather fine in early growth-stages and gradually increase in coarseness with growth. *S. patricki* possesses straight ribs which are rather coarse in the early growth-stage, becoming fine and biconcave in the later stage.

*Shasticrioceras nipponicum* Matsumoto has some similarity to the present species in the general features of shell form and ornamentation, but differs in its remarkable clavate tubercles and coarse ribs which are frequently branched at the umbilical margin.

*Occurrence.* Lower Barremian, Monobe Member of the Ryoseki Formation.

### *Shasticrioceras intermedium* sp. nov.

*Derivation of name.* The present species has lateral tubercles on the major ribs although other species of the *Shasticrioceras* do not have them. Therefore, the species possesses generic characters of both *Shasticrioceras* and *Paracrioceras*.

Text-fig. 5

1976 *Shasticrioceras* sp. Obata and Ogawa, pl. 1, fig. 5.

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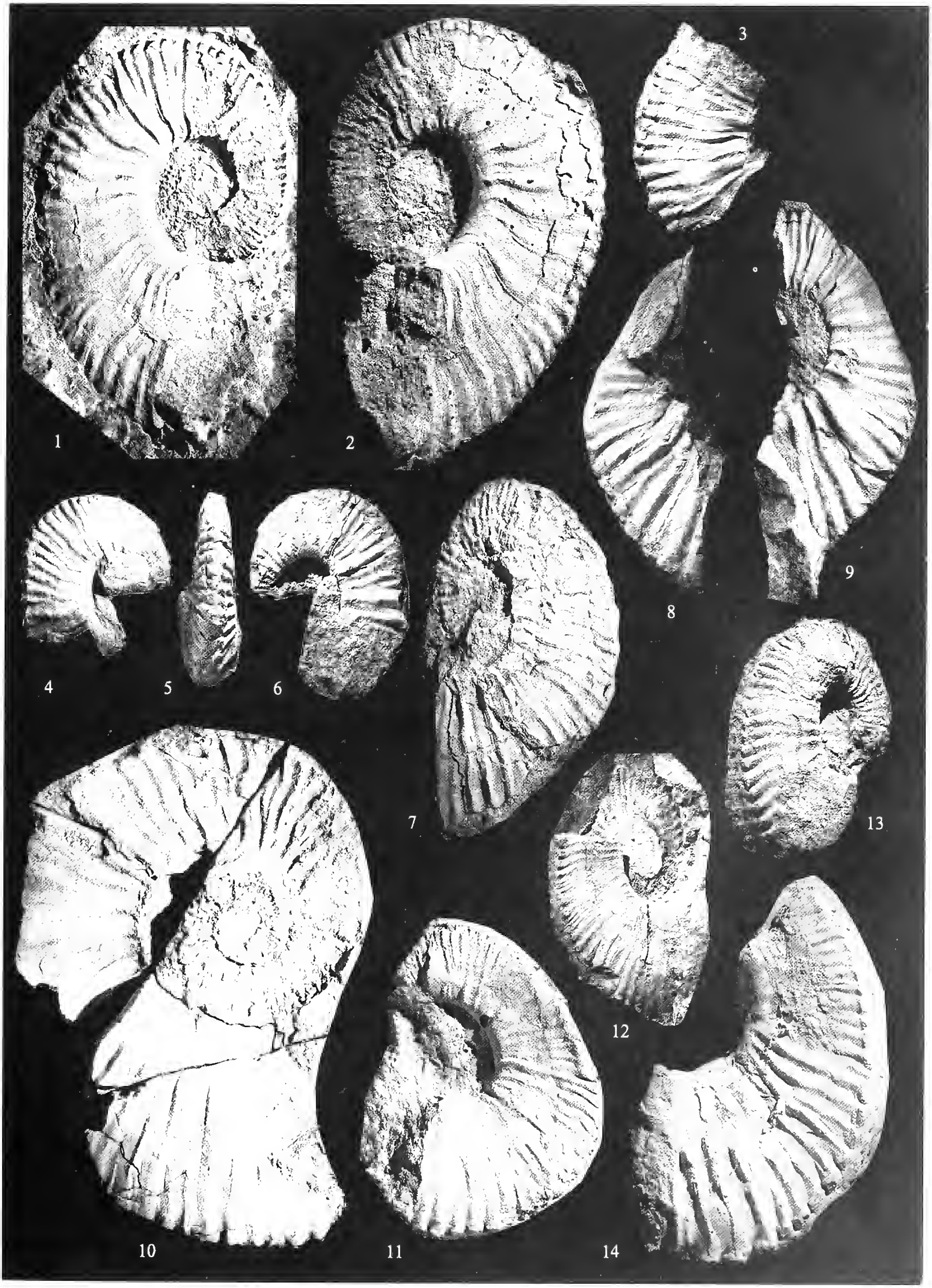
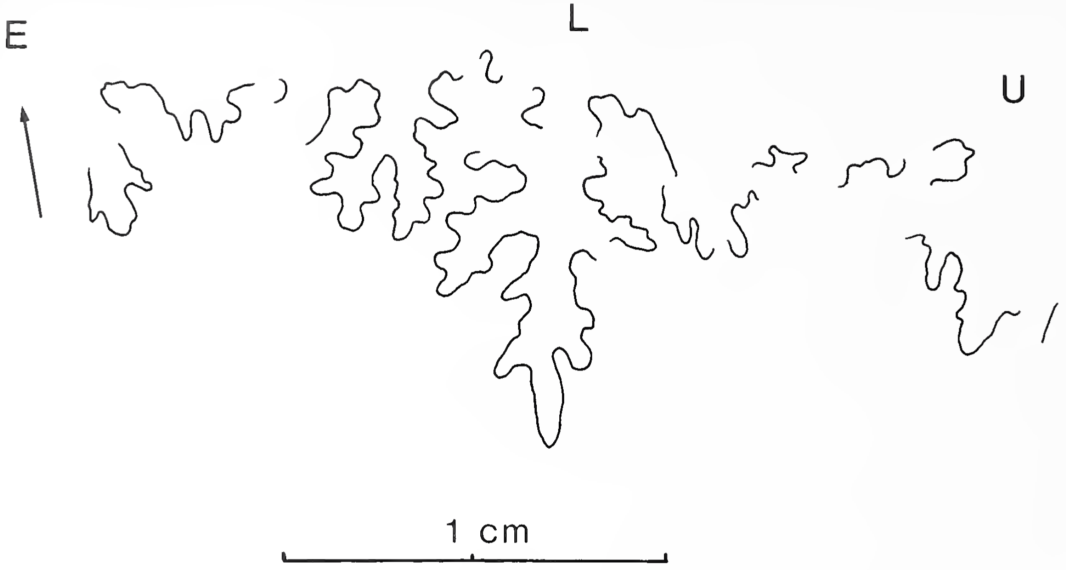
### EXPLANATION OF PLATE 3

Figs 1–14. *Shasticrioceras nipponicum* Matsumoto. 1–6, 8–14, Lower Barremian, upper part of the Arida Formation. 1–2, NSM-PM 7635; locality 1711; internal mould (1) and rubber cast from the same external mould (2); lateral views, × 1. 3, NSM-PM 7625; locality 1703; lateral view, × 1. 4–6, NSM-PM 7626; locality 2505; lateral (4 and 6) and ventral (5) views, × 1·2. 8–9, NSM-PM 7637; locality 2505; lateral views, × 1·2. 10, YM-1004; locality 1711; lateral view, × 0·6. 11, NSM-PM 7627; locality 1711; lateral view, × 1. 12, NSM-PM 7628; locality 1919; lateral view, × 1·2. 13, NSM-PM 7636; locality 1711; lateral view, × 1. 14, NSM-PM 7444; locality 2505; lateral view, × 0·8. 7, EE-AM 1002; Lower Barremian, upper part of the Hanoura Formation; locality 4052; lateral view, × 1·2.

PLATE 3



MATSUKAWA and OBATA, *Shasticrioceras*



TEXT-FIG. 4. Suture line of *Shasticrioceras patricki* Murphy. External suture, the second last suture of EE-AM 1003; locality R2, Yunoki, Monobegawa area (see Pl. 2, fig. 5).

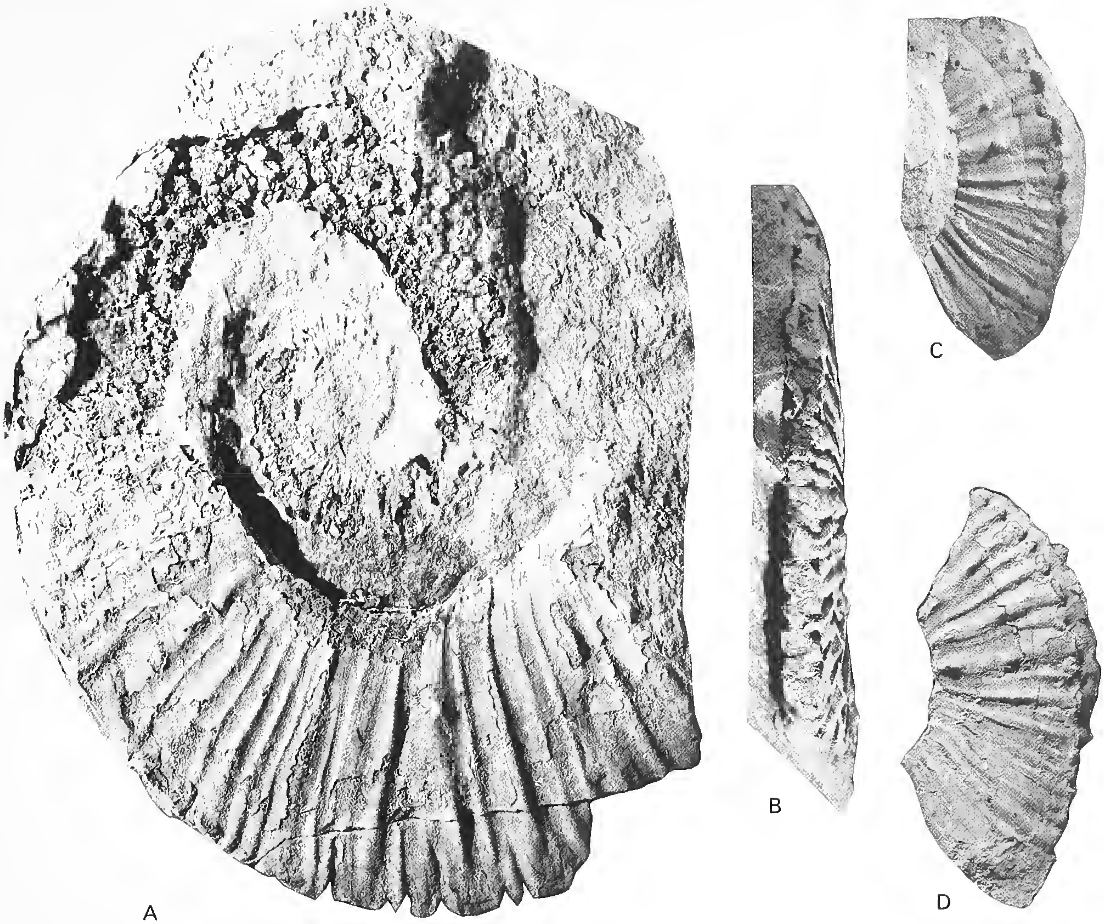
*Material.* Holotype: NSM-PM 7446. Paratypes: NSM-PM 7630 and NSM-PM 7631. All from locality 1405 in the Arida Formation (Y. Ogawa Colln).

*Diagnosis.* Very compressed species of *Shasticrioceras* with one, two, or three tubercles on major ribs in the adult stage.

*Description.* The shell attains large size (120 mm in maximum diameter). The whorl is of ancyloceratid type with an openly coiled whorl even at the early growth-stage (e.g. in NSM-PM 7446, less than 18 mm in diameter). The whorl section is compressed, planulate, and oblong with slightly flattened flanks and flattened venter. The ventro-lateral shoulder is angular, but the dorsal shoulder is rather rounded. The whorl is ornamented with numerous nearly radial, but very slightly sinuous, ribs which are sometimes tuberculated. Ribs arise at the umbilical margin and become weaker on the venter. Both major and minor ribs are present, but sometimes it is difficult to distinguish between them. In early growth-stages the ribs are crowded and equal to the interspaces in width. They gradually increase in coarseness and become one-third as wide as the interspaces in the adult growth-stage. Mono- to trituberculate major ribs appear irregularly at the latest stage. Distinctly clavate tubercles are found on the periphery of the venter of the major ribs and umbilical bullae and lateral spines are weak. The top of each clavus is rather flattened. The suture line is unknown.

*Measurements.* (in mm; see Text-fig. 3 for explanation of the symbols used).

| | Dx | H | B | B/H | Ux |
|---|---|---|---|---|---|
| NSM-PM 7446 (holotype) | 195+ | 27+ | 11·1 | 0·41 | 54·3 |
| NSM-PM 7630 | | 14·6 | 4·1 | 0·28 | |
| NSM-PM 7631 | | 17·4 | 6·0+ | 0·34+ | |



TEXT-FIG. 5. *Shasticrioceras intermedium* sp. nov., Lower Barremian, upper part of the Arida Formation. A–B, NSM-PM 7446; holotype; locality 1405; lateral and ventral views, respectively, × 1. C, NSM-PM 7630; paratype; locality 1405; lateral view, × 1·2. D, NSM-PM 7631; paratype; locality 1405; lateral view, × 1·3.

*Comparisons.* The present species is closely related to *Shasticrioceras nipponicum* Matsumoto in having a planulate and oblong whorl section, flat venter, and major and minor ribs which are interrupted on the venter and show ventro-lateral clavi. The two species are distinguished by the presence of one, two or three lateral tubercles on the major ribs of *S. intermedium*.

*Shasticrioceras poniente* Anderson, the type species of *Shasticrioceras*, from the upper part of the Lower Barremian of California, has a much more swollen whorl than the present species. The ribs of *S. poniente* are continuous around the whorl, but on *S. intermedium* are interrupted on the venter. Furthermore, some major ribs in the latter have lateral tubercles.

*Remarks.* The presence of lateral tubercles on the major ribs of *S. intermedium* might lead to a revised definition for the genus *Shasticrioceras*.

*Occurrence.* Lower Barremian. Arida Formation, Arida area.

## DISCUSSION

### *Palaeogeography*

Barremian ammonite faunas in Japan contain northern, high latitude elements including Boreal *Simbirskites* (*Milanowskia*), northwest European *Crioceratites* (*Paracrioceras*) and northern Pacific *Shasticrioceras*. The distribution of these ammonites in Japan has been explained by the presumed marine connections during a transgressive period (Matsukawa 1988; Obata and Matsukawa 1988). It is worthy of note that these northern ammonites, accompanied by Tethyan ones, are found at several localities in southwest Japan but not in northeast Japan (see Text-fig. 1). This is in contrast to the segregated northern and Tethyan ammonite faunas which are found in northern and southern localities, respectively, in the southern Caucasus and Crimea (Kakabadze 1981).

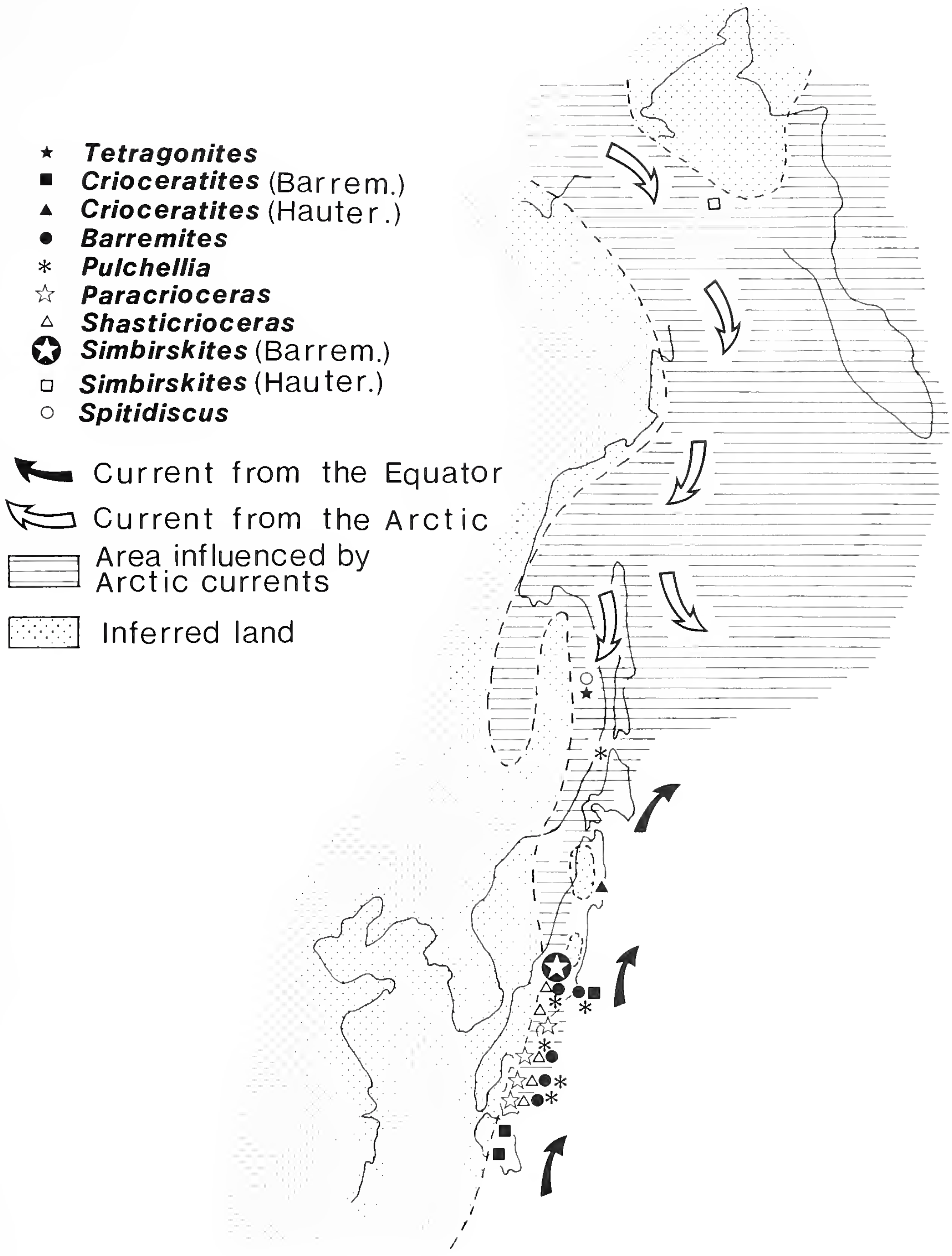
The presumed palaeocurrent directions (Obata and Matsukawa 1988) and palaeogeography of Japan during Barremian time provide an explanation. Oceanic circulation patterns are useful in explaining the global distribution of some Tethyan and Boreal ammonites in Barremian time (Obata and Matsukawa 1988). A warm current presumably passed northward from the equator, turning to the east near the position of present-day Hokkaido, whereas a cool current was directed southward from the Arctic, turning west by Coriolis force to reach near Kyushu. If northeast Japan was part of the eastern margin of the Asiatic continent, the area must have been influenced by the Arctic current. However, only Tethyan ammonites have been found in northeast Japan. As an explanation of the problem, a seaway for the cool current from the Arctic is considered to have existed between northeast Japan and the Asiatic continent. This seaway makes it possible to explain the occurrence of northern ammonites only in southwest Japan (see Text-fig. 6). In southern Sikhote-Alin, northwest European and Tethyan ammonites, including *Spitidiscus* sp. aff. *S. rotula*, have been reported from the Barremian, and Boreal bivalves, including *Aucella crassicolis*, *A. volgensis* and *A. okensis*, from the Valanginian (Avdeiko 1968). This occurrence suggests that both Equatorial and Arctic currents reached Sihotaryn during the Barremian. The southward current probably occurred at a greater depth as an undercurrent because the Arctic Ocean consisted of cool waters (e.g. Jeletzky 1971). This concurs with the common heteromorphs in the northern faunas from Japan because they are interpreted to have had a benthic mode of life (e.g. Klinger 1980). The occurrence of only one specimen of *Pulchellia*, a characteristic Tethyan genus, from Rebun in the northern part of northeast Japan, probably suggests that the current from the Equator reached northward at least that far.

*Shasticrioceras patricki* Murphy is found in middle Barremian strata of both California and Japan. This species is interpreted to have been carried to these widely separated areas by currents from the Arctic, or to have been a migrant via high latitudes from Japan to California, or vice-versa. Some species of the genus *Shasticrioceras* from Barremian strata of Arctic Canada were also likely to have been immigrants from the northern Pacific Ocean (Text-fig. 7). The occurrence of *S. bifurcatus* Dimitrova in the Barremian of Bulgaria (Dimitrova 1967) might support the hypothesis that the genus was derived from a Tethyan ancestor because *Shasticrioceras* is not known to occur between the Bulgarian and northern Pacific areas and where non-marine facies occur.

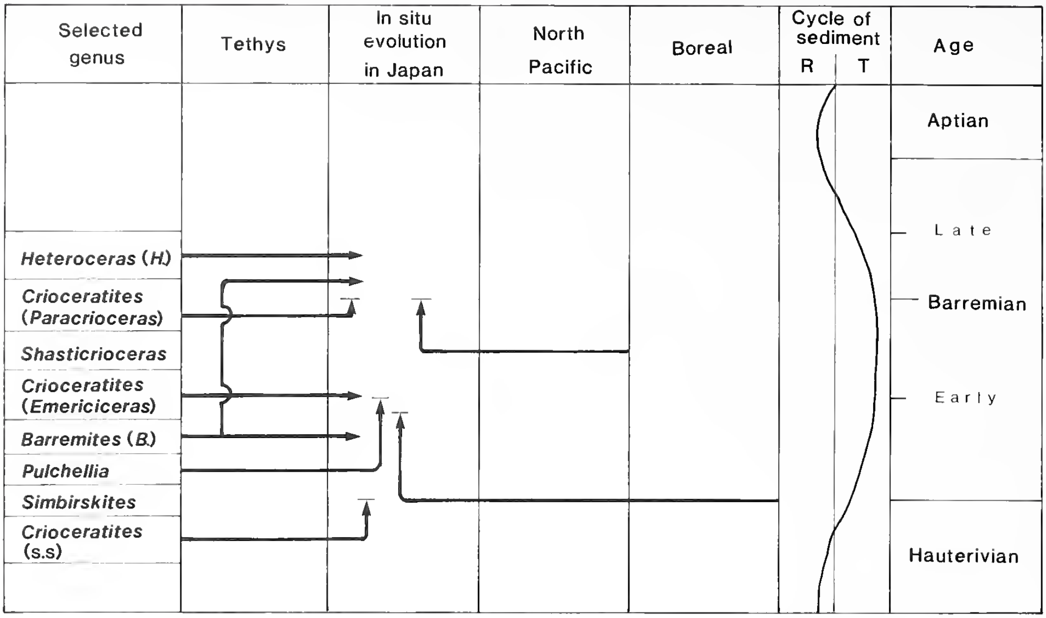
### *Evolution of* Crioceratites *in Japan*

Three species of *Crioceratites*, *C.* (*C.*) *ishiwarai*, *C.* (*E.*) *emerici* and *C.* (*Paracrioceras*) *asiaticum*, are known to occur in statigraphical order in the mid-Hauterivian to early Barremian of Japan.

*C.* (*C.*) *ishiwarai* from the middle Hauterivian, allied to *C.* (*C.*) *nolani* or *C.* (*C.*) *duvali* of Europe, is characterized by having a tightly coiled whorl, trituberculate major ribs with five to eight minor ribs between them in the adult stage, and by a tendency to bifurcation of ribs near the ventral border (Yabe and Shimizu 1926). *C.* (*E.*) *emerici* from the Japanese lower Barremian is characterized by loose coiling, trituberculate major ribs and four continuous minor ribs between major ribs in the adult stage. *C.* (*P.*) *asiaticum* is distinguished by having tight to loose coiling as the shell grows, trituberculate major ribs and one to two minor ribs between major ribs in the adult stage.



TEXT-FIG. 6. Distribution of some Barremian ammonite genera and the presumed palaeogeography and palaeocurrents around Japan.



TEXT-FIG. 7. Origin of some Barremian and Hauterivian ammonite species from Japan.

Examining the Japanese material in its stratigraphical context, it is seen that the whorl changes successively from tightly coiled to loosely coiled, and back again to tightly coiled. Ribs consist of trituberculate major ribs and minor ribs. The number of minor ribs between major ribs decreases stratigraphically, from five or eight to one or two through four. Some minor ribs bifurcating near the ventral border in *C.* (*C.*) *ishiwarai* are not seen in other species. From the above characters, it can be seen that the number of minor ribs shows a tendency to decrease through time. Furthermore, *C.* (*P.*) *asiaticum* does not have similar morphological features to *C.* (*E.*) *emerici* and *C.* (*C.*) *ishiwarai* throughout its ontogeny. Thus, *C.* (*E.*) *emerici* seems not to be recognizably related to *C.* (*P.*) *asiaticum* in the same lineage.

Each of the Japanese species has a close resemblance to European forms: *C.* (*C.*) *ishiwarai* is similar to species of the *C. nolani* and *duvali* group; *C.* (*P.*) *asiaticum* resembles *C.* (*P.*) *elegans*; and specimens identified as *C.* (*E.*) *emerici* from Japan and Europe belong to one and the same species. According to Immel (1978), one of two crioceratid lineages including *C.* (*E.*) *emerici* (referred to as *C.* (*C.*) *emerici* by Immel) which developed in southern Europe (Tethyan province), is made up of *C.* (*C.*) *nolani*, *C.* (*C.*) *journoti*, *C.* (*E.*) *emerici*, and *C.* (*E.*) *barremense* in order, and is characterized by a decreasing number of minor ribs. Another lineage comprising *C.* (*P.*) *elegans* (referred to as *C.* (*C.*) *elegans* by Immel) is highly developed in northwest Europe (Boreal province) and is characterized by having no distinction between major and minor ribs and being loosely to tightly coiled as the shell grows.

Thus, morphological affinities are, as described above, not recognizable between the three species from Japan, but all of these species appear closely similar to some European species.

*Crioceratites* (*Paracrioceras*) in northwestern Europe is interpreted to have descended from southern European *Crioceratites* (*Crioceratites*) species migrating northward during mid-Hauterivian time (Immel 1978; Kemper *et al.* 1981).

According to P. F. Rawson (pers. comm. February 1991), by the Barremian northwest Europe had apparently lost contact with areas to the north: the Barents Shelf had become non-marine, and the Russian Platform and northern Siberia partly so. No heteromorphs are known from these areas in either the Barremian or the Hauterivian, with the exception of three specimens from the Russian

Platform. All the evidence suggests that the NW European heteromorphs came originally from western Tethys and never migrated farther into the Boreal Realm. Thus, it is suggested that the ancestor of *C.* (*P.*) *asiaticum* is more likely to have been derived from Tethys. *C.* (*P.*) *asiaticum* is interpreted to have evolved in parallel to the European crioceratid lineage and to have a common ancestor.

Consequently, it may be a reasonable interpretation that the three Japanese crioceratid species are immigrant species from the Tethys, and that *C.* (*C.*) *ishiwarai* and *C.* (*P.*) *asiaticum* developed in Japan (see Text-fig. 7).

## CONCLUSIONS

Four species representing three genera of ammonites from four Barremian formations in southwest Japan are described in this paper. These genera were mainly distributed in the northwest European and northern Pacific provinces in Barremian time. They are interpreted to have migrated between these areas via high latitude seas.

The occurrence of only Tethyan ammonite faunas in northeast Japan and of mixed Tethyan and northern faunas in southwest Japan suggests that a Barremian seaway existed between northeast Japan and continental Asia. This is based on oceanic circulation patterns and concordant global distribution of ammonites during the Barremian.

Three species belonging to *Crioceratites* from Japan appear morphologically more closely related to some species from Europe than to each other. It may be reasonable to interpret these three species from Japan as immigrant species from the Tethys or their descendants.

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# POPULATION ANALYSIS AND ORIENTATION STUDIES OF GRAPTOLOIDS FROM THE MIDDLE ORDOVICIAN UTICA SHALE, QUEBEC

*by* SUSAN RIGBY

ABSTRACT. Three large populations of graptoloids from the Middle Ordovician Utica Shale of Quebec contain *Orthograptus quadrimucronatus micracanthus* and *Amplexograptus praetypicalis*. Detailed orientation studies show that the two species reached the bedding plane at different times and were probably present in the water mass as monospecific shoals. Some size ranges of each population are orientated, suggesting that current sorting occurred. Few siculae are present, either because of current winnowing or because of geographical separation of growth stages in life. Length–frequency graphs of complete specimens suggest that both species grew throughout life. Survivorship analysis indicates that some populations died from constant environmental stress while others lived long enough for increasing length (or age) to become a handicap. The origin of synrhabdosomes is considered to be taphonomic.

ALTHOUGH graptoloids are often very abundant when they are found, few studies of such populations have been undertaken. A notable exception is the work of Cisne and Chandlee (1982), who analysed a large number of specimens collected from a transect across late Middle Ordovician sediments in the Mohawk Valley, New York, USA. This transect included the Utica Shale and its shallow water equivalents. The graptoloids were identified at the generic level and analysed for relative and absolute abundances to elicit environmental information. The graptoloid samples were collected over 1 m thick packets of rock, each representing approximately 50000 years of deposition.

The present study is a pilot attempt to investigate the information-carrying potential of individual graptoloid populations preserved on single bedding planes and which presumably lived and died over a short period of time.

## GEOLOGICAL SETTING

The Utica Shale, deposited during the late Middle Ordovician (Riva 1969), was interpreted (Bradley 1989) as having been laid down in deep water within a small and closing ocean basin. This basin was situated between mainland Laurentia and the approaching Taconic island arc. Collision occurred later in the Quebec area than to either north or south. This was attributed to a local but deep embayment of the coastline. The enclosed Taconic Ocean probably had a width of 500–900 km at its fullest development.

In the Neuville area of Quebec, Canada, the Utica Shale is well exposed on the shores of the St Lawrence River and in roadside cuttings and cliffs. It contains abundant and well-preserved graptoloids. The fauna is otherwise sparse, but includes coiled gastropods, small brachiopods and orthocone nautiloids. From this low diversity and preponderance of planktonic organisms, and from the high carbon content of the rocks, it is probable that low oxygen availability made the bottom conditions inimical to life at the time of deposition.

Slabs with a surface area in excess of 0·7 m$^2$ of fine grained, petroliferous marly shale were extracted from the Shore Road below, and 200 m to the west of, the Egaré Motel at Neuville. Two species of graptoloid are present – *Orthograptus quadrimucronatus micracanthus* (Ruedemann, 1947)

[Palaeontology, Vol. 36, Part 2, 1993, pp. 267–282.]

TEXT-FIG. 1. Graptoloids from Utica 3 (SM X.23262); Shore Road, Neuville, Quebec, Canada; Utica Shale, Middle Ordovician. A–C, *Orthograptus quadrimucronatus micracanthus*. D–E, *Amplexograptus praetypicalis*. Scale bars divided into mm.

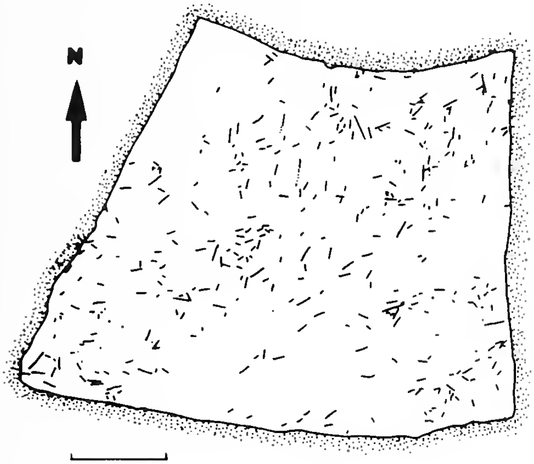
(Text-fig. 1A–C) and *Amplexograptus praetypicalis* Riva, 1987 (Text-fig. 1D–E), both in great numbers. This limited assemblage is consistent with a stratigraphical position within the *C. spiniferus* Zone, close to the base of the Utica Shale as redefined by Riva (1969).

## MATERIALS

Three slabs were analysed in detail. Labelled Utica 1, Utica 2 and Utica 3, they have areas of 0·1669 m$^2$, 0·7700 m$^2$ and 0·7610 m$^2$ respectively and are stored in the Sedgwick Museum, Cambridge (SM X.23260–X.23262). On all three slabs the majority of graptoloids appear to be unbroken, which is rather unusual (Crowther 1978). Both sicula and nema are visible on most specimens, and relatively few graptoloids overlap one another.

The slabs were bleached with 10 per cent hydrochloric acid to lighten the matrix and improve contrast between rock and fossils. In the process, some of the periderm was removed by the violence of the reaction, leaving the outlines of the graptoloids complete but their interiors fragmented (Text-fig. 1). This does not affect identification, as the overall shape is sufficient to distinguish between the two species. Preservation was also affected by weathering; graptolites on those bedding surfaces which had been exposed were more poorly preserved than those which were freshly split.

The bleached slabs were drawn to true scale on sheets of transparent acetate. These were then photocopied and the copies used to measure lengths, widths and orientations of all complete specimens on the slabs (Text-fig. 2). Identification of the graptoloids was made at the time of drawing, which although time-consuming, ensured that each specimen could be located again if necessary. Two of the three slabs were broken during passage from Quebec to Cambridge but the drawings were put together to reconstruct the complete bedding plane. As the slabs were collected from frost-shattered and slip-rotated areas on the roadside, an arbitrary 'North' value (000°) was chosen for each slab and no correlation attempted between them.



TEXT-FIG. 2. Utica 1 (SM X.23260). Lines represent the orientation and length of graptoloids. Scale bar = 100 mm.

## METHODS

### *Statistical techniques for testing directionality*

Few studies have been carried out on the orientation of bedding plane associations of graptoloids, so that their precise behaviour in the presence of currents of varying speeds is unknown. Rickards (1975) suggested that those monograptids with hooked thecae were probably orientated differently with respect to currents than those with simple thecae. Assuming that in most species the proximal and distal ends of the colony had different properties (e.g. width and weight), it seems reasonable to assume that graptoloids generally provide directional data, rather than just orientational data. In the present study, the facing direction of the proximal end is given relative to the arbitrary 'North' (see above).

On each of the three slabs, the facing direction of the sicula and total length of a set of 100 specimens was recorded. The length of specimens was in most cases grouped into 1–5 mm, 6–10 mm, 11–15 mm and > 15 mm classes. The data were then broken down into species and length categories, and analysed statistically for evidence of preferred orientation. If a preferred direction appeared to be present, or if the sample size of a particular sub-group was too small, more colonies were chosen at random and counted until a large enough sample had been measured.

A rose diagram was plotted for each data set. The data sets were then analysed to find the mean direction and mean resultant length. It was assumed that directional data would follow a von Mises distribution, which is the circular equivalent of a normal distribution. A Rayleigh test for preferred orientation was then applied, using the null hypothesis that there is no preferred direction expressed by the data. If data are bimodal or have another form of complex distribution, then this parametric test is inappropriate and can lead to misleading conclusions (Davis 1984). To help weed out inappropriate uses of this kind, rose diagrams gave a visual check on the veracity of the results derived from the statistical technique (as suggested by Davis 1984) and thus some of the apparent results were discarded. The directional data are summarized in Table 1.

TABLE 1. Orientation and statistical likelihood of random occurrences of different sizes and species of graptoloids from Utica 1–3 (SM X.23260–X.23262).

| Slab | Species | Size fraction (mm) | Sample size | $\bar{R}$ | Significance (%) | Mean direction |
|---|---|---|---|---|---|---|
| Utica 1 | *O. q. micracanthus* | All | 163 | 0·406 | 1 | 43 |
| | | 1–5 | 69 | 0·409 | 1 | 41 |
| | | 6–10 | 63 | 0·326 | 1 | 53 |
| | | 11–15 | 21 | 0·578 | 1 | 31 |
| | | > 15 | 10 | 0·595 | 2·50 | 45 |
| Utica 2 | *O. q. micracanthus* | All | 251 | 0·045 | Random | |
| | | 1–5 | 102 | 0·202 | 5 | 349 |
| | | 6–10 | 48 | 0·267 | 5 | 340 |
| | | 11–15 | 75 | 0·191 | Random | |
| | | > 15 | 26 | 0·325 | 10 | 97 |
| | *A. praetypicalis* | All | 91 | 0·176 | Random | |
| | | 1–5 | 1 | | | |
| | | 6–10 | 10 | 0·462 | Random | |
| | | 11–15 | 19 | 0·181 | Random | |
| | | > 15 | 61 | 0·178 | Random | |
| | | [> 20 | 63 | 0·311 | 1 | 161] |
| | Both | All | 342 | 0·045 | Random | |
| Utica 3 | *O. q. micracanthus* | All | 223 | 0·192 | | 210 |
| | | 1–5 | 62 | 0·219 | | 217 |
| | | 6–10 | 85 | 0·065 | Random | |
| | | 11–15 | 43 | 0·23 | Random | |
| | | > 15 | 33 | 0·456 | 1 | 209 |
| | *A. praetypicalis* | All | 108 | 0·258 | | 212 |
| | | 1–5 | 8 | 0·468 | Random | |
| | | 6–10 | 20 | 0·181 | Random | |
| | | 11–15 | 31 | 0·398 | 1 | 294 |
| | | > 15 | 49 | 0·364 | 1 | 34 |
| | Both | All | 331 | 0·069 | Random | |

### *Population and survivorship studies of graptolites*

All complete specimens on the slabs were measured for use in population studies. The principal techniques used were the generation of length–frequency curves and survivorship analysis. Length–frequency distributions can show whether growth of individuals was seasonal (in which case the graph should show one or more peaks) or if growth terminated before death (in which case a peak appears at the upper size range of the population). It also gives a view of the overall population structure, but this is better seen in survivorship curves.

The use of survivorship techniques is probably best known to most palaeontologists from their application to rates of species extinction (Van Valen 1973). Several population studies on fossils have been carried out using survivorship analysis, notably on Silurian ostracodes from Gotland (Kurten 1964). In this technique, the rates at which a population is dying between consecutive ages is assessed and plotted on a semi-log scale against age. At a simple level, two extremes of survivorship curve are seen. At one end of the scale, an individual within a population has an equal chance of dying at any time, regardless of its age. This results in a straight survivorship curve, and is commonly seen where environmental stress is high and mediates mortality within the population under study. At the other end of the scale, an individual in a population may live to senility, dying from internal causes. In this case, a convex survivorship curve results and the environment is considered a minor factor in mediating lifespan, the major control being internal and metabolic (Raup and Stanley 1978).

In population biology, survivorship analysis is used with caution. Many factors affect the shape of a survivorship curve for any population. These include intrinsic factors such as potential lifespan and periodicity of reproduction, and extrinsic factors such as seasonality in the environment and population changes unrelated to birth and death – immigration and emigration to and from the area of study. Some of the classical studies of population biology have been done on islands, specifically to minimize this effect (e.g. Clutton-Brock and Ball 1987).

When the technique is applied to palaeontological data, the problems of information-loss during taphonomy serve to complicate the data much further. In any species with a soft-bodied larval stage, for example, the population preserved in the fossil record will be skewed in favour of older individuals. Current-winnowing at a later post-mortem stage can severely affect the remaining population. Bedding plane assemblages of fossils may represent gradual mortality over a period of time, or the sudden death of all of the population at once. In the first case, the population has been frozen at a series of different times, in the second it has been frozen at a single point in time (Raup and Stanley 1978). The palaeontologist can only use judgement to determine which is more likely to account for any observed fossil population.

For population studies each species on each of the Utica slabs was investigated separately. In each case length–frequency graphs were used to generate composite, age-specific survivorship curves as there was no evidence for a mass mortality event either in the graptoloids or in the sediments. Although the graptoloids were concentrated on some bedding planes, they were present throughout the rock sequence and there was no visible change in the sediment which defined graptoloid-rich beds. All populations were corrected to cohorts of 1000 before being plotted as survivorship curves (Hutchinson 1978).

To draw survivorship curves for graptoloid populations it was assumed that the length of each graptoloid was proportional to its age. In the following study, most survivorship curves are shown with the length and age of the rhabdosome on the horizontal axis. The idea that length of a graptoloid colony is proportional to its age has long been implicit. Recent studies (Rigby and Dilly in press) suggest that this assumption is justified for at least some shapes of rhabdosome, including the biserial forms studied here.

### *Calculating the lifespan of* O. q. micracanthus *and* A. praetypicalis

Two models, both based on growth rates, for estimating the lifespan of graptoloids are available, one based on *Rhabdopleura* and one on *Cephalodiscus* (Rigby and Dilly in press); both living relatives of graptoloids which possess a skeleton.

Using the latter model, the plan area of a graptoloid colony is calculated and related to the growth rates of extant *Cephalodiscus* as measured in plan view by successive drawings of growing colonies. In experiments, this growth rate was shown to be 0·065 $mm^2$ per zooid per day. Using the *Rhabdopleura* model, the rate of addition of collagenous rings is used to estimate the minimum age at death of a graptoloid colony. *Rhabdopleura* zooids build their colony by the addition of such rings to 'thecal' apertures. One complete ring can be added in eight hours, and each is considered analogous to two half-rings on a graptoloid theca. The numbers of half rings required to build an average sicula and an average theca have been measured from isolated graptoloids. These suggest that about 22 days were required for the secretion of a sicula and 6·6 days for a theca. These averages take into account the variation in the number of increments that occurs within one colony and between species. These two methods of calculation can be used to give an estimate of minimum lifespan for any graptoloid.

In the case of *O. q. micracanthus*, the plan area of six specimens drawn from the Utica slabs was measured at 2 mm intervals along their lengths. The colony width changes little with distance from the proximal end, broadening quickly to its maximum value. This means that the calculated relationship between *Cephalodiscus*-based age estimates and length is effectively linear. For the *Rhabdopleura*-based age modelling, the number of thecae was measured with increasing distance from the proximal end. On average there were fourteen thecae in the first 5 mm, plus the sicula. In subsequent 5 mm intrvals there were twelve thecae. This again gives a roughly linear relationship, after the first 5 mm, between the length of the rhabdosome and the calculated age of the colony.

*Amplexograptus praetypicalis* specimens were measured from the Utica slabs studied here and also from drawings given by Riva (1987). It is a graptoloid species which widens gradually over the first 10–12 mm before reaching its maximum dorso-ventral width. This means that in calculating their age from *Cephalodiscus* models of colony growth, the linear relationship between length and age breaks down somewhat, because the model predicts that less time would be required to build a narrow colony than a wide one. The implications of this observation for interpretation of survivorship curves for this species are discussed below. Observations of the number of thecae per unit length for this species show that the relationship between thecal number and length is linear after the first 5 mm. Seventeen thecae plus the sicula are present in the first 5 mm, and thirteen thecae for every 5 mm thereafter. This is a close enough approximation to a linear relationship to leave unaltered any survivorship curves generated by the *Rhabdopleura* method. All survivorship curves were plotted on a single length axis, with ages calculated from the pterobranch models added, except for the data for *A. praetypicalis* where age was calculated using the *Cephalodiscus* method. In this case separate survivorship curves are drawn for *Cephalodiscus*-based age calculations.

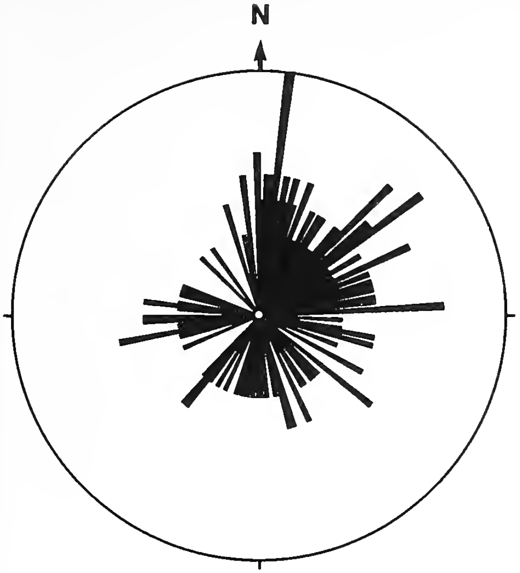
### *Modifications to the survivorship data*

Two modifications were made to the raw survivorship information. Any part of a survivorship curve with fewer than five members of the population left was discounted. This is common practice in the analysis of human survivorship curves (Martin Bland *pers. comm.*). Any part of the curve referring to graptoloids less than three millimetres long was also discounted, for two reasons. First, very few isolated siculae are present; they may have been winnowed out, or they may have lived in geographical separation from the larger colonies (Rigby 1992). Whichever is the case, it is certain that more small graptoloids were part of the population than are recorded on this bedding plane but the amount of discrepancy is unknown. Second, the justification for using length to approximate the age of a graptoloid colony is the assumption that there is a linear relationship between the two parameters, as discussed above. Whether the growth of graptoloids was more similar to that of *Rhabdopleura* or to that of *Cephalodiscus*, the linear relationship would almost certainly have broken down in the transition from sicula to colonial graptoloid. It might be that this stage was passed as quickly as possible, to minimize the time spent in a hydrodynamically unstable form. Alternatively, it might have taken more time, because of the need to bud multiple soft-tissue clones and build several new thecae in close succession. Either way, once the assumption of a linear relationship is rejected, those individuals below true colonial size should be disregarded in an analysis of survivorship within the population.

## DIRECTIONAL DATA ANALYSIS

### *Utica 1*

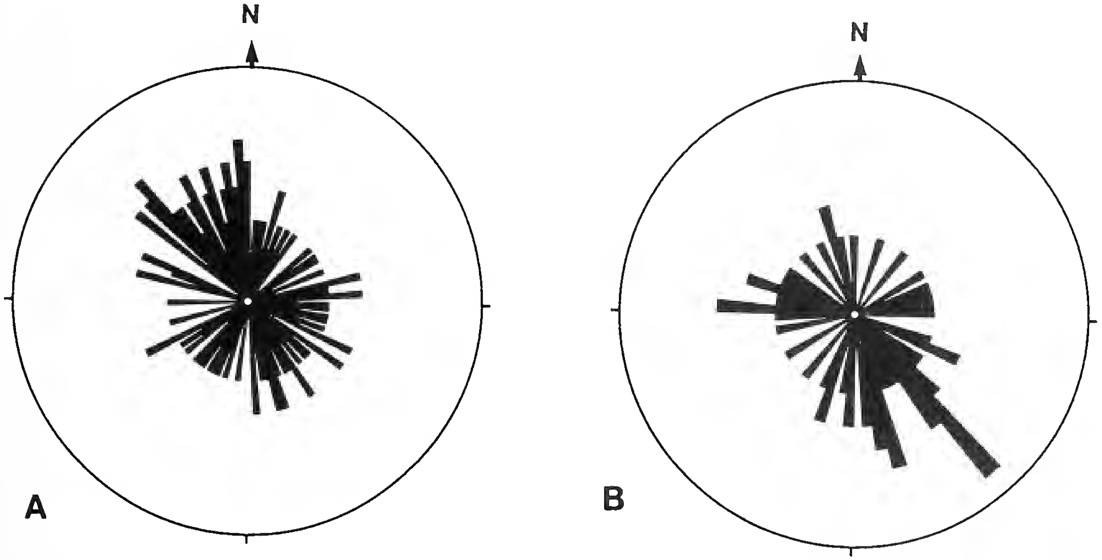
In the population overall, a preferred orientation was observed which was significant at the 1 per cent level (Text-fig. 3). All size groups showed the same result, except for the > 15 mm size division, which had a small sample size and showed a preferred orientation significant at the 2·5 per cent level. These data are consistent with orientation by a single current capable of transporting all sizes of graptoloid.



TEXT-FIG. 3. Orientation of all sizes of *Orthograptus quadrimucronatus micracanthus* on Utica 1 (SM X.23260); (n = 163; segment interval = 2°).

*Utica 2*

Overall, both species appeared to have a random distribution, and their size groups had random distributions, with three exceptions – the two smallest of *O. q. micracanthus* and specimens of *A. praetypicalis* more than 20 mm in length (Text-fig. 4).



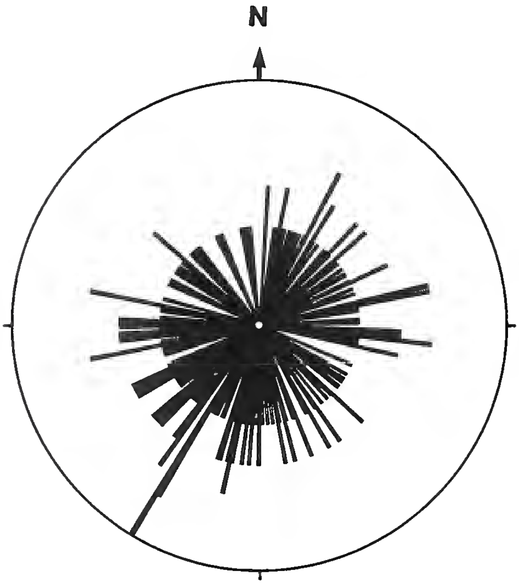
TEXT-FIG. 4. Orientation of graptoloids on Utica 2 (SM X.23261). A, small specimens of *Orthograptus quadrimucronatus micracanthus* (n = 102; segment interval = 3°). B, large specimens of *Amplexograptus praetypicalis* (n = 63; segment interval = 5°).

I think that it is not possible for a single current to have produced the observed results. As large specimens of *A. praetypicalis* are affected, but large specimens of *O. q. micracanthus* are not, it would be reasonable to assume that the specimens of *A. praetypicalis* arrived first on the seabed and were orientated before the arrival of the second species. Small specimens of *O. q. micracanthus* could have been orientated later, in a different direction, by a more gentle current of insufficient strength to affect larger colonies. Very few small specimens of *A. praetypicalis* are present.

This is a testable hypothesis, because there are places on this slab where one specimen lies on top of another. In total, thirty-three cases were found where preservation was good enough for the order of overlap to be determined. Of these, fourteen cases showed two specimens of *O. q. micracanthus* one on top of the other, seven cases showed two specimens of *A. praetypicalis* one on top of the other, ten cases showed *O. q. micracanthus* on top of *A. praetypicalis* and only two cases showed the reverse. This strongly supports the hypothesis that the two species arrived on the bedding plane at different times, with *A. praetypicalis* arriving first.

### *Utica 3*

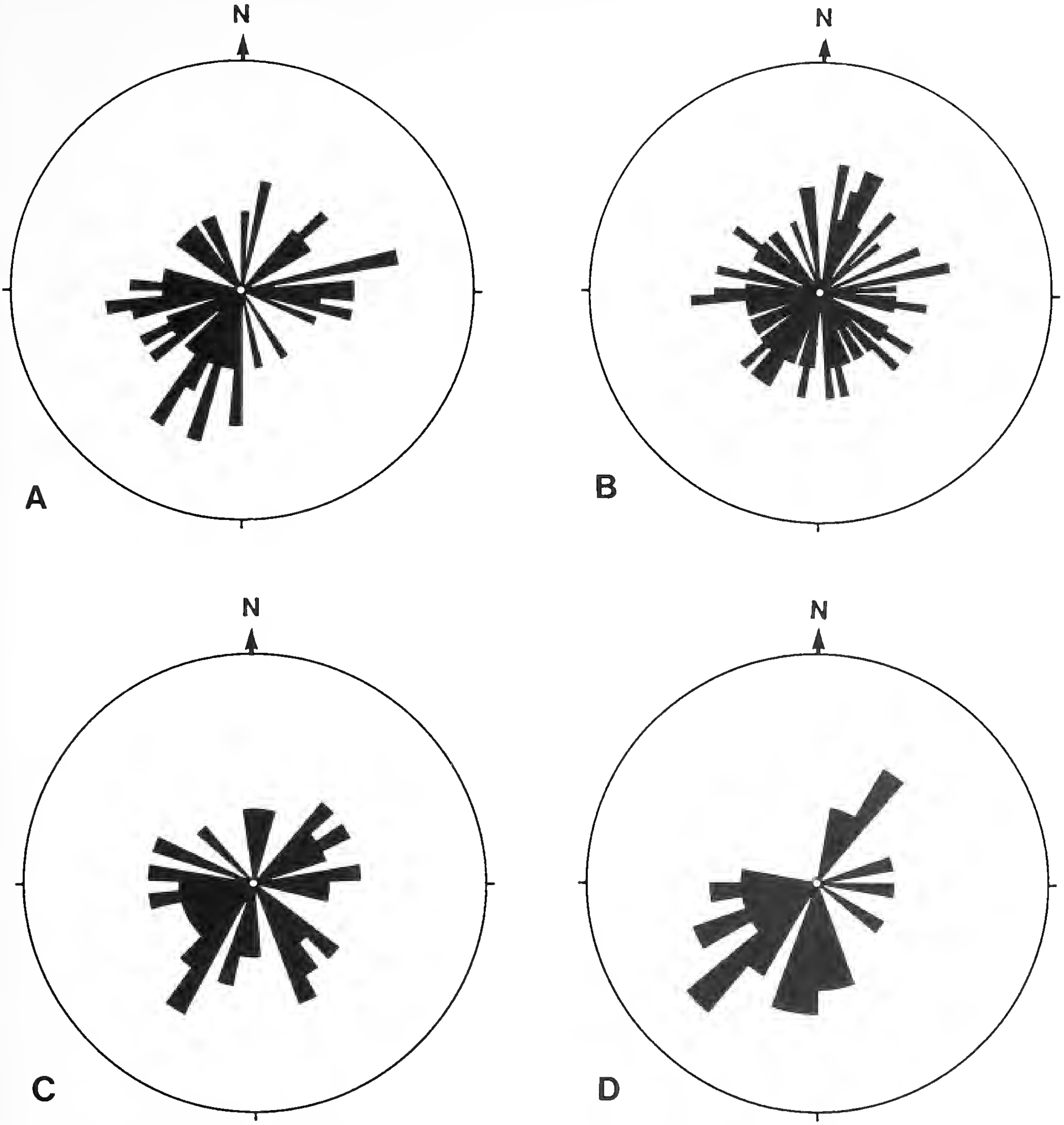
Considered together, the *O. q. micracanthus* data showed a statistically significant preferred orientation. However, cursory inspection of the rose diagram (Text-fig. 5) was enough to show that this was a function of assuming a von Mises distribution when a more complicated distribution pattern is actually shown. When the data were broken down by size, an equivocal result emerged. There was a preferred direction in specimens between 1–5 mm in length (but only significant at the 10 per cent level) and over 15 mm in length. The intermediate size ranges appeared to have a random distribution (Text-fig. 6).



TEXT-FIG. 5. Orientation of all sizes of *Orthograptus quadrimucronatus micracanthus* on Utica 3 (SM X.23262), (n = 223; segment interval = 1°).

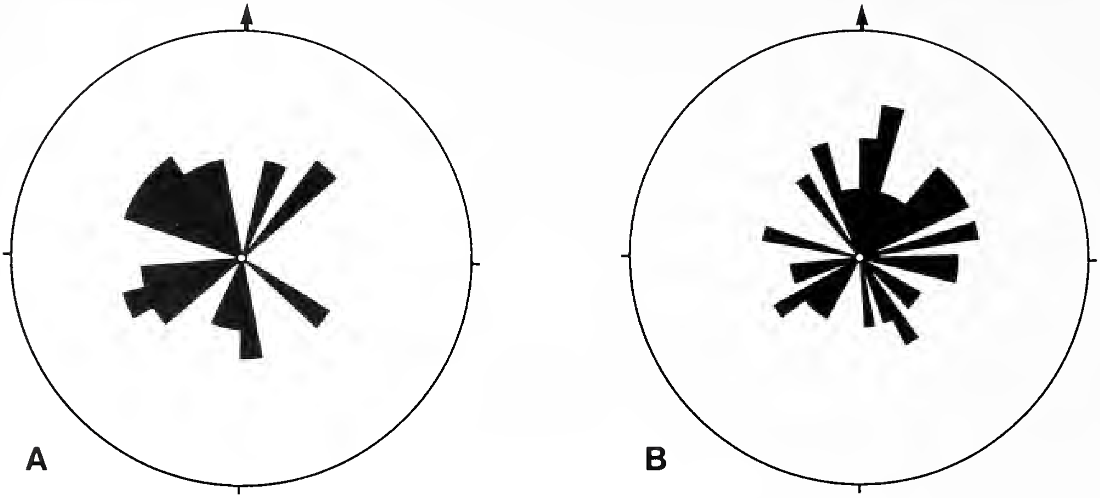
The small specimens of *A. praetypicalis* (in the 1–5 mm and 6–10 mm size ranges) showed a random distribution of direction. However, both of the larger size groups (11–15 mm and > 15 mm) showed preferred directions significant at the 1 per cent level (Text-fig. 7).

In summary, all of the larger graptoloids on this slab are orientated, but with different mean orientations. Preservation on this fragmentary slab is too poor to determine the order of arrival of



TEXT-FIG. 6. Orientation of different size-groups of specimens of *Amplexograptus praetypicalis* on Utica 3 (SM X.23262). A, 1–5 mm (n = 62; segment interval = 5°). B, 6–10 mm (n = 85; segment interval = 1°). C, 11–15 mm (n = 43; segment interval = 8°). D, > 15 mm (n = 33; segment interval = 10°).

the different species. Several currents might have been involved, but the obvious problem is that large graptoloids are orientated when small ones are not. Perhaps large and small colonies arrived at different times, which would support a seasonal growth for graptoloid colonies, possibly with annual or biannual periods of 'bloom', leading to the presence of different sizes of colony in the water column at different times of year.



TEXT-FIG. 7. Orientation of large specimens of *Amplexograptus praetypicalis* on Utica 3 (SM X.23262). A, 11–12 mm (n = 31; segment interval = 12°). B, > 15 mm (n = 49; segment interval = 8°).

## POPULATION ANALYSIS

### *1.* O. q. micracanthus

Three populations are available:

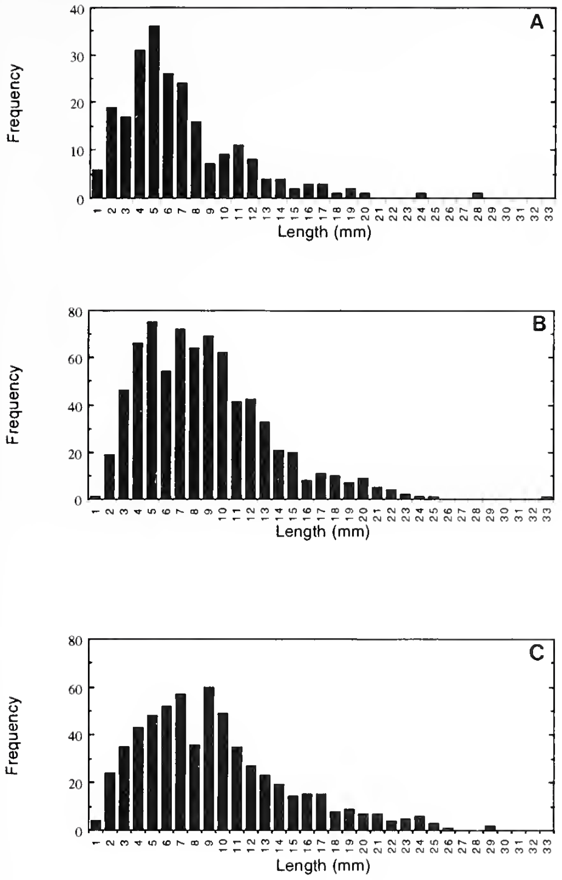
On Utica 1 (population, n = 232) the largest specimen is 28 mm long, and 5 mm is the commonest length. The length/frequency plot is a left-skewed normal distribution. (Text-fig. 8). The smooth nature of the curve suggests that growth was continuous, rather than strongly seasonal, and the absence of a terminal bulge shows that growth was continuous throughout life. These data converted into a survivorship curve (Text-fig. 9) show an initial increase in mortality rate with age followed by a long period of constant probability of death, and finally a rather irregular increase in mortality rate to the point where no individuals survive. When individuals less than 3 mm long are removed from consideration, along with those rare last specimens to survive, the remaining part of the curve is almost straight.

On Utica 2 (n = 744) a left-skewed, normal distribution of length with frequency is observed, with the commonest length of graptoloids again being 5 mm. The largest specimen is 33 mm long, which slightly exceeds the maximum length given by Elles and Wood (1901–18) for this species (Text-fig. 8). Smooth and continuous growth is suggested by the data. When the data for this slab and species are converted into a survivorship graph (Text-fig. 9), the result is distinctly convex, even with very small and very large specimens removed. With an occasional variation, the mortality rate increased continuously with length in this example.

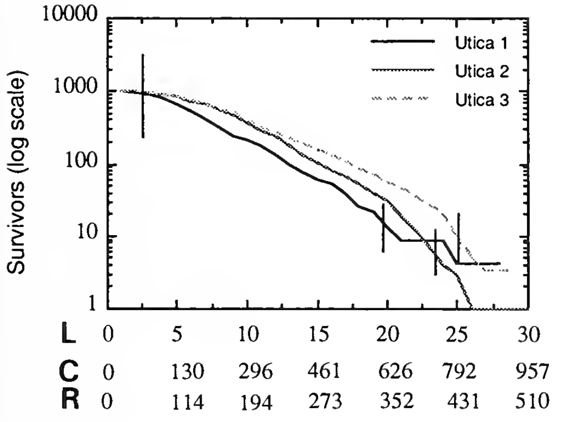
On Utica 3 (n = 609) the largest specimen is 29 mm long, and the commonest length is 9 mm. From the length–frequency graph (Text-fig. 8) it appears that continuous growth went on throughout life. When a modified survivorship curve is plotted (Text-fig. 9), the result is equivocal. Whilst definitely convex in overall form, a large segment of the survivorship curve is straight.

### *2.* A. praetypicalis

Two populations are available. (Utica 2 and 3). Both are smaller than those of *O. q. micracanthus*, and the size-range larger.

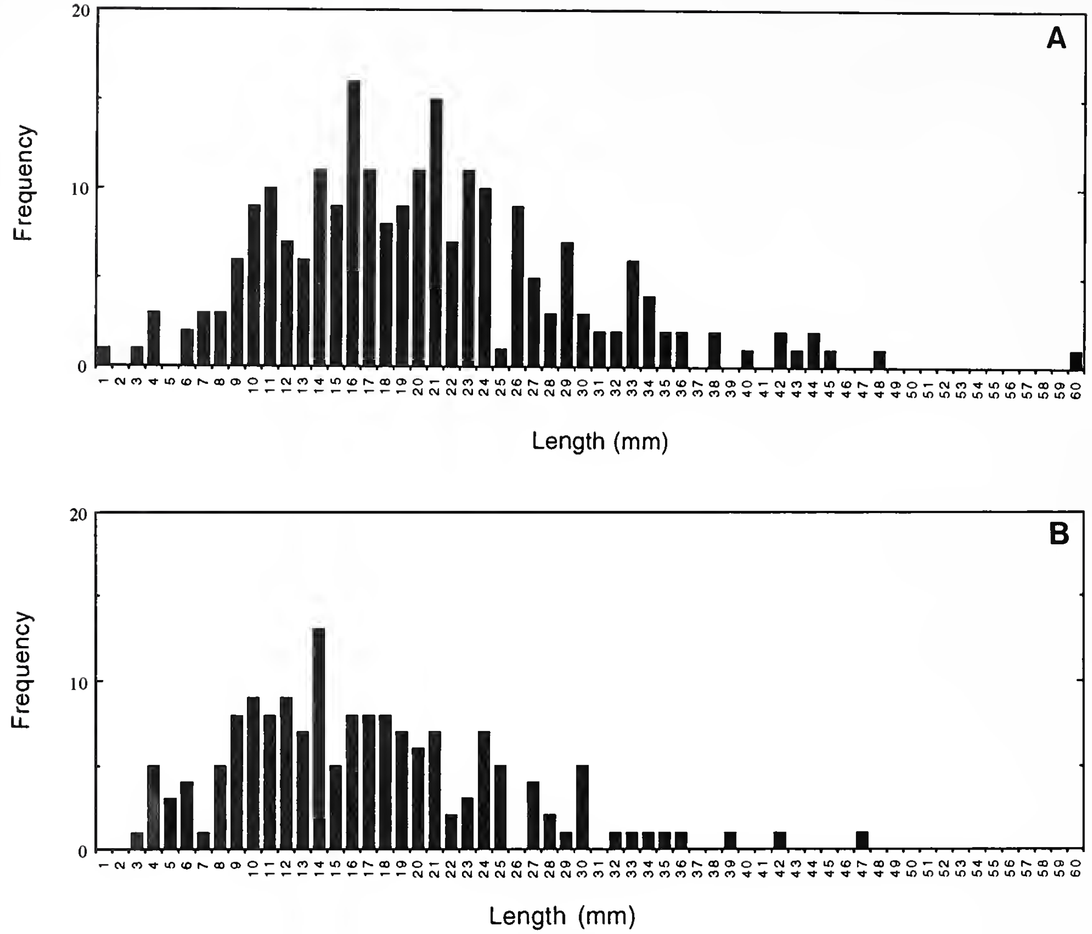


TEXT-FIG. 8. Length/frequency distributions of *Orthograptus quadrimucronatus micracanthus*. A, Utica 1 (SM X.23260). B, Utica 2 (SM X.23261). C, Utica 3 (SM X.23262).



TEXT-FIG. 9. Survivorship curves for *Orthograptus quadrimucronatus micracanthus* from Utica 1–3. L = length of specimens; C = age in days calculated from the *Cephalodiscus* model; R = age in days calculated from the *Rhabdopleura* model. Vertical bars mark the cut-off points for the data discussed in the text.

On Utica 2 (n = 266) the largest specimen is 60 mm long, and the commonest length is 16 mm. Length-frequency graphs for this species and slab are more irregular than for *O. q. micracanthus* because of the smaller sample size and greater range in length. However, the primary signal seems similar, with a left-skewed normal distribution (Text-fig. 10), indicating continuous growth through

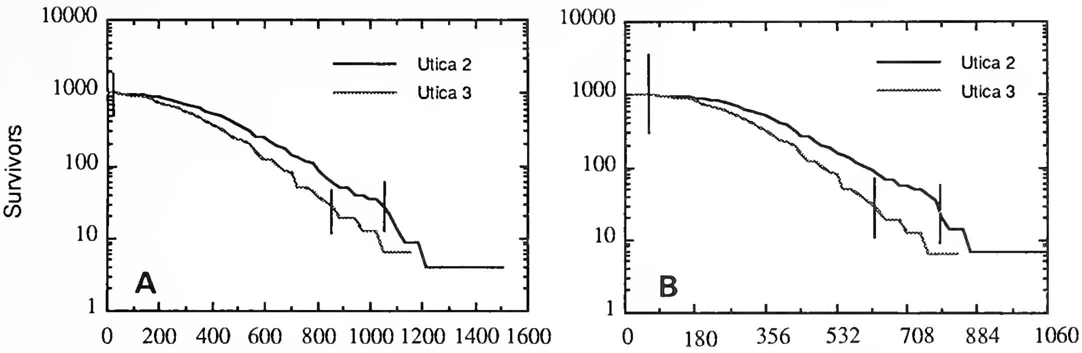


TEXT-FIG. 10. Length/frequency distributions of *Amplexograptus praetypicalis*. A, Utica 2 (SM X.23261). B, Utica 3 (SM X.23262).

life. A modified survivorship curve for these data has a convex shape (Text-fig. 11B), but with a long straight middle segment similar to the *O. q. micracanthus* curve from Utica 3.

On Utica 3 (n = 160) the largest specimen is 47 mm long and the commonest length is 14 mm. Growth appears to have been continuous (Text-fig. 10). The modified survivorship curve generated by this data (Text-fig. 11B) is clearly convex.

When age-based (rather than length-based) survivorship curves are generated using the *Cephalodiscus* model, the data points are changed because there is not a linear relationship between the age and length of this particular graptoloid for at least the first centimetre of stipe. Because the earlier growth stages are narrower, they should have taken less time to build than later growth stages, and so should represent smaller increments of time. When the graphs are corrected for this by causing the early growth stages to represent smaller periods of time, more individuals appear to have died off earlier, straightening the curve to some extent (Text-fig. 11A). The mortality rate of young specimens is increased in this method of calculation. However, for both Utica 2 and Utica 3 the overall effect is small and the curves remained noticeably convex.



TEXT-FIG. 11. Survivorship curves (calculated age in days on horizontal axis) for *Amplexograptus praetypicalis*. A, from the *Cephalodiscus* model. B, from the *Rhabdopleura* model. Vertical bars mark the cut-off points for the data discussed in the text.

## DISCUSSION

### *Directional observations*

In all three slabs there was some evidence of current orientation. The most highly orientated population is on Utica 1, where all size ranges show evidence of current sorting. The least affected slab appears to be Utica 2. On all three slabs it is possible that currents not only produced a directionality in the graptoloid population, but also a size bias due to winnowing. In the following analysis of graptoloid populations, this possibility is ignored, because the pattern of currents playing over the study area at the time of deposition was clearly complex, with several current events interspersed between the arrival of different graptoloid species (Utica 2) and possibly different sizes of the same species of graptoloid (Utica 3). The population analyses of the three slabs show strong similarities in the analysis of the same species on different slabs, and clear differences between analyses of the two species. It therefore seems likely that current winnowing had less effect than the primary controls on each species population. Having said that, it is apparent that the following study of graptoloid populations must be viewed in the light of their subsequent complex taphonomic history.

### *An interpretation of the graptoloid populations of the Utica Shale*

Graptoloid populations from the Utica Shale produce survivorship curves that are to some extent convex. This means that mortality rate increased with age for both species present on the slabs. This could be interpreted to indicate that, in all the populations studied, inate senility was a factor in mortality. Clearly environmental stresses were also a common cause of death for members of these populations, as shown by the divergence of these curves from ideal convex shapes. The relative importance of each type of mortality varies from one slab to another. The specimens on Utica 1, which shows an almost straight survivorship curve, seem to have suffered from constantly high environmental stress, while those on Utica 2 and 3 seem generally to have experienced greater mortality with increasing age.

A large degree of environmentally-mediated mortality is to be expected in any planktonic organism, where chance water movements may remove the individual from its source of food or oxygen. Moreover, in a narrow basin such as the Taconic Ocean, it is to be expected that small changes in lateral position would have been accompanied by large changes in oceanographic parameters, as observed by Cisne and Chandlee (1982) in their 83 km transect across the basin.

It is unexpected to find any physiologically mediated overprint to this environmentally moderated mortality, because graptoloids were colonial. Colonies such as corals can live indefinitely, because they can replace dead colony members by asexual budding. Although genetic defects may eventually build up in the genome until mortality occurs, this process, if it happens at all, will take in the order of thousands of years (Jackson and Coates 1986).

An alternative interpretation of the survivorship curves is that as length increased so did the likelihood of dying-off during the next short time interval. In the populations analysed here there is evidence from the length–frequency curves for continuous growth of the graptoloid colony through life. Perhaps this suggests another explanation for the observed data. If graptoloids continued to grow throughout life, then their hydrodynamic and feeding properties, as well as their food needs, would have changed as well. For biserial forms, this change would have been a continuous increase in feeding intensity (i.e. a need for increasingly food-rich water) as the colony grew (Rigby 1992). Perhaps large individuals eventually outgrew the food availability in the water around them. In this case, environmental stresses would have operated preferentially on large colonies, and a convex survivorship curve could be generated without the need for internally controlled changes in mortality rate. This theory offers the possibility eventually of using graptoloid populations to determine oceanographic parameters like food availability and dependability for the seas in which they lived.

### *Synrhabdosomes*

Many synrhabdosomes were found during the collection of samples from the Utica Shale. Four poorly preserved examples occur on Utica 3 (the best preserved is shown in Text-figure 12) all belonging to *O. q. micracanthus*. As in the example drawn here, they are preserved with the nemata overlapping and the sicular apertures directed outwards. This is the same orientation as those seen by Ruedemann (1947) and many other workers, and in the opposite orientation to the synrhabdosomes of *Rhaphidograptus toernquisti* described by Bjerreskov (1976). The present synrhabdosomes show a range of rhabdosome size, but no extremely large or small colonies, in contrast to those described by Ruedemann (1895, 1947) which contain graptoloids in all stages of developments, and to those of Bjerreskov (1976), in which all the constituent graptoloids are the same size.

It has been suggested that synrhabdosomes have one of two origins. They either might have been primary, serving some biological purpose, or grown by asexual budding of one colony (Kozłowski 1948; Zalasiewicz 1984). The latter would need soft part connection of colonies at an early stage and would accord well with Ruedemann's (1895, 1947) observations. Alternatively, they could be of taphonomic origin. If the first suggestion is correct the populations analysed in this paper might have been substantially different in life, especially if the formation of synrhabdosomes was common, and their duration long. If the latter suggestion is correct, perhaps many of the orientation studies conducted here give apparently random results because single graptoloid colonies were not the prime units affected by currents.

Can the occurrence of synrhabdosomes in this study suggest anything about their mode of formation? One factor that seems to be of relevance is their relative rarity. On almost 1·7 $m^2$ of graptoloid-rich bedding plane, only four synrhabdosomes were found (although all on the same slab). This must suggest that they were either unusual or temporary aggregates, implying that normal graptoloid reproduction was unlikely to have occurred in this way. Alternatively, they could have been common in life but disaggregated quickly after death.

On the bedding plane where the synrhabdosomes lie, some current sorting can be seen to have occurred which has affected the larger specimens of both species. Could current sorting have generated or affected the synrhabdosomes? It is hard to explain how this could have occurred. Bjerreskov (1976) observed that the synrhabdosomes she described are present in beds in which other graptoloids are strongly current orientated. This suggested to her that the synrhabdosomes had to form at a different time to the current sorting-event, most probably while the colonies were still floating high in the water column.

The solution that seems most likely to me is as follows. A major contributor to the organic content of the sea bed at the present time is marine snow. This is macroscopic aggregates of organic

TEXT-FIG. 12. Synrhabdosome of specimens of *Orthograptus quadrimucronatus micracanthus* from Utica 3 (SM X.23262). Scale bar = 5 mm.

detritus and living organisms, bonded largely by the mucus feeding-webs of zooplankton (Alldredge and Silver 1988). Marine snow collects substantial amounts of debris as it falls through the water column and brings large aggregates of organic matter to the sea bed in a single mass. Although largely composed of mucus, marine snow has considerable physical strength and will withstand high energy dissipation rates (Alldredge *et al.* 1990). Perhaps graptoloid synrhabdosomes were caught in this way. They would be uncommon, as most graptoloids would fall to rest alone, and they would be in masses too large to be affected by currents that later orientated individual colonies. The soft organic debris associated with the synrhabdosomes would have had a low preservation potential, but might have contributed to an overall increase in organic carbon within the sediment.

This interpretation must be regarded with due suspicion, as it is backed up by no firm evidence. In many ways it mirrors the suggestion (Rickards 1975) that synrhabdosomes were bound together by soft tissue. The major difference is that the soft tissue here is considered to have come from another source than the graptoloids themselves, making synrhabdosomes a taphonomic product.

*Acknowledgments*. The help of John Riva was invaluable during fieldwork in Quebec. Thanks go to Martin Bland, of St George's Medical School, Tooting, UK, for advice on survivorship analysis, to Dan Goldman for help in identifying specimens, and to Michael Fuller and Barrie Rickards for improving the manuscript. This work was carried out during the tenure of a Research Fellowship at Emmanuel College, Cambridge for which I am very grateful.

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# A NEW RHABDOPLEURID HEMICHORDATE FROM THE MIDDLE CAMBRIAN OF SIBERIA

*by* PETER N. DURMAN *and* NIKOLAI V. SENNIKOV

ABSTRACT. *Rhabdopleura obuti* sp. nov. is described from the late Middle Cambrian Mayan Stage of the Sukhan Depression, Siberia, and is the second rhabdopleurid to be described from the Cambrian. It is probably one of the oldest 'living fossils', remaining unchanged for over 520 Ma. This colonial pterobranch consists of stolonal and zooidal tubes. The creeping portion commonly found in most pterobranchs is reduced, with the colony adopting an erect growth habit. The stolonal tubes frequently show dichotomies and contain stolons. It is the earliest record of stolons. The zooidal tubes widen distally and occasionally show branchings to form other zooidal tubes. Fuselli are common and possess a very irregular zig-zag suture. There is no thecal dimorphism. There are several dark bodies occurring within the zooidal tube which have been interpreted as dormant buds and zooidal material. The best preserved zooid occurs in an open-ended tube and is cigar shaped (0·7 by 0·2 mm) and attached proximally to a stolon. This is the earliest record of zooid material. A review of hemichordate zooids in the fossil record is presented. *Rhabdopleura obuti* is compared with other pterobranchs and graptolites, with the conclusion that it represents an early rhabdopleurid but has characters which represent the start of the graptolite evolutionary story.

THE close phylogenetic relationship between the pterobranchs and the graptolites, which was first suggested by Schepotieff (1905) and substantiated through the work of Kozlowski (1938, 1949*a*), is now well established from a variety of morphological, ultrastructural and chemical evidence (summarized by Rickards and Dumican 1984; Urbanek 1986). Predictions based on this close phylogenetic relationship suggest the occurrence of pterobranch-like ancestors in the Cambrian (Andres 1977, p. 89; Rickards 1979; Rickards *et al.* 1984). Attention has been focused on the early graptolite and pterobranch record in order to untangle the early evolution of these groups. The record of Middle Cambrian graptolites has developed over the last eighty years (North America: Ruedemann 1908, 1931, 1947; Australia: Chapman 1919; Chapman and Thomas 1936; Quilty 1971; Europe: Sdzuy 1974) with a substantial Siberian component (Obut 1964, 1974). Middle Cambrian graptolite material further suggests an early occurrence of pterobranchs. The discovery of *Rhabdopleura* at this stratigraphical level will have great bearing in the study of the evolution of the pterobranchs and their relationship with the Graptolithina. A detailed study involving a phylogenetic classification of these groups and the origin and early evolution of the graptolites is currently being prepared for publication (by P.N.D.).

The material consists of a number of well-preserved, semi-transparent tubular colonial fossils with fusellar structures and sclerotized stolons constituting the earliest record of preserved stolon material. The fossils occur in a light-grey bedded limestone which can be easily prepared with acids. It is the earliest Cambrian pterobranch material to have been found in Siberia. It also represents a group which has remained unchanged for over 500 million years and is probably one of the oldest 'living fossils' (see below for discussion).

The only other record of a pterobranch from the Middle Cambrian is *Rhabdotubus johanssoni* Bengtson and Urbanek, 1986, from southern Sweden and Norway (see also Öpik 1933). The material described here was discovered in the collections of A. M. Obut at the Institute of Geology and Geophysics, Academy of Sciences, Novosibirsk during a visit made by Durman. It had been collected by K. S. Zaburdin in 1957 (Field specimen No. 1738B) from a locality on the River Ukukit which is a western tributary from the middle region of the Rover Olenek, on the western flank of the Sukhan Depression. This is part of the Olenek structural region in the Yudoma–Olenek facies

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region of the Siberian Platform (Kobanjikov 1959), in the Zelenotsvetnaya Formation. In modern usage this formation correlates with the Djahtaz and Siligir horizons from the Mayan Stage of the late Middle Cambrian (Shabanov *et al.* 1983). *Rhabdotubus johanssoni* is from the *Eccaparadoxides pinus* Biozone of the early Middle Cambrian, the earliest record of a pterobranch.

## SYSTEMATIC PALAEONTOLOGY

Phylum HEMICHORDATA Bateson, 1885
Class PTEROBRANCHIA Lankester, 1877
Order RHABDOPLEURIDA Fowler, 1892
Family RHABDOPLEURIDAE Harmer, 1905
Genus RHABDOPLEURA Allman, 1869

*Type species. R. normani* Allman 1869*a*, p. 311 (see also Allman 1869*b*, p. 439; Allman 1869*c*, p. 58, pl. 8); Recent, from the Shetland Sea, Scotland, at 90 fathoms.

### *Rhabdopleura obuti* sp. nov.

Plate 1, figs 1–4; Plate 2, figs 1–6; Text-figs 1–4

*Derivation of name.* After the Soviet graptolite worker Professor A. M. Obut who described much of the Siberian Cambrian graptolite material.

*Material.* The specimens are on five pieces of rock of which two fragments are housed at the Palaeontological Department of the Central Siberian Geological Museum in the Institute of Geology and Geophysics, Novosibirsk; registration number IGiG No. 962. Three other pieces of rock are deposited at the Sedgwick Museum, Cambridge (SM X.23262–23264).

*Holotype.* IGiG No. 962.

*Paratypes.* SM X.23262–23264.

*Horizon and locality.* Zelenotsvetnaya Formation, late Middle Cambrian, River Ukukit, Siberia.

*Associated species. Siberiodendrum robustum* Obut, 1964 and *Archaeolafoea* sp. are in the same collection made by V. Ya Kobanjikov from this locality (housed at IGiG).

*Diagnosis.* Coenoecium consisting of stolonal and zooidal tubes. Colony habitus largely erect with limited, encrusting, proximal portion. Stolonal tubes are 0·25–0·75 mm wide with irregular branchings. Sclerotized stolons common showing bifurcation at branch nodes. Stolon thickness between 60 and 80 $\mu$m. The erect zooidal tubes are 6·6 mm long on average widening gradually to an aperture of about 1 mm. Branching of zooidal tubes occurs quite commonly. No thecal dimorphism or indication of cortical bandaging. Fusellar structures found throughout the whole colony with traces of very irregular zig-zag sutures in the stolonal tubes. Fusellar heights vary

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EXPLANATION OF PLATE 1

Figs 1–4. *Rhabdopleura obuti* sp. nov. Zelenotsvetnaya Formation of the Mayan Stage, Middle Cambrian; River Ukukit (western tributary of River Olenek), Siberia. 1, IGiG No. 962, holotype; showing overall colony form with stolonal and zooidal tubes, fuselli and stolons visible, × 10. 2, SM X.23264; possible coiled thecorhiza, × 16·6. 3, SM X.23264; zooid in place within tube showing proximal stolon attachment, × 4·8. 4, SM X.23264; zooid within tube with distal lophophore structure and proximal attachment point for stolon, × 4·8.

PLATE 1

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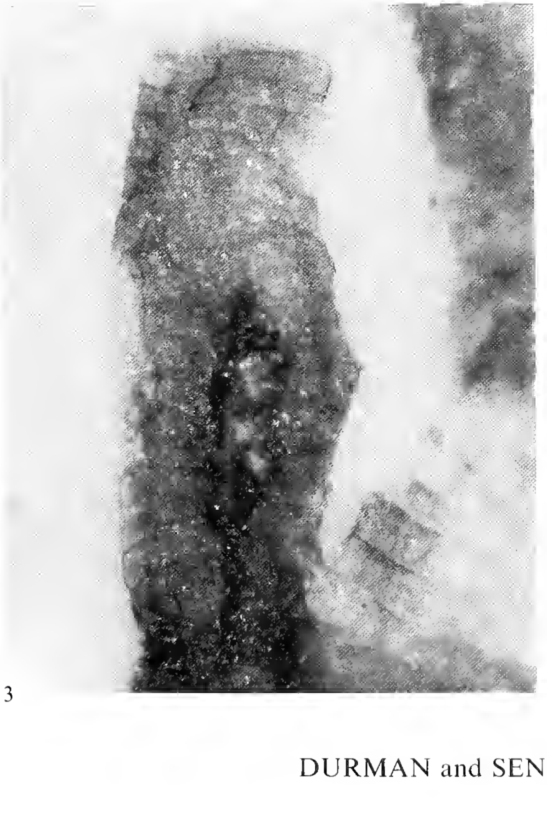

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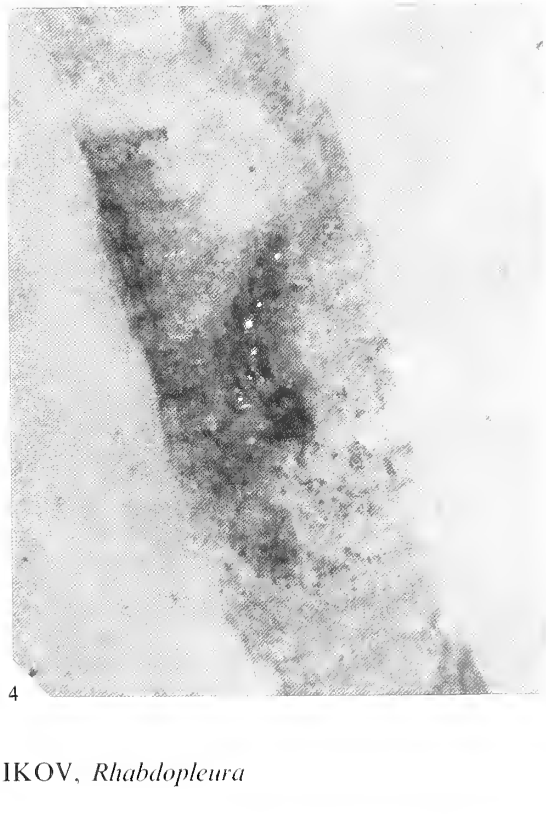

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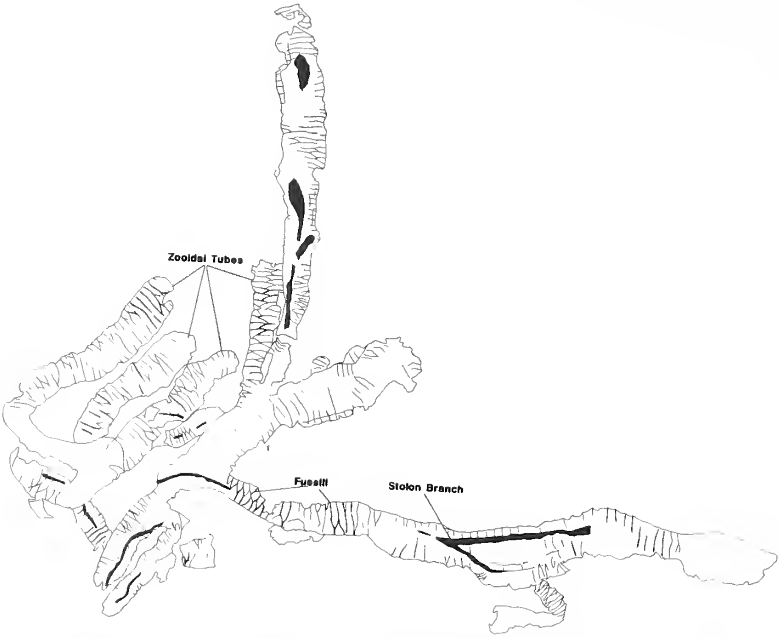
DURMAN and SENNIKOV, *Rhabdopleura*



TEXT-FIG. 1. Camera lucida drawing of the holotype of *Rhabdopleura obuti* sp. nov. (IGiG No. 962) illustrating the overall colony form with fusellar structures and stolons. Dark bodies represent probable zooids or dormant buds, × 7.

75–150 μm in stolonal tubes and 50–100 μm in zooidal tubes. Buds and zooids preserved within the tubarium with zooids measuring about 0·2 by 0·7 mm.

### *Description*

*Coenoecium.* The material consists of several distinct semi-transparent rhabdosomes and a number of isolated zooidal tubes (Plates 1–2; Text-figs 1–2). The overall colony form, such as any division into repent and erect tubes, is difficult to discern because the rhabdosomes have been flattened on burial. This flattening has also caused tubes to overlie one another and occur in a closer proximity to each other than they would have in life. The holotype has twelve distinct tubes and measures 12 by 9 mm (Pl. 1, fig. 1; Text-fig. 1). The upright zooidal tubes are the most common.

*Stolonal tubes.* The primary tubes have diameters of about 0·25–0·75 mm and are often seen with the better preserved stolon material (Pl. 2, figs 2, 5–6). The flattened tube diameters of 2·5 mm are associated with the very proximal tube portions nearest to the dichotomies. One tube fragment displays an area devoid of fuselli, running longitudinally down one side of the tube (Pl. 2, fig. 1). It has been interpreted as the structureless lower layer that occurs typically on the lower side of the creeping tubes in *Rhabdopleura* and also in some graptolites, for example the crustoids (Kozlowski 1962; Urbanek 1986). One specimen (Pl. 1, fig. 2) appears to be a coiled creeping tube forming a typical thecorhiza. No indication could be found in any of the material for any form of diaphragm or transverse structures which are found in Recent *Rhabdopleura*.

*Zooidal tubes.* The erect zooidal tubes arise by lateral branching from the primary stolonal tubes (Pl. 1, fig. 1; Pl. 2, fig. 2) and appear at a variety of orientations from the primary tube; they tend to form a lateral branch which twists around the main axis so that they run parallel to it, or can bend outwards at angles of up to 90°. The porus in the primary tube (where a zooidal tube emerges) is of the same diameter as the initial portion of the zooidal tube; branching apparently occurred by perforatory budding. The zooidal tubes vary in size: the longest complete tube is 8·5 mm (on the holotype); an average tube length is 6·6 mm ($n = 22$ complete tubes). The tubes are generally parallel sided or display a slight widening towards the aperture (Pl. 2, fig. 3). The diameter increase is about 0·5 mm over an average tube length, often with a greater expansion at the very terminal portion giving rise to a funnel-shaped aperture (Pl. 2, fig. 3). The apertures of the tubes range from 0·47 to 1·25 mm in diameter (average about 0·87 mm; $n = 31$). Aperture ornamentation is not apparent but there is the possibility in some of the material that the apertures may have an oblique margin at an angle of 20°–30° to the edge of the tube; however, this may be a taphonomic affect. These variations described are probably due to preservational or local growth differences rather than any form of thecal dimorphism. The coenoecia of the zooidal tubes are often darker more proximally and become lighter distally, a feature related to secondary thickening which is more prevalent proximally or to greater proximal sclerotization.

*Fusellar structure.* Full fusellar rings are most prevalent; rarer half-rings occur most frequently proximally and in the stolonal portions. The zig-zag suture is very indistinct and irregular but can be seen over short lengths (Pl. 2, fig. 2; cf. *Rhabdopleura kozlowskii* Kulicki, 1969). Zooidal tubes mainly comprise complete fusellar rings with an oblique suture which is often irregularly placed as in the case of most rhabdopleurids and some graptolites. The distal parts of the fuselli frequently protrude to give the appearance of a collar which is very characteristic of the rhabdopleurid fusellar arrangement (Pl. 2, fig. 5). The height of the fuselli (i.e. the distance between the growth lines) varies with position in the colony: the stolonal tubes have fusellar heights in the range 75–150 $\mu$m, the zooidal tube fuselli 50–100 $\mu$m. Thus over a 2·5 mm portion, the stolonal tubes have about 18–22 fuselli compared with 25–35 fuselli in zooidal tubes.

*Stolons.* The stolons are very common throughout the colonies and more frequent in the repent tubes. The stolons appear as dark rods often with relief. Their common occurrence is due to the sclerotization which toughens the material and makes their preservation potential greater. The longest stolon is 6·38 mm with a thickness of 60 $\mu$m; stolon thickness ranges from 60 to 80 $\mu$m. The stolons frequently appear to bifurcate at the lateral branches (Text-fig. 1). The stolons swell at these nodes (Pl. 2, figs 2, 5–6).

*Buds and zooids.* At a number of places, there are dark bodies which may be interpreted as dormant buds or zooids. However, it is possible to confuse areas of tube overlap with these zooids as they both appear darker than the surrounding region and care must be taken in the interpretation. The clearest example of a preserved zooid occurs in an open-ended tube; it is cigar shaped, measuring 0·7 mm long by 0·2 mm wide (Pl. 1, fig. 3; Text-fig. 3). It is attached proximally to a 67 $\mu$m wide stolon and is preserved in three dimensions but no further anatomical details can be seen. In one specimen (SM X.23264; Pl. 1, fig. 4) there is a suggestion of a lophophore. At the distal end of the zooid in SM X.23262 there is a small projection which may be remnants of the pre-oral disc or cephalic shield (Pl. 1, fig. 3). The size compares well with accounts of Recent rhabdopleuran zooids which measure $<0·5–1·0$ mm (Bulman 1970; Stebbing 1970) and with the unique record of graptolite zooids recorded as being 'rather less than half a millimetre' (Rickards and Stait 1984).

*Discussion.* The general appearance of the coenoecium with the proximal semi-annular fuselli and zooidal tubes displaying irregular, annular fuselli is in itself sufficient to place these specimens in *Rhabdopleura*; the occurrence of sclerotized stolon and zooidal bodies makes this placement conclusive. Other features, such as the development of the secondary thickening in the proximal areas, are common in *Rhabdopleura normani*. The absence of thecal dimorphism prevents inclusion in the graptolites (as thecal dimorphism is essentially a graptolitic character secondarily lost in the graptoloids). The only character which is not properly accounted for within extant *Rhabdopleura* is the occurrence of distally widening tubes (although Andres has reported them in specimens from Bergen, Norway – see below). The proposal to erect a new genus or subgenus was considered at length (see later for comparison and discussion), but it was decided that the differences between the extant species were no greater than the differences between them and *R. obuti*, and the proposal was abandoned. There is a series of parallel-sided lines which run longitudinally in some of the tubes which look similar to cortical bandages. However, a number of the lines converge and cross which suggests that they are due to wrinkling from tube flattening; if they were cortical bandages, the lines would be expected to maintain a parallel relationship along their entire length. There is no indication of any type of solid substrate such as shell material, and presumably the good preservation indicates the colony has not been transported any great distance. Text-figure 4 illustrates the authors' concept of how the organism *Rhabdopleura obuti* might have appeared in life.

## COMPARISON WITH OTHER PTEROBRANCHS AND GRAPTOLITES

Despite the simple morphology of the rhabdopleurids, their ecophenotypic variability has made classification confused in the past. Identification of extant species of *Rhabdopleura* has been much debated with great deal of synonymizing and species splitting (Thomas and Davies 1949*a*). This is mainly due to the very varied forms that the genus can adopt, related to substrate interaction. Fossil species have similarly undergone much discussion but this debate has often been at a higher taxonomic level and, due to Mierzejewski (1986), at the family level. Bulman (1970) was the first to place all the fossil pterobranchs into the family Rhabdopleuridae, as previous workers such as Kozlowski showed a reluctance to use families in classification. Mierzejewski (1986) adopted a different approach with the different fossil genera representing three families with three distinct phylogenetic lines.

### *Comparison with Recent* Rhabdopleura

Seven Recent species of *Rhabdopleura* have been described; Thomas and Davies (1949*a*) gave an account of their classification and its problems. It was suggested by van der Horst (1936) that these seven species can be synonymized into three, based on a geographical distribution (*R. normani* – Atlantic; *R. striata* – Sri Lanka; and *R. annulata* – New Zealand, Celebes and Tasmania). This scheme has been adopted by most workers. *R. normani* is very variable with the zooidal tubes arising with poorly to well developed adherent portions (Lankester 1886, p. 625). *R. annulata* lacks an adherent portion but the creeping portion is well developed. *R. obuti* differs from most of the Recent examples of *Rhabdopleura* in lacking a distinct and significant creeping portion of the stolonal tubes, with a very irregular and limited zig-zag suture in the stolonal tubes which widen distally. However, there are rare examples of other rhabdopleurids demonstrating characters such as distally widening tubes, e.g. *Rhabdopleurites primaevus* Kozłowski, 1967 and Recent *Rhabdopleura* from Bergen, Norway (Dietmar Andres pers. comm.). Branching of the zooidal tubes is rare in Recent *Rhabdopleura* but has been reported (Schepotieff 1907, pls 17, 21; Kozłowski 1949*a*, fig. 14); Kulicki 1971, fig. 2G–H). It is rarely seen in *R. normani* (Noel Dilly pers. comm.). The limited creeping portion of *Rhabdopleura obuti* is perhaps a reflection of the soft substrate on which it lived. Rhabdopleurids are usually found associated with hard substrates such as pebbles, corals, ascidians and shells, although *R. mirabilis* Sars, 1874 is reported to be attached to mud, sand particles, and associated foraminiferal tests. *R. normani* is known to grow on sand particles off the Faeroe Islands (Noel Dilly pers. comm.).

### *Comparison with fossil rhabdopleurids*

*Rhabdopleura eocenica* Thomas and Davies, 1949*b* (Yprésian, Eocene, Lower Swanwick, Hampshire); *R. vistulae* Kozłowski, 1949*b* (Upper Cretaceous, Poland); *R. delmeri* Mortelmans, 1955 (Viséan, Turnhout, Belgium); *R. kozlowskii* Kulicki, 1969 (Bathonian, southern Poland); *R.*? sp. Mierzejewski, 1978 (Ludlow, Silurian, Poland) and *R. hollandi* Rickards *et al.*, 1984 (Upper Llandovery, Powys, Wales) all display features very much like Recent *Rhabdopleura*. *R. obuti* is very comparable with these forms and only differs from them in the characters listed above.

Many of the rhabdopleurids described by Kozlowski (*Rhabdopleuroides exspectatus* Kozłowski,

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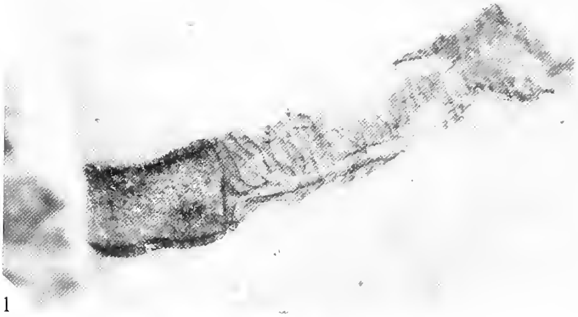
EXPLANATION OF PLATE 2

Figs 1–6. *Rhabdopleura obuti* sp. nov. Zelenotsvetnaya Formation of the Mayan Stage, Middle Cambrian; River Ukukit (western tributary of Rover Olenek), Siberia. 1, SM X.23263; stolonal tube illustrating structureless lower layer, × 17·5. 2, SM X.23262; stolonal tube with branch, fuselli and stolons, × 35. 3, SM X.23264; typical zooidal tube with funnel-shaped aperture and fuselli, × 14·2. 4, SM X.23264; collection of branching zooidal tubes, × 3·7. 5, SM X.23262; stolonal tube with stolon and collar-shaped fuselli, × 40. 6, SM, X.23262; stolonal tube with branching stolon, × 17·7.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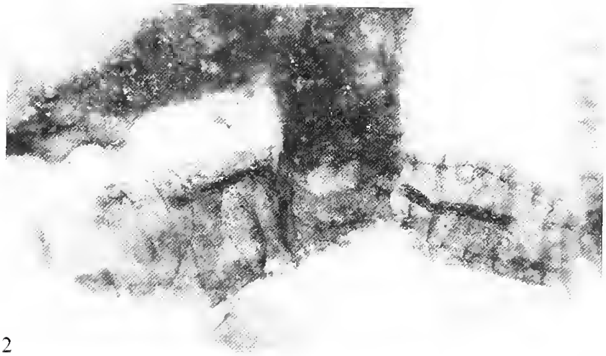
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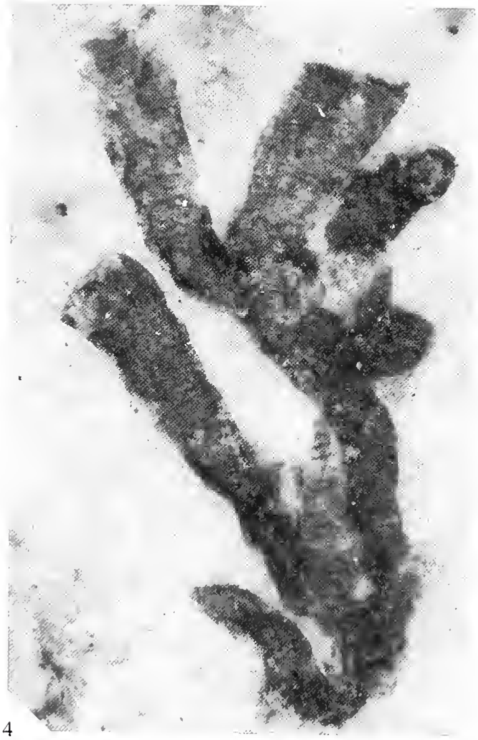
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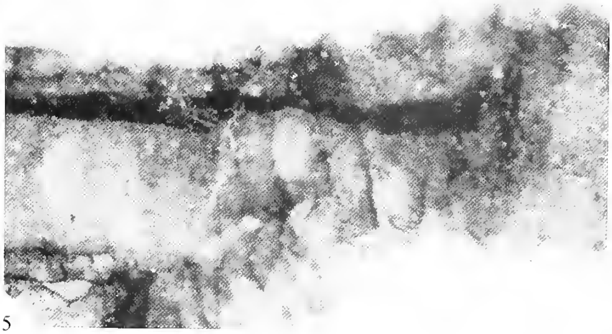
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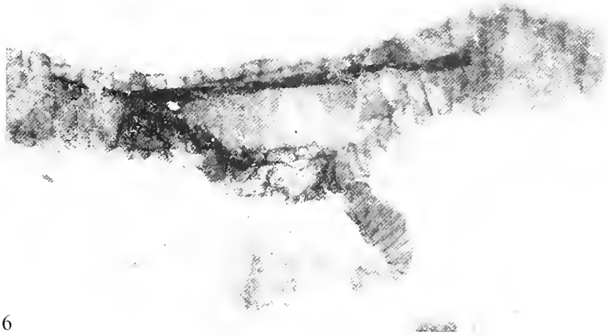
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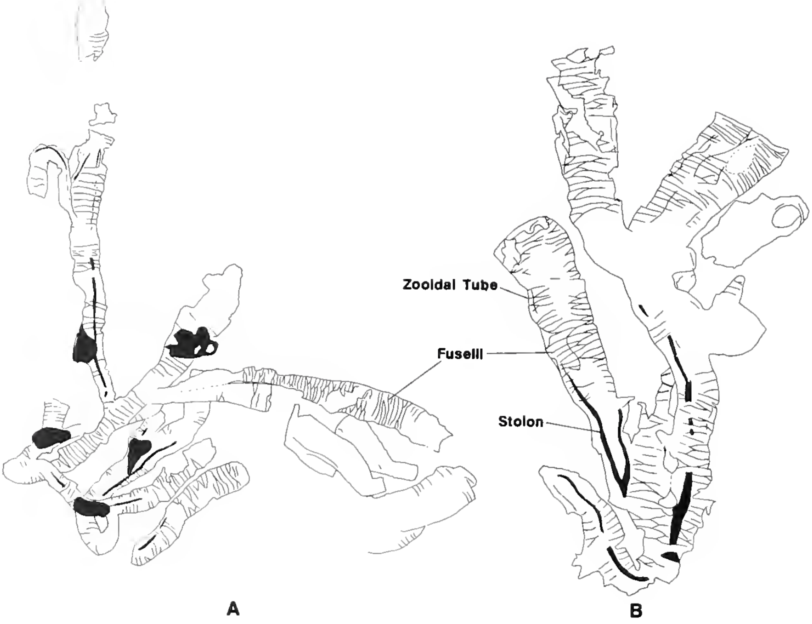
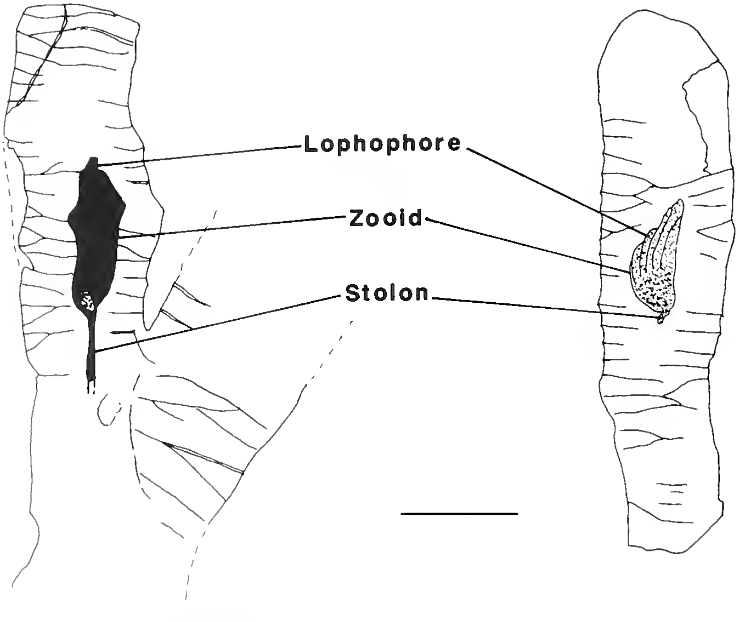
DURMAN and SENNIKOV, *Rhabdopleura*



TEXT-FIG. 2. *Rhabdopleura obuti* sp. nov. showing overall colony arrangement. A, SM X.23262; large dark bodies are probable zooids, × 5. B, SM X.23264; collection of branching zooidal tubes, × 2·5.



TEXT-FIG. 3. Zooids belonging to *Rhabdopleura obuti* sp. nov. SM X.23264. Both zooids occur within zooidal tubes displaying fuselli and possibly exhibit lophophores distally and stolon structures proximally. Scale bar represents 0·5 mm.

1961 (Upper Ordovician, Poland); *Rhabdopleurites primaevus* Kozłowski, 1967 (Ordovician, Poland) and *Kystodendron* Kozlowski, 1959 (Ordovician, Poland)) appear to be very similar to Recent *Rhabdopleura*. However, they are differentiated on the basis of a few characters listed as follows: *R. exspectatus* lacks dormant buds, possesses apertural languettes and the zooidal tubes are attached throughout their length; *R. primaevus* possesses non-fusellar portions, but the sterile buds are missing and it is based on very fragmentary material; and *Kystodendron* (includes *Eorhabdopleura* Kozłowski, 1970) has major stolons and peduncular stolons of cysts of sterile buds which lack diaphragms. We believe that these characters are not sufficient to define taxa separate from *Rhabdopleura*. The characters on which these taxa are defined are often absence characters which are not useful when dealing with fossil material. Clearly, the lack of a character may be simply related to its poor preservation. Additionally, Kozłowski's material was mainly derived from acid isolation techniques which have been useful in obtaining new material but can also cause damage to specimens.

The only other Middle Cambrian rhabdopleurid, *Rhabdotubus johanssoni* Bengtson and Urbanek, 1986 has a very similar appearance to the material described here. *Rhabdotubus* has tubes displaying creeping portions and zooidal tubes which widen distally, with very similar fusellar arrangements. There are lateral branches to the zooidal tubes and the colony sizes are very comparable. However the colonies of *Rhabdotubus* differ by having a more discrete basal structure and also the erect zooidal tubes occur frequently as adnate bundles. *Rhabdotubus* also seems to show a preference for firm substrates such as brachiopod valves, which may be the reason why there is a better developed thecorhiza. There is an absence of stolons or related structures in *Rhabdotubus*, which has been interpreted as a lack of stolon sclerotization (Bengtson and Urbanek 1986).

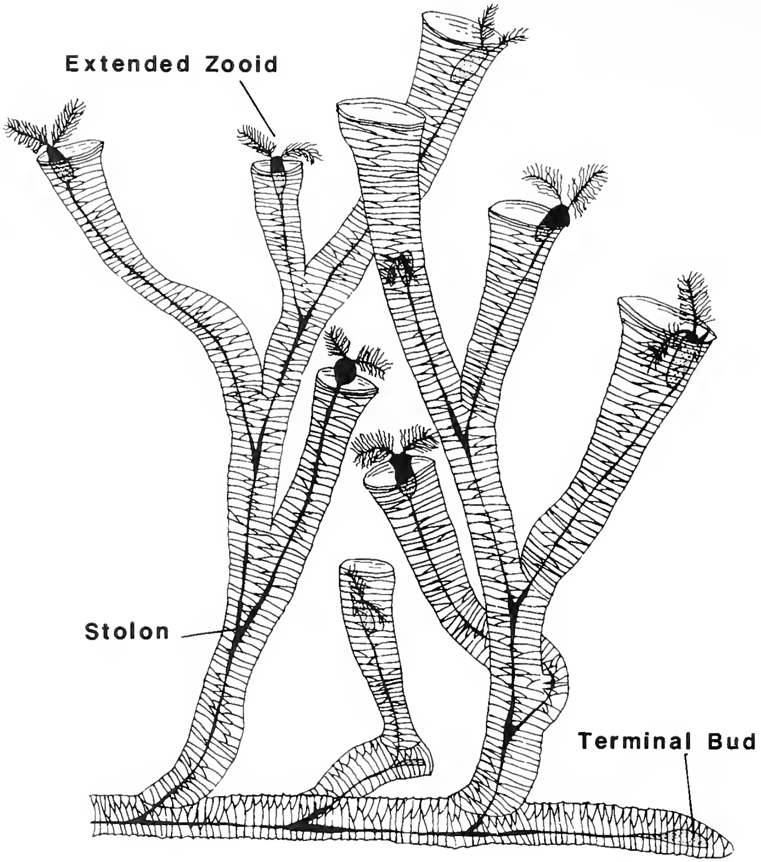
Bengtson and Urbanek (1986) proposed that *Rhabdotubus* is an intermediate form between the rhabdopleuran pterobranchs and the tuboid graptolites with a mosaic of characters from both groups. The main points of evidence that they have for the association with the tuboids are: the striking resemblance of the colony habitus; the occurrence of a ventral apertural lip; and the steady increase of the zooidal tube diameter and the lack of a scelerotized stolon system. *Rhabdopleura obuti* is probably more closely related to Recent rhabdopleurids than *Rhabdotubus*, but also shows some characters that are seen in the tuboid graptolites such as the distally widening tubes. These Middle Cambrian rhabdopleurans provide evidence for the divergence of the rhabdopleurid and tuboid groups which is an important phase of hemichordate evolution.

### *Comparison with* Fasciculitubus *Obut and Sobolevskaya, 1967*

This genus is remarkably similar to *Rhabdotubus* and they are probably synonymous; however, for the present *Fasciculitubus* should merely be removed from the graptolite Idiotubidae to the pterobranch Rhabdopleuridae. It has a very comparable colony habitus with a distinct basal portion and erect cylindrical tubes. Urbanek (pers. comm.) agrees that *Rhabdotubus* and *Fasciculitubus* are very similar.

## *RHABDOPLEURA*: A 'LIVING FOSSIL'

The discovery of rhabdopleurids at this stratigraphical level indicates the remarkably conservative nature of the group. The basic morphology has remained unchanged for 520 Ma, consisting of a series of creeping tubes with erect zooidal tubes and a branching system of sclerotized stolons. This represents one of the oldest 'living fossils', characterized by a low species diversity and a set of morphological traits which persist over an extraordinarily long time range. The existence of 'living fossils' has been considered paradoxical in the sense that changing environments over such a long period would surely have prompted some form of evolutionary change. 'Living fossils' have been considered in terms of rates of evolution. The two main explanations are that slow transformation, producing little anatomical diversity, accounts for low observed taxonomic diversity or, in reverse, that low rates of speciation have slowed the acquisition of morphological diversity (Eldredge 1984).



TEXT-FIG. 4. Reconstruction of *Rhabdopleura obuti* sp. nov. with branching zooidal tubes, bifurcating stolons, terminal bud and feeding zooids. The overall zooid morphology is taken from the preserved material and by comparison with Recent species. The zooids are mainly shown feeding at the tube rims. A dormant bud at the terminal portion is also indicated. The attached portion of the colony is somewhat reduced, with a dichotomizing system of zooidal tubes above. The zooidal tubes show the distally widening tubes with funnel-shaped apertures.

Our understanding of why *Rhabdopleura* is a 'living fossil' is hampered by a limited knowledge of its geographical distribution through time, and the fragmentary fossil record. So, although it is difficult to explain the occurrence of *Rhabdopleura* in terms of evolutionary rates, it is somewhat easier to speculate how this organism has succeeded to defy extinction.

Recent *Rhabdopleura* is commonly found inhabiting cryptic environments such as on the concave surface of bivalve shells. During a dredging study off Stoke Point, Plymouth, 61 per cent of the colonies were found on this inner surface of shells such as *Glycimeris glycimeris* (Stebbing 1970). Observations of colonies in life position at the same locality (by SCUBA diving) revealed that the dead shells were in abundance, and all the separated valves were lying concave side downwards. The specificity of habitat is likely to be related to selection by the larvae on settling, enabled by its mobility, but its exact mode is unknown (Dilly 1973). Other cryptic environments have been utilized such as dead serpulid tubes, in the holes left by the sponge, *Cliona celata*, or in the burrows of boring polychaetes (Stebbing 1970). The cryptic nature of the habitat is clearly advantageous with respect to avoiding predation, adverse conditions etc. and, although *Glycimeris* has not existed as long as

*Rhabdopleura*, there were presumably other suitable host shells during earlier times, such as trilobite moults. 'Living fossils' are often seen to inhabit restricted environments; for example, *Nautilus* lives in deep, fore-reef slope environments. It is thought that *Nautilis* retreated to deeper waters (facilitated by the ability to survive in low-oxygen conditions) to avoid competition with the newly evolved fast-moving fish (Wells *et al.* 1992). Similarly, representatives of the Pleurotomariidae (Gastropoda) are widely known from the Cambrian, but today they are only known from deep water environments ($>200$ m), of low latitudes and hard substrates (Hickman 1984). These groups have been known from much broader environments in the geological past but today are restricted to *refugia*-type environments.

Another factor which may have favoured their survival is the ability to overwinter by encystment. Recent *Rhabdopleura* produce buds consisting of a spherical or ovoid mass of yolky globules which are sometimes enclosed in a darkly pigmented case (Dilly 1975). These have been variously referred to as hibernacula (Lankester 1884), sterile buds (Schepotieff 1907) or dormant buds (Stebbing 1970). There are commonly several dormant buds in each colony. They are formed from the base of the contractile stalks of adult zooids and became separated from them into a chamber in the repent coenoecium by the secretion of a septum across the tube. The material composing the dormant bud wall (which is very similar to graptolite periderm) is clearly very resistant as it is commonly preserved in the fossil record. This resulting yolk store is contributed by many of the zooids in the colony, but it is not clear as to whether this food supply is generally available in times of shortage. It is perhaps more likely that the colony dies back in the winter and that fresh zooids develop from dark cells surrounding the yolk within the bud (Dilly 1975). This adaptation to overwintering has enabled the group to survive through periods of low food levels and other adverse conditions. It is not known how resistant these dormant buds are; perhaps they could survive for several years to produce viable colonies. The acquisition of the dormant buds occurred early in the phylogeny of the group, as it has been proposed that the graptoblasts, associated with the crustoid graptolites, represent structures homologous to dormant buds (Urbanek 1983). Graptoblasts are found as early as the Lower Ordovician. Dormant buds are not found in any of the other Hemichordata; they first appeared in the pterobranchs and were subsequently lost at some point during the evolution of the graptolites (Durman unpublished). Their occurrence in the rhabdopleurids could have been a significant factor for the survival of the group through mass extinctions.

The simple morphology of the rhabdopleurids has allowed substantial ecophenotypic variation enabling adaptation to changing environments. This has been assisted further through its modular development of its colonial habit allowing variability within the colony. The reproductive strategies have also been an aid to its survival. *Rhabdopleura* is able to reproduce sexually (probably during more favourable times) and can bud asexually as part of the growth of the colony and reproduction (during less favourable times). The exact bathymetric range of *Rhabdopleura* is unknown but *R. normani* tends to be a relatively deep water form with *R. compacta* occurring in comparatively shallower waters (Plymouth Sound and the coast of Bermuda, respectively). Although it is most commonly found in cryptic environments, it has also been reported from coarse sandy substrates and even mud. *Rhabdopleura* appears to have quite a wide tolerance of physical conditions, but seems to select cryptic environments over non-cryptic. A combination of the cryptic life habit, a persistent life-cycle strategy and adaptability has allowed the survival of this remarkable genus to the present day.

## HEMICHORDATE ZOOIDS IN THE FOSSIL RECORD

The first account of zooids in the fossil record was by Rickards and Stait (1984; see also Rickards *et al.* 1991) where several zooids were found in the thecae of *Psigraptus jacksoni* (Tremadoc); they are pyritized and preserved in three dimensions. Previous to these accounts, deductions about the size and function of zooids had to be made by comparison with living pterobranchs and by analysis of the structures these zooids made, i.e. the fuselli and cortical bandages of the rhabdosomes (Crowther and Rickards 1977). A recent paper by Sudbury (1991) proposed a formula for the size of the zooid based on its relationship with fusellus height (FH), that is, the graptolite zooid would be 1·5 FH wide and 4·5 FH long. It is quite likely that such a relationship exists as the fuselli are structures secreted by the cephalic shield of the zooid. The discovery of preserved zooid material associated with *Rhabdopleura obuti* is an ideal opportunity to test some of these ideas (Pl. 1, figs 3–4; Text-fig. 3). Measurements of the fusellar heights from a tube containing a zooid range from 67 to 84 μm and average 75 μm. If the formula is applied to these measurements, a zooid measuring 113 μm wide by 338 μm long would be expected to have built the tube. The zooid within the tube measures 200 by 700 μm, about double the dimensions predicted by the formula. If one assumes that the formula is accurate, the measurements represent the size of the zooid that built the tube, suggesting that the zooid has doubled in size following its completion. This increase in size could be related to a change in life functions such as sexual reproduction. Sudbury (1991, p. 384) mentioned that the graptolite zooids of her study appear to produce over large thecae and, she proposed that the tubes were built rapidly and that the construction of fuselli was part of the earlier stages of the ontogeny. After the tube was complete the zooid could then embark on the final stage of its ontogeny, including the production of gonads for sexual reproduction, causing a further increase in zooid size. The measurements here concur with Sudbury's predictions.

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# A NEW EARLY DEVONIAN GALEASPID FROM BAC THAI PROVINCE, VIETNAM

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ABSTRACT. A new large galeaspid, *Bannhuanaspis vukhuci* gen. et sp. nov., is described from the top part of the Si Ka Formation or the base of the Bac Bun Formation (Early Devonian, Late Lochkovian or Early Pragian) in the Phu Luong District, Bac Thai Province, northern Vietnam. The overall shape of its head shield is suggestive of the 'Polybranchiaspidiformes', but this morphology is regarded as a primitive feature for the Galeaspida. Its transversely elongated median dorsal opening, broad posterior margin of head shield and posterolaterally directed main lateral-line are also regarded as primitive galeaspid characteristics. However, it shares with the 'Polybranchiaspidiformes' and Huananaspidiformes a large number of gill openings, and with the Galeaspidiformes very short and rounded cornual processes.

THE Galeaspida, a group of Silurian and Devonian jawless vertebrates endemic to China and Vietnam, were first described by Y. H. Liu (1965), but it is now clear that the small fragments of exoskeleton referred to by Mansuy (1915, pl. 1, figs 2–5) as 'ostracoderme indéterminé', from the Si Ka Formation of Northern Vietnam (Lung Co-Si Ka section) is the earliest known record of this group. Y. H. Liu (1975) restricted the name Galeaspida to the genus *Galeaspis*, and considered this group as allied to the Osteostraci, within the Cephalaspidomorphi. The other jawless vertebrate genus he recorded from the Devonian of China, *Polybranchiaspis*, was thus placed in a group of its own, the Polybranchiaspida, which he regarded as related to the Heterostraci (Y. H. Liu 1975). Halstead Tarlo (1967) lumped the two groups into the Galeaspida, and he was later followed by Janvier (1975) and all subsequent writers. *Galeaspis* turned out to be preoccupied and was replaced by *Eugaleaspis* (Y. H. Liu 1980), but the change of Galeaspida into Eugaleaspida or Galeaspidiformes into Eugaleaspidiformes (Y. H. Liu 1980) was unnecessary, since the rules of nomenclature do not apply to taxa above the family-group level, and since these higher taxa were not preoccupied. Therefore, the names Galeaspida and Galeaspidiformes Liu are retained here.

Besides the fragments collected by J. Deprat around 1910, and described by Mansuy in 1915, the first evidence of determinable galeaspids from Vietnam dates back to 1973, when three incomplete head shields collected by Ta-Thanh Trung in the Si Ka Formation of Tong Vai, Quan Ba district, Ha Giang Province, were sent to China for identification. These have been determined as *Polybranchiaspis* 'nov. sp.', close to *P. liaojaoshanensis* Liu (Ta-Thanh 1978; Pan Jiang, unpublished report to the Institute of Geology and Mineral Resources, Hanoi, 1978). Tông-Dzuy and Janvier (1987), on the basis of photographs, suggested that they might rather belong to *P. gracilis* Cao, 1986, which, however, may well be a mere individual variation of *P. liaojaoshanensis*. The three specimens, quoted as lost by Tông-Dzuy and Janvier (1987), have now been found to be deposited in the Geological Institute of the Academia Sinica, Beijing.

Fragments, scales, or incomplete shields of galeaspids have also been recorded from more southerly localities in Vietnam, namely in Trang Xa (Bac Thai Province: Tông-Dzuy and Janvier 1987), and Dong Mo (Lang Son Province: Tông-Dzuy and Janvier, 1990).

The present description of a new and unusually large galeaspid from Vietnam is based on material collected in 1991 in the locality of Ban Nhuan, Phu Luong district, Bac Thai Province. The specimen belongs to the collection of the Department of Geology of the University of Hanoi (UHDG, VND 50-52).

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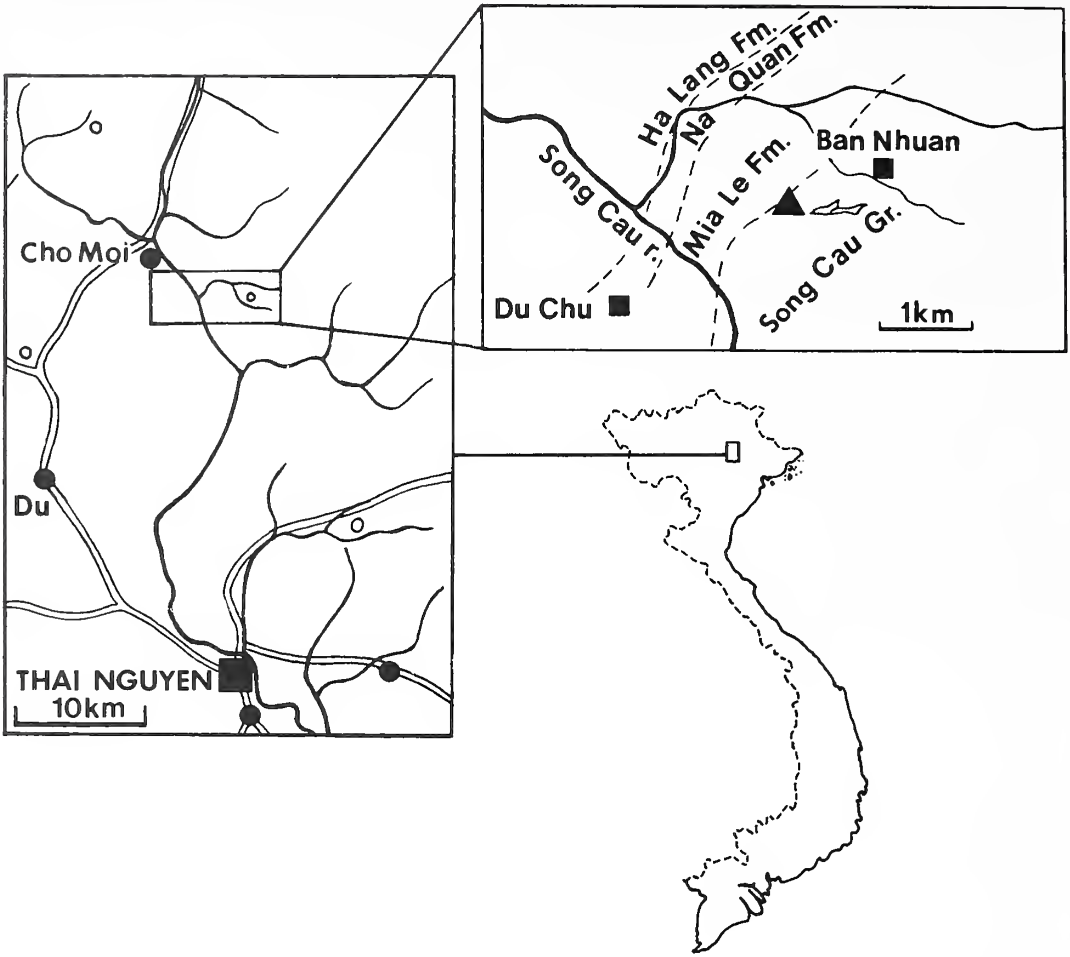


TEXT-FIG. 1. Locality map, showing the distribution of the Song Cau Group and the Mia Le, Na Quan and Ha Lang Formations across the Song Cau river. The galeaspid locality near Ban Nhuan is indicated by a black triangle.

## GEOLOGICAL SETTING

Early Devonian vertebrate faunas of Vietnam occur exclusively in the Si Ka and Bac Bun Formation of the Bac Bo (formerly the Tonkin), both united as the Song Cau Group (Tông-Dzuy 1980). Their age was first believed to be Eifelian (Long 1967), but recent re-examination of the associated or overlying invertebrate faunas (in particular brachiopods and corals) has shown that they were rather Late Lochkovian or Early Pragian in age (Tông-Dzuy 1980; Tông-Dzuy *et al.* 1986; Tông-Dzuy and Janvier 1990). This new dating is also supported by faunal comparisons with the Early Devonian vertebrate-bearing localities of southern China, in particular Qujing, Yunnan, and Liujing, Guangxi. The fish-bearing parts of the Si Ka and Bac Bun Formations could thus be correlated with the lower part of the Cuifengshan Formation of Yunnan or the uppermost part of the Lianhuashan Formation of Guangxi (Pan and Dineley 1988), that is the 'Siegenian' (Upper Lochkovian–Lower Pragian) in the sense of S. T. Wang (1991). Previous work (Pham-Dinh 1967), as well as field investigations carried out since 1985 by the present authors, suggests that there are several fish horizons in the Si Ka and Bac Bun Formations, and that, despite similarities in the higher taxonomic composition, differences at the specific or generic level may be due to slight differences in age rather than to differences in environmental conditions (Tông-Dzuy and Janvier, submitted). The new galeaspid described here from Ban Nhuan, for example, has never been observed in any of the major fish localities of the Bac Bo (Tranx Xa, Dong Mo), even in the form of exoskeletal fragments.

The locality of Ban Nhuan is situated 18 km north east of the town of Du, in the Phu Luong District, approximately 30 km north of Thai Nguyen, on the southern margin of a large Palaeozoic anticlinorium (Text-fig. 1). There, the Si Ka and overlying Bac Bun Formation (Song Cau Group) outcrop at the base of the hills, their top being generally made up of the limestone of the Mia Le and Na Quan Formations and the siliceous shales of the Ha Lang Formation. All these formations are intersected by the Song Cau river. The best exposures occur along the path leading from the Song Cau river to Ban Nhuan, about one kilometre before arriving at the village. There, several bone-beds are clearly visible within the massive dolomitic sandstone of the top of the Si Ka Formation. The large galeaspids described herein occur in a very fine-grained dolomitic sandstone at the top of the formation, probably just below the uppermost bone-bed. This type of sediment corresponds to a low-energy environment which permitted the preservation of the extremely thin and fragile galeaspid exoskeleton. Fragments of exoskeleton with a similar structure occur also in the bone-beds, in association with numerous fragments of plates and scales of yunnanolepid antiarchs and youngolepid sarcopterygians. From the lithology, these fish-bearing beds can be placed near the boundary between the clastic Si Ka Formation and the dolomitic Bac Bun Formation.

These large galeaspid shields are associated with some antiarch plate fragments, one of which could be determined as an anterior ventrolateral plate of *Yunnanolepis* sp.

## SYSTEMATIC PALAEONTOLOGY

Class GALEASPIDA Liu, 1965
Order and Family undetermined
Genus BANNHUANASPIS gen. nov.

*Derivation of name*. After Ban Nhuan, the type locality of the type species.

*Type species*. *Bannhuanaspis vukhuci* sp. nov.

*Diagnosis*. As for the type species

### *Bannhuanaspis vukhuci* sp. nov.

Text-figs 2–6

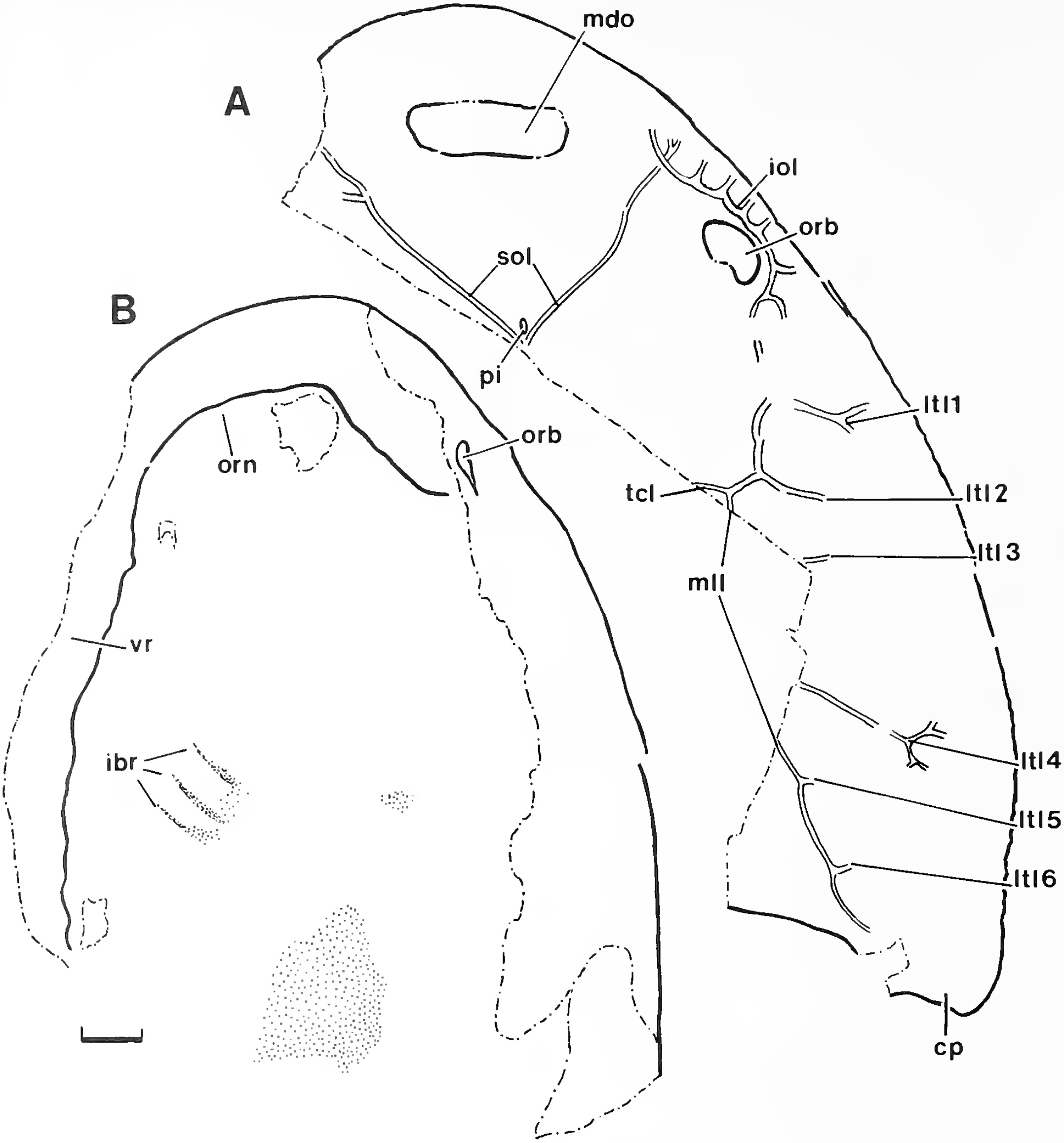
*Derivation of name*. The species is dedicated to Dr Dang Vu Khuc, Geological Museum, Hanoi.

*Diagnosis*. A very large polybranchiaspidid-like galeaspid, with orbits situated close to the shield margin and a transversely elongated median dorsal opening. The maximum breadth of the shield is situated in its rearmost part.

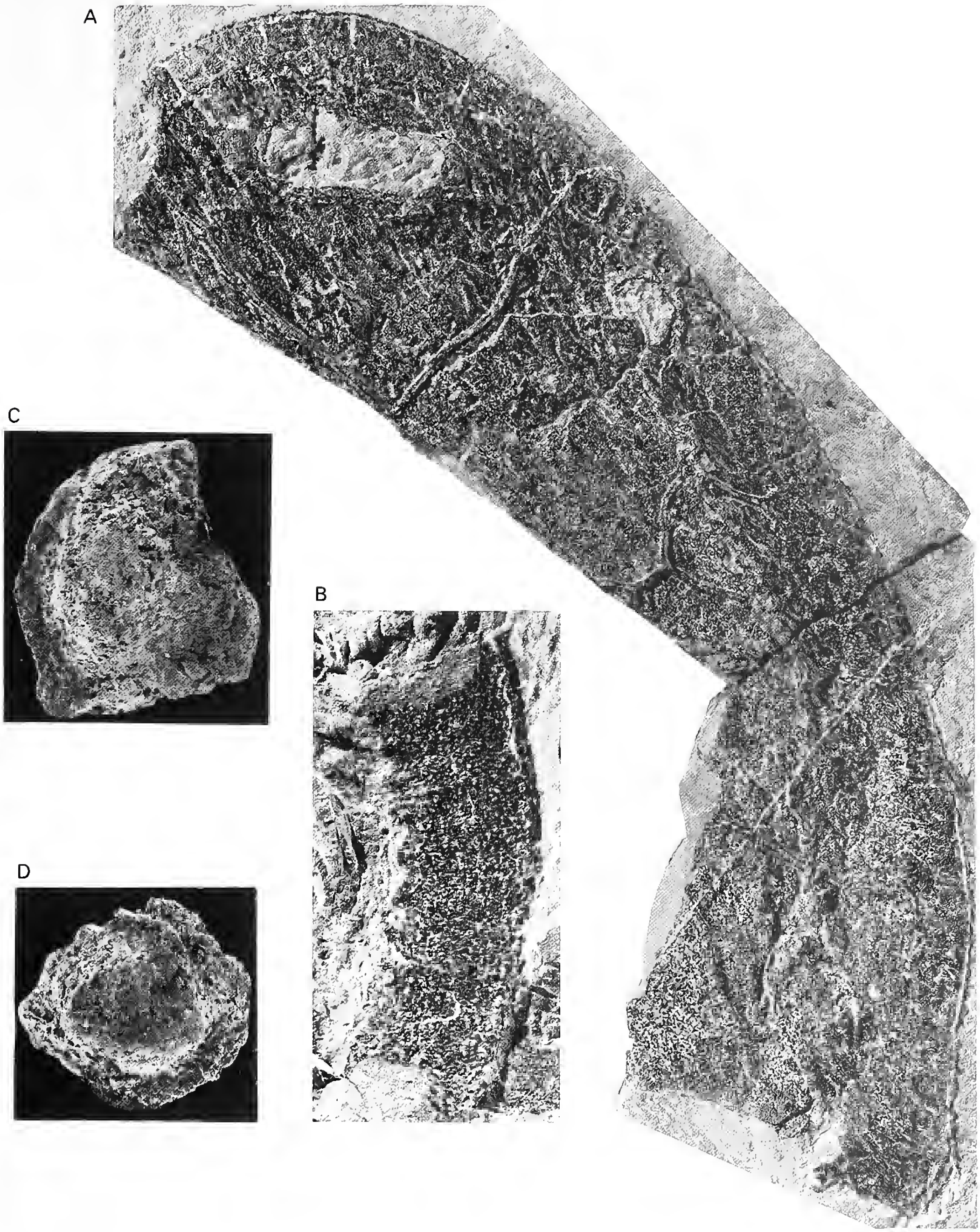
*Holotype*. An incomplete head shield (University of Hanoi, Department of Geology, VND 50; Text-figs 2, 3A), part and counterpart.

*Type locality*. Ban Nhuan, North East of Du, Phu Luong District, Bac Thai Province, Vietnam (Text-fig. 1)

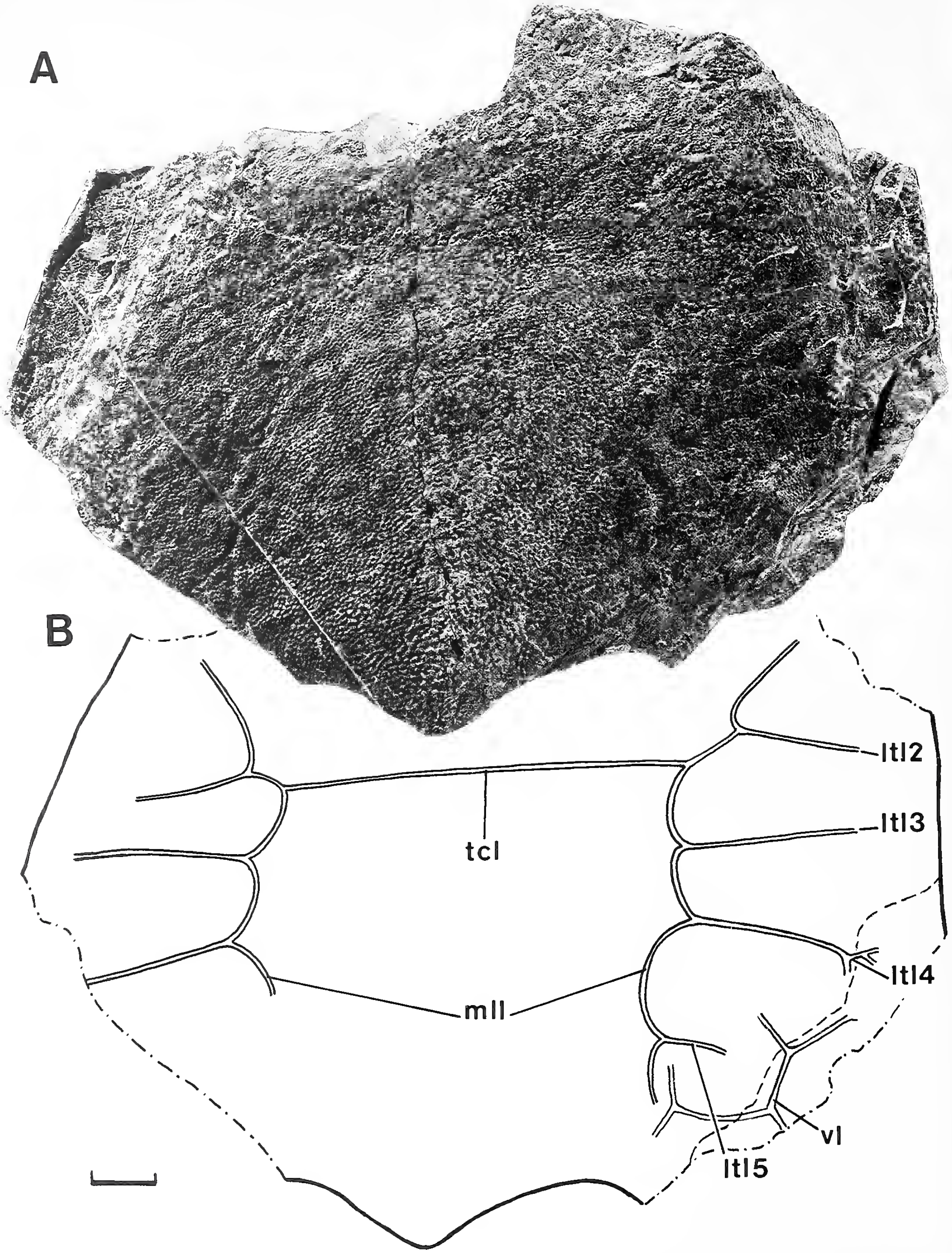
*Type horizon*. Uppermost part of the Si Ka Formation or lowermost part of the Bac Bun Formation, Lower Devonian, Late Lochkovian to Early Pragian.



TEXT-FIG. 2. *Bannhuanaspis vukhuci* gen. et sp. nov. Lower Devonian (Late Lochkovian to Early Pragian), top part of Si Ka Formation or base of the Bac Bun Formation; Ban Nhuan, Phu Luong district, Bac Thai Province, Vietnam; holotype (VND 50); interpretive scheme of head shield. A, dorsal part of incomplete dermal head shield in ventral view, showing the canals of the sensory-line system. B, counterpart of the latter specimen, showing part of the marginal region and ventral rim of the dermal head shield in dorsal view; traces of perichondral bone from endoskeleton dotted. Scale bar = 10 mm. Abbreviations: *cp*, cornual process; *ibr*, trace of interbranchial ridges; *iol*, infraorbital portion of main lateral line; *ltl 1–6*, lateral transverse lines; *mdo*, median dorsal opening; *mll*, main lateral-line; *orb*, orbit; *orn*, oral notch; *pi*, pineal foramen; *sol*, supraorbital line; *tcl*, transverse commissural line.



TEXT-FIG. 3. *Bannhuanaspis vukhuci* gen. et sp. nov. Lower Devonian (Late Lochkovian to Early Pragian), top part of Si Ka Formation or base of the Bac Bun Formation; Ban Nhuan, Phu Luong District, Bac Thai Province, Vietnam. A, Incomplete head shield (holotype, VND 50), exoskeleton in ventral view (for interpretation see Text-fig. 2A), × 1. B, fragment of ventral rim of head shield (VND 52), showing branchial notches, (for interpretation see Text-fig. 5A), × 1. C–D, isolated scales of the body squamation, associated with the holotype; scanning electron micrographs of the external surface, × 50.


A
B
ltl2
tcl
ltl3
ltl4
mll
vl
ltl5

*Referred material*. Posterior median dorsal part of the head shield (VND 51, Text-figs 4, 5A), isolated fragment of ventral rim of the shield (VND 52, Text-fig. 3B, Text-fig. 5A) isolated scales in association with the latter specimens (Text-fig. 3C–D).

*Remarks*. *Bannhuanaspis vukhuci* is one of the largest known galeaspids, together with the primitive Silurian genus *Hanyangaspis* (N. Z. Wang 1986), *Dongfangaspis major* (Y. H. Liu 1975) and *Antiquisagittaspis* (Y. H. Liu 1985). Its closest overall resemblance is to *Polybranchiaspis*, from which it differs however by the more lateral position of the orbits, the more posteriorly placed and more transversely elongated median dorsal opening, the broader posterior limit of the head shield, and its larger size. Although the sensory-line pattern is broadly similar to that of *Polybranchiaspis*, it differs from the latter in that the posterior part of the main lateral-line is posterolaterally – and not posteriorly – directed (*mll*, Text-figs 2A, 4B). This feature was previously known only in *Hanyangaspis* and *Xinshuiaspis* (N. Z. Wang 1991).

The question of the systematic position of *Bannhuanaspis* can only be answered in the context of the question of the monophyly of the 'Polybranchiaspidiformes', which will be briefly discussed below.

*Description*. The holotype VND 50 is a slightly distorted and incomplete head shield, the dorsal aspect of which is known from the ventral surface of the dorsal exoskeleton (Text-figs 2A, 3A). The canals of the sensory-line system, which, in galeaspids, lie against the basal surface of the exoskeleton (Janvier 1990), are thus clearly visible. The median dorsal opening (*mdo*, Text-fig. 2A) is transversely elongated, roughly rectangular in shape, with rounded angles, and situated relatively far behind the anterior margin of the shield. One of the orbits is visible on the left side, although slightly distorted by crushing (*orb*, Text-fig. 2A). A pineal foramen is present (*pi*, Text-fig. 2A).

The posterior median dorsal shield fragment VND 51 (Text-figs 4, 5A), which was used for completing the reconstruction in Text-figure 5B, exhibits the dorsal surface of the exoskeleton. Therefore, no sensory-line canal is visible in external aspect, beside a minute series of slits by which these canals open to the exterior (Text-fig. 6). The pattern of these canals in this specimen could, however, be traced on a radiograph (Text-fig. 4B). This specimen, which is similar in size to the holotype, and which was found in the same block, could be assembled to the latter, thanks to the position of the posterior margin of the shield and of the transverse commissural sensory-line canal (*tcl*, Text-figs 2A, 4B). Clearly, there is only one commissural canal, a condition which is regarded as a synapomorphy of all the galeaspids, apart from *Dayongaspis*, *Xinshuiaspis* and *Hanyangaspis* (Janvier 1984; N. Z. Wang 1991). There are probably six lateral transverse sensory-lines (*ltl 1–6*, Text-figs 2A, 4B). The infraorbital portion of the main lateral-line (*iol*, Text-fig. 2A) sends off numerous side-branches toward the shield margin, and is connected anteriorly with the distal part of the supra-orbital line (*sol*, Text-fig. 2A). Although no sensory-line canal has ever been reported in the ventral exoskeleton of the Chinese galeaspids, this specimen clearly shows such a canal extending on the lateral part of the dermal postbranchial bar and of the ventral rim (*vl*, Text-figs 4B, 5B1). It displays a zig-zag pattern which differs from that of the dorsal lateral-line canals.

The posterior margin of the shield is remarkably broad, with only shallow embayments on either side of a median dorsal process. There is no distinct median dorsal crest, but a slight median elevation in the rearmost part of the shield. Laterally, the posterior margin of the shield is produced into a slight lobe, which may have extended beyond the level of the body and may represent an incipient cornual process (*cp*, Text-fig. 2A).

The ventral surface of the head shield is known from the counterpart of the holotype, which displays a slight oral notch (*orn*, Text-figs 2B, 5B), and from the ventral side of isolated median shield fragment, which shows part of the ventral rim of the oralobranchial fenestra (*vr*, Text-fig. 5A). With this specimen, there is also an isolated portion of ventral rim detached from another shield (Text-figs 3B, 5A). These latter two specimens clearly show the series of branchial notches (*brn*, Text-fig. 5A–B), which are quite numerous and suggest thus a condition comparable to that in *Polybranchiaspis* or *Duyunolepis*, though the precise number of these notches

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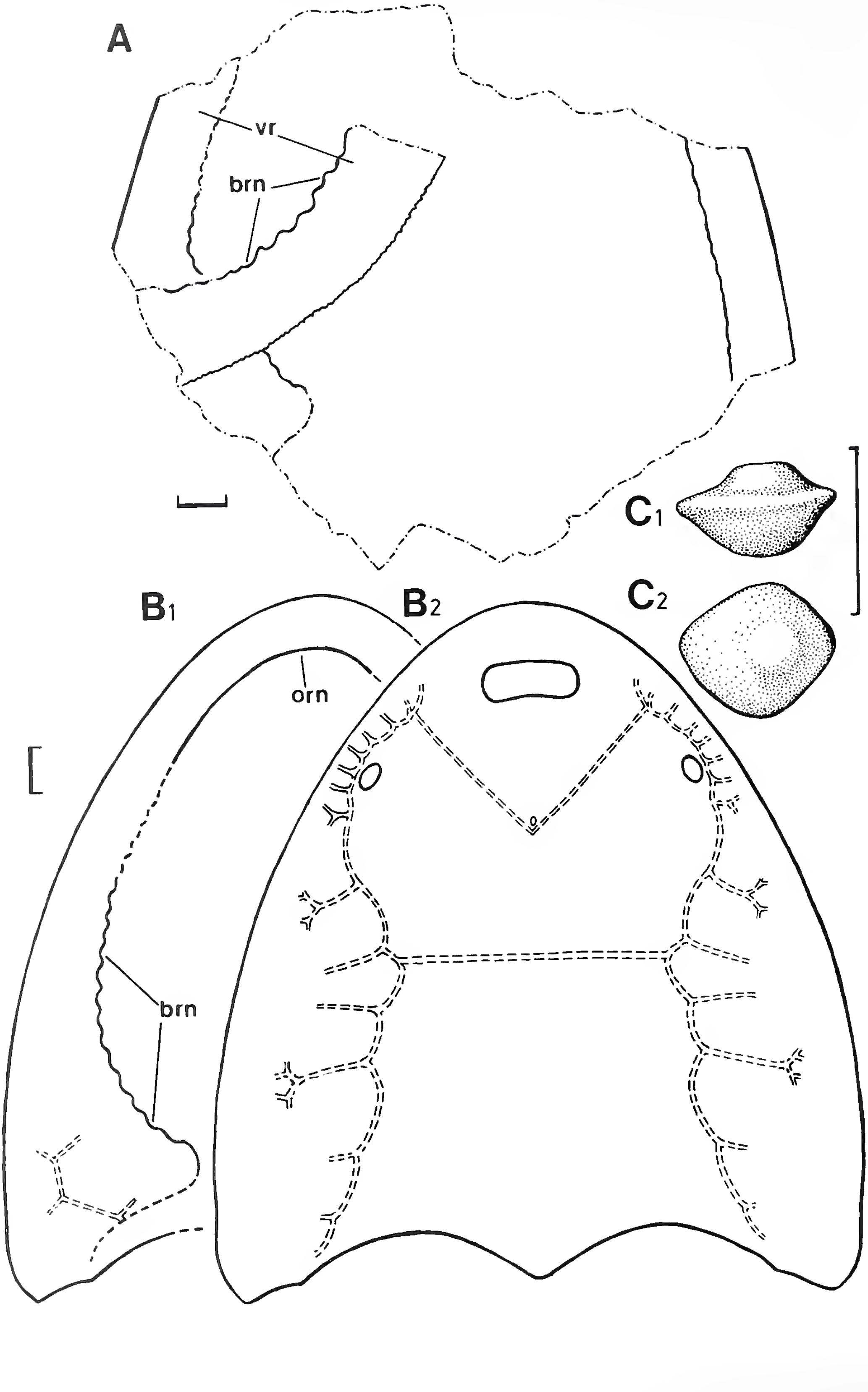
TEXT-FIG. 4. *Bannhuanaspis vukhuci* gen. et sp. nov. Posterior median part of head shield (VND 51), same locality and level as the holotype. A, specimen in dorsal view, showing the external aspect of the exoskeleton, and some sensory-line canals of the ventral exoskeleton on the right side. B, distribution of the sensory-line canals, based on a radiograph of the specimen. Scale bar = 10 mm. Abbreviations: *ltl 2–5*, lateral transverse lines; *mll*, main lateral-line; *tcl*, transverse commissural line; *vl*, ventral sensory-lines.


A
vr
brn
C1
C2
B1
B2
orn
brn

remains unknown (Text-fig. 5B1). The dermal postbranchial bar does not seem to be complete (Text-fig. 5A, B1). The dermal covering of the oralobranchial fenestra is unknown.

Some slight traces of perichondral bone from the endoskeleton are visible in the counterpart of the holotype, within the sediment which fills the oralobranchial fenestra. A series of transverse strands of perichondral bone may represent traces of the interbranchial ridges of the roof of the oralobranchial chamber (*ibr*, Text-fig. 2B).

The organization of the exoskeleton is quite similar to that described in *Polybranchiaspis* sp. by Janvier (1990) and N. Z. Wang (1991). It consists of loosely assembled, minute dermal units, each of which bears a single tubercle covered with a shiny hard tissue (possibly an enameloid). The exoskeleton is completely recrystallized and its microstructure cannot be studied.

Numerous scales occur in the sediment in association with the shields, sometimes arranged into parallel series which suggest that they retain their original position, as described by S. F. Liu (1983) in *Eugaleaspis*. All the scales are minute rounded units (Text-figs 3C–D, 5D–E), quite similar in shape and structure to the individual units of the dermal head shield. They have no pulp cavity and bear a single boss, or tubercle (Text-fig. 5C) covered with a shiny hard tissue (Text-fig. 3D).

## DISCUSSION

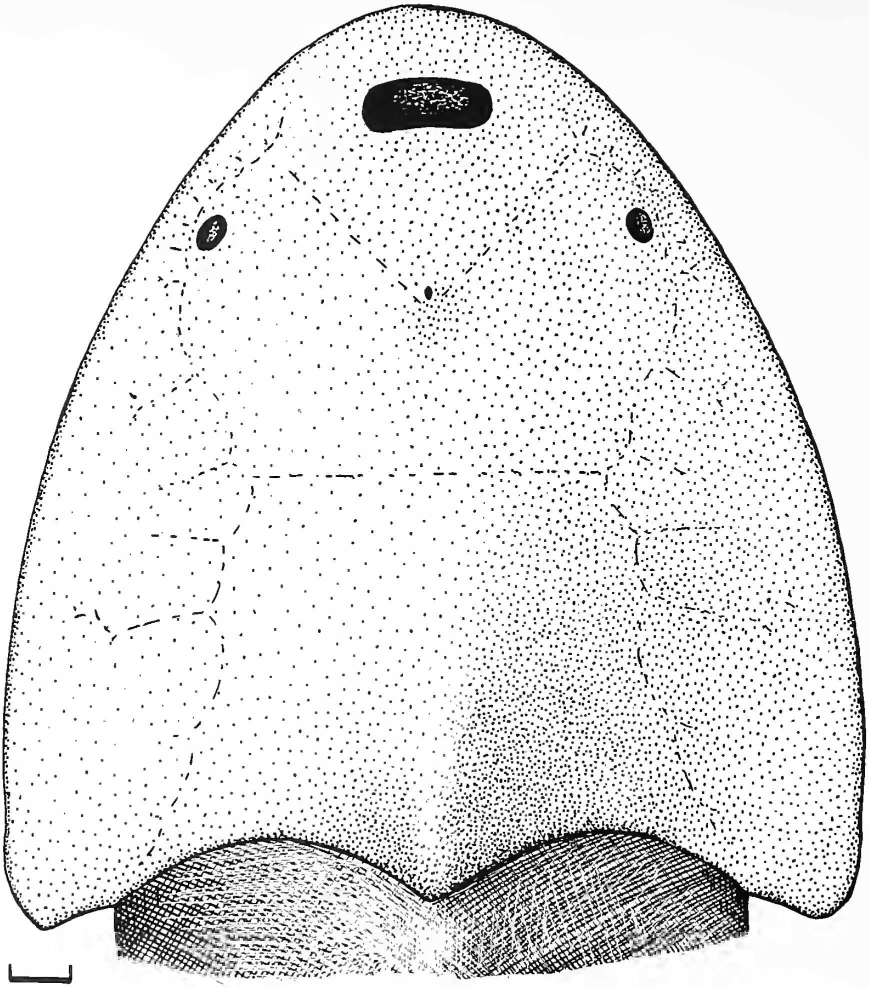
The phylogenetic interrelationships of the Galeaspida have been briefly discussed by Janvier (1984), S. F. Liu (1986) and in more detail by N. Z. Wang (1991). The first question that arises in this connection is that of the sister-group of the Galeaspida, which may serve as an out-group to evaluate character-state polarities. The Galeaspida have been regarded as the sister group of the Osteostraci (Janvier 1975; Halstead 1982; Young 1991), the Osteostraci+Gnathostomata (Forey 1984; Janvier 1984; Maisey 1986), the Gnathostomata alone (N. Z. Wang 1991), or also in a trichotomy with the Osteostraci and Gnathostomata (Young 1991, as a second possibility).

The current classification of the Galeaspida comprises four orders: the Hanyangaspidida: (*Hanyangaspis*, *Xiushuiaspis*, *Dayongaspis*); the Polybranchiaspidiformes (*Polybranchiaspis*, *Dongfangaspis*, *Diandongaspis*, *Laxaspis*, *Damaspis*, *Siyingia*, *Cyclodiscaspis*, *Duyunolepis*, *Paraduyunaspis*, *Neoduyunaspis*); the Huananaspidiformes (*Huananaspis*, *Asiaspis*, *Nanpanaspis*, *Lungmenshanaspis*, *Sanqiaspis*, *Sanchaspis*, *Wumengshanaspis*, *Sinoszechuanaspis*); and the Galeaspidiformes (*Eugaleaspis*, *Sinogaleaspis*, *Yunnanogaleaspis*, *Meishanaspis*, *Tridensaspis*). In addition, there are some genera *incertae sedis*, based on too poorly preserved material (*Antiquisagittaspis*, *Kwangnanaspis*, *Qingmenaspis*).

The Hanyangaspidida and the Polybranchiaspidiformes are most probably paraphyletic. *Hanyangaspis* is now regarded as being the sister-group of all other Galeaspida (Janvier 1984). The Polybranchiaspidiformes cannot be defined on the basis of a unique derived characteristic.

The number of characters available to reconstruct galeaspid phylogeny is quite limited because of the generally poor preservation of the specimens. They are: (1) the shape and position of the median dorsal opening, (2) the position of the orbits, (3) the overall shape and proportions of the head shield, (4) the pattern of the sensory-line canals, and (5) the number of gill openings or corresponding gill compartments. Features of the internal anatomy and ventral dermal covering of the oralobranchial chamber are so rarely preserved, and apparently so homogeneous throughout the entire group (apart from the more or less sinuous course of the dorsal jugular vein or the extension of the dorsal wall of the abdominal cavity), that they are not considered at the moment to be useful for unravelling the relationships within the Galeaspida. However, there are probably more characters to be found in the ventral dermal covering of the head shield, but this remains poorly known.

TEXT-FIG. 5. *Bannhuanaspis vukhuci* gen. et sp. nov. A, drawing of the ventral side of the specimen in Text-figure 2, showing part of the ventral rim of the dermal head shield, as well as a fragment of the ventral rim of a presumably different specimen of the same species (VND 52). B, reconstruction of dermal head shield in ventral (B1) and dorsal (B2) aspect, with the pattern of the sensory-line canals reconstructed on the basis of the specimens in Text-figures 2 and 4. C, reconstruction of an isolated body scale in lateral (C1) and external (C2) view. Scale bar: A–B = 10 mm, C = 1 mm. Abbreviations: *brn*, branchial notches; *orn*, oral notch; *vr*, ventral rim.



TEXT-FIG. 6. *Bannhuanaspis vukhuci* gen. et sp. nov., reconstruction of the head and anterior part of trunk squamation in dorsal view. Scale bar = 10 mm.

Out-group comparison does not tell us much of the plesiomorphic state of most of these characters. The median dorsal opening is apparently unique to the Galeaspida. Although Janvier (1981, 1984) regarded it as homologous to the nasopharyngeal duct of hagfishes and to the presumed prenasal sinus of the Heterostraci. In this case, the closer this median dorsal opening is to the anterior shield margin, the more plesiomorphic it is. *Hanyangaspis*, in which this opening is almost terminal in position, would thus show the most generalized condition for the Galeaspida. Moreover, a transversely elongated opening (as in *Hanyangaspis*) would be plesiomorphic relatively to an oval, elliptic, rounded, heart- or slit-shaped opening, if evaluated by reference to the Heterostraci. Conversely, the rounded opening of *Dayongaspis* would be plesiomorphic if assessed by reference to hagfishes.

The generalized position of the eyes for the vertebrates is a lateral position, and the dorsally placed eyes of some galeaspids is thus presumably derived. Therefore, the more laterally placed the eyes are, the more plesiomorphic is the condition. This condition is again met with in *Hanyangaspis* and possibly in a few other galeaspid taxa (*Cyclodiscaspis*, *Sanqiaspis*, *Huananaspis*).

The overall shape and proportions of the head shield are quite diverse in galeaspids, and the elongated shape of the head shield of *Hanyangaspis* recalls strikingly that of the head in many thelodonts (e.g. *Turinia*), a group of supposedly jawless vertebrates regarded as an ensemble of generalized primitive vertebrates. This might be an indication that the morphology of *Hanyangaspis* is closest to the plesiomorphic state for the galeaspids. The 'Polybranchiaspidiformes' would thus be slightly derived, relatively to *Hanyangaspis*, in having a somewhat narrower and more oval shield, some of them having, in addition, a deep posterior median embayment. In this respect, the shield shape of *Bannhuanaspis*, with its wide and shallow posterior embayment, would be closer to that of *Hanyangaspis* than to that of other 'Polybranchiaspidiformes'.

The pattern of the sensory-line canals is unique to the Galeaspida, with a typically festooned pattern of the main lateral-line, but the supraorbital lines, meeting behind the pineal foramen, may be regarded as a generalized vertebrate feature. Yet, these lines seem to be lacking in *Hanyangaspis*, *Dayongaspis* and *Xiushuiaspis* (see, however, contradictory interpretations in Y. H. Liu 1986). The sensory-line canal pattern in quite homogeneous in all galeaspids, yet with minor differences, such as the connection between the supraorbital and medial longitudinal lateral lines in the Eugaleaspidiformes (Y. H. Liu 1986), or the presence of two transverse commissural lines in *Dayongaspis*, *Xiushuiaspis* and *Hanyangaspis*, a feature regarded by Janvier (1984) as plesiomorphic and N. Z. Wang (1991) as apomorphic. In fact, several transverse commissural canals occur in primitive heterostracans, osteostracans and gnathostomes (Y. H. Liu 1986). The presence of a single commissural canal in all galeaspids except these three genera may thus be regarded as apomorphic. In some galeaspids, the distal end of the lateral transverse canals, branching off laterally from the main lateral-line canal, seems to display a peculiar star-shaped pattern which may be unique to a monophyletic group within the 'Polybranchiaspidiformes', and which would thus include *Laxaspis*, *Diandongaspis*, *Cyclodiscaspis*, and *Dongfangaspis*. Such a structure has not been observed in *Bannhuanaspis*, although the distal end of the transverse canals is branched (Text-fig. 2A).

The number of external branchial openings or branchial compartments varies from seven to ten in most Silurian and Devonian jawless vertebrates (Heterostraci, Osteostraci, Thelodonti), except in the Anaspida, where it may reach fifteen or more. In the Galeaspida, *Hanyangaspis* and *Xiushuiaspis* possess only seven branchial openings or branchial compartments (N. Z. Wang 1986, 1991). In most other galeaspids, except the Galeaspidiformes (*Sinogaleaspis*, *Yunnanogaleaspis*, *Eugaleaspis* and possibly *Tridensaspis*), the number of gill openings and branchial compartments is very high (up to twenty-four pairs in *Paraduyunaspis*). The phylogenies of the Galeaspida proposed by Janvier (1984) and N. Z. Wang (1991) both imply the paraphyly of the 'Polybranchiaspidiformes' and a reversal to a low number of branchial compartments in the Galeaspidiformes (six or seven: Y. H. Liu 1975; Pan and Wang 1980). In both phylogenies, the sister-group of the Galeaspidiformes is the Huananaspidiformes, which are characterized by a rostral process, but clearly possess a much higher number of branchial compartments (Y. H. Liu 1975; Pan and Wang 1981). The two groups share cornual processes, that is, lateral expansions of the lateral shield margin. This supposedly reversed condition of the Galeaspidiformes with respect to the number of gill openings is in contradiction with their early occurrence (Late Wenlockian), together with rather plesiomorphic galeaspid genera such as *Xiushuiaspis*. It would be premature, at this level of knowledge of galeaspid anatomy, to produce one more phylogeny of the Galeaspida, and the remarks above are only aimed at showing that, if one considers *Hanyangaspis*, *Xiushuiaspis* or *Dayongaspis* (or all three: see N. Z. Wang 1991) as the sister-group of all other galeaspids, one may recognize among the latter two major monophyletic groups: the Huananaspidiformes, possessing a rostral process, and the Galeaspidiformes, possessing a short head shield and a slit-shaped median dorsal opening. In contrast, the 'Polybranchiaspidiformes' cannot be defined on the basis of a unique character, their oval shield shape being most probably plesiomorphic, as it occurs also in *Xiushuiaspis*, and they have a large number of gill openings, like the Huananaspidiformes. *Bannhuanaspis* shares with the Galeaspidiformes a posteriorly broad head shield with short cornual processes, and with the 'Polybranchiaspidiformes' and Huananaspidiformes a large number of gill openings. The transversely (yet moderately) elongated median dorsal opening is a general galeaspid feature, variously modified within this group. Although *Bannhuanaspis* possesses a single transverse commissural canal which puts it among 'higher' galeaspids ('Polybranchiaspidiformes'+Huananaspidiformes+Galeaspidiformes), it seems to retain a posterolaterally directed main lateral-line, a feature found with certainty only in *Hanyangaspis*, *Xiushuiaspis* and possibly *Dayongaspis*, thus, most probably a general galeaspid character.

## CONCLUSION

*Bannhuanaspis vukhuci* is an unusually large galeaspid from the uppermost part of the Late Lochkovian to Early Pragian Si Ka Formation of Bac Bo (Vietnam). Its closest overall resemblance is with the 'Polybranchiaspidiformes' of the Early Devonian of China. However, it differs from all the genera classically included in the latter group by its transversely elongated median dorsal opening, laterally-placed orbits, and broad posterior shield margin with small cornual processes. *Bannhuanaspis* is more advanced than *Hanyangaspis*, *Xiushuiaspis* and *Dayongaspis* in possessing a single transverse commissural sensory-line. It shares with the Galeaspidiformes a posteriorly broad head shield with short cornual processes, and with the 'Polybranchiaspidiformes' and Huananaspidiformes a large number of gill openings. Its transversely elongated median dorsal opening, rather laterally placed orbits and posterolaterally directed main lateral-line are all generalized galeaspid characters.

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# SEXUAL DIMORPHISM IN MID-CRETACEOUS HEMIASTERID ECHINOIDS

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ABSTRACT. Fossil hemiasterid echinoids of *Hemiaster* (*Leymeriaster*) are sexually dimorphic, females having wider gonopores than males. No other conspicuous morphological differences permit the two sexes to be distinguished, but in certain populations females achieve larger sizes than males and consequently seem hypermorphic.

SEXUAL dimorphism, common in modern echinoids, in many cases affects only gonopore size (Smith 1984) with specimens considered to be female having wider genital pores (e.g. David *et al.* 1988). However, a few species living in cold or deep waters show more spectacular types of sexual dimorphism, a commoner one being the presence of marsupia on the female test (Pearse and McClintock 1990; Schatt and Féral 1991). Another type of morphological sexual dimorphism, recently discovered by David and Mooi (1990), is the presence of internal brooding pouches in the female test of Antarctic urechinid echinoids.

Of these different types of sexual dimorphism, only the last is still unknown in fossil species. Indeed, the size of genital pores has been described as a sexually dimorphic character for several fossil clypeasteroids (Kier 1967, 1968, 1969) and for a few cassiduloids (Philip 1963; Kadil'nikova and Moskvin 1984). Moreover, Kier (1969) and Philip and Foster (1971) have reported the presence of marsupia in fifteen Cretaceous and eleven Cenozoic species, including arbacioids, clypeasteroids, spatangoids and one phymosomatoid.

Apart from the Maastrichtian spatangoid *Cyclaster platornatus* from Belgium (Jagt and Michels 1990), which are as sexually dimorphic as the Tertiary species of *Cyclaster* (Henderson 1975), almost all dimorphic Cretaceous echinoids are regular species (Kier 1969). So, until now, only allusions to sexual dimorphism have been made by palaeontologists studying Cretaceous hemiasterids (see below). This paper presents the first example of conspicuous sexual dimorphism among these fossil spatangoid echinoids.

## PREVIOUS ALLUSIONS TO SEXUAL DIMORPHISM IN FOSSIL HEMIASTERID ECHINOIDS

Lambert (1889) distinguished between North European species of Cretaceous hemiasterids, with petals flush with the test as in *Hemiaster* (*Bolbaster*) *nasutulus*, and North African species, with deep ambulacra excavated like a marsupium as in *Mecaster latigrunda*. However, he used the term 'marsupium' in a descriptive way, never introducing the notion of sexual dimorphism and brooding pouches. Gauthier (1902) defined a morphological variety of *Mecaster noemiae*, named '*gulgulensis*', which was more extended posteriorly than typical specimens, and was also more inflated. Because this variety had fundamental similarities of ambulacra, peristome and periproct with *Mecaster noemiae*, Gauthier supposed that its morphological differences from the typical specimens might be sexual differences. Moreover, Fourtau (1911) described, among other Turonian echinoids from Egypt, two species of *Mecaster*, *M. aly* and *M. lumei*, considering the first to be male, and the second female. A few years later, Lambert (1913) noticed the presence of morphologically intermediate specimens and ironically asked if they corresponded to hermaphrodites. Finally,

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Devriès (1960) considered that the petals of *Mecaster fourneli* were sufficiently excavated to act as marsupia, developing the hypothesis introduced by Lambert (1933) for a single small *M. fourneli* with deep ambulacra. None of these authors founded their interpretations on biometric analysis or genital characteristics.

Only Cottreau (1922) has presented a detailed example of morphological dimorphism among fossil hemiasterids, describing dimorphism in *Hemiaster* (*Bolbaster*) *madagascariensis* relating to the shape of the test. The species comprised two morphological groups, one corresponding to individuals with a slightly inclined aboral surface, a non-angular posterior edge between non-divergent petals, and a weakly posterior apical system; the other, with an angular, more inclined test with a short and hard posterior edge, and conspicuously posterior apical system. Cottreau found no morphologically intermediate specimens and thought that differences between the two groups corresponded to a sexual dimorphism. Unfortunately he gave no information about the gonopore size and therefore no genital dimorphism can be associated with these morphological differences.

## SEXUAL DIMORPHISM IN CENOMANIAN–TURONIAN HEMIASTERIDS

### *Material and methods*

To test the hypotheses of sexual dimorphism in hemiasterid echinoids, numerous species of these spatangoids have been subjected to biometric analysis. Three examples are selected to illustrate the main results: (1) *Hemiaster* (*Leymeriaster*) *similis* from the Upper Cenomanian of the west coast of France (fifty-five specimens from Port-des-barques, Charente-Maritime, and thirty-three others from Challans-Commequiers, Vendée); (2) *H.* (*L.*) *leymeriei* from the Lower Turonian of west-central France (thirty-seven specimens from Briollay, Anjou); and (3) *Mecaster cenomanensis* from the Lower Cenomanian of Charente-Maritime, west coast of France (seventy-five specimens). For each species, several populations have been biometrically analysed to detect interpopulational and intraspecific differences.

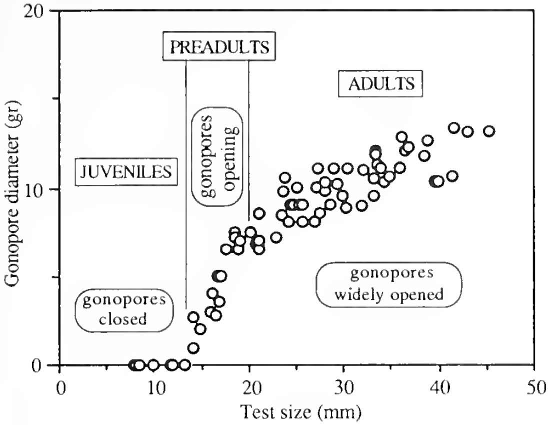
For each species, all the specimens of a single population come from one thin lithological unit of a single outcrop. In order to analyse homologous measurements statistically, the gonopore sizes as a whole correspond to the right posterior genital pore. Its largest diameter was measured with an ocular micrometer. After the distinction of genital dimorphism, several morphological parameters, particularly the shape of test and ambulacra, have been analysed in relation to the gonopore diameter to detect possible secondary sexual differences between males and females.

The material used in this study is housed in Centre des Sciences de la Terre, Université de Dijon (STD).

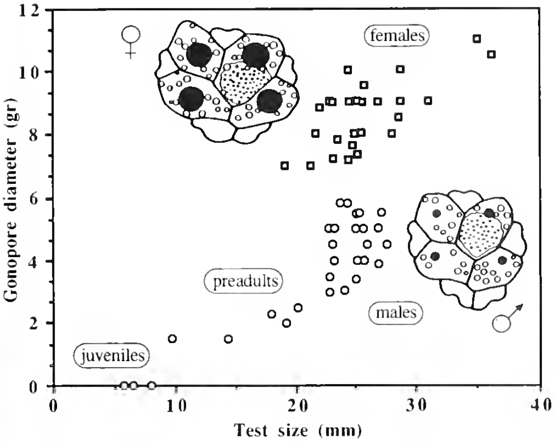
### *Biometric results and interpretations*

*Sexual maturity and relative age of fossil hemiasterid echinoids.* Previous biometric analyses of gonopore diameter variation in fossil hemiasterid populations (Néraudeau 1990) have shown that it is often easy to distinguish juveniles from adults and to characterize an intermediary stage corresponding to a pre-adult phase of development. Indeed, the ontogeny of fossil hemiasterid echinoids comprises two main morphological crises: the first when the genital pores open, showing the end of the juvenile stage; and the second preceding the acquisition of the final adult morphology and sexual maturity (Text-fig. 1). Between these two crises, associated with two precise size limits, there is a rapid increase in the diameter of the gonopores characterizing the pre-adult stage (David 1980; David and Laurin 1991; Néraudeau 1991).

*Growth stages of* Hemiaster (L.) similis. The genital pores of *Hemiaster* (*Leymeriaster*) *similis* are generally closed until a test size of 10 mm, sometimes even 12 mm, is reached (Néraudeau and Moreau 1989) (Text-fig. 2). The smallest individuals, without gonopores, can be considered as sexually immature juveniles. These juveniles are always infrequent in fossil populations of adult individuals, being often grouped apart in marly lithofacies, whereas adults abound in chalky ones (Néraudeau 1989).



TEXT-FIG. 1. Sexual maturity and relative age of a fossil hemiasterid echinoid defined by the variations in gonopore diameter (30 gr. = 1 mm). Example given is for the Turonian species *Mecaster verneuili*. Individuals with closed gonopores are juveniles. The rapid opening of gonopores corresponds to a pre-adult stage of development preceding the acquisition of sexual maturity. When the gonopores are widely open, the echinoids are adults and sexually mature.



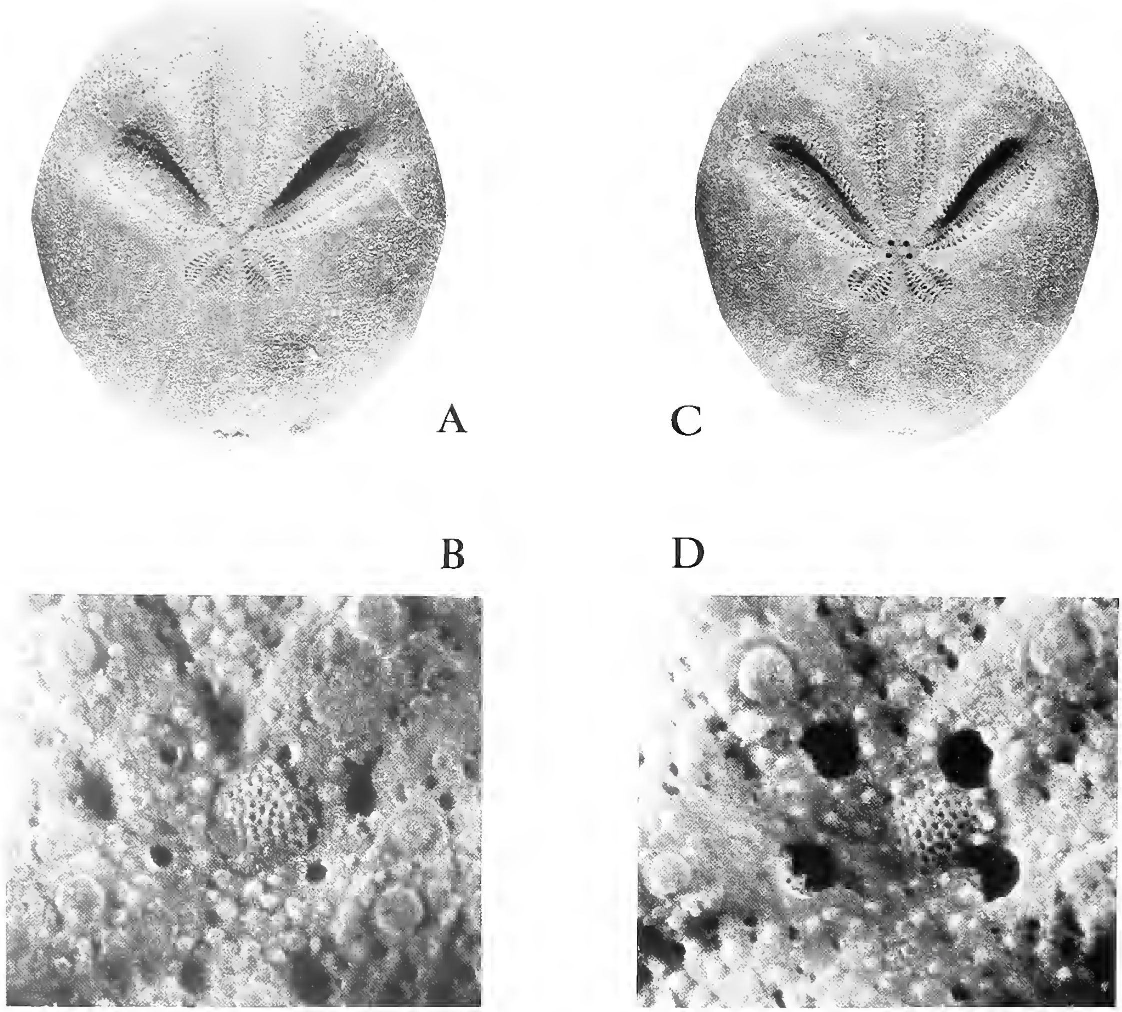
TEXT-FIG. 2. Scatter diagram showing the variations in the diameter of the gonopores (30 gr. = 1 mm) according to the test sizes for *Hemiaster* (*Leymeriaster*) *similis* from the Upper Cenomanian of Port-des-barques, Charente-Maritime. The specimens without genital pores correspond to juveniles. The opening of the gonopores, between 10 and 20 mm, mark the pre-adult stage. Specimens longer than 19–20 mm are adult, sexually mature and dimorphic, the females having gonopores conspicuously wider than the male ones, as indicated on the apical systems illustrated.

After the gonopores open, they rapidly increase in diameter during an ontogenic stage where the test has not achieved all the characteristics of the species morphology. This pre-adult stage of development, like the juvenile stage, is demographically poorly represented in the populations. Finally, the adult-specific morphology is achieved at sizes between 19 and 21 mm, when most of the morphological characters reach relative stability.

*Sexual dimorphism in adult* Hemiaster (L.) similis. Variations in gonopore diameter distinguish two groups of adult individuals, with wide and small genital pores respectively (Text-fig. 2). In accordance with the recent sea-urchin dimorphism, specimens with large gonopores can be considered to be females (Tahara *et al.* 1960; Kier 1967; David *et al.* 1988). The other specimens, whose gonopore diameter corresponds on average to 55 per cent of that of the female, can be considered to be males.

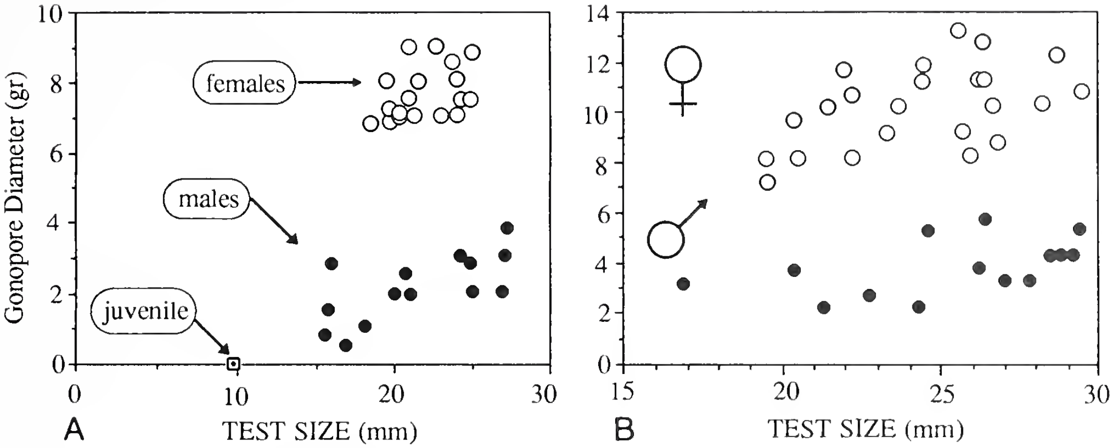
In this reference population, twenty-five adult individuals can be considered to be females, twenty-two to be males and, therefore, females are slightly more numerous than males with a proportion of fifty-three per cent (in adult specimens only). The result of a binomial probability statistic ($P = 0{\cdot}1$) shows that these ratios deviate significantly from a random sampling of a 50:50 male to female ratio. However, no palaeontological or sedimentological information permits definition of the fossil assemblage as a 'census assemblage' (Cadée 1982; Néraudeau 1991) where the male and female numbers would reflect exactly the sex ratio and the demographic structures of a local echinoid settlement.

*Stratigraphical and geographical variations of the dimorphism. Hemiaster* (*L.*) *similis* and closely related species are rather common in the outcrops of Cenomanian to Turonian age in northern Aquitaine and Anjou, France. Different populations, analysed in the same way as the reference population, show a conspicuous genital dimorphism where the females have gonopores two to three times wider than those of the male (Text-fig. 3). Moreover, females are often more numerous than males in the populations, the male to female ratios deviating significantly from random sampling of 50:50 male to female ratio, according to binomial probability statistics ($P < 1{\cdot}5$ for the following examples).



TEXT-FIG. 3. Male and female of the hemiasterid *Hemiaster* (*Leymeriaster*) *leymeriei* (Agassiz), Lower Turonian of Briollay, Anjou. A, dorsal view of a male specimen (STD B1M), × 2. B, apical system of the same specimen showing the four small gonopores, × 24. C, dorsal view of a female specimen (STD B2F), × 2. D, apical system of the same specimen showing the four wide gonopores, × 24.

Contemporaneous populations of *H.* (*L.*) *similis* show conspicuous sexual dimorphism, whatever their geographical location. For example, for *H.* (*L.*) *similis* from Challans-Commequiers, 200 km

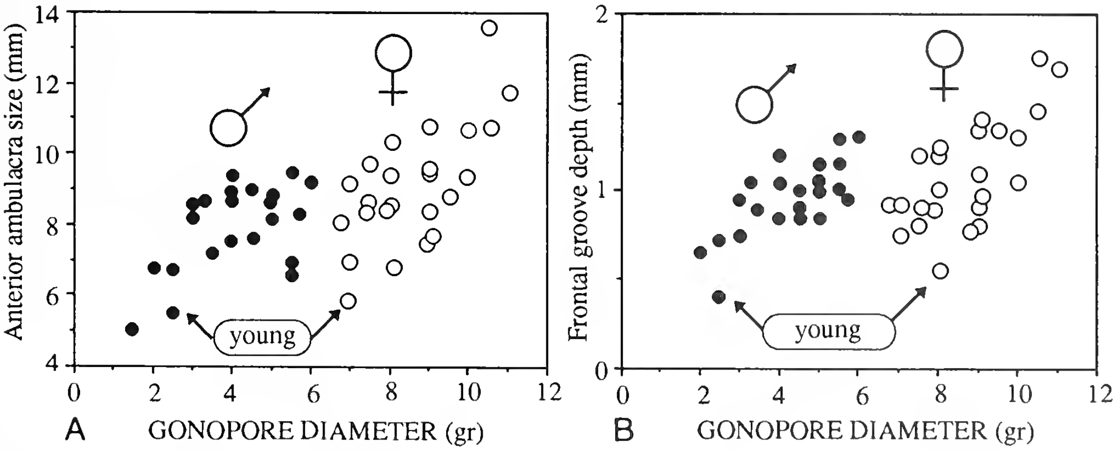


TEXT-FIG. 4. Diagrams showing the variation in gonopore diameter (30 gr. = 1 mm) according to test size in two *Hemiaster* (*Leymeriaster*) populations closely related to the reference population in Text-fig. 2. A, *H.* (*L.*) *similis* from Challans-Commequiers, contemporaneous with the reference population but geographically distant. B, *H.* (*L.*) *leymeriei* from Briollay, Anjou, a Turonian descendant of *H.* (*L.*) *similis*.

to the north of the reference population, adult individuals comprise eighteen females (56 per cent) and fourteen males (44 per cent) in the sample studied (Text-fig. 4A).

Moreover, compared to the Cenomanian species *H.* (*L.*) *similis*, the dimorphism of its Turonian descendant *H.* (*L.*) *leymeriei* seems conspicuously expressed too. Males of *H.* (*L.*) *leymeriei* have gonopores whose diameter corresponds on average to 34 per cent of that of the female (Text-fig. 4B). In the sample studied, twenty-two specimens from the thirty-seven adult individuals collected are females (62 per cent) and only fourteen of them are males (38 per cent).

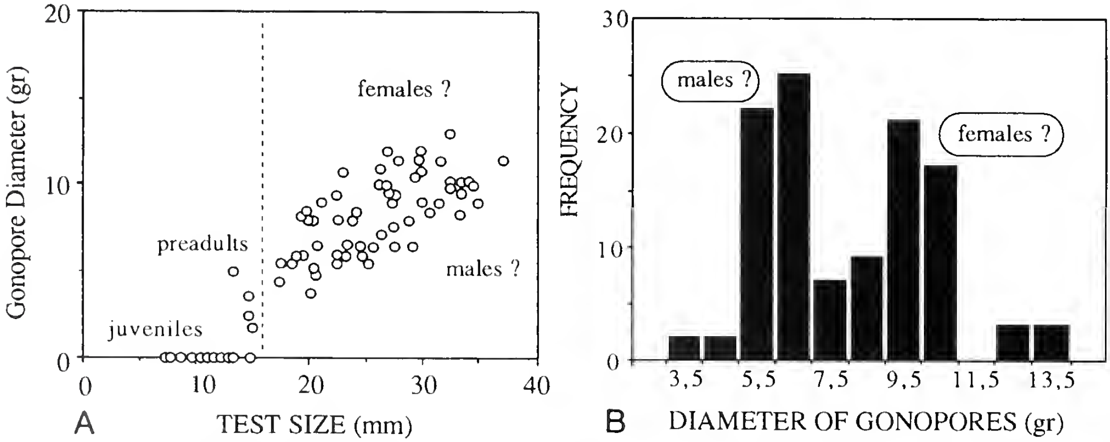
*Research of secondary sexual differences.* Exhaustive biometric analyses of *H.* (*L.*) *similis* and *H.* (*L.*) *leymeriei* (Néraudeau 1990) reveal that the two sexes of these species present no real morphological differences associated with the genital dimorphism. But in several populations, such as the reference



TEXT-FIG. 5. Scatter diagrams showing the variation in depth of the frontal groove (A) and the variation in size of the anterior ambulacra (B) in the reference population of *Hemiaster* (*Leymeriaster*) *similis* from the Upper Cenomanian of Port-des-barques, Charente-Maritime.

population of *H.* (*L.*) *similis*, the females achieve a larger size than males and consequently show more excavated ambulacra, particularly the anterior pair and the frontal groove (Text-fig. 5A). The anterior petals of the females are, in these cases, more extended than those of the males, both in depth and length (Text-fig. 5B). The accentuation of these morphological parameters for the females does not constitute a true difference with the males. There is no acceleration of their morphology (McNamara 1986), only an hypermorphosis of ambulacra, correlated with the larger adult size.

However, for the other populations of *H.* (*L.*) *similis* and *H.* (*L.*) *leymeriei*, and in the limits of the samples under study, males and females have the same adult maximum size. The apparent hypermorphosis detected for some females *H.* (*L.*) *similis* cannot be recognized. Consequently, it is impossible to define the maximum size difference between males and females as a general sexual characteristic and, moreover, it is difficult to say if it is real or simply a sampling artefact.



TEXT-FIG. 6. Variation in gonopore diameter of *Mecaster cenomanensis* (Lower Cenomanian of Les Renardiéres, Charente-Maritime) according to the test sizes showing a rather large variability and no conspicuous genital dimorphism.

*Comparison with* Mecaster *species.* As mentioned above, several North African species of the hemiasterid genus *Mecaster* have been described as sexually dimorphic. Unfortunately, none of the authors have documented conspicuous genital differences associated with the morphological differences. In my own experience, an exhaustive morphological analysis of Cretaceous hemiasterids (Néraudeau 1990) has shown that sexual dimorphism can be detected biometrically for several globular species of North European hemiasterids, but never conspicuously for North African *Mecaster* species.

In most cases, the frequency distribution of gonopore diameter is almost unimodal for *Mecaster* species and the variations in gonopore diameter according to the size of individuals show a great variability (Néraudeau 1990; Text-fig. 6). That variability in gonopore diameter is too marked to permit the distinction of any sexual dimorphism and, therefore, *Mecaster* species would be characterized by tests showing no conspicuous sexual dimorphism.

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# A EUTHYCARCINOID ARTHROPOD FROM THE SILURIAN OF WESTERN AUSTRALIA

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ABSTRACT. The Euthycarcinoidea is a superclass of the arthropod phylum Uniramia and one of the rarest groups of fossil arthropods. Only seven species in five genera have been described, from rocks of Late Carboniferous age in France and the USA, and of Middle Triassic age in France and eastern Australia. Here, a much older euthycarcinoid, from a mixed sequence of fluviatile and aeolian sandstones of probable Late Silurian age in Western Australia, is described as *Kalbarria brimmellae* gen. et sp. nov. Because of their uniramian affinities, it has previously been suggested that euthycarcinoids may be the closest ancestral relatives of hexapods. Although previous evidence had indicated that the earliest hexapod predated the earliest euthycarcinoid, the discovery of a euthycarcinoid about 120 million years older than the previous oldest record, and predating the oldest known hexapod, provides strong support for the view that the hexapods may have evolved from the Euthycarcinoidea. A model illustrating euthycarcinoid origins from myriapods, and hexapod origins from euthycarcinoids is proposed, based on paedomorphic loss of appendages.

IN July 1990 a single specimen of a fossil arthropod (Western Australian Museum specimen number WAM 90.158) was collected from the rim of the Murchison River gorge in Western Australia (Text-fig. 1). The fossil (Text-fig. 2) came from the Tumblagooda Sandstone, a unit that exceeds 1000 m in thickness in the Murchison section. The part of the sandstone sequence from which the fossil was collected was interpreted by Hocking (1981, 1991) as having been deposited in a mixed braided fluvial and aeolian sandsheet environment. However, Trewin (1993) reinterpreted it as a mixed fluvial and aeolian sandsheet deposit. The arthropod is the first body fossil to be collected from the Tumblagooda Sandstone, despite the presence of a rich trace fossil assemblage (Trewin and McNamara work in progress), in particular extensive trackways thought to have been made by a number of different types of arthropods, including eurypterids (McNamara 1981).

## AGE OF THE TUMBLAGOODA SANDSTONE

Although palaeomagnetic data have suggested an Early Ordovician age for the Tumblagooda Sandstone (Schmidt and Hamilton 1990), palaeontological evidence indicates that the sandstone is probably younger. Simple trilete spores and acritarchs recovered from borehole material attributable to the Tumblagooda Sandstone are indicative of a Silurian age (B. E. Balme, pers. comm.). Similarly, the Dirk Hartog Formation, which conformably overlies the Tumblagooda Sandstone, has yielded a conodont assemblage that indicates a Late Silurian age (Philip 1969). Most of the conodonts that were identified are long-ranging Ludlow species that extend into the Early Devonian. The presence of *Ozarkodina ziegleri tenuiramea* Walliser, 1964 and *O.* aff. *fundamentata* (Walliser, 1957) suggest a correlation with the mid-Ludlow *ploekensis* Zone. Higher in the unit the presence of *O. jaegeri* Walliser, 1964 and *Neoprioniodus bicurvatus* (Branson and Mehl, 1933) indicate a Late Ludlow age. The brachiopod *Conchidium* that was recovered from the Dirk Hartog Formation by Glenister and Glenister (1957) also suggests a Silurian age. It should be noted that the borehole from which this material was recovered is some distance from Kalbarri, making lateral facies variation a possibility and the correlation perhaps tenuous.

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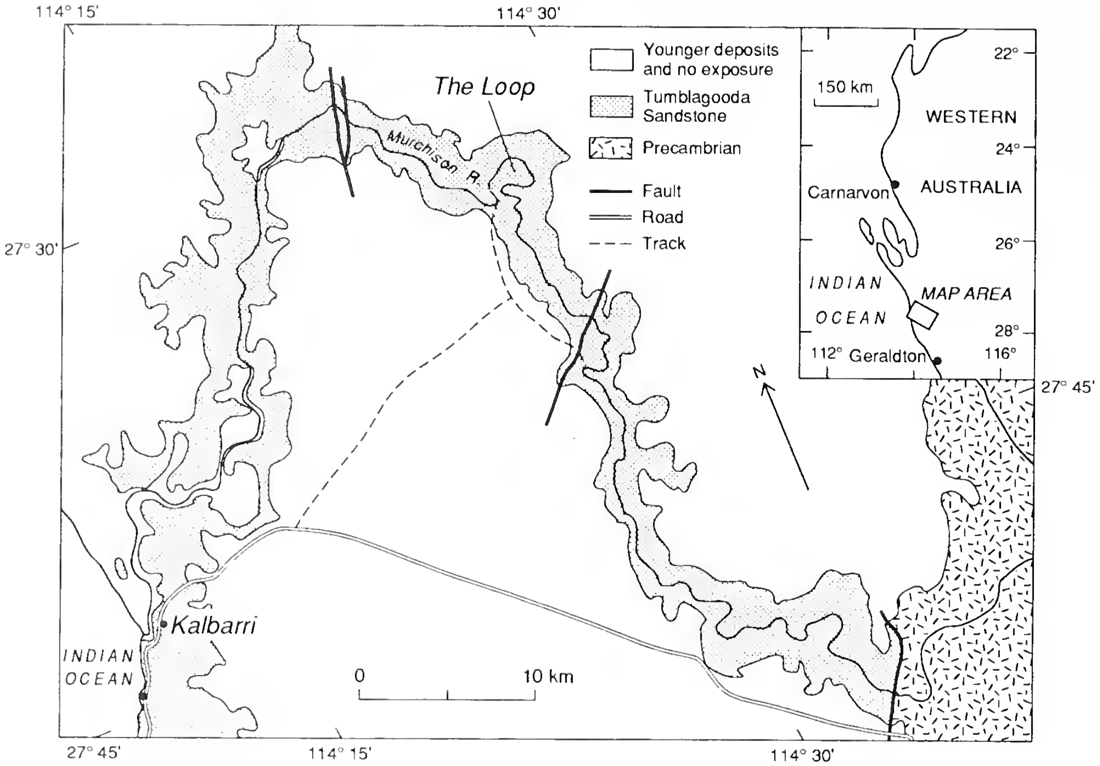


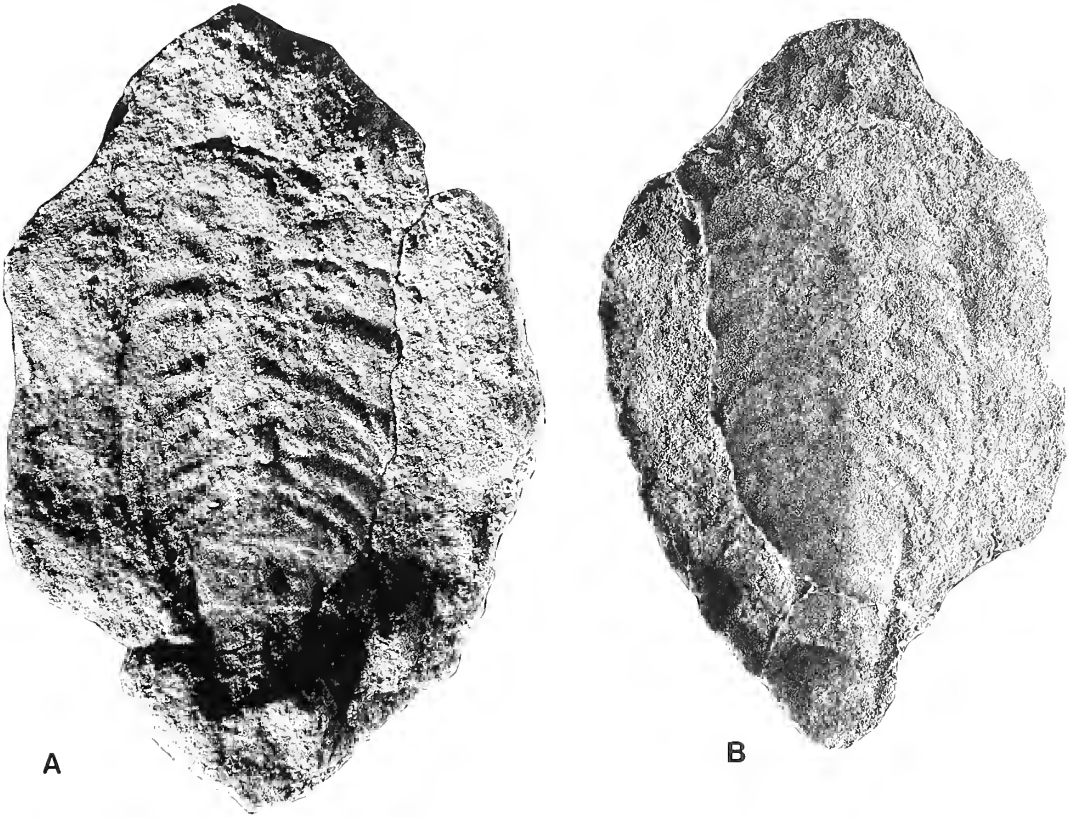
TEXT-FIG. 1. Locality map for the Murchison Gorge area of Western Australia, showing the extent of the exposures of the Tumblagooda Sandstone. The specimen described below was collected at The Loop.

The trace fossil assemblage (Trewin and McNamara work in progress) is in many respects similar to a trace fossil assemblage in the Beacon Supergroup in Victoria Land, Antarctica (Bradshaw 1981; Gevers and Twomey 1982). In particular there are similar large trackways attributable to the ichnogenus *Diplichnites* (= *Beaconichnus*). Other ichnogenera in common include *Didymaulichnus*, *Beaconites*, *Diplocraterion* and *Heimdallia*. The lowest part of the Beacon Supergroup is dominated by a *Heimdallia–Diplichnites* ichnocoenosis (Bradshaw 1981). This ichnoceonosis is also a common component of the Tumblagooda Sandstone. While Bradshaw attributed a Devonian age to the lower part of the Beacon Supergroup, Gevers and Twomey (1982) noted that the upper part of the Beacon Supergroup contains Early to Middle Devonian lycopod stems (Plumstead 1964), suggesting that the lower part of the supergroup may extend possibly as low as the Silurian. Either way, the palaeontological evidence indicates a similar age for the two sequences, perhaps close to the Silurian–Devonian boundary.

Further argument against an Ordovician age is provided by the age of mineralization adjoining dolerite dykes in the Northampton Block, that occur immediately south of the exposure of the Tumblagooda Sandstone. This has been dated at 434 ± 15 Ma (i.e. Early Silurian), yet there is no evidence of this phase of mineralization having effected the Tumblagooda Sandstone (Blockley *in* Hocking *et al.* 1987).

## PRESERVATION OF THE SPECIMEN

The fossil arthropod, which has a preserved length of 115 mm, occurs in a light brown, medium to coarse, quartz sandstone. The grains are between 0·1 and 1·0 mm in diameter, with most between 0·3 and 0·5 mm. The individual grains are well rounded and subspherical. The organism is preserved as an external mould of the ventral surface, apart from the anteriormost tergite (T1) – the gnathocephalon, and presumed procephalon. Both of these elements were folded beneath the body prior to fossilization and are consequently preserved as external moulds of the dorsal surface, impressed on the ventral surface (Text-fig. 2A). By 'unfolding' the carapace, the original length of the arthropod would have been 133 mm. Subsequent attempts to locate the counterpart of the specimen, which presumably would have preserved the dorsal surface, proved unsuccessful, as were attempts to locate more specimens.



TEXT-FIG. 2. *Kalbarria brimmellae* sp. nov. Western Australian Museum specimen number WAM 90.158; holotype; Murchison River, Western Australia; (?) Late Silurian, Tumblagooda Sandstone, ×0·75. A, external mould of the ventral surface in sandstone. B, latex cast.

Preservation of the arthropod in such a coarse-grained rock is surprising; not only are the tergites preserved, but so too are the appendages, implying that these elements were relatively well sclerotized. The ventral somites, however, are poorly preserved, suggesting that they may have been less well sclerotized.

The presence in the specimen of a small procephalon, six dorsal tergites and eleven preabdominal appendages, combined with an appendage-free abdomen of five segments, confirms the identification of the Tumblagooda Sandstone arthropod as a member of the Euthycarcinoidea. This group of rare, exclusively freshwater arthropods has previously been known only from Late Carboniferous and Middle Triassic strata in eastern France, the United States and eastern Australia (Gall and

Grauvogel 1964; Riek 1964, 1968; Schram 1971; Schram and Rolfe 1982; Rolfe 1985). Euthycarcinoids are characterized by the possession of mono-, diplo- and/or triplopodous dorsal segmentation. The presence of a euthycarcinoid in the Tumblagooda Sandstone therefore extends the range of this superclass by about 120 million years, back into the Silurian.

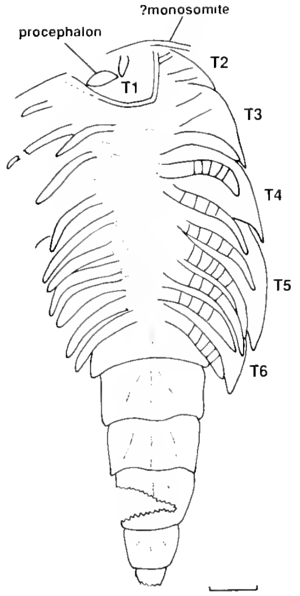
## EUTHYCARCINOID RELATIONSHIPS

Until quite recently, this group of arthropods had proved hard to assign with confidence to any higher taxonomic group. Handlirsch (1914) indicated his belief that they were crustaceans in his choice of the name 'Euthycarcinoidea' (literally meaning 'straight crab'), when describing the first known species, *Euthycarcinus kessleri*, from the Triassic of eastern France. He considered that euthycarcinoids represented a primitive form of copepod crustacean. When they redescribed *E. kessleri*, Gall and Grauvogel (1964) placed it in a separate new class of crustaceans. However, as Schram (1971) noted, euthycarcinoid segmentation bears little resemblance to that of any other known group of crustaceans. Furthermore, Schram (1971) observed that the 'mandibles' and postoral appendages are very obscure in euthycarcinoids and do not indicate the phylogenetic relationships of the group.

Schram (1971), in describing *Kottixerxes gloriosus* from the Late Carboniferous at Mazon Creek, USA, preferred to include the euthycarcinoids in the Merostomoidea, as a distinct order. Riek (1964) had earlier considered *Synaustrus brookvalensis*, the species that he described from the Middle Triassic of New South Wales, Australia, to be a merostomoid trilobitoid. However, following the publication of Gall and Grauvogel's (1964) paper, and a re-examination of the material, Riek (1968) agreed with them on the more likely crustacean affinity of euthycarcinoids. But rather than viewing them as copepods, Riek suggested that they belonged in the Branchiopoda.

It was not until Bergström (1980) re-evaluated the phylogenetic relationships of early arthropods, including the euthycarcinoids, and new material from the USA (Schram and Rolfe 1982) and France (Heyler 1981; Rolfe *et al.* 1982; Rolfe 1985) was examined, that a new and more radical reassessment of the likely phylogenetic relationship, and hence systematic position, of the Euthycarcinoidea was made. All previous taxonomic assignments had inferred that euthycarcinoids possessed biramous appendages. However, as Bergström (1980) observed from studying *Synaustrus brookvalensis* and *Kottixerxes gloriosus*, euthycarcinoids possessed uniramous appendages. This was later confirmed by the studies of Schram and Rolfe (1982) on *Kottixerxes*, *Sottyxerxes* and *Smithixerxes*, and supported by this study of the Western Australian euthycarcinoid. The presence of two pairs of antennae, such as Riek (1964, 1968) reported in *Synaustrus*, has not been substantiated, either by the re-examination of his material by one of us (K.J.M.), or by the study of other euthycarcinoid species. Furthermore, the absence of uropods makes crustacean affinities unlikely. The presence of diplo- and triplosegments, combined with a uniramian limb, led Bergström (1980) to state that the Euthycarcinoidea 'seem to show important similarities only with the uniramian groups and probably represent a distinct uniramian group comparable in rank with the Myriapoda and Hexapoda'.

In their review of the Carboniferous euthycarcinoids from France and the USA, Schram and Rolfe (1982) formalized Bergström's concept and recognized the Euthycarcinoidea as a subphylum of the Uniramia. However, the concept of the Uniramia *sensu* Manton (1977) as a separate phylum comprising the Onychophora, Myriapoda and Hexapoda has come under much criticism (e.g. Kristensen 1975, 1981, 1991; Patterson 1978; Boudreaux 1979). The general consensus is that, while the Hexapoda and Myriapoda can be regarded as sister-groups, the Onychophora represents a separate phylum from the Uniramia. While Boudreaux (1979) regarded the Hexapoda and Myriapoda as classes, Kristensen (1991) considered them to be superclasses, rather than subphyla. Kristensen pointed out how the Hexapoda and Myriapoda have been combined as either the 'Atelocerata', 'Antennata' or 'Tracheata'. However, there are problems with using any of these names. For instance, it is debatable whether the evolution of a tracheal system occurred only once during the evolution of the myriapod/hexapod lineage. The other alternative is to follow Harvey



TEXT-FIG. 3. *Kalbarria brimmellae* sp. nov. Camera lucida drawing based on latex cast of original (Text-fig. 2B). T1 to T6 are dorsal tergites 1 to 6, the lateral extremities of which protrude beyond the ventral appendages. The limb-bearing section comprises the preabdomen; the narrower, appendage-free section the postabdomen. Scale bar = 10 mm.

and Yen (1989) who used the concept of the Uniramia as a phylum exclusive of the Onychophora. This is followed here, with the Uniramia being considered to comprise the Hexapoda, Myriapoda and Euthycarcinoidea.

Starobogatov (1988) proposed a new classification of the euthycarcinoids, incorporating the Cambrian arthropod family Aglaspidae. This group had been considered by other authors to be either xiphosuran merostomes (Størmer 1955), or a separate class of merostomes (Bergström 1971), while Briggs *et al.* (1979) doubted whether they were merostomes at all. From their redescription of *Aglaspis spinifer*, Briggs *et al.* (1979) deduced that the assignment of the aglaspids to the Merostomoidea was unwarranted. Although Repina and Okuneva (1969) had described what they interpreted as gill branches in the aglaspid *Khankaspis bzahnovi*, Briggs *et al.* (1979) considered that aglaspids had uniramous appendages. However, in their opinion more work needed to be done on elucidating the nature of aglaspid appendages before assignment to any class could be considered.

Starobogatov (1988), without further analysis of other material, accepted the uniramian nature of the limbs of aglaspids and placed them in the Euthycarcinoidea. However, there are a number of major problems with this interpretation. Aglaspids, unlike euthycarcinoids, have a large headshield that incorporates at least four appendages (Briggs *et al.* 1979); a comparable headshield is not present in euthycarcinoids (Schram and Rolfe 1982). The thoracic segments are monosegments in aglaspids, unlike all euthycarcinoids where at least some of the segments are diplo- or triplosegments. Furthermore, there is no distinct postabdomen of five or six segments, such as occurs in euthycarcinoids. On these grounds alone there seems little justification for incorporating the aglaspids in the Euthycarcinoidea. Hence in this paper the composition of the Euthycarcinoidea is deemed to be the same as that envisaged by Schram and Rolfe (1982), with the addition of *Kalbarria*.

## TERMINOLOGY

Schram and Rolfe (1982) considered that the small structure Bergström (1980) interpreted as the head was probably a procephalon, because in well-preserved material from elsewhere it was seen to carry a single pair of antennae, 'eyes' and the labrum. Previously, the first tergite had been interpreted as the head (e.g. Gall and Grauvogel 1964; Riek 1964). In their discussion of the uniramian affinities of euthycarcinoids, Schram and Emerson (1991) interpreted the structure, referred to as 'tergite 1' by Schram and Rolfe (1982) and considered by them to be part of the preabdomen, as the gnathocephalon. There is some justification for this, in as much as the labrum (sternite 1 *sensu* Schram and Rolfe 1982, text-fig. 1) and sternite 2, thought to be involved with feeding, are situated beneath tergite 1. The small monosomite recognized in *Kottixerxes* and in *Sottyxerxes* (Schram and Rolfe 1982) has been regarded as separating the preabdomen into two regions. Re-examination of the holotype of *Synaustrus brookvalensis* by one of us (K.J.M.) has revealed that a similar small monosomite is present between tergites 1 and 2. Thus, in this study, tergite 1 is interpreted as the gnathocephalon, and tergites 2 and 6 part of the preabdomen, Schram and Rolfe (1982) referred to the small monosomite as tergite 1. However, as there was probably little dorsal expression of this somite it is not viewed herein as a tergite.

## SYSTEMATIC PALAEONTOLOGY

Phylum UNIRAMIA Manton, 1973
Superclass EUTHYCARCINOIDEA Gall and Grauvogel, 1964
Family EUTHYCARCINOIDAE Handlirsch, 1914
Genus KALBARRIA gen. nov.

*Derivation of name.* After Kalbarri, Western Australia, the closest town to the site of discovery.

*Type species. Kalbarria brimmellae* sp. nov.

*Diagnosis.* Preabdomen broad, with five tergites of varying widths; tergite 1 less than half the width of tergite 5. Postabdomen relatively wide anteriorly, tapering strongly posteriorly. Postabdominal segments bearing ventral sagittal and diagonal ridges.

### *Kalbarria brimmellae* sp. nov.

Text-figs 2–3.

*Derivation of name.* Named after Kris Brimmell who so astutely recognized the specimen in the field.

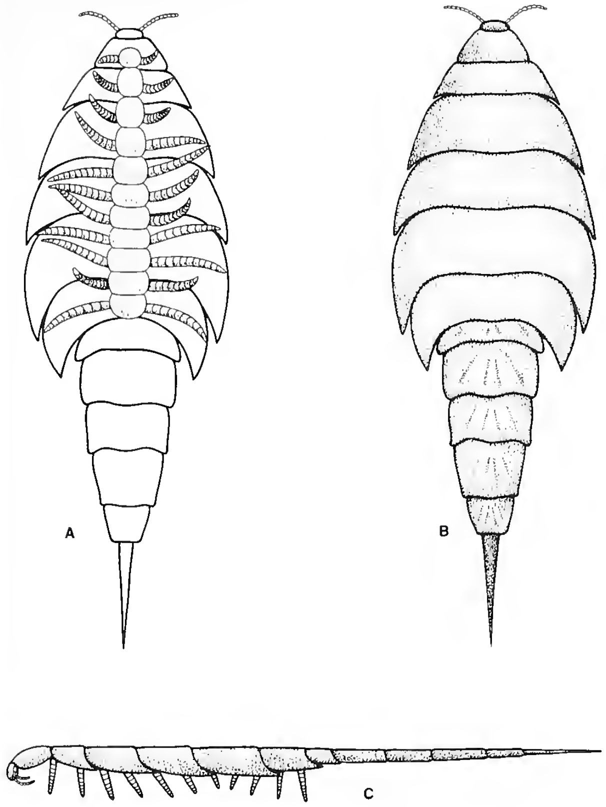
*Holotype.* Western Australian Museum specimen number WAM 90.158.

*Locality and horizon.* On the rim of the gorge of the Murchison River in the region of The Loop, near Kalbarri, Western Australia (Text-fig. 1); Tumblagooda Sandstone (? Late Silurian). Full locality details are kept on file in the Department of Earth and Planetary Sciences, Western Australian Museum, Perth.

*Diagnosis.* As for genus.

*Description.* Procephalon small, broadly ovoid, with a width (5·4 mm) twice that of its length; gently convex. Gnathocephalon (tergite 1) trapezoidal, with an anterior width the same as that of the procephalon, which is just 11·5 per cent of maximum preabdominal width (MPW); increases markedly in width posteriorly to 37 per cent MPW; occupies 17 per cent of combined gnathocephalic and preabdominal lengths; tergal margins gently curved. Thin, ridged structure situated between tergite 1 and tergite 2 may possibly represent the small monosomite observed in this position in *Kottixerxes gerem* (Schram and Rolfe, 1982, pl. 2, fig. 4).

Preabdomen progressively widens posteriorly from tergite 1 to tergite 5, then narrows to tergite 6. Relatively wide, length:width ratio of 1·54. Tergite 2 is a monosegment, reaching up to 88 per cent of MPW posteriorly; tergal margins very slightly curved and, like all subsequent tergites, subtended into slight postero-lateral prolongations. Tergite 3 is a diplosegment, reaching up to 96 per cent of MPW posteriorly, with slightly more curved tergal margins than the preceding two tergites. Tergite 4 is also a diplosegment and is slightly wider than tergite 3, attaining about 98 per cent of MPW. Tergite 5 is the widest and is a triplosegment; its tergal margin



TEXT-FIG. 4. *Kalbarria brimmellae.* sp. nov. Reconstruction of A, dorsal; B, ventral; and C, lateral views. Length of antennae and telson conjectural, as is size and shape of sternites, ×0·5.

is slightly less curved than the preceding two tergites. Tergite 6, a diplosegment, is much narrower than the preceding segments, being only 70 per cent of MPW. Its postero-lateral margins are produced into quite prominent prolongations. Tergites show a progressive increase in length posteriorly, from tergite 2, which is 13 per cent of maximum preabdominal length (MPL), through tergite 3, 16 per cent of MPL, tergite 4, 18·5 per cent of MPL to tergite 5, 22 per cent of MPL. Tergite 6, as well as being narrower, is also shorter than preceding tergites, being 16 per cent of MPL.

Preabdomen with eleven pairs of uniramous appendages that do not extend laterally beyond the tergites. Compared with other described euthycarcinoid appendages, they are relatively stout. They have suffered slight post-mortem disarrangement, but show that they extend from the somites with a slight curvature. At about three-quarters of the transverse distance, they curve strongly backwards through an angle of between 50° and 60°. Proximally, the appendages are of similar diameter throughout (ranging between 3·0 and 3·4 mm) apart from the posteriormost which is slightly narrower at a diameter of 2·4 mm. Total number of segments in appendages not known, but in some appendages up to six segments are preserved, and these are wider than long. Appendages terminate in a single terminal spine.

The sternites, the ventral plate to which the limbs would have attached, are poorly preserved, due to their probably weaker degree of sclerotization.

Postabdomen of five gently curved segments; less than half width of preabdomen and two-thirds its length. Anterior segment chevron-shaped; width posteriorly 48 per cent of MPW; tapers strongly anteriorly to a width of just 20 per cent of MPW. Second segment rectangular, 47 per cent of MPW; wider than long, width being almost twice the length. Distal margins gently curved. Third segment widest anteriorly, being 41 per cent of MPW; tapers evenly posteriorly to 37 per cent of MPW; length similar to that of first segment, thus width is less than twice length, being 1·65 times length anteriorly, and 1·5 times length posteriorly. Fourth segment continues tapering trend, being only 25 per cent of MPW posteriorly; anteriorly width 1·47 times length, posteriorly 1·07 times length. Fifth segment tapers to just 21 per cent of MPW; anteriorly width 1·32 times length, posteriorly 1·19 times length. The anterior part of a sixth segment is just visible. This may represent the proximal part of a telson. Postabdominal segments bear ornamentation of raised ridges that extend posteriorly and posterolaterally from the anterior margins of the segments.

*Discussion.* The fusion of the tergites is manifested in this specimen by the tergite 2 being a monosomite, tergites 3 and 4 being diplosegments, as is tergite 6, but with tergite 5 being a triplosegment. This sequence differs from all other known euthycarcinoids. However, Schram and Rolfe (1982) did not place great reliance on this character as a differentiating feature, considering that the diplo- and triplotergites were able to move relative to the sternites, as they were connected by arthrodial membranes.

The small, oval structure impressed on the folded-under tergite 1 is interpreted as the procephalon, in part because this ovoid shape would appear to be characteristic of euthycarcinoid procephala, as interpreted by Schram and Rolfe (1982, Text-fig. 1), but also because its longer dimension is similar to the anterior width of tergite 1, to which the procephalon would have been attached. Due to its relatively poor state of preservation, it is not possible to determine the nature of the eyes of *Kalbarria*. Preservation of the procephalon and tergite 1, the gnathocephalon, impressed beneath tergite 2 and part of tergite 3, is not surprising. Schram and Rolfe (1982) suggested that the procephalon in euthycarcinoids may have been carried in a vertical orientation, much as in some insects and myriapods. The inverted preservation of the cephalon, plus tergite 1 suggests the possibility that during life tergite 1 may also have been orientated at a higher angle to the horizontal plane, than other tergites (Text-fig. 4). The location of the small monosomite between the preabdomen and gnathocephalon is likely to have been a site of greater articulation.

In reconstructions of other euthycarcinoids (e.g. Schram and Rolfe 1982, text-fig. 2) where appendages are depicted, they are shown as projecting laterally beyond the tergites. This would not appear to have been the case in *Kalbarria*, the ventral aspect of the preservation revealing that the gently curving appendages do not project beyond the distal margins of the tergites. The relatively consistent degree of limb curvature suggests that it had limited ability to flex. While the total number of segments in each appendage is not known, the sizes of those that can be identified indicate that it was unlikely that there were as many as the twenty-four reported in *Kottixerxes gloriosus* (Schram and Rolfe 1982, p. 1437). The size of the leg segments of *Kalbarria* suggest that there were less than half this number present.

A number of previously-described euthycarcinoids are characterized by the possession of well-developed setae on their appendages, one per segment. In the case of *Kottixerxes gloriosus* they are developed as long, flap-like structures (Schram and Rolfe 1982, pl. 1, fig. 3). Although the appendages in *Kalbarria brimmellae* are not as well preserved as in *Kottixerxes gloriosus*, there is no evidence of the possession of setae. The impression made by the appendages in *Kalbarria brimmellae* indicate a moderately convex, cylindrical appendage. Compared with other euthycarcinoids the appendages are appreciably wider. It is therefore possible that a primitive character in euthycarcinoids was the possession of a walking leg that was shorter and stouter than in later euthycarcinoids and was either free of setae, or at the most possessed only very fine setae.

Apart from its relatively greater width, the postabdomen differs little in overall structure from other euthycarcinoids. It does, however, bear ornamentation not recorded in other species, in the form of both sagittal and oblique ridges on the ventral surface. Whether or not these were also present on the dorsal surface and on the preabdomen is not known.

Of other euthycarcinoids, *Kalbarria* most closely resembles species of the Late Carboniferous *Kottixerxes* and the Middle Triassic *Synaustrus*. Like *Kalbarria*, both have a preabdomen composed of five tergites and an appreciably smaller postabdomen, a characteristic feature of the family Euthycarcinidae. *Kalbarria* can be distinguished from the two species of *Kottixerxes* (*K. gloriosus* from the Late Carboniferous at Mazon Creek, Illinois, USA and *K. gerem* Schram and Rolfe, 1982 from the Upper Carboniferous at Montceau-les-Mines, France) by virtue of its larger size, broader, more elliptical, preabdomen and broader, more strongly tapering postabdomen that bears an ornamentation of posteriorly diverging, straight ridges. It similarly differs from the Middle Triassic *Synaustrus brookvalensis* (see Riek 1964, 1968) in its larger size and relatively broader preabdomen and postabdomen. Although Riek (1964, 1968) considered that *Synaustrus* possessed only four postabdominal segments, re-examination of the original material shows that, like other euthycarcinids, it too possessed five.

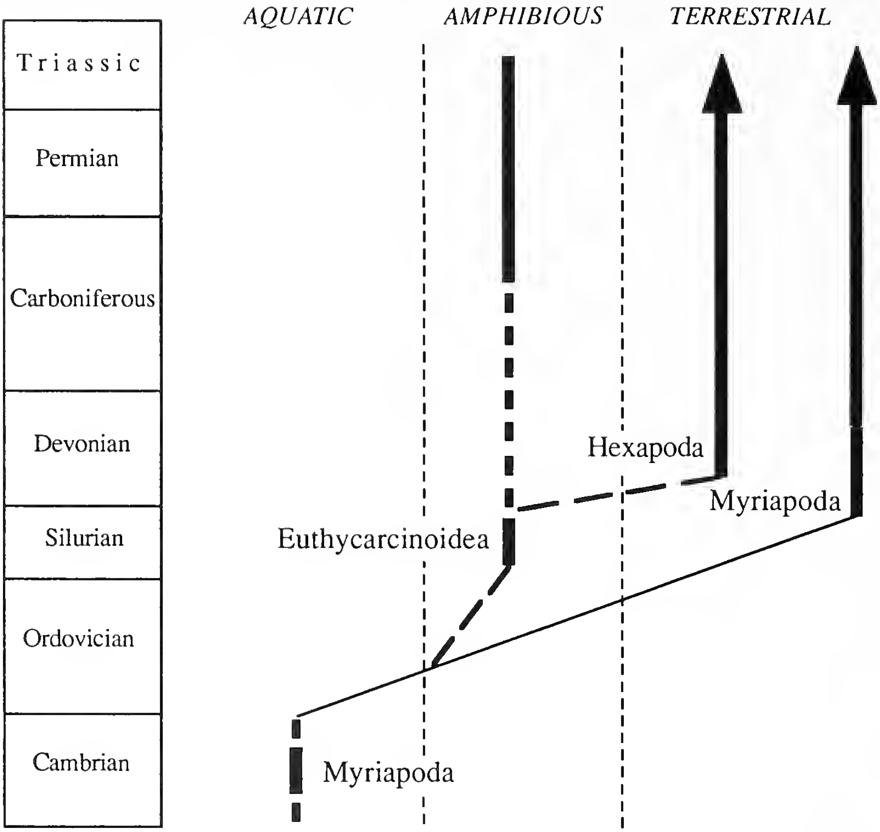
*Kalbarria brimmellae* bears a superficial resemblance to the Late Devonian *Oxyuropoda ligioides* Carpenter and Swain, 1908, an arthropod of uncertain status that has at various times been referred to the Tanaidacea, Isopoda, Arachnomorpha and the Phyllocarida (Rolfe 1969). However, unlike *K. brimmellae*, *O. ligioides* possesses a more parallel-sided body, very much shorter postabdomen, and paired caudal rami. Although nothing is known about the appendages of *Oxyuropoda*, the overall similarity to the euthycarcinoid bodyplan indicates that, as Schram (1971) suggested, further consideration should be given to including this form within the Euthycarcinoidea.

## EUTHYCARCINOIDS AND THE EVOLUTION OF THE HEXAPODA

### *Heterochrony and the myriapod–euthycarcinoid–hexapod transition*

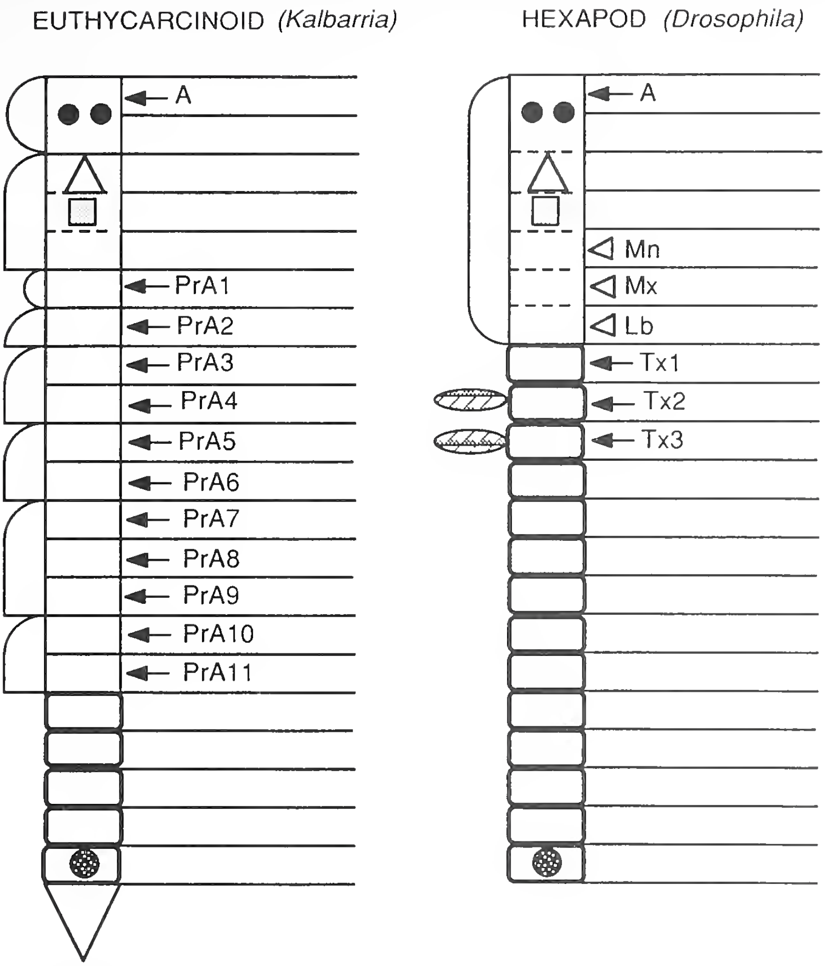
Perhaps the most radical suggestion made by Schram and Rolfe (1982, p. 1448) was that the Euthycarcinoidea may have been involved in the evolution of the Hexapoda: '...the dramatic reduction of limbs noted between [*Sottyxerxes* and *Kottixerxes*] during...phylogeny, might be regarded as an interim stage en route to hexapody...'. The ancestors of hexapods, like most other major groups of organisms, are unknown. To many workers the most plausible explanation for the evolution of the Hexapoda has been that they derived from some hypothetical myriapodous ancestor (de Beer 1958; Anderson 1973; Manton 1977; Mamayev 1977; Manton and Anderson 1979; Boudreaux 1979; Little 1983; Anderson 1987; Kristensen 1991). Anderson (1987) postulated that a group of hypothetical myriapods might have hatched as hexapodous juveniles, then subsequently produced a further eleven leg-bearing segments through ontogeny, to reach sexual maturity with a complement of fourteen pairs of trunk limbs. By progenesis (paedogenesis of Anderson 1987) at a juvenile stage, when only three pairs of appendages had been produced, an adult organism would have existed that possessed just three pairs of appendages, such as in hexapods. While there is little doubt that heterochrony has played a major role in evolution in most, if not all, groups of organisms from the intraspecific to the suprageneric level (McKinney and McNamara 1991), such a scenario is little more than speculation. While it might be argued that the Euthycarcinoidea are too specialized a group to be the ancestors of another subphylum, such arguments are based purely on consideration of the morphological features of the adult organism. As it seems likely that the mechanism for the evolution of hexapods was paedomorphosis, operating at early stages of development of the ancestor, it would have been the morphologically much simpler juvenile form that would have been the target of selection. While little is known of early euthycarcinoid development, Schram (1971) described a juvenile of *Kottixerxes gloriosus* only 14 mm long. It had eleven preabdominal segments, but differed from adults in the absence of fusion of the tergites, indicating the more generalized form of juveniles.

The recognition that euthycarcinoids belong in the same phylum as the hexapods and myriapods, and are characterized by one major feature that is present in hexapods but lacking in myriapods, the subdivision of the postcephalic segments into limb-bearing and limb-free sections, makes them the most suitable candidate amongst known organisms for being ancestors of the hexapods (Text-fig. 5). Their multilimbed state and less complex head region are both more primitive states than corresponding structures in the hexapods. However, while their subdivision into a pre- and post-abdomen is a more derived state than in the myriapods, their cephalic region is more primitive than in living myriapods. Whereas myriapods have only limb-bearing postcephalic segments, in hexapods there are three pairs of limb-bearing postcephalic segments (the thorax) followed by eleven or fewer limb-free segments (the abdomen), making a total of 14 post-cephalic segments. In euthycarcinids there are eleven limb-bearing segments (the preabdomen), followed by five limb-free segments (the postabdomen). Schram and Rolfe (1982) considered that in *Kottixerxes gerem* there are eleven limb bearing segments plus one or two limb-free segments in the preabdomen. This would



TEXT-FIG. 5. Stratigraphical ranges of euthycarcinoids, hexapods and myriapods in the Palaeozoic, and their suggested relationships. Note the general trend to terrestriality through time.

seem to indicate that in euthycarcinids there are up to eighteen (Text-fig. 6) post-cephalic segments. The euthycarcinids would thus seem to be over-endowed with segments, as Anderson (1987) had considered that the hexapod ancestor would require a total of fourteen trunk segments. However, as Schram and Rolfe (1982) pointed out, the euthycarcinoid head would appear to be much simpler than the hexapod head, which is known to be composed of six basic segments, fused into a cephalon, plus an antennate segment (Text-fig. 6). While the cephalic region of euthycarcinoids is still poorly known, it would seem that it might correspond to a procephalon, consisting of a single pair of antennae and sphaeroidal 'eyes', plus a gnathocephalon. Schram and Emerson (1991) pointed out that 'The...head is not well known, but appears to resemble Snodgrass' (1952) hypothetical primitive arthropod head, with an anterior procephalon bearing a single pair of antennae and a distinct posterior gnathocephalon bearing the mouth and a set of rarely preserved mandibles.' Schram and Rolfe (1982) hypothesized that formation of the gnathocephalon might have occurred by fusion of the first three euthycarcinoid post-procephalic segments. To form the hexapod head, this gnathocephalon would have had to have fused to the procephalon and a further two segments (PrA1 and PrA2 of Text-fig. 6) would have been needed to be incorporated into the head region. If this were the case, with the preabdomen losing two limb-bearing segments to the conjoined procephalon and gnathocephalon, then fourteen post-cephalic segments would remain, the same as in the hexapods (Text-fig. 6), PrA3-PrA5 of the euthycarcinoid being homologous with the three



TEXT-FIG. 6. Schematic representation of the segmentation of a euthycarcinoid (*Kalbarria*) and a hexapod (*Drosophila*). Representation is based on Schram and Emerson (1991, figs 9–10), the euthycarcinoid being represented by *Kalbarria*, rather than *Kottixerxes*. One difference in the interpretation is that Schram and Emerson (1991) assumed that each postabdominal segment in the euthycarcinoid was a duplosomite. There is no evidence for this, and it is herein suggested that each segment equates to a monosomite. This interpretation results in the anus being on the 21st monosomite in both euthycarcinoids and hexapods. In this model the three hexapod thoracic segments are considered to be homologous to the euthycarcinoid preabdominal segments T3 to T5. Abbreviations: A, Antennate somite; PrA, Preabdominal somites; Mn, Mandibular somite; Mx, Maxillar somite; Lb, Labial somite; Tx, Thoracic somite. Symbols: small circles = eyes; triangle = labrum; square = mouth; shaded large circle = anus; black arrows = appendage-bearing somites.

appendage-bearing segments of the hexapod thorax (Tx1-Tx3 of Text-fig. 6). With this model, the anus would be on the homologous segment in the euthycarcinoids and hexapods, the terminal segment.

The second change that would have occurred in the transition from a euthycarcinoid to a hexapod would have been the suppression of development of the posterior six pairs of appendages by paedomorphosis. However, there would have been retention of the same number of segments, these becoming part of the post-abdomen (= abdomen in hexapods). Typically in uniramians, segmentation precedes formation of appendages, limb primordia being established shortly after the blastoderm stage, at which time the embryo has been subdivided by the activity of segmentation genes (Cohen 1990). Detailed experimental work on *Drosophila* has shown how one specific gene, the *Distal-less* gene, plays a crucial role in controlling the position of limb formation. Its activity is exerted by differential regulation of subordinate genes. In experimentally induced mutants in which the *Distal-less* gene is deleted, the primordia of the appendages are not developed. As Cohen (1990) noted, because *Distal-less* gene acts as a developmental switch defining the identity of cells as limb, activation of expression of this gene is crucial in determining limb primordia in the embryo. If, as seems likely, such a gene system operated in euthycarcinoids, then it could be suggested that suppression of expression of this gene would have resulted in failure of some appendages to develop. It can be conjectured that during euthycarcinoid ontogeny the full complement of cephalic and post-cephalic segments was formed, following which pairs of appendages developed sequentially from the anterior to the posterior, as in other uniramians (Boudreaux 1979; Minelli and Bortoletto 1988; Cohen 1990).

While the number of appendages is fixed very early in embryological development in the hexapods, the full number in some myriapods is not attained until after a number of post-larval moults. For instance, in symphylan myriapods (Ravoux 1962) the newly hatched larvae possess five to seven pairs of legs (Boudreaux 1979). After three moults, the ninth segment develops a pair of legs (the preceding segments each having already developed a pair of legs earlier in development). After two more moults, legs have developed on the tenth and eleventh segments, but the twelfth and thirteenth segments are appendage-free. Precocious maturation in such forms could have the effect of producing an adult form with fewer appendages than its ancestral adult, but with retention of appendage-free posterior segments. Boudreaux (1979) noted how a number of 'specialised' millipedes fail to develop legs on the last few segments. This he attributed to 'neoteny' (= paedomorphosis).

With such a propensity in myriapods for paedomorphic loss of posterior limbs, it would not seem developmentally too difficult for an ancestral form to have ceased limb generation at an earlier ontogenetic stage, while segments were still generated at the ancestral rate. Such dissociated heterochrony is quite common in many groups of organisms (McKinney and McNamara 1991). The paedomorphic reduction in limb number could have occurred by one of three methods: (1) by premature maturation (progenesis), following production of only three pairs of appendages; (2) by a delay on timing of onset of appendage development (postdisplacement); or (3) by a reduction in the rate of appendage development resulting in cessation of production of further pairs of appendages. Either of the first two processes are the more likely. However, whichever paedomorphic process was involved, a form would be produced with three pairs of appendages, and a postabdominal, limb-free region of eleven segments, as is the case in the hexapods. Both of these seemingly major structural changes (the fusion of anterior dorsal segments, and the increase in number of postabdominal segments at the expense of the preabdomen) merely continue the trends apparent from a hypothetical evolution of euthycarcinoids themselves from myriapods (Text-fig. 5), and myriapods from a lobopod ancestor. Reductions in both segment and limb numbers could quite plausibly have been induced by perturbations to the gene regulatory system, principally by failure of specific genes to trigger segment or appendage formation in the later stages of early embryonic development.

One area where some of the later euthycarcinoids seem to differ appreciably from other uniramians is in the number of leg segments. *Kottixerxes* has up to twenty-four segments (Schram and Rolfe 1982). However, *Euthycarcinus* would appear to have had only twelve (Gall and Grauvogel 1964). From the size of those present in *Kalbarria*, a similar number to *Euthycarcinus* might be postulated. Kristensen (1991) considered that the relatively few number of leg segments (six) in hexapods is another hexapod autapomorphy. However, some have an extra four, which is the number present in Palaeozoic muriapods. The morphological significance of these numbers remains debatable. Kukalová-Peck (1987) considered that the hexapod leg evolved from an ancestral leg with a groundplan of no fewer than eleven segments. Again, the smaller number of leg segments in living hexapods argues for a paedomorphic reduction in number.

Like euthycarcinoids, myriapods possess diplosegments, but they have many more body segments (up to 191 in some Geophilomorpha – Minelli and Bortoletto 1988). Of the two families of euthycarcinoids, the Sottyxerxidae are more 'primitive' in possessing up to thirty-five post-cephalic somites. But being euthycarcinoids, they have attained six limb-free postabdominal segments. The trend for paedomorphic reduction in segment number is continued to the Euthycarcinoidae, with sixteen post-cephalic somites. The loss of segments from myriapods to euthycarcinoids accords with Demange's (1967, 1969) model of 'metameric reduction' in myriapods, in other words an evolutionary trend towards reduction of number of segments. Segment number does not change between the Euthycarcinoidea and the Hexapoda, just the number of appendages. The dorsal fusion of the cephalon, with six somites beneath one dorsal tergite (the head), is a further continuation of the trend to dorsal fusion apparent in the euthycarcinoid preabdomen. Boudreaux (1979) suggested that the tagmosis of the three gnathal segments could have occurred in a single step. In the sottyxerxids only diplosegments are known, but in the euthycarcinids, such as *Kalbarria*, triplosegments are developed. The gnathocephalon of the hexapods is equivalent to the triplosegments of euthycarcinoids, with dorsal fusion of three segments.

This overall reduction in variability of firstly, segment number and secondly, limb number between myriapods, euthycarcinoids and hexapods, combined with segment number and, in particular, appendage number becoming firmly fixed, parallels the phylogenetic 'hardening' of developmental regulation seen in another arthropod group, the Trilobita (McNamara 1986). Early trilobites, in particular Early Cambrian forms, show high variability in segment number within species, as well as between species. As forms evolved through the Cambrian, so the segment number became more fixed, firstly at the specific level, then at the supraspecific level. By the Ordovician, thoracic segment number largely had become fixed at the ordinal level. Such developmental 'hardening' (see McKinney and McNamara 1991) is likely to be a reflection of improved refinement in the control of developmental regulation.

### *Ecological and physiological factors*

It might seem a little surprising, given the close morphological similarity between euthycarcinoids and hexapods, that more emphasis has not been given to the possible rôle of euthycarcinoids in hexapod evolution. One obvious reason is that prior to the discovery of *Kalbarria brimmellae*, the earliest fossil hexapod remains pre-dated the earliest euthycarcinoids. Whereas the earliest euthycarcinoids were thought to be Late Carboniferous, the earliest known hexapod is the Early Devonian collembolan *Rhyniella* from Scotland (Whalley and Jarzembowski 1981) and the earliest insect the wingless archaeognathan machilid from the Middle Devonian of New York State (Shear *et al.* 1984). (Some doubt exists over the validity of *Gaspea palaeoentognatha*, a specimen from the Early Devonian of Quebec that was described by Labandiera *et al.* 1988 as the first true insect, Jeram *et al.* 1990.) However, with the recognition of a euthycarcinoid in Silurian rocks that pre-date the earliest hexapod (Text-fig. 5), the case for euthycarcinoids being a link between early myriapods and the hexapods is strengthened.

Emerson and Schram (1990) and Schram and Emerson (1991) suggested that diplopodous uniramians, such as euthycarcinoids, may also have played a rôle in the evolution of arthropods that bear biramous appendages, perhaps having been close to a possible ancestor of the remipede crustacean *Tesnusocaris*. The fusion of the dorsal tergites in euthycarcinoids that resulted in a single dorsal segment being associated with a pair of ventral sternites could be seen as presaging the evolution of duplosegments in *Tesnusocaris* and thence biramous appendages in crustaceans as a whole.

While the case for the evolution of hexapods from euthycarcinoids can be made on anatomical and developmental grounds, there are ecological and physiological factors that need to be taken into consideration. The first potential problem lies with the fact that the earliest unequivocal myriapods from the Upper Silurian of Shropshire (Jeram *et al.* 1990) are interpreted, like the earliest hexapods, as being terrestrial. Euthycarcinoids, on the other hand, have only been described from freshwater environments. The presence of the large flap-like setae on *Kottixerxes* argues for an active swimming way of life in this particular Carboniferous form. It would appear from this that on ecological grounds there are problems with suggesting that euthycarcinoids were ancestral to the hexapods. However, there are indications from the Tumblagooda Sandstone, in the form of fossil trackways, that suggest that Silurian euthycarcinoids were able to walk out of water.

There is strong evidence that eurypterid and other trackways from this unit were made subaerially (Trewin 1993). Trackways, similar in width to *Kalbarria brimmellae* and made by an animal with probably eleven walking appendages found close to the *K. brimmellae* specimen and at the same stratigraphical level, are most likely to have been made by a euthycarcinoid. The preservation and character of the trackways are like the eurypterid tracks, indicative of them having been formed subaerially. The relatively stout appendages of *K. brimmellae* are not inconsistent with their utilization for subaerial locomotion. The existence of aeolian sands overlaying fluvatile, track-covered sands and the preservation of very fine detail, argues for the trackways having been made in wet sand, but subaerially. It is quite possible that the preservation of *K. brimmellae* itself may have occurred by the animal having been overwhelmed in a sandstorm whilst traversing wet sand, resulting in rapid impression of the animal into the soft wet sediment, and immediate burial.

Another potential problem with the evolution of a group of initially terrestrial organisms from an aquatic group, is the question of respiration. It is not known how euthycarcinoids respired. However, as all other uniramians utilize tracheal respiration, it is possible that euthycarcinoids, like eurypterids (Selden 1985), may have possessed some form of pseudotracheal respiration in the aquatic environment, which preadapted them to terrestrial respiration. After all, forms that today are wholly terrestrial, such as the myriapods, had aquatic ancestors (Robison 1990). If the earliest hexapods were indeed very small then they probably, like other small arthropods, were able simply to respire directly through the thin cuticle.

The existence of true terrestrial arthropods, including centipedes and trigonotarbid arachnids in Late Silurian strata elsewhere (Jeram *et al.* 1990), combined with the probable amphibious behaviour of eurypterids and euthycarcinoids in Late Silurian strata in Western Australia, suggests that early attempts at colonization of land were perhaps more out of necessity to survive, than any attempt to colonize a vacant niche. Evidence is available (Trewin and McNamara work in progress) that eurypterids were walking in and out of pools of water on large sand flats. It is likely that as one pool dried up following river flooding, the eurypterids and other arthropods, including the euthycarcinoid, moved from pool to pool in an attempt to get back to the river.

The evidence that the early land arthropods were predominantly carnivorous (Jeram *et al.* 1990; Shear 1991), means that for early hexapods to survive in a generally hostile environment, it would have been necessary for them to adopt a cryptic habit to avoid predation pressure (Kukalová-Peck 1991). The likelihood that the early hexapods were very small, as the earliest fossils indicate (Whalley and Jarzembowski 1981, Shear *et al.* 1984), suggests that their evolution by paedomorphosis from euthycarcinoids may indeed have been by progenesis. Attainment of sexual maturity at an early growth stage would have meant not only retention of just three pairs of appendages, but also a very small body size. In fact it may have been this very small body size that was the prime target of selection, rather than the possession of three pairs of appendages. In an environment replete with predators, one of the most successful anti-predation strategies is the possession of a small body size. In what is likely to have been a very unstable environment, other *r*-selected life history strategies, such as rapid reproduction, combined with large numbers of offspring, would have been the ideal springboard for the rapid evolution of a major evolutionary novelty.

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Schultka (1991) has described a further species of *Euthycarcinus* from the Upper Carboniferous of Nordrhein-Westfalen, Germany. He also favours a uniramian affinity for the Euthycarcinoidea, as a group separate from, but of equal taxonomic status to, the Myriapoda and the Hexapoda.

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# PETRIFIED STEMS BEARING *DICROIDIUM* LEAVES FROM THE TRIASSIC OF ANTARCTICA

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ABSTRACT. Anatomically preserved one to five year-old stems are described from a Triassic site in the central Transantarctic Mountains. They are assigned to *Kykloxylon fremouwensis* gen. et sp. nov. and are regarded as related to the corystosperm stem *Rhexoxylon* on the basis of wood and pith anatomy and leaf trace organization. *Kykloxylon* axes possess a solid vascular cylinder of secondary xylem of the *Dadoxylon* type, but lack centripetal wood and a narrow pith. The bases of leaves attached to one-year-old stems of *K. fremouwensis* are similar to the leaves of *Dicroidium fremouwensis* described from the same locality in Antarctica. The '*Dicroidium*/*Kykloxylon* plant' from Antarctica is branched and more complex than the hypothetical '*Dicroidium*/*Rhexoxylon* plant' reconstructed from disarticulated remains from the Ischigualasto Formation of Argentina. It is suggested that the '*Dicroidium*/*Rhexoxylon* plant' may have been dominant in western Gondwana, whereas the *Dicroidium* plants with *Kykloxylon* stems might have had a wider geographical distribution in Gondwana.

PETRIFIED plant stems from the late Palaeozoic and Mesozoic are common throughout Gondwana (Kräusel *et al.* 1962; Maheshwari 1972; Prasad 1982; Smoot *et al.* 1985; Bose *et al.* 1989; Taylor and Taylor 1990). They are represented typically by isolated trunks and branches that have been transported to the site of deposition. These fossils are generally decorticated axes and have resulted in a profusion of form genera based almost exclusively on features of the secondary xylem. One of the most interesting aspects of these stems is the potential information that is available on past climates based on growth ring analysis (Jefferson 1982; Jefferson and Taylor 1983; Francis 1986; Taylor 1989). Of biological interest are the *in situ* stumps from the Cretaceous of Alexander Island (Antarctica) described by Jefferson (1982). An analysis of the size and distribution of these stumps has provided the opportunity to reconstruct a Cretaceous forest. The species composition of such forests continues to remain problematic since the systematic affinities of the trees are still uncertain.

The excellent preservation of the plant assemblages occurring in the silicified peat at Fremouw Peak is significant in that it provides, for the first time, an accurate image of the vegetation that inhabited this Triassic site in Antarctica. Small herbaceous plants such as sphenophytes (Osborn and Taylor 1989) and a variety of ferns (Schopf 1978; Millay and Taylor 1990) have already been described as well as a cycad with a slender growth habit (Smoot *et al.* 1985) and a conifer with podocarpaceous affinities (Meyer-Berthaud and Taylor 1991). In addition, a *Pteruchus*-like pollen organ (DeVore and Taylor 1988), multiovulate cupules (Taylor and Taylor 1987) and leaves of *Dicroidium fremouwensis* (Pigg 1990) have also been reported from this locality. The present study is based on the distal parts of a plant that bore leaf bases of the *D. fremouwensis* type. This is the first report of stems and leaf bases with similar anatomy that differ significantly from the stems of *Rhexoxylon*, the Triassic genus generally believed to have borne *Dicroidium* foliage at some localities.

## MATERIAL AND METHODS

Numerous twigs and stems were collected from a silicified peat in the Transantarctic Mountains during the 1985–1986 field season (Taylor *et al.* 1986). The collecting locality is a col at an elevation of 2408 m just north of Fremouw Peak in the Queen Alexandra Range (84° 17′ 409″ S, 164° 21′ 483″ E (Global Positioning System),

**[Palaeontology, Vol. 36, Part 2, 1993, pp. 337–356, 4 pls.]**

Buckley Island Quadrangle; Barrett and Elliott 1973) (Text-fig. 1A). The locality occurs in the upper part of the Fremouw Formation and is considered to be early mid-Triassic in age based on palynostratigraphy (Farabee *et al.* 1990) and the occurrence of the vertebrate *Cynognathus* (Taylor and Taylor 1990) (Text-fig. 1B).

Cellulose acetate peels of the specimens were prepared for light microscopy by etching the rock surfaces with 48 per cent hydrofluoric acid for 1–5 minutes. The largest specimen was cut into two slabs and eighty serial transverse-oblique peel sections were prepared. This stem was less than 1 cm long and it was not possible to correct the original plane of section in order to obtain information about the phyllotaxy. One of the remaining slabs was re-cut longitudinally to provide anatomical details of the secondary xylem in both radial and tangential planes. Information on the pattern of leaf trace emission and vascularization of the leaf bases was obtained by a series of peel sections made from three leafy twigs (10,415 A; 10,525 A; 10,628 E1B).

Slides and peels are deposited in the Palaeobotanical Collections, Department of Plant Biology, The Ohio State University under the acquisition numbers 14,768–14,862

## SYSTEMATIC PALAEONTOLOGY

### Class GYMNOSPERMOPSIDA
### Order CORYSTOSPERMALES
### Family CORYSTOSPERMACEAE Thomas, 1933
### KYKLOXYLON gen. nov.

*Type species. Kykloxylon fremouwensis* sp. nov.

*Diagnosis.* Gymnospermous plant with undivided cylinder of secondary xylem in 1–5 year-old stems. Stems with non-septate pith containing lacunae, sclerotic nests and occasional bands of periderm-like tissue. Primary xylem endarch, with small tracheids in radial files; secondary xylem pycnoxylic with growth rings, rays uniseriate and short with smooth cell walls. Tracheids with 1–3 rows of bordered pits with circular pores on the radial walls; pits sometimes spaced when uniseriate, either opposite or alternate when multiseriate. Pits in cross fields simple, oval-horizontal and variable in number. Cortex parenchymatous with lacunae and sclerotic nests as in pith; cortical periderm homogeneous and composed of several rows of cuboidal cells, often with dark contents. Vascular system to the leaf originating from four axial bundles and consisting of several endarch strands, dividing near periphery of cortex in a three-dimensional pattern; vascular supply in leaf base consisting of adaxial row of endarch bundles and two incomplete rings of abaxial vascular strands.

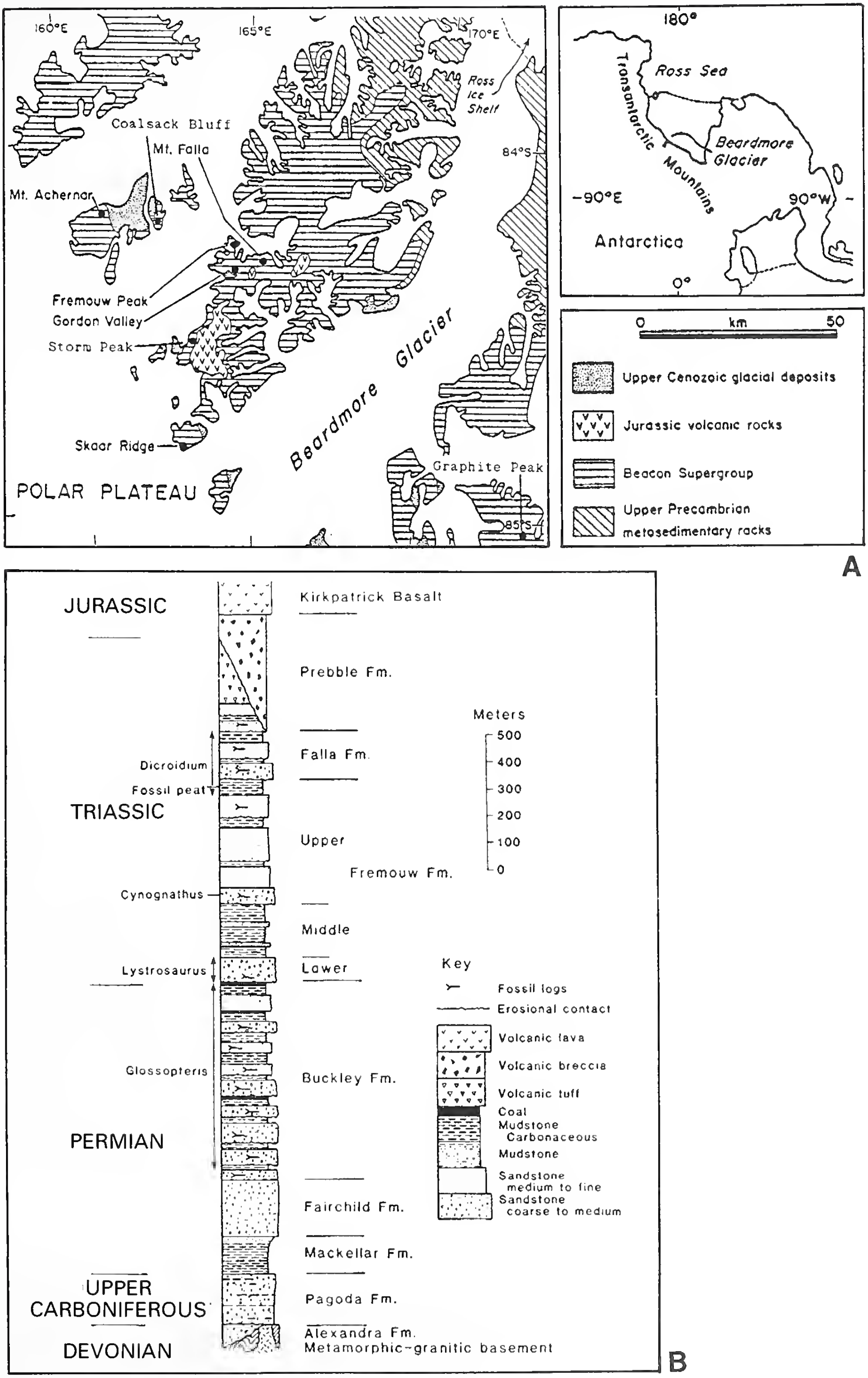
### *Kykloxylon fremouwensis* sp. nov.

Plate 1, figs 1–5; Plate 2, figs 1–6; Plate 3, figs 1–6; Plate 4, figs 1–7; Text-figs 2–5

*Derivation of name.* The generic name *Kykloxylon* refers to the continuous cylinder of secondary xylem (Gr. '*kyklos*', ring; '*xylon*', wood) and the specific epithet *fremouwensis*, to the Fremouw Peak collecting locality.

*Diagnosis.* Gymnospermous axes up to 15 mm in diameter; pith composed of parenchyma, sclerotic nests up to 300 × 650 μm wide and 400 μm high and lacunae up to 250 μm in diameter; and occasional periderm-like tissue. Primary xylem of radially aligned tracheids 5–17 μm in diameter. Secondary xylem with growth rings of variable thickness; late wood of 1–3 cell rows; tracheids polygonal to square in transverse section, up to 55 μm both in radial and tangential dimensions, pits on radial walls bordered, 8 × 10 μm to 10 × 14 μm in diameter; 3–9 simple pits in cross fields arranged in vertical tiers; cross field pits oval–circular, horizontally elongate and 7 × 10 μm to 10 × 25 μm; rays uniseriate, 1–10 cells high, ray cells 15–20 μm wide and 35–65 μm high. Cells of cortical periderm up to 35 × 50 μm wide, frequently with dark contents. Leaf venation originating

TEXT-FIG. 1. A, Map of the Beardmore Glacier area, Transantarctic Mountains. B, Stratigraphical column of the Beacon Supergroup; Central Transantarctic Mountains.


160°E
165°E
170°E
Ross Ice Shelf
Coalsack Bluff
Mt. Falla
Mt. Achernar
84°S
Fremouw Peak
Gordon Valley
Storm Peak
Skaar Ridge
Beardmore Glacier
POLAR PLATEAU
Graphite Peak
85°S
180°
Ross Sea
Transantarctic Mountains
Beardmore Glacier
-90°E
90°W
Antarctica
0°
0 km 50
Upper Cenozoic glacial deposits
Jurassic volcanic rocks
Beacon Supergroup
Upper Precambrian metasedimentary rocks
A
JURASSIC
Kirkpatrick Basalt
Prebble Fm.
Meters
500
400
300
200
100
0
Falla Fm.
Dicroidium
Fossil peat
TRIASSIC
Upper
Fremouw Fm.
Cynognathus
Middle
Lystrosaurus
Lower
Key
Fossil logs
Erosional contact
Volcanic lava
Volcanic breccia
Volcanic tuff
Coal
Mudstone Carbonaceous
Mudstone
Sandstone medium to fine
Sandstone coarse to medium
Glossopteris
Buckley Fm.
PERMIAN
Fairchild Fm.
Mackellar Fm.
UPPER CARBONIFEROUS
Pagoda Fm.
Alexandra Fm.
DEVONIAN
Metamorphic-granitic basement
B

as two pairs of traces from four axial bundles; subsequent divisions in cortex and leaf base leading to a row of adaxial bundles and two incomplete rings of bundles toward the abaxial surface.

*Holotype.* Specimen 10,628 E.

*Paratypes.* Specimens 10,397 D(1); 10,415 A–B; 10,440 C(3); 10,525 A(6); 10,891 D(7)–E; 10,891 F(2).

*Locality.* Col just north of Fremouw Peak, GPS 84° 17′ 409″ S, 164° 21′ 483″ E (Buckley Island Quadrangle).

*Stratigraphical level.* Top of the upper portion of the Fremouw formation, Beacon Supergroup, early Middle Triassic.

### *Description*

This paper is based on the description of twelve stem specimens that occur in the same peat blocks as *Antarcticycas schopfii* (Smoot *et al.* 1985), *Dicroidium* foliage (Pigg 1990) and filicalean fern stems and petioles (Millay and Taylor 1990). No specimens of *Kykloxylon* have been found associated with the conifer *Notophytum krauselii* (Meyer-Berthaud and Taylor 1991) or with sphenophyte twigs known from this locality which may be part of a different plant community (Taylor and Taylor 1990).

The smallest axis, which represents the apical portion of a leafy shoot, is 3·2 × 4·3 mm wide, and includes leaf bases (Text-fig. 2G). The six other leafy shoots range from 5 to nearly 10 mm in diameter. They show a single ring of xylem in transverse section and have a single year's growth (Pl. 1, figs 1–2; Text-fig. 2C–F). Leaves are densely arranged on the shoots. The occurrence of several bands of periderm just beneath the leaf bases suggests that the leaves were probably shed early, perhaps during the first year of growth.

Four stems have a vascular cylinder with more than one growth ring and contain no leaves (Pl. 1, figs 3–4; Text-fig. 2A–B). The largest stem has five rings of secondary xylem and measures 10 × 15 mm in diameter (Pl. 1, fig. 3; Text-fig. 2A). All of the axes that are approximately one year old possess axillary buds; a larger axis approximately five years old has what appears to be an axillary bud, but this may also represent an adventitious bud (Text-fig. 2A, C–D, F–G).

*Pith.* The diameter of the pith varies from 0·5 mm in the apical portion of the shoot to 1·8 × 2·6 mm in the largest stem (Pl. 1, figs 1, 3–5). This represents 16–40 per cent of the total diameter of the axes without leaf bases and 22–75 per cent of the diameter of the vascular cylinder. The pith parenchyma is rarely preserved except in the vicinity of what we interpret as sclerotic nests, which are present in all specimens including the apical portion of a shoot (Pl. 1, figs 2, 5; Pl. 2, fig. 1). These nests are up to 650 $\mu$m wide (transverse section) and 100–400 $\mu$m high (longitudinal section) in the largest stems; 110–150 $\mu$m in width (TS) and up to 150 $\mu$m high (LS) in the apical stem sections. Nests are composed of polyhedric cells, 30–80 $\mu$m wide, that sometimes possess reticulate or pitted thickenings on their walls. The parenchyma cells preserved in the vicinity of these nests measure up to 90 $\mu$m in diameter. Another conspicuous feature of the pith is the presence of ovoid-spherical cavities that do not exceed 250 $\mu$m in diameter (Pl. 1, figs 1–2, 5; Pl. 4, fig. 7). Some of these spheres superficially resemble chlamydospores of fungi, but it is our belief that most represent pith lacunae that are an anatomical feature of this taxon. Lacunae of this type have not been recorded in any other plant material from the Fremouw peak locality but they resemble the 'resinous cells' described in the cortex of *Dicroidium* leaves (Pigg 1990) and *Pteruchus*-like pollen organs (DeVore and Taylor 1988). One additional potentially important anatomical feature in *Kykloxylon* is a band of small rectangular cells arranged in files that occasionally traverse

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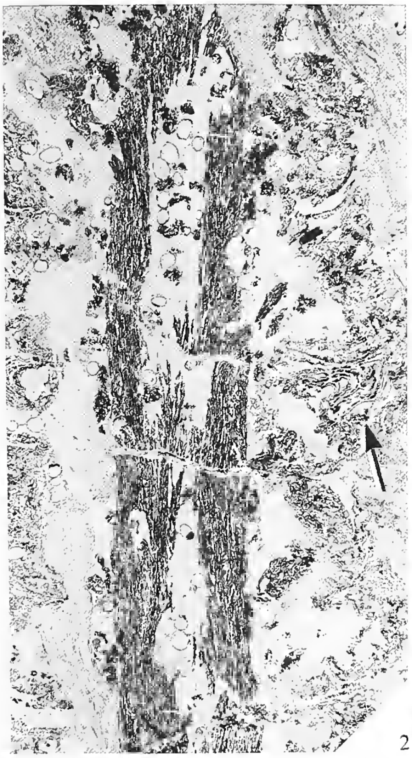
EXPLANATION OF PLATE 1

Figs 1–5. *Kykloxylon fremouwensis* gen. et sp. nov. Middle Triassic; Queen Alexandra Range, Transantarctic Mountains. 1, 10,628 E(1)BT. 17; transverse section (TS) of a leafy shoot; holotype specimen, × 10. 2, 10,397 D(1)T. 5; longitudinal section (LS) of a leafy shoot with a bud at arrow, × 10. 3, 10,891 F(2)T. 5; TS 5 year-old stem with two leaf traces at arrows, × 6·5. 4, 10,891 D(3)T. 2; TS 3 year-old stem, × 20. 5, 10,440 C(3). 3; TS central pith region of the apical portion of a shoot; note sclerotic nests (N) and lacunae (L), × 25.

PLATE 1


1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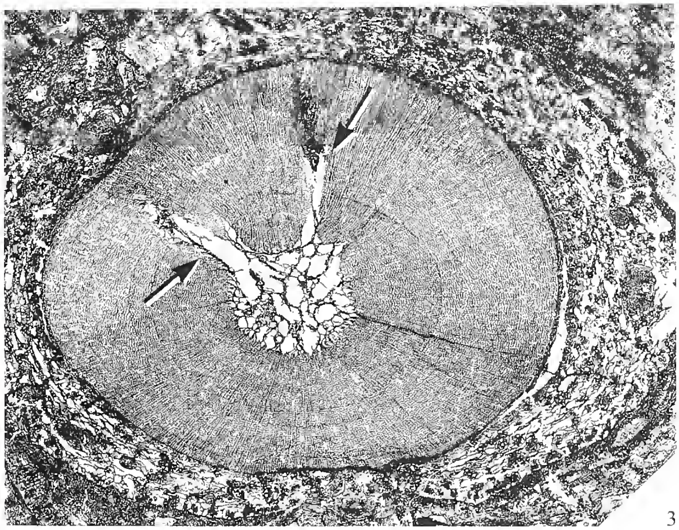
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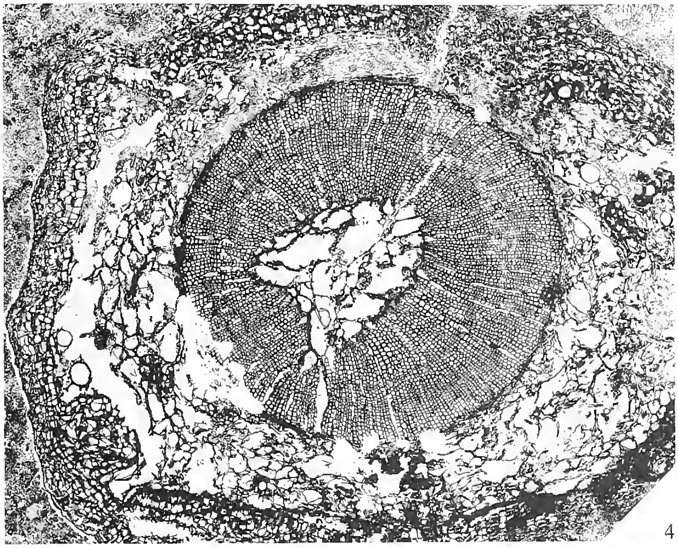
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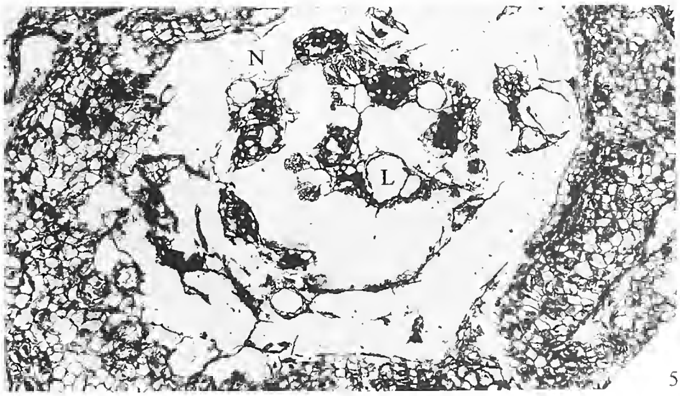

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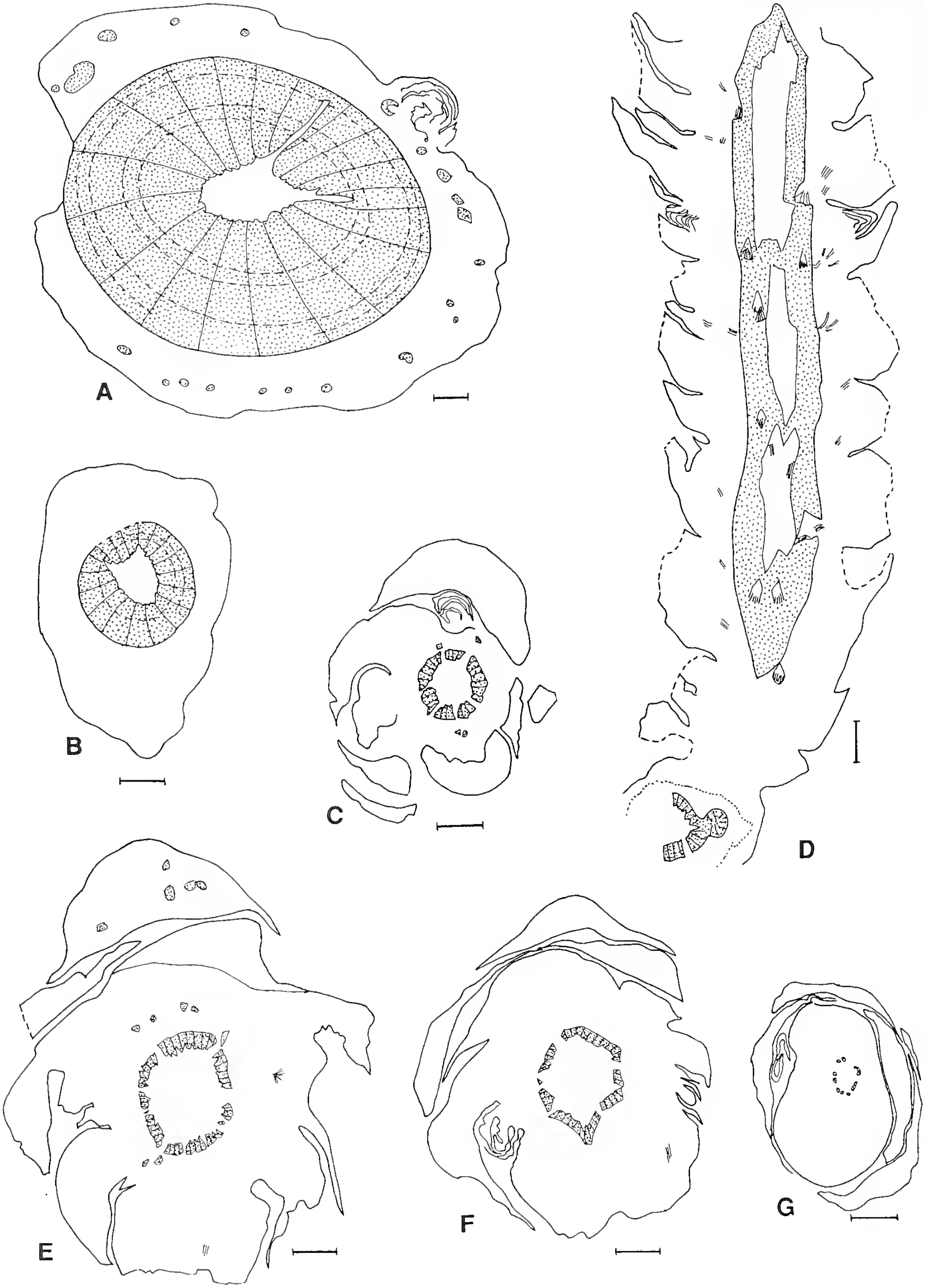
MEYER-BERTHAUD *et al.*, *Kykloxylon*


A
B
C
D
E
F
G

the pith. While this zone of cells superficially resembles a periderm-like tissue, the origin and subsequent fate of these cells is not known.

*Primary xylem.* The primary xylem in *Kykloxylon* is composed of a few rows of radially aligned tracheids that differ from those of the secondary xylem by their smaller diameters (5–17 $\mu$m wide) (Pl. 2, figs 1–2). A transverse section in the apical portion of a shoot clearly shows that the primary xylem is arranged in paired clusters of tracheids suggesting that the axial bundles also occur in pairs (Pl. 1, fig. 5; Pl. 2, fig. 1). Order of primary xylem maturation is endarch. Tracheids with scalariform to reticulate secondary thickenings compose the major portion of this tissue.

*Secondary xylem.* In transverse section, the secondary xylem ranges from 200 $\mu$m wide in the leafy twigs to 3·5 mm in the largest stem. Tracheids are polygonal in the region of the pith and square to rectangular in the outermost rings of the five year-old stem. In the early-wood, tracheids range from 25 to 70 $\mu$m in tangential dimension and from 25 to 55 $\mu$m radially. The radial dimension of the tracheids in stems with growth rings is reduced in the latewood which is composed of 1–3 rows of cells (Pl. 1, figs 3–4). Rays are 1–10 cells high and uniseriate (Pl. 2, fig. 5). Ray cells range from 15 to 20 $\mu$m wide and 35 to 65 $\mu$m high. Axial parenchyma is absent.

Pitting on the radial walls of the tracheids is variable. In the oldest specimen, most of the tracheids, including those close to the primary xylem, show contiguous biseriate pits that are arranged either in an alternate or opposite pattern; otherwise the radial pitting is uniseriate and either spaced or contiguous (Pl. 2, fig. 3). A few large tracheids possess triseriate radial pitting (Pl. 2, fig. 6). Pits are bordered and range from $8 \times 10$ $\mu$m to $10 \times 14$ $\mu$m wide. Apertures are circular to oval and average 6 $\mu$m in diameter. In most of the pits, the centre is occupied by a circular black dot up to 3 $\mu$m in diameter (Pl. 2, figs 3–4; Text-fig. 3). If this dot represents a torus, its small diameter compared with the size of the pith aperture makes its function questionable. An alternative hypothesis is that the pit aperture is conical rather than cylindrical (Text-fig. 3). The dot, then, would be the black image of the outer aperture (facing the pit chamber).

Pits in the cross fields are simple and range from 3 to 9 (Pl. 2, fig. 3). The shape of these pits is oval; in some, it is horizontally elongate. Pit size ranges from $7 \times 10$ $\mu$m to $10 \times 25$ $\mu$m. Oval pits are numerous and arranged more or less in an alternate pattern. Horizontally elongate pits occur in vertical tiers and give the cross field a scalariform appearance (Pl. 2, figs 3, 6). The dimensions and arrangement of the pits suggest that the large horizontally elongated ones may result from the fusion of two contiguous oval pits. The horizontal walls of the ray cells are smooth and approximately 4 $\mu$m thick. Periclinal walls are rarely observed.

*Phloem.* Some secondary phloem is preserved in the largest stem where it is sectioned obliquely (Pl. 3, fig. 5). This phloem zone is about 300 $\mu$m thick and composed of small sieve cells up to 30 $\mu$m in radial dimension. Uniseriate rays are also visible. Due to the relatively poor preservation of extraxylary tissues the exact organization of the phloem is uncertain, and thus it is not known whether fibres are present. Nothing is known about the primary phloem of *Kykloxylon.*

*Cortex and periderm.* Cortical tissues are similar to those of the pith and include numerous spherical cavities (Pl. 3, fig. 4; Pl. 4, figs 5–6). Some parenchyma cells may be present surrounding the sclerotic nests. These cells measure $20 \times 50$ $\mu$m to $55 \times 65$ $\mu$m in the largest stem. Almost all of the axes possess one to several bands of periderm just beneath the leaf bases (Pl. 3, fig. 4). The development of this tissue occurs early in the ontogeny of the stem since cortical cells of the apical fragment of a shoot show some evidence of periclinal divisions. The periderm is composed of cells that are square-rectangular in both transverse and longitudinal sections. These elements measure up to $35 \times 50$ $\mu$m wide and frequently possess dark contents.

*Leaf trace emission and phyllotaxy.* The vascularization of a leaf originates as four traces (Ia, Ib, IIa, IIb) arranged in two pairs (I, II) that are variously separated (650–800 $\mu$m) depending on the diameter of the stele

TEXT-FIG. 2. *Kykloxylon fremouwensis* gen. et sp. nov. Middle Triassic; Queen Alexandra Range, Transantarctic Mountains; general views of a selection of representative axes; all specimens except D in transverse section. A, 10,891 F(2)aT. 41. B, 10,891 D(3)T. 2. C, 10,525 A. 6. D, 10,397 DT. 2. E, 10,628 E(1)BT. 28; holotype specimen. F, 10,743 DT. 3. G, 10,440 C(3). 3. Scale bars = 1 mm.

(Pl. 4, figs 1–4; Text-fig. 4A). The two traces of a pair (Ia, Ib) are emitted with a slight delay from two different bundles separated by a narrow parenchymatous zone (Pl. 4, figs 2–4, 7). Traces follow a slightly ascending course through the cortex (Pl. 4, figs 1–4, 6; Text-fig. 4B–C) until the two inner bundles (Ib, IIb) become reorientated at 90° (Pl. 4, fig. 5; Text-fig. 4D, F). As a result of this change in orientation the protoxylem of these bundles shifts from an adaxial to a lateral position. The inner and outer traces of each pair subsequently divide in different planes that are approximately perpendicular (Text-fig. 4F). In each pair of traces, the bundles arising from the division of the outer trace (either Ia or IIa) are arranged in a horizontal row; those arising from the division of the inner trace (either Ib or IIb) tend to be arranged in a ring rather than remaining vertically aligned (Pl. 3, figs 1–3, 6; Text-fig. 4E–F).

In leafy twigs, the leaves are crowded and the phyllotaxy difficult to interpret. A series of transverse sections has been prepared through a complete internode of a five-year-old stem and a selection of the most representative ones is illustrated in Text-figure 5A–C. In Text-figure 5D, which shows these sections superimposed, leaf vascular supplies I+II (including Ia, Ib, IIa, IIb) and I′+II′ (including I′a, I′b, II′a, II′b) are separated by an angle approaching 130°. This suggests that the leaves were arranged in a single sinistrorse helix according to the Fibonacci series. On the basis of this specimen it would appear that the buds are axillary (Text-fig. 5A, C). However, additional specimens will have to be critically examined to confirm this hypothesis.

*Leaf bases.* Leaf bases are widely inserted on the twigs (Pl. 1, figs 1–2) and all are broken at a distance of 1–2 mm from the stem surface. The bases are flat or slightly concave on the adaxial surface, and hemispherical on the abaxial side (Pl. 3, figs 1–2; Text-fig. 4E); none of the leaf bases observed showed evidence of tapering. Bases measure up to 2 mm high and 5 mm wide. The ground tissue is composed of an outer part that consists of several rows of cuboidal cells with dark contents and an inner zone of parenchymatous cells that often appear disorganized. The inner zone also contains numerous sclerotic nests and lacunae (Pl. 3, fig. 1; Text-fig. 4E). The vascular system in the leaf bases is bilateral and complex. Each half of the leaf vascular supply consists of an adaxial series of bundles and, near the middle of the leaf base, an incomplete ring of traces that are close to the abaxial surface (Pl. 3, fig. 1; Text-fig. 4E). Bundles range from 150 to 350–550 $\mu$m wide and often occur in a lacuna. In the best preserved portions of the leaf bases, they are ensheathed by 2–3 rows of elongate cells that are slightly flattened in transverse section (Pl. 3, fig. 6). Each bundle consists of up to 10 rows of radially aligned tracheids that are $5 \times 10$ $\mu$m to $15 \times 20$ $\mu$m wide. Primary xylem maturation is endarch in the bundles of the adaxial series. Protoxylem has an inner lateral position in the traces of the ring (Pl. 3, figs 3, 6). External to the tracheids is a zone of phloem that consists of radially aligned thin-walled cells which are up to 45 $\mu$m wide. No further information is available of the leaf base or leaf distally.

## DISCUSSION

### *Comparison with form genera based on petrified wood from Gondwana*

There have been numerous reports of silicified wood fragments from the late Palaeozoic and Mesozoic of Antarctica since the initial description of *Antarcticoxylon* by Seward (1914). However, in most instances these reports lack information about anatomical features. To date, the best-known fossil woods from the Antarctic regions are those described by Maheshwari (1972) from different Permian localities of Antarctica, two specimens referred to as *Taeniopitys scotti* and *Dadoxylon allani* by Kraüsel (1962) from the Permian of the Allan Hills (South Victoria Land), and specimens of *Australoxylon* (*Dadoxylon*) *bakeri*, *D. lafoniense* and *Dadoxylon* cf. *D. angustum* from the Permian of the Falkland Islands (Halle 1911; Seward and Walton 1923; Marguerier 1973). In

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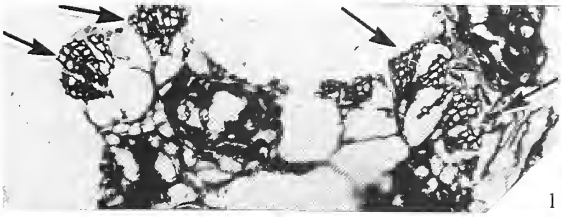
EXPLANATION OF PLATE 2

Figs 1–6. *Kykloxylon fremouwensis* gen. et sp. nov. Middle Triassic; Queen Alexandra Range, Transantarctic Mountains. 1, 10,440 C(3). 3; detail of TS stele showing 2 pairs of bundles (arrows) in the apical portion of a shoot, × 100. 2, 10,891 D(3)T. 2; radially aligned tracheids of primary bundles seen in figure 1 and larger tracheids of the secondary xylem, × 170. 3, 10,891 F(2)IIS. 1; secondary xylem in radial section; cross fields at top, × 335. 4, 10,891 F(2)IIS. 1; bordered pits with a central black dot on the radial wall of a tracheid, × 800. 5, 10,891 F(2)IS. 1; secondary xylem with short uniseriate rays in tangential section, × 150. 6, 10,891 F(2)IIS. 1; triseriate pitting on the radial wall of a tracheid, × 200.

PLATE 2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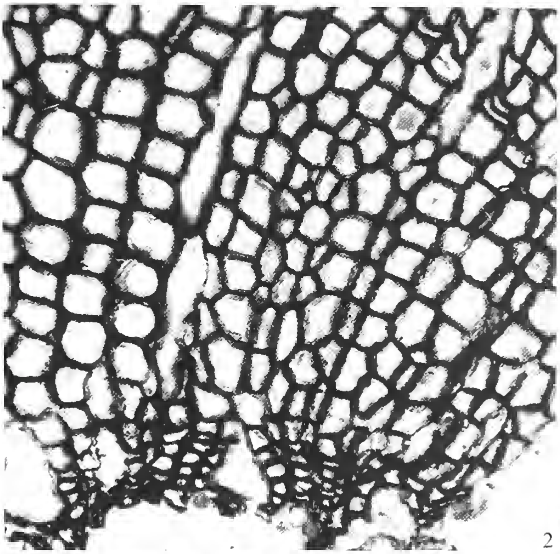
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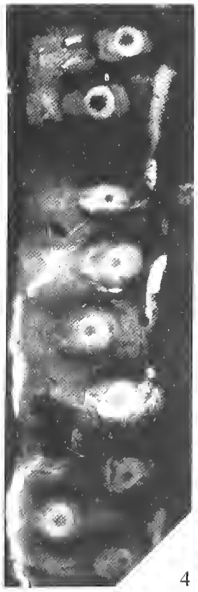
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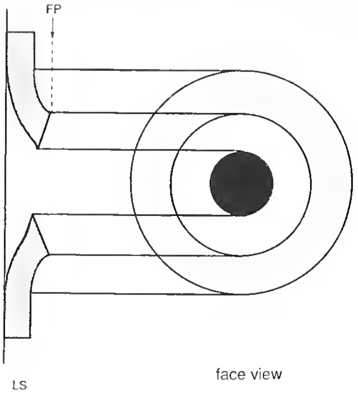
MEYER-BERTHAUD *et al.*, *Kykloxylon*



TEXT-FIG. 3. Interpretation of the features of a bordered pit on the radial wall of a secondary xylem tracheid. FP, focusing plane; LS, longitudinal section.

most species, as in *Kykloxylon*, ray cells have thin, unornamented walls and pits in the cross fields are simple. Depending on the taxa, cross field pits are either small and numerous or large and unique. In three species, *T. scotti*, *D. allani* and *A. bakeri*, variations in pit organization from one type to the other occur within a single specimen. Despite these variations, none shows the large, horizontally elongated pits arranged in vertical tiers that characterize some cross fields in the wood of *Kykloxylon*. In addition, unlike *Kykloxylon*, *T. scotti* and *A. bakeri* are characterized by a special outer parenchymatous 'sheet' that surrounds the pith (Kraüsel *et al.* 1962). The description by Halle (1911) of 2–5 small simple pits that are rounded or elliptical, and then almost horizontal in the cross fields of the wood of *Dadoxylon* cf. *D. angustum* is reminiscent of the cross field pits in *Kykloxylon*. In the former species, the ray cells are especially narrow (10–15 $\mu$m), the rays are taller (1–25 cells) and pits on the radial walls of the tracheids have an elliptical pore.

The wood of *Damudoxylon indicum* (Holden 1917; Maheshwari 1972) from the Permian of India has short rays (2–7 cells) and 1–4 simple pits that tend to fuse in the cross fields. But unlike *Kykloxylon*, the pith of *D. indicum*, which is devoid of sclerotic cells and lacunae, is lined by a sheath of small reticulate cells. In addition, the primary xylem is associated with a large amount of parenchyma at the nodes, a feature that has not been observed in the Antarctic specimens. One feature that deserves mention in a comparison with *Kykloxylon* is the report of paired leaf traces extending almost horizontally through the wood of *D. indicum* (Holden 1917).

### *Relationships of* Kykloxylon fremouwensis *and* Dicroidium fremouwensis

*Dicroidium fremouwensis* occurs in the peat of Fremouw Peak and is the first species of *Dicroidium* known with anatomically preserved specimens. It includes bifurcating fronds that might have been

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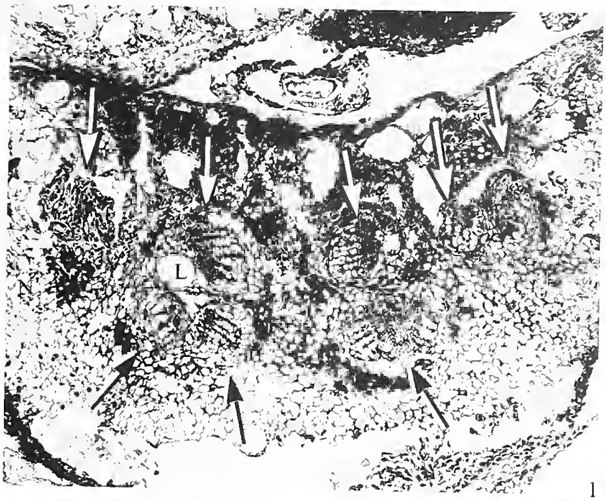
EXPLANATION OF PLATE 3

Figs 1–6. *Kykloxylon fremouwensis* gen. et sp. nov. Middle Triassic; Queen Alexandra Range, Transantarctic Mountains. 1, 10,628 E(1)BT. 82; TS leaf base showing an adaxial line of bundles and two incomplete rings of bundles placed oppositely on the abaxial side (arrows); note sclerotic nest (N) and lacuna (L); compare with Text-fig. 4E; holotype specimen, × 22. 2, 10,628 E(1)BT. 22; oblique TS leaf base showing a 3-dimensional arrangement of the bundles; holotype specimen, × 22. 3, 10,628 E(1)BT. 82; detail of figure 1 showing the two abaxial groups of bundles arranged in opposite rings and two adaxial bundles at right (arrows), × 45. 4, 10,397 DT. 5; LS wood, cortex and periderm from right to left; note a leaf trace running through the cortex, × 40. 5, 10,891 F(2)B. 12; secondary phloem in oblique TS showing two rays with enlarged cells, × 80. 6, 10,415 A. 55; detail of a pair of perpendicularly arranged leaf traces within cortex of a leafy shoot; at left, outer trace with protoxylem pointing upwards and at right, inner leaf trace shifted; adaxial side at top, × 45.



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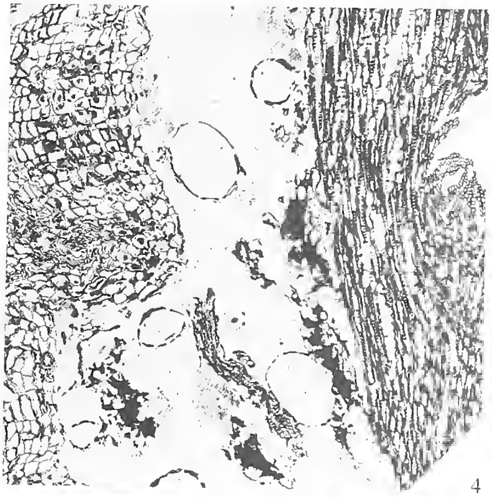

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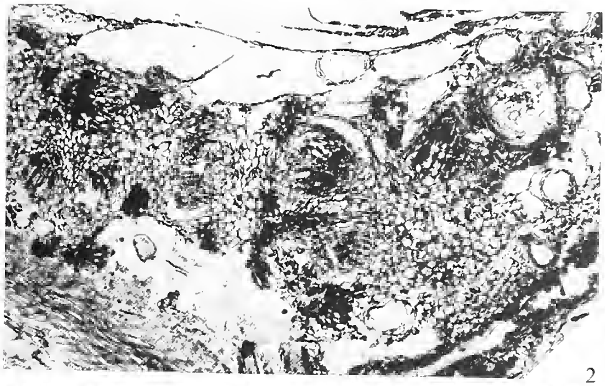

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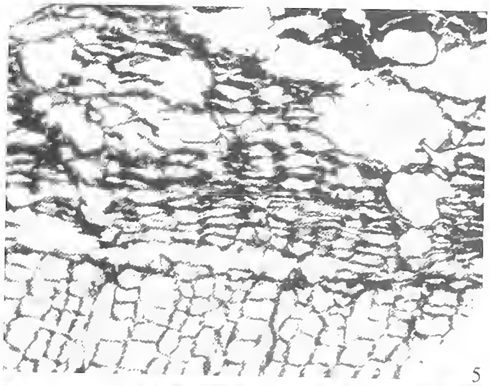

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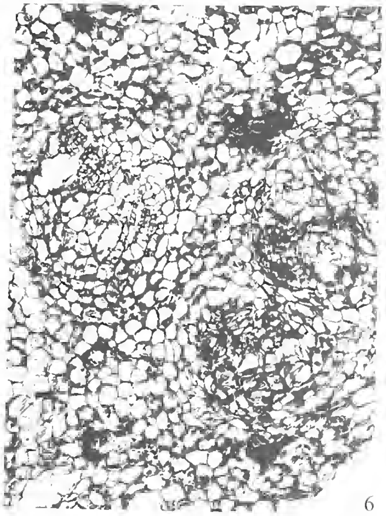

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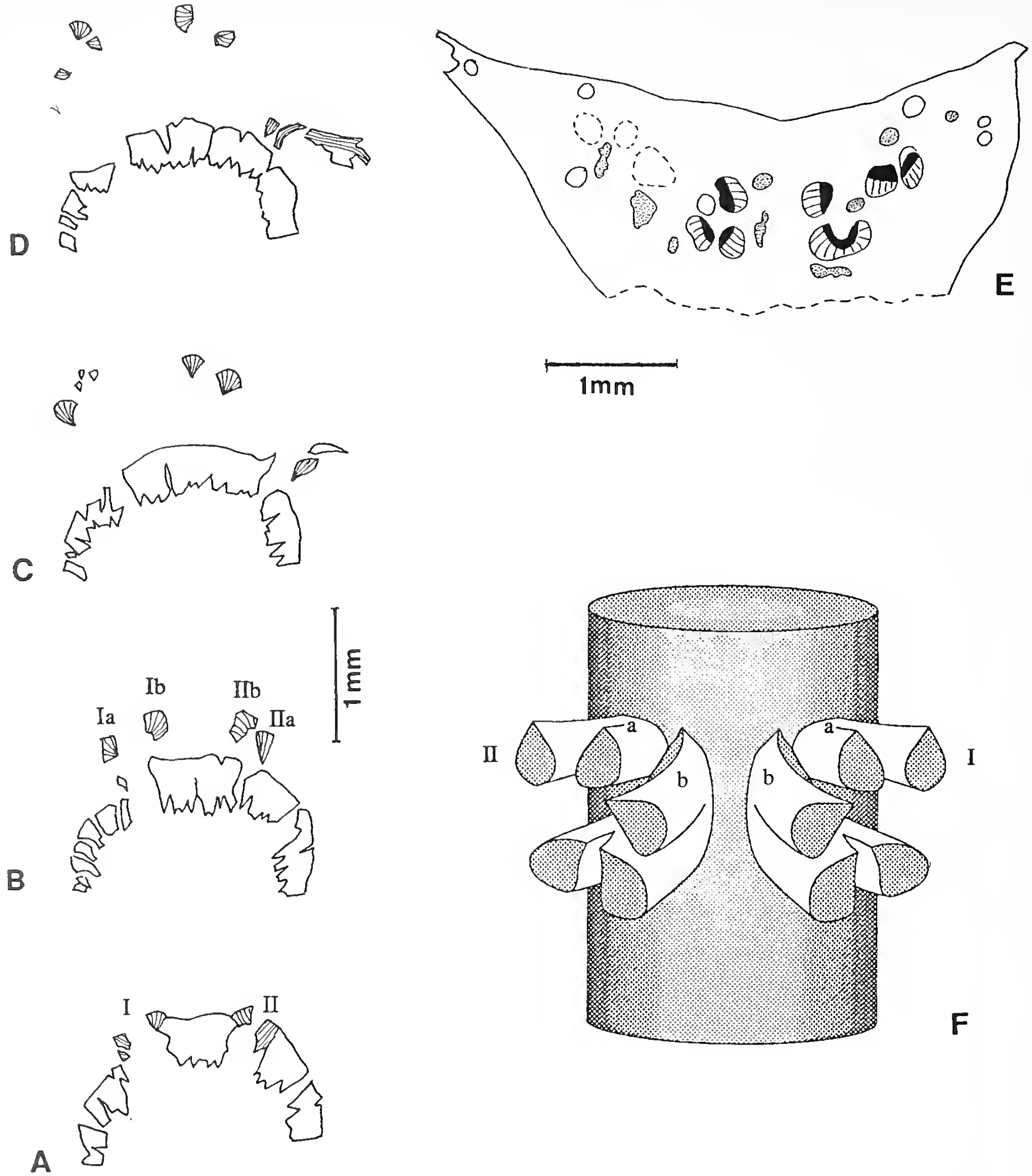
MEYER-BERTHAUD *et al.* *Kykloxylon*



TEXT-FIG. 4. *Kykloxylon fremouwensis* gen. et sp. nov. Middle Triassic; Queen Alexandra Range, Transantarctic Mountains. A–D. Series of sections from proximal (A) to distal levels (D) showing the emission of two pairs of leaf traces (Ia, Ib and IIa, IIb) that compose the vascularization of a leaf; compare with Plate 4, figs 5–7; holotype specimen; A, 10,628 E(1)BT. 41; B, 10,628 E(1)BT. 34; C, 10,628 E(1)BT. 26; D, 10,628 E(1)BT. 21; E, 10,628 E(I)BT. 82; oblique transverse section of a leaf base showing the three-dimensional arrangement of the leaf traces. Stippled areas = sclerotic nests; solid white circles = secretory cavities; areas encircled by a dotted line = putative position of unpreserved bundles; blackened areas in bundles = xylem; stripped areas in bundles = phloem. F, three-dimensional reconstruction showing the division of the leaf traces that form the vascularization of a single leaf.

up to 150 mm long with petioles measuring 5 mm proximally (Pigg 1990). Although remains of *D. fremouwensis* are abundant at Fremouw Peak, nothing is known of proximal petiole anatomy because specimens discussed in Pigg (1990) are known only at and distal to the frond bifurcation into pinna rachides. On the contrary, a wealth of information is known on the anatomy of the rachides and pinnae. Rachides are unique in possessing a three-dimensional vascular system with an adaxial row of bundles and one abaxial ring of strands. The strands are ensheathed by 1–3 layers of elongated cells. They consist of several rows of radially aligned tracheids limited abaxially by a zone of secondary phloem. Adaxial bundles are endarch (Pigg 1990, pl. 3, figs 2–5). Two zones are recognized in the ground tissue of the rachides: an outer zone of cuboidal cells with dark contents and an inner zone of loose parenchyma elements in which large 'resinous cells' are scattered.

*Kykloxylon fremouwensis* and *Dicroidium fremouwensis* are associated in the same plant assemblage within the Fremouw Peak peat and share a striking number of similar anatomical features. The dimensions of the petioles of *D. fremouwensis* are comparable to those of the leaf bases attached to *Kykloxylon*. The two-part organization of the ground tissue is similar in both species. The lacunae described in pith, cortex and leaf bases of *Kykloxylon* resemble the 'resinous cells' (Pigg 1990) of *Dicroidium*. The absence of sclerotic nests in *Dicroidium* rachides and pinnae may be related to the distal position of these parts in the frond architecture. The arrangement of leaf traces is dorsiventral both in *D. fremouwensis* rachides and *K. fremouwensis* leaf bases and differs only in the number of abaxial rings. The composition of the strands is similar in both species. Based on these anatomical features and the occurrence of both taxa within the same peat, we believe that *Kykloxylon fremouwensis* and *Dicroidium fremouwensis* represent parts of the same biological species. We interpret the reduction from two abaxial rings of strands in *Kykloxylon* leaf bases to one ring only in *Dicroidium* rachides as the result of the dichotomy that is known to occur in the distal part of *Dicroidium* petioles.

This is a different interpretation for the biological affinities of *Dicroidium* from that seen at Triassic localities in Argentina and elsewhere in South America, where *Dicroidium* is consistently associated with *Rhexoxylon* stems (Archangelsky 1968). This latter reconstruction was subsequently supported by Petriella (1981) and by Retallack and Dilcher (1988), who reconstructed the '*Dicroidium*/*Rhexoxylon* plant'. These two viewpoints as to the biological affinities of *Dicroidium* are not contradictory. Rather, they underscore a common situation in palaeobotany in which one type of leaf is ultimately demonstrated to have been produced by a variety of stem-genera. This is certainly the possibility with *Dicroidium*, a leaf morphotype which is highly variable throughout the Triassic of Gondwana.

### *The relationship between* Rhexoxylon *and* Antarcticoxylon

*Rhexoxylon* has been described from various Triassic localities of South Africa and South America, and four species are currently recognized: *R. africanum* (Bancroft 1913), *R. tetrapteridoides* (Walton 1923), *R. piatnitzkyi* (Archangelsky and Brett 1961; Brett 1968) and *R. brasiliensis* (Herbst and Lutz 1988). *Rhexoxylon waltoni*, which was described by Kraüsel (1956) on the basis of a special tissue ('Fransenxylem') lining the secondary xylem, was synonymized with *R. africanum* by Archangelsky and Brett (1961), a decision that has been supported by the work of Herbst and Lutz (1988). In addition, a specimen with *Rhexoxylon*-like secondary anatomy was recently reported from the Triassic of Antarctica (Taylor 1992). All specimens assigned to these species are characterized by a cylinder of secondary xylem that is divided into sectors by large wedges of parenchyma and the development, within the pith, of strands of secondary xylem that are either centripetal or both centripetal and centrifugal. This vascular organization superficially resembles that of modern lianas (Walton 1923). In addition, the stems assigned to these species are characterized by a large pith, a pycnoxylic type of wood and tracheids of secondary xylem that show alternate and contiguous ('araucarian') bordered pits on the radial walls. Anomalous xylem development in tangential cracks of the wood is also a common feature of these taxa.

The problem of associating *Antarcticoxylon priestleyi* with *Rhexoxylon* is a complex one. Two decorticated specimens have been assigned to *Rhexoxylon* (*Antarcticoxylon*) *priestleyi* by Walton (1925); the original stem described by Seward (1914) from an erratic boulder on the Priestley Glacier (Antarctica) and a second, better-preserved specimen from the Triassic of South Africa (Walton 1925, 1956). The association of the Antarctic specimen with a two-winged pollen grain that resembles those produced by *Pteruchus* suggests a Triassic age for this specimen. Like the four species of *Rhexoxylon* mentioned above, both specimens have a pycnoxylic type of wood, tracheids of secondary xylem of the 'araucarian' type and anomalous xylem development in the wood. However, they also possess a massive undivided cylinder of secondary xylem and, in this respect, differ from these taxa. Because of the bad state of preservation of the Antarctic specimen, the presence of centripetal xylem at the periphery of the pith has never been established and many other critical characters of the primary and secondary xylem have not been observed in this stem. For these reasons, we propose to maintain *Antarcticoxylon* as a form genus including a single valid representative, the specimen from Antarctica (Meyer-Berthaud and Taylor 1991). The specimen from South Africa has a well-preserved ring of centripetal secondary xylem at the periphery of the pith and in this respect resembles *Rhexoxylon*. However, it is not clear whether stems with an undivided cylinder of secondary xylem should be included within *Rhexoxylon*. According to Walton (1923, 1925, 1956), the *Rhexoxylon* stems probably possess a continuous cylinder of secondary xylem at an early stage of development that becomes segmented radially by the secondary tissue development. During this phase of growth, vascular strands with both centripetal and centrifugal secondary xylem are formed at the periphery of the pith. However, after the discovery of a young stem of *R. piatnitzkyi*, Archangelsky and Brett (1961) suggested a different pattern of growth. They interpret the vascular tissues of *Rhexoxylon* as discrete vascular segments with both centripetal and centrifugal xylem from the earliest stages of development. According to this idea, the increase in diameter of the stems results from a tangential splitting of the original strands and the formation of secondary xylem along the margins of the wedges of wood that have become separated. In the present paper, the specimen from South Africa is referred to as '*Rhexoxylon priestleyi*'.

### *Comparison between* Kykloxylon, Antarcticoxylon *and* Rhexoxylon

A comparison of the available anatomical features of *Kykloxylon*, *Antarcticoxylon* and *Rhexoxylon* indicates that these taxa have numerous characters in common (Table 1). The secondary xylem in all three is pycnoxylic with uniseriate rays. Pitting on the radial walls of the tracheids is uni- or biseriate, rarely triseriate. Pits are bordered with a circular, sometimes slightly elliptical, aperture. They are generally polygonal and contiguous (of 'araucarian' type) when multiseriate. Pits in the cross field are simple. Those in *Rhexoxylon* are few and wide. We mentioned a tendency for a reduction in the number of cross field pits, possibly by fusion, in the wood of *Kykloxylon*.

A consistent character of most *Rhexoxylon* and possibly *Antarcticoxylon* stems is the presence of sclerotic nests and lacunae (also called 'reservoirs' or 'cysts'; Table 1) that might have been secretory in the pith. These characters have been mentioned by some authors (Walton 1923; Archangelsky and Brett 1961) as indicators of the potential affinities with the medullosan

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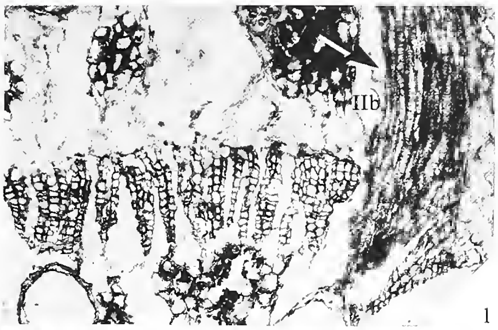
EXPLANATION OF PLATE 4

Figs 1–7. *Kykloxylon fremouwensis* gen. et sp. nov. Middle Triassic; Queen Alexandra Range, Transantarctic Mountains. 1–4, series of oblique sections showing the pattern of emission in three traces (Ia, Ib, IIb at arrows) that are part of a single leaf vascular supply, from distal (1) to proximal levels (4); holotype specimen; all × 70. 1, 10,628 E(I)BT. 8. 2, 10,628 E(I)BT. 13. 3, 10,628 E(I)BT. 17. 4, 10,628 E(I)BT. 20. 5–7, series of transverse sections showing the pattern of emission of four traces (Ia, Ib, IIb, IIa) that are part of a single leaf vascular supply, from distal (5) to proximal levels (7); note the shift of the inner bundles (Ib, IIb) in fig. 5 (arrows); compare with Text-fig. 4A–D; holotype specimen; all × 45. 5, 10,628 E(1)BT. 21. 6, 10,628 E(1)BT. 28. 7, 10,628 E(1)BT. 41.

PLATE 4



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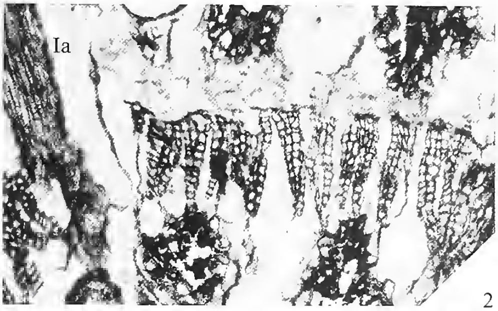

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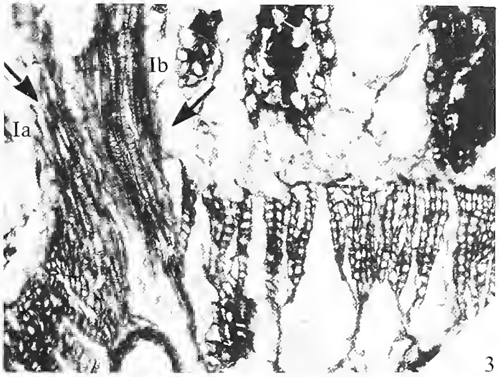

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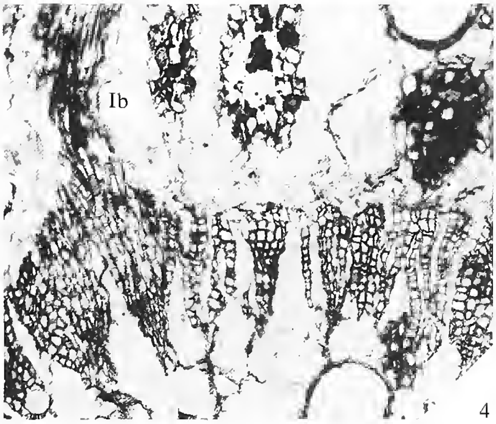

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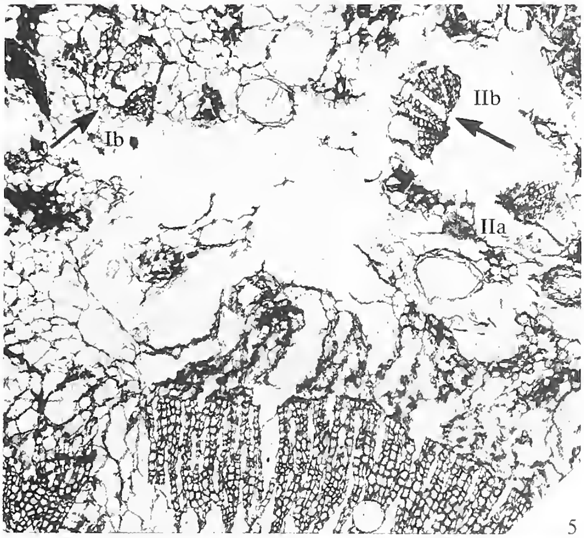

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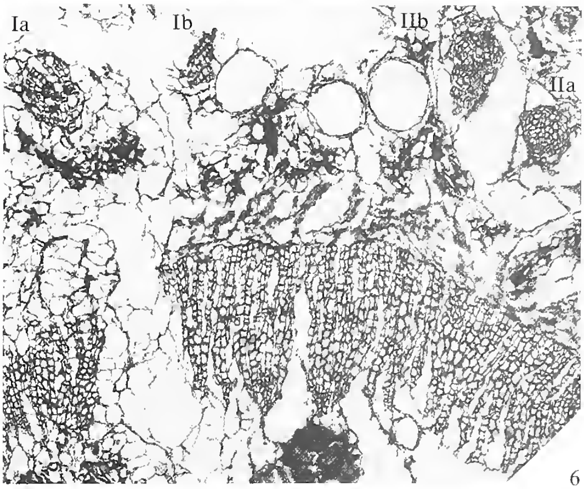

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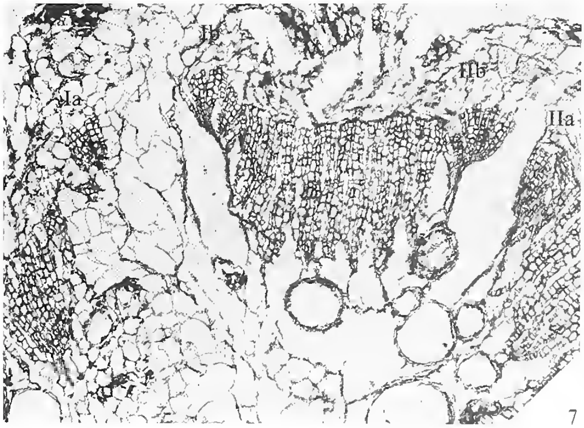

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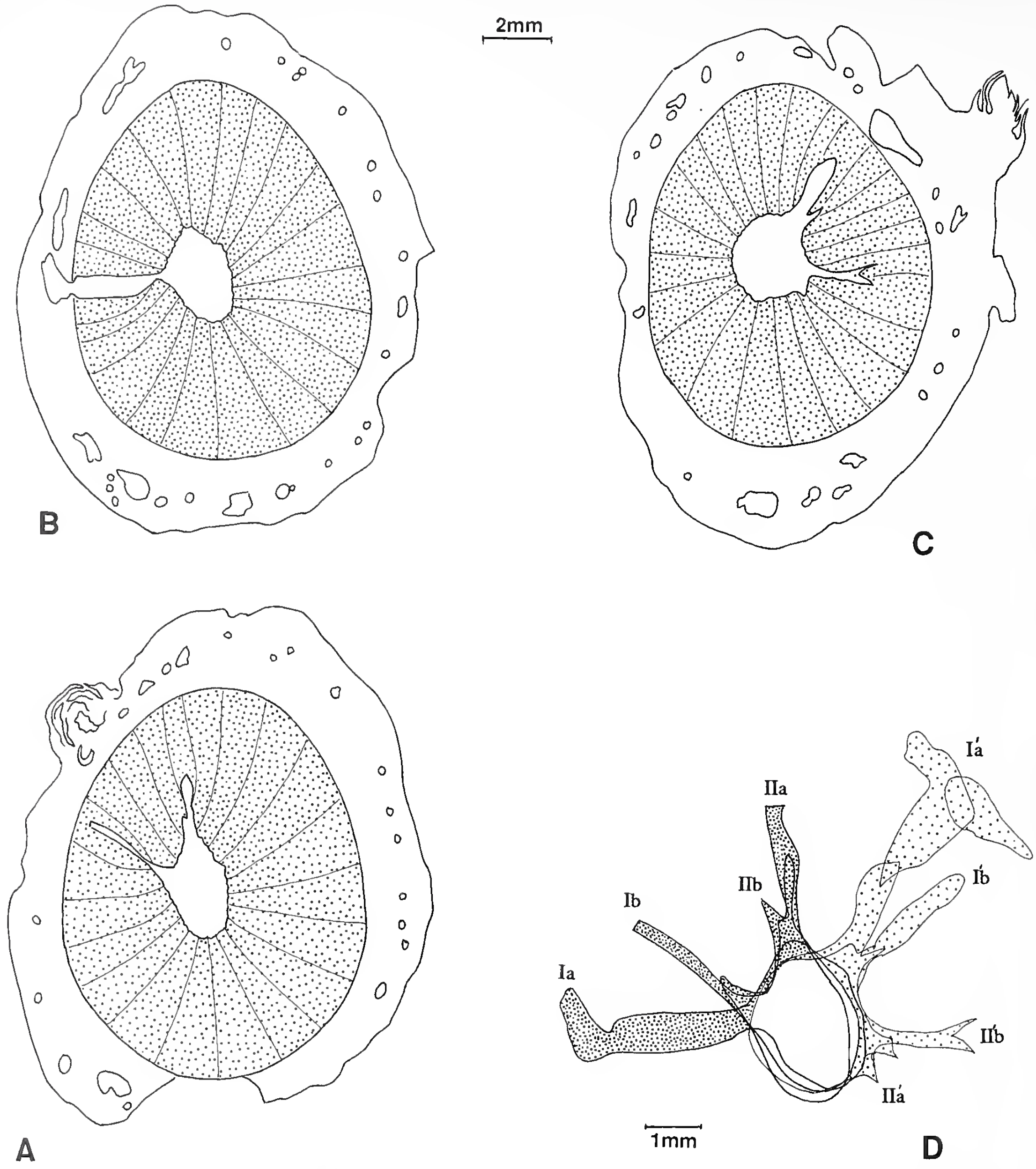
MEYER-BERTHAUD *et al.*, *Kykloxylon*



TEXT-FIG. 5. *Kykloxylon fremouwensis* gen. et sp. nov. Middle Triassic; Queen Alexandra Range, Transantarctic Mountains. A–C, emission of two successive leaf vascular supplies from proximal (A) to distal levels (C), ×3. A, 10,891 F(2)aT. 41; B, 10,891 F(2)aT. 4; C, 10,891 F(2)aT. 5. D, superimposed transverse sections showing the emission of two successive leaf vascular supplies (I+II and I′+II′) separated by an approximate angle of 130°.

pteridosperms. We emphasized similar features in *Kykloxylon* with a special mention to the lacunae since within the Fremouw Peak flora the latter are known from these stems, the leaves and petioles of *Dicroidium* and certain reproductive structures. The bands of periderm-like tissue extending

TABLE 1. Comparison of anatomical characters of *Kykloxylon* gen. nov., *Antarcticoxylon* Seward and *Rhexoxylon* Bancroft.

| | *Kykloxylon fremouwensis* | *Antarcticoxylon priestleyi* | *"Rhexoxylon priestleyi"* | *Rhexoxylon tetrapteridoides* | *Rhexoxylon africanum* | *Rhexoxylon brasiliensis* | *Rhexoxylon piatnitzkyi (small)* | *Rhexoxylon piatnitzkyi (trunks)* |
|---|---|---|---|---|---|---|---|---|
| AUTHOR(S) | | Seward 1914<br>Walton 1923, 25 | Walton 1925, 56 | Walton 1923 | Bancroft 1913<br>Walton 1923 | Herbst<br>& Lutz 1988 | Archangelsky<br>& Brett 1961 | Brett 1968 |
| LOCALITY | Antarctica | Antarctica | South Africa | South Africa | South Africa<br>Rhodesia | Brasil | Argentina | Argentina |
| DIAMETER (cm) | up to 1 x 1.5 | > 2 x 9 | 6 | up to 17 | > 25 | up to 37 x 43 | 8 | up to 100 |
| SECONDARY XYLEM | | | | | | | | |
| Divided in sectors | No | No | No | Yes | Yes | Yes | Yes | Yes |
| Centripetal wood | No | ? | Yes | Yes | Yes | Yes | Yes | Yes |
| Type | Pycnoxylic | Pycnoxylic | Pycnoxylic | Pycnoxylic | Pycnoxylic | Pycnoxylic | Pycnoxylic | Pycnoxylic |
| Ray width | Uniseriate | Uni(bi)seriate | Uniseriate | Uniseriate | Uniseriate | ? | Uniseriate | Uniseriate |
| Ray height | 1 to 10 | 1 to 24 cells | 1 to 8 cells | 5 to 7 cells | 1 to 17 cells | ? | 1 to 22 cells | 1 to 22 cells |
| Radial pitting | Uni-triseriate | Uni-biseriate | Uni-biseriate | Uni-biseriate | Uni-triseriate | ? | Uni-biseriate | Uni-biseriate |
| Cross field pits | 3 to 9 | Not preserved | 4 to 7 | 1 | 1 to 3 | "in 2 rows" | 1 to 3 | 1 to 3 |
| PROTOXYLEM | Endarch | Endarch ? | Endarch | Endarch | Endarch | Endarch | Mesarch | ? |
| PITH | | | | | | | | |
| Sclerotic nests | Yes | ? | Yes | Yes | Yes | Yes | No | Yes |
| Lacunae | Cavities | ? | "Reservoirs" | "Reservoirs" | ? | "Cysts" | "Cysts" | "Cysts" |
| Periderm-like zone | Yes | No | No | Yes | Yes | No | No | Yes |
| CORTEX | | Not preserved | Not preserved | | Not preserved | | | Not preserved |
| Sclerotic nests | Yes | | | Yes | | No | No | |
| Lacunae | Cavities | | | Secretory cells | | No | "Cysts" | |

through the pith in *Kykloxylon* have also been reported in *R. africanum* (Bancroft 1913), *R. tetrapteridoides* (Walton 1923) and *R. piatnitzkyi* (Archangelsky and Brett 1961). It is not known whether this tissue is the result of some wound or represents some form of growth that is a feature of these plants.

The pattern of leaf trace emission in *Kykloxylon* is complex and initially involves four bundles. As a result of repeated divisions the two pairs of traces that originate from the axial strands eventually give rise to an adaxial row of vascular bundles and two abaxial rings of strands in the leaf base. A comparable pattern has been reported in a young axis of *Rhexoxylon piatnitzkyi* (Archangelsky and Brett 1961). Here also the vascularization of the leaf is supplied by traces originating from several axial bundles that occur in pairs, the bundles of each pair being separated by a small amount of parenchyma. Within the cortex the traces divide to form a three-dimensional pattern. In *R. piatnitzkyi* this pattern results in the formation of seven to eight groups of bundles arranged in a semi-circle. It should be pointed out that the two leaf bases illustrated in Archangelsky and Brett's Figure 5 (1961) are incomplete and thus the possibility cannot be ruled out that the bases also contained bundles near the adaxial leaf base surface. The pattern of leaf base vascularization has not been studied in any other specimens of *Rhexoxylon* and *Antarcticoxylon*. But a horizontal or low-angled course of the leaf traces has been reported in *R. tetrapteridoides* (Walton 1923) and *R. piatnitzkyi* (Archangelsky and Brett 1961). This feature which has been observed in *Kykloxylon* may characterize the whole group of plants presently discussed. Finally, the presence of buds on small axes of *R. piatnitzkyi* (Archangelsky and Brett 1961) and *Kykloxylon* is noteworthy.

One of the primary difficulties in discussing the affinities of *Kykloxylon* with *Rhexoxylon* is brought about by the fact that the former are known only from young axes (with up to five years' growth) while most species of the latter are known only from fragments of trunks or older branches. According to Walton, the arrangement of the secondary xylem has no systematic value since young *Rhexoxylon* axes might have had an undivided cylinder of xylem. However, the single five year-old stem (based on ring count from Archangelsky and Brett 1961, fig. 2; pl. 1, fig. 21) of *R. piatnitzkyi* has the vascular tissue divided into sixteen vascular segments with both centripetal and centrifugal wood.The oldest specimen from Fremouw Peak, which is also approximately five years old, shows an undivided ring of wood and no centripetal development of the secondary xylem. In addition, the pith of *Kykloxylon* is much smaller and the vascularization of the leaf bases is quite different from that of *R. piatnitzkyi*. It is currently impossible to state with certainty that all of the young axes of *Rhexoxylon* species are anatomically similar to *R. piatnitzkyi*; however, at our current level of knowledge this feature is sufficient to distinguish those specimens from *Kykloxylon*.

The axis from South Africa referred to herein as '*Rhexoxylon priestleyi*' resembles *Kykloxylon* in having a continuous cylinder of pycnoxylic wood. However, the lack of information concerning the pattern of leaf trace emission and leaf base venation in this axis prevents any close comparison with the specimens from Fremouw Peak.

Finally, the differences between *Kykloxylon*, *Antarcticoxylon* and *Rhexoxylon* must not understate the unique set of characters shared by these taxa. It is our belief that they form a natural group, the Corystospermaceae, characterized by the following vegetative characters: pycnoxylic wood with uniseriate rays, possibly related to the tree habit of these plants; 'araucarian' type of pitting on the radial walls of the tracheids of secondary xylem; cross-field pits simple that tend to be few and wide; pith with sclerotic nests and lacunae or secretory structures; leaf vascular system complex, originating from several axial bundles, three-dimensional and dorsiventral in leaf bases.

## CONCLUSION

This study represents the first step in the reconstruction of a '*Dicroidium* plant' from Antarctica. The distal parts of the plant are constructed of axes with a solid cylinder of pycnoxylic wood of the *Dadoxylon*-type, a form-genus that is widespread in the Mesozoic of Gondwana (Giraud 1991). Distal-most twigs bear helically arranged leaves of the *Dicroidium fremouwensis*-type. Because of the consistent occurrence of buds on stems, it is assumed that this plant possessed a more complex branching pattern than the tree fern-like habit of the '*Dicroidium*/*Rhexoxylon* plant' suggested by Petriella (1981) on the basis of specimens from the Triassic of Argentina. The presence of *Pteruchus* pollen organs at the same locality (DeVore and Taylor 1988), also with characteristic cortical lacunae, strongly suggests that this was the microsporangiate organ of the Antarctic *Dicroidium* plant.

Stems are assigned to a new genus, *Kykloxylon*, which differs from *Rhexoxylon* axes of comparable ontogenetic age by a different arrangement of the vascular cylinder and features associated with the leaf bases and their vascular pattern. The liana-like anatomy of *Rhexoxylon* can no longer be used to characterize all plants that produced *Dicroidium* foliage. Perhaps the '*Dicroidium*/*Rhexoxylon* plants' inhabited the western regions of Gondwana (South Africa, South America and rarely Antarctica) whereas the '*Dicroidium*/*Kykloxylon* plants' might have had a wider geographical distribution in Gondwana.

To date our knowledge of Triassic plants has been fragmentary, owing to the relatively few taxa described and especially to the few known permineralized specimens that provide a suite of anatomical features useful in whole plant reconstruction. The relationships between *Dicroidium* foliage and *Kykloxylon* axes illustrated here represent the first attempt to document the biological relationships of two Triassic taxa based on such a suite. It is important to underscore our belief that the plants that bore *Dicroidium* foliage may have been of several types and that the Antarctic *Dicroidium*/*Kykloxylon* plant was just one of many forms that inhabited the Triassic of Gondwana. Although the reproductive organs are still poorly known, the vegetative parts based on anatomical evidence suggest that at least two of the taxa (*Rhexoxylon* and *Kykloxylon*) shared a number of features, especially those relating to leaf trace emission. As subsequent studies of permineralized Triassic plants continue it may be possible to resolve more accurately the relationships between these Mesozoic seed ferns and their putative Palaeozoic ancestors based on both vegetative and reproductive organs.

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# REMAINS OF AN ORNITHISCHIAN DINOSAUR IN A PLIOSAUR FROM THE KIMMERIDGIAN OF ENGLAND

*by* MICHAEL A. TAYLOR, DAVID B. NORMAN *and*
ARTHUR R. I. CRUICKSHANK

ABSTRACT. A specimen of the Kimmeridgian pliosaur *Pliosaurus brachyspondylus* includes three elements which do not appear to be plesiosaurian. A pair of left and right dermal scutes are ascribed to an unidentified armoured thyreophoran ornithischian dinosaur, and a single fragment is less definitely ascribed to the same animal. It is presumed that the pliosaur had been scavenging a dinosaur corpse shortly before its own death, and that the scutes were transported inside the pliosaur's stomach. This hypothesis cannot be verified because the pliosaur skeleton was severely disarticulated before burial, and partly destroyed before collection.

IN 1980 the skull, mandible and some other bones of a large Kimmeridgian pliosaur *Pliosaurus brachyspondylus* were discovered in the *Aulacostephanus eudoxus* Zone of the Lower Kimmeridge Clay, Lower Kimmeridgian Stage, Upper Jurassic, in the Blue Circle Company's claypit at Westbury, Wiltshire. The animal, known as the 'Westbury Pliosaur', was briefly announced at the time of discovery (Crane 1980) and has now been placed on public display after lengthy preparation and mounting (Swansborough 1989; Taylor 1989). This paper describes, and attempts to identify, three anomalous dermal scutes found with the pliosaur which is itself described by Taylor and Cruikshank (in press).

## MATERIAL

The three bones appear to be dermal scutes, from their texture and the apparent lack of articular or sutural faces, at least in the case of the complete pair. However, dermal scutes have never been reported in plesiosaurs, although many complete skeletons have been found from Jurassic and Cretaceous strata. We consider these bones far more likely to be from another animal, probably a thyreophoran dinosaur. As dinosaurs of any kind are scarce in British Jurassic marine sediments, we think these scutes worthy of report, although we have been unable to identify the original dinosaur.

The material is housed in the Geology Section, Bristol City Museum and Art Gallery (abbreviation BRSMG), Queens Road, Bristol BS8 1RL, UK.

*Description.* Two of the three bones form a symmetrical pair, identical except for their left- and right-handedness. One (BRSMG Cc332eu) is crushed, but the other (BRSMG Cc332j) is uncrushed and almost intact (Text-figs 1A–C, 2A–C). The latter is a broadly triangular bone, concave internally. The convex exterior surface bears a flat process (pr) merging into the remainder of the bone. This process is damaged in BRSMG Cc332j. Neither bone bears any evidence of a joint with another bone, and appears instead to have been a scute embedded in the dermis, as suggested by the roughening around and within the internal concavity. We identify these scutes as a pair from opposite sides of the original animal.

The third bone is a single isolated fragment (BRSMG Cc332du; Text-figs 1D–E, 2D–E). It appears to be the tip of a flat, narrow bone. Its maximum thickness, as preserved, is about 4 mm. One side

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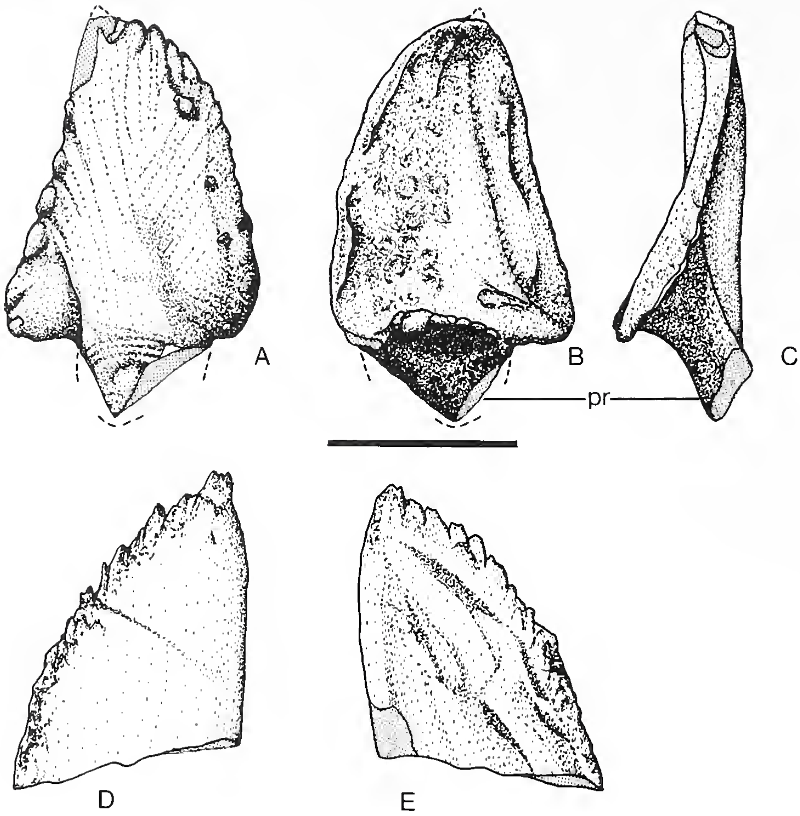
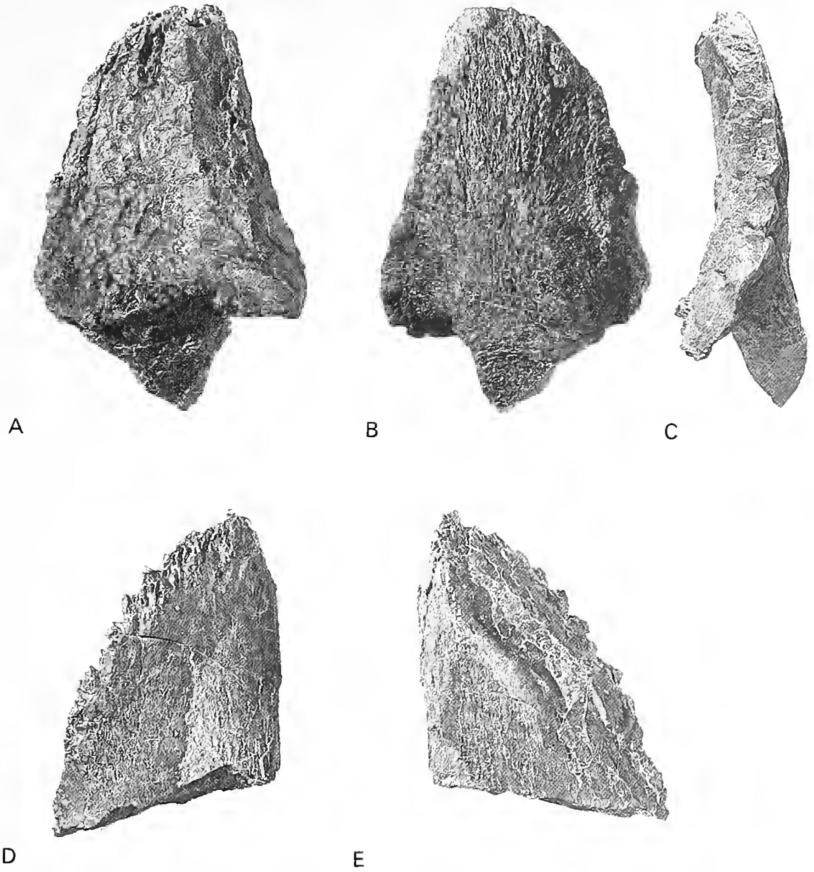


TEXT-FIG. 1. Presumed thyreophoran dinosaur dermal scutes; Kimmeridgian; Westbury, England. A–C, BRSMG Cc332j, one of a handed pair; A, presumed external surface; pr, process; B, presumed internal surface; C, side view. D–E, BRSMG Cc332du, isolated fragment. Scale bar = 50 mm.

is smooth but the other is irregular. It tapers obliquely to a thin, irregular edge which appears to be textured as if to attach to dermis. We are uncertain of its provenance but provisionally identify it as a fragment of dermal scute. We cannot rule out the possibility that it is a fragment of pliosaur bone, possibly one with pathological texture, especially as the snout and parietal crest of the pliosaur show regions of pathological bone growth.

*Taphonomy.* The taphonomy of the pliosaur is not fully understood, and much of the skeletal association appears to have been destroyed before discovery. Even if the single broken bone is indeterminate, we have to account for the presence of paired left and right scutes. These must have travelled together to the site, probably in the same piece of dinosaur hide. It is conceivable that they fell from a drifting carcass, and landed accidentally on the pliosaur's burial spot. We think this extremely improbable. It seems far more likely that the scutes travelled to the burial spot inside the pliosaur, which had been scavenging a drifting dinosaur carcass.

One of the paired scutes (BRSMG Cc332eu) was found and still remains crushed into the dorsal surface of the palate inside the left orbit of the pliosaur, while the location of the other (BRSMG Cc332j) was not recorded. The single element (BRSMG Cc332du) was found loose between the disarticulated skull and mandible, which lay a few metres apart (BRSMG Geology Section archives). The precise location of the scutes is not, however, significant as they would in any case



TEXT-FIG. 2. Presumed thyreophoran dinosaur dermal scutes; Kimmeridgian; Westbury, England. A–C, BRSMG Cc332j, one of a handed pair; A, presumed internal surface; B, presumed external surface; C, side view. D–E, BRSMG Cc332du, isolated fragment. All ×0·5.

have been displaced during the decomposition and subsequent disturbance of the pliosaur skeleton. The external texture of the scutes reveals no evidence of etching by stomach acids, but the bone could have been protected by its dermal cover.

*Identification.* Amongst large reptiles known to us from the Kimmeridgian of Europe, only the crocodilians and the thyreophoran dinosaurs had dermal scutes. We do not consider these scutes to be crocodilian, because they lack the typical indented waffle-like pattern. The scutes, on the other hand, resemble in basic form the known dermal armours of thyreophoran dinosaurs such as stegosaurs and ankylosaurs (e.g. reviews by Carpenter 1990; Coombs and Maryańska 1990; Dong 1990; Galton 1990). The paired elements bear some resemblance to cervical scutes of known forms, in having a broad base and separate but ill-defined process. The single fragment could be part of the base of a longer spine, as is known in the tail of stegosaurs. We have been unable to match them precisely with any known forms, so they may come from a novel taxon. However, British Jurassic thyreophoran dinosaurs are relatively poorly known, and we cannot rule out the possibility that the scutes come from a previously undiscovered portion of a described taxon. It is not justifiable to erect a new taxon on these scutes, and we therefore ascribe them to an undetermined thyreophoran ornithischian, presumably an ankylosaur or stegosaur.

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# *TELMATOSAURUS TRANSSYLVANICUS* FROM THE LATE CRETACEOUS OF ROMANIA: THE MOST BASAL HADROSAURID DINOSAUR

*by* D. B. WEISHAMPEL, D. B. NORMAN *and* D. GRIGORESCU

ABSTRACT. The hadrosaurid dinosaur *Telmatosaurus transsylvanicus* from the Late Cretaceous of the Haţeg region of Romania is redescribed and its phylogenetic position among hadrosaurids and successive sister-taxa is evaluated. Hadrosauridae is defined and diagnosed as a monophyletic group on the basis of twelve of the best-known genera and species previously referred to this higher taxon. *T. transsylvanicus* lacks a number of features (among them, narrow mandibular condyle of the quadrate, narrow dentary teeth, single large carina on dentary teeth) that diagnose remaining members of Hadrosauridae. As a consequence, our study indicates that *T. transsylvanicus* is the most basal of known hadrosaurids. The late Maastrichtian age of *T. transsylvanicus* suggests that this species was an evolutionary relict, isolated from its sister taxon (all remaining hadrosaurids) for at least fifteen million years. The geographical distribution of *T. transsylvanicus*, across an archipelago of European islands at the end of the Cretaceous, may well account for such an evolutionary relationship.

WHEN Ilona Nopcsa, the sister of Franz Baron Nopcsa, discovered remains of hadrosaurid dinosaurs on their Transylvanian estate in 1895, only twenty-four species of these ornithopod dinosaurs were known elsewhere in the world. Since 1899, when Franz Baron Nopcsa reported on these specimens before the Viennese Academy of Sciences (Nopcsa 1900), the majority of early-named hadrosaurid species have been ignominiously relegated to the taxonomic scrap-heap (Weishampel and Horner 1990). Nopcsa's species from Transylvania, however, is one of the survivors of modern revisions.

This hadrosaurid from the Haţeg Basin of western Romania was originally named *Limnosaurus transsylvanicus* (Nopcsa, 1900). Because the name *Limnosaurus* was preoccupied by a fossil crocodilian (Marsh 1872), Nopcsa (1903) replaced it with *Telmatosaurus* (see Paris and Taquet 1973; Weishampel and Reif 1984; Brinkmann 1988). The holotype and referred material of *T. transsylvanicus* range from nearly complete, isolated cranial specimens to isolated axial and appendicular elements. On the basis of the preservation, completeness, and abundance of this material, *Telmatosaurus transsylvanicus* ranks as one of the best-known dinosaur taxa from Romania, and perhaps even all of Europe, during the Late Cretaceous.

Despite these claims, *T. transsylvanicus* was not included in several important reviews of hadrosaurid taxonomy and systematics (e.g. Lull and Wright 1942; Ostrom 1961; but see Brinkmann 1988). These studies were restricted solely to consideration of North American taxa, for which there is considerably better preserved and more diverse material. As a consequence, *T. transsylvanicus* has also not been featured in studies of Late Cretaceous faunistics, palaeoecology, and biogeography, nor in the controversies about Cretaceous–Tertiary extinction patterns.

Earlier we presented some of the historical context of work on the Haţeg fauna (Weishampel *et al.* 1991; see also Weishampel and Reif 1984). Most early work centred on Nopcsa's detailed taxonomic work on the dinosaurs from the Sînpetru Beds (now split into the Sînpetru and Densuş-Ciula formations), but also included his synthetic work on the island biogeography of these same animals. At the end of Nopcsa's life, the fauna included a number of dinosaurs (*Telmatosaurus transsylvanicus*, *Rhabdodon priscus*, '*Struthiosaurus*' *transilvanicus*, *Magyarosaurus dacus*, *Meg-*

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*alosaurus hungaricus*), a crocodile (*Allodaposuchus precedens*), a turtle (*Kallokibotion bajazidi*), and a pterosaur, the material of which is presently missing.

Very little sustained field research was conducted in the Haţeg Basin from the time of Nopcsa's death in 1933 until work by the Universitatea Bucureşti in the mid-1970s. This most recent work in Transylvania, under the direction of one of us (D.G.), has considerably enlarged the fauna. In addition to what had been known previously, new taxa included acipenseriform and characid fishes, amphibians, a species of multituberculate mammal (*Paracimexomys*? *dacicus*), large and small theropod dinosaurs, hatchling ornithopod dinosaurs, and dinosaur eggs (Grigorescu *et al.* 1990, in press; Weishampel *et al.* 1991).

Our review of the osteology of *Telmatosaurus transsylvanicus* is based on material originally collected by Ilona and Franz Baron Nopcsa in the late nineteenth and early twentieth century, by Kadić O. in 1914, and by the Universitatea Bucureşti since the 1970s. The goal of this study is to place *T. transsylvanicus* in its proper phylogenetic position and thereby address its importance to Late Cretaceous palaeoecology and biogeography.

## ABBREVIATIONS

BMNH, Natural History Museum, London, England; FGGUB, Facultatea de Geologie şi Geofizică, Universitatea Bucureşti, Bucharest, Romania; MAFI, Magyar Állami Földtani Intézet, Budapest, Hungary; MJH, Muzeul Judeţean Hunedoara, Deva, Romania; MNHN. Muséum National d'Histoire Naturelle, Paris, France; MNMB, Magyar Nenzeti Múzeum, Budapest, Hungary; PIN, Palaeontologiceski Institut, Akademii Nauk, Moscow, Russia; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

## SYSTEMATIC PALAEONTOLOGY

### ORNITHOPODA Marsh, 1881
### Family HADROSAURIDAE Cope, 1869
### Genus TELMATOSAURUS Nopcsa, 1903
### *Telmatosaurus transsylvanicus* (Nopcsa, 1900)

Text-figs 1–6

*Holotype*. BMNH R3386, a relatively complete, but crushed skull.

*Referred material*. BMNH R2967, R3387, R3388, R3401, R3809, R3828, R3841, R3842, R3843, R3844, R3845, R3846, R3847, R3848, R4878, R4879, R4897, R4910, R4911, R4913, R4914, R4915, R4973, R5614, R10981, R10983, R11108, R11109, R11110, R11111, R11112, R11113, R11114, R11539, R11545, FGGUB 1000, 1005, 1006, 1008, 1010, 1015, 1018, 1033, 1040, 1051, 1078, [4], [5], [11], [15], [24], [40], [42], MAFI Ob.1943, Ob.3079, Ob.3107, Ob.3108, Ob.3109, Ob.3110, Ob.3111, Ob.3112, Ob.3113, Ob.3115, Ob.3116, Ob.3117, Ob.3118, Ob.3120, Ob.3121, Ob.3122, Ob.3123, Ob.3124, Ob.3126, Ob.3127, Ob.3128, Ob.3129, Ob.3130, Ob.3283, Ob.3284, Ob.4212, v.10338, v.13495, v.13497, v.13503, v.13504, v.13526, v.13513, MJH 66, 70, MNMB v.60. These specimens consist of isolated cranial elements, articulated and isolated cervical, dorsal, sacral, and caudal vertebrae, and various appendicular elements including scapulocoracoid, humerus, ulna, femur, tibia, and pedal elements. Referral of these postcranial elements to *T. transsylvanicus* is based principally on Nopcsa's personal account of their association (through notes, museum acquisition records, and publications).

*Provenance*. Sînpetru and Densuş-Ciula formations, Upper Maastrichtian; Haţeg Basin, Judeţul Hunedoara, Romania.

*Diagnosis*. A hadrosaurid dinosaur (see Weishampel and Horner 1990 for familial diagnosis) of small body size (a dwarf?), having a large caudal ectopterygoidal shelf, an isosceles triangle-shaped rostral process of the jugal, a relatively long post-metotic braincase, relatively large basipterygoid processes, a relatively large scar for *m. protractor pterygoideus* on the lateral aspect of the basisphenoid, a well-developed channel for the palatine branch of the facial nerve that also accommodated the median cerebral vein, absence of a diastema between the predentary and dentary dentition, and a slightly bowed femur.

## DESCRIPTION

### *Skull, mandible, and dentition*

Although the most complete cranial material of *T. transsylvanicus* is the crushed holotype (BMNH R3386), referred material was used in conjunction with this deformed specimen to reconstruct the undistorted skull of this species (Text-fig. 1; see also Weishampel *et al.* 1991). The following description is based on both sources. Except where noted, all measurements are taken from the reconstructed skull.

In lateral view (Text-fig. 1A), the undistorted skull of *T. transsylvanicus* is relatively long (440 mm) compared with its height (215 mm, measured from the mandibular condyle of the quadrate to the top of the skull roof). Such skull proportions are similar to those of *Camptosaurus dispar*, species of *Iguanodon*, and *Ouranosaurus nigeriensis*, while different from many hadrosaurids. The dorsal margin of the skull rises in a gentle curve from the muzzle to immediately over the orbits. In dorsal view (Text-fig. 1B; see also Weishampel *et al.* 1991), the muzzle itself is approximately 85 mm at its widest, while across the orbits and adductor chambers it is 185 mm wide. In caudal view, the skull is at least 175 mm wide (measured across preserved portions of the squamosals).

Although known from the majority of cranial elements, existing material of *T. transsylvanicus* does not include the prefrontal (nor a palpebral, should one have existed), most of the postorbital, the quadratojugal, portions of the jugal, most of the palate, and the predentary. Most of the braincase is preserved, but intracranial sutures tend to be fused and/or obliterated by maturity and/or erosion of the specimens. However, using comparative material, it is possible to reconstruct the braincase of *T. transsylvanicus* (Text-fig. 2) with some confidence.

We begin our description of the skull of *T. transsylvanicus* with elements of the facial skeleton, continuing with the braincase, palate, and mandible.

*Premaxilla.* In dorsal view, the premaxilla of *T. transsylvanicus* (BMNH R3386, R3842, R4911; FGGUB 1008, 1015) is not particularly expanded (Text-fig. 1B). In this feature, it is more like *Camptosaurus dispar* and species of *Iguanodon* (Gilmore 1909; Norman 1980, 1986; Weishampel and Bjork 1989) than *Ouranosaurus nigeriensis* and other hadrosaurids. In lateral view, the ventral margin of the premaxilla is depressed well beneath the level of the maxillary tooth row.

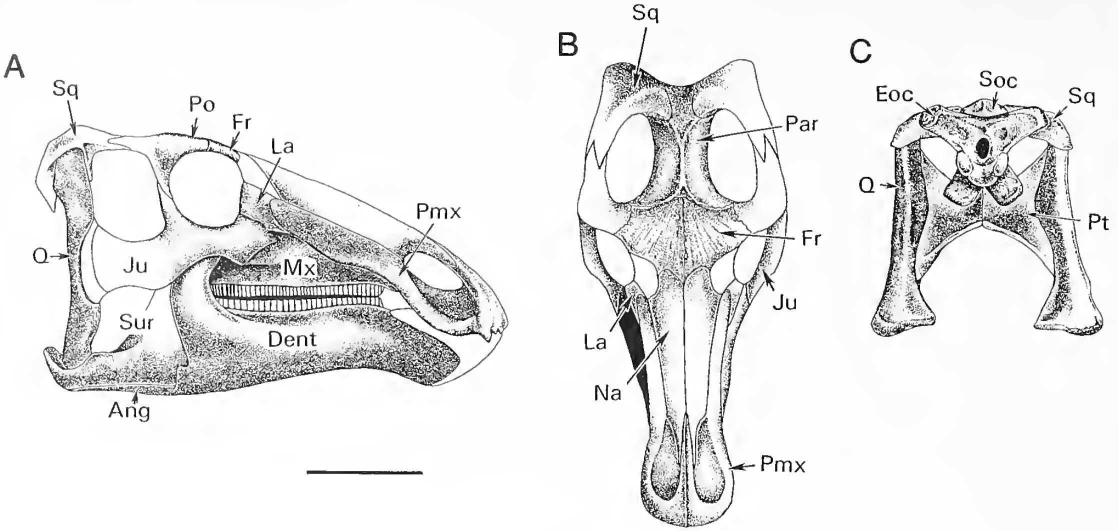
The oral margin of the premaxilla is strongly denticulate (Text-fig. 3A-B), again reminiscent of that found in *Iguanodon atherfieldensis*, *I. bernissartensis*, *I. lakotaensis*, and *Ouranosaurus nigeriensis* (Taquet 1976; Norman 1980, 1986; Weishampel and Bjork 1989). These denticles are restricted to the more medial aspect of the oral margin of the premaxilla; in BMNH R3386, there are three projections on each premaxilla, while in FGGUB 1015 there are two. In addition, the oral margin and adjacent rostral surface of the premaxilla is roughened by short, vertical striations and pitting, suggesting a rhamphothecal covering in life.

The body of the premaxilla flares slightly to form an approximately horizontal floor for the narial fossa (Text-fig. 3A). Within the fossa, the external nares are relatively small and forwardly placed on the muzzle. There is no evidence of a circumnarial depression. Extending caudally from the floor of the narial fossa, the caudolateral process of the premaxilla extends to and subsequently laps the lateral surface of the lacrimal. Thus, the nasal and maxilla are separated by the premaxilla in lateral view (BMNH R3386).

The ventral surface of the premaxilla is perforated by a premaxillary foramen (*sensu* Horner 1983). This foramen (not seen in BMNH R3386, but visible in FGGUB 1008 and 1015; Text-fig. 3B) enters the central portion of the premaxilla, about 12 mm from the interpremaxillary suture (FGGUB 1008). It is not clear from currently known material whether this foramen communicates via a canal with the narial fossa.

*Nasal.* Although dorsoventrally crushed, the nasal does not appear to be strongly arched in BMNH R3386 (nor in a specimen from the Upper Cretaceous of southern France here referred to *Telmatosaurus*, MNHN FMR 12). Instead, it continues the gentle upward slope of the muzzle that was established by the dorsal margin of the premaxilla (Text-fig. 1A).

*Frontal.* In dorsal view, the frontal of *T. transsylvanicus* (BMNH R3386, R3828, R4911, R4915) is a relatively flat, triangular element (Text-fig. 1B). The paired frontals are unfused, but form a slightly sinuous interfrontal suture. Along the forward edge, there are deep excavations to receive the caudal ends of the nasal and



TEXT-FIG. 1. *Telmatosaurus transsylvanicus*. A–C, skull in right lateral, dorsal, and caudal views respectively. All figures based in large part on BMNH R3386 and R3387. Scale = 100 mm. A–B after Weishampel *et al.* 1991. Abbreviations: Ang = angular; Dent = dentary; Eoc = exoccipital; Fr = frontal; Ju = jugal; La = lacrimal; Mx = maxilla; Par = parietal; Pmx = premaxilla; Po = postorbital; Pt = pterygoid, Q = quadrate; Soc = supraoccipital; Sq = squamosal; Sur = surangular.

prefrontal. The margin of the excavation for the nasal is slightly raised in BMNH R4915. Medially, the paired frontals extend between the nasals as an oblique wedge. Ventrally, divergent ridges mark the suture between the frontal and laterosphenoid and the margins of the olfactory tracts.

The lateral edge of the frontal forms of the forward half of the orbital rim (Text-fig. 1A), as in *Gryposaurus notabilis*, *G. incurvimanus*, *Anatotitan copei*, and species of *Edmontosaurus*, among hadrosaurids, and virtually all other iguanodontians (e.g. *Camptosaurus dispar*, species of *Iguanodon*). Caudally and laterally, the frontal–postorbital suture is interdigitate and extends rostrolaterally from the forward margin of the supratemporal fenestra. The frontal–parietal articulation sweeps across the skull roof (also in an interdigitate fashion) to meet the frontal–postorbital suture along the rim of the supratemporal fenestra. There is no evidence of a medial gap accommodating an extension of the parietal (the 'interparietal' process *sensu* Lull and Wright 1942). Immediately rostral to the frontal–parietal articulation, the frontal is raised into a low transverse ridge.

*Parietal.* The parietals are fused into a single plate (known only in BMNH R3386) which is relatively long (90 mm), suggesting that the adductor chamber was large (Text-fig. 1B), as in *Camptosaurus dispar* and species of *Iguanodon*, and *Gryposaurus notabilis*, *G. incurvimanus*, and *Kritosaurus navajovius* among other hadrosaurids (Horner 1992). In *T. transsylvanicus*, there is a modest sagittal crest. In dorsal view, the parietal is hour-glass shaped. Rostrally, it is bounded by the frontal and postorbital, while caudally it articulates with the squamosal and supraoccipital. Ventrally, the parietal articulates with the laterosphenoid, prootic, and opisthotic.

*Postorbital.* Only the most rostral portion of the postorbital, where it contacts the frontal (see above), is known in *T. transsylvanicus*. Morphological details beyond those already given are non-existent.

*Squamosal.* The squamosal is incompletely known (BMNH R3386; Text-fig. 1A). Missing are the rostral process (which contacts the postorbital) and most of the medial process (which contacts the parietal and paroccipital process). The body of the squamosal forms a deep cotylus for reception of the head of the quadrate. The base of the prequadratic process preserves the scar for *m. adductor mandibulae externus superficialis*.

*Maxilla.* The maxilla (Text-fig. 3C) is known from a number of specimens, among them FGGUB 1010, MAFI Ob.3108, Ob.3109, and BMNH R3386, R3388, R4911, R5164. This triangular element is relatively long and low (195 mm and 70 mm respectively for FGGUB 1010). The dorsal process is located approximately halfway along the length of the maxilla. Rostral to the dorsal process, the concave dorsal surface of the maxilla receives the caudal portion of the body and caudolateral process of the premaxilla. Because of poor preservation, it is unclear whether a rostromedial maxillary process was present in *T. transsylvanicus*. Immediately lateral to the dorsal maxillary process is the articular surface for the jugal. This nearly triangular surface is slightly offset from the lateral surface of the maxilla. However, unlike other hadrosaurids, there is not much scarring in this region.

The lateral wall of the maxilla bears no indication of a laterally-positioned antorbital fenestra and fossa. Instead, the more caudal region of the premaxillary articular surface contains a relatively large, oval foramen that communicates with the region behind the dorsal maxillary process. This foramen has been argued to be the antorbital foramen among hadrosaurids (Weishampel and Horner 1990). A series of foramina mark the lateral surface of the maxilla, the largest of which is beneath and slightly forward of the articular surface for the jugal. Together, these foramina fall irregularly in a longitudinal row and probably represent neurovascular canals that conduct branches of the maxillary nerve and vessels to the buccal cavity and cheek region, as in other ornithischians. Beneath this position, the maxilla becomes slightly emarginated, such that the maxillary dentition is inset from the side of the face.

Caudal to the dorsal process and jugal articular surface, the maxilla bears a prominent ectopterygoidal shelf. This shelf is relatively broad and slightly undulatory, thus producing a slightly bulbous caudal extreme. Medial to the ectopterygoidal shelf, the maxilla is drawn up into a well-striated edge that supports the base of the palatine (BMNH R3388, R4911). The medial side of the maxilla is relatively flat and covered by an arc of special foramina (Edmund 1957) that mark the base of each alveolar chamber.

Ventrally, the maxillary tooth row is laterally concave, much as in *Iguanodon atherfieldensis* and hadrosaurids generally. It contains more tooth positions than more basal iguanodontians of approximately the same size (cf. 31 in FGGUB 1010, 19 in *Iguanodon lakotaensis*, 22 in *Ouranosaurus nigeriensis*) and about the same as other similar-sized hadrosaurids (approximately 30 in *Gilmoreosaurus mongoliensis*, 35 in *Prosaurolophus maximus*).

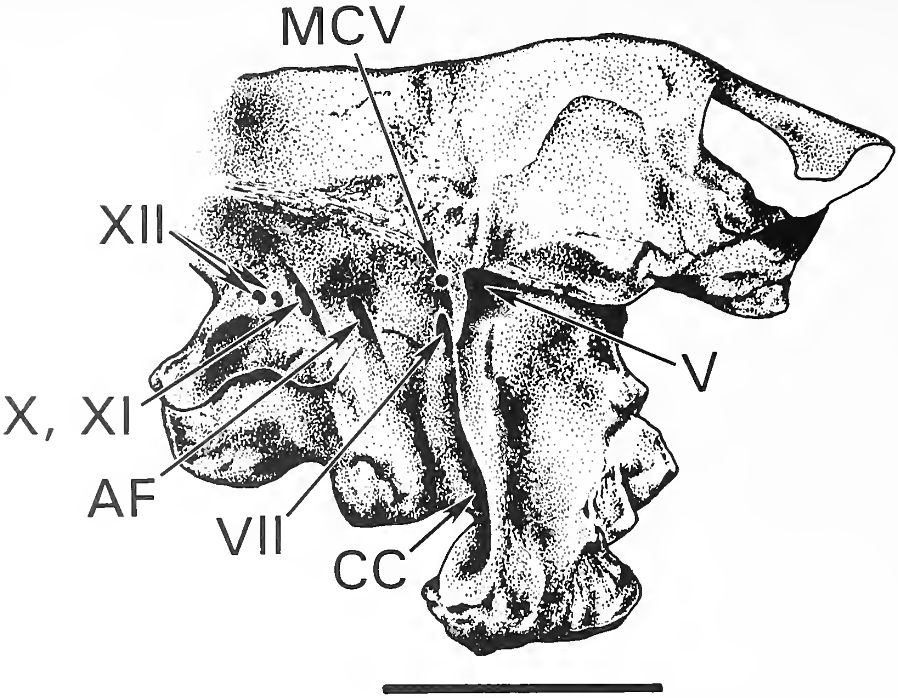
*Lacrimal.* Much of the detail of the lacrimal is lost as the result of crushing in BMNH R3386, the only specimen preserving this element. Nonetheless, it appears to be typically triangular, overlapped rostrally by the caudolateral process of the premaxilla (Text-fig. 1A).

*Jugal.* The rostral portion of the jugal (BMNH R3386, R4911, R11545; Text-fig. 1A) appears to form an isosceles-triangle-like articulation with the maxilla. The inner surface of this rostral portion is strongly striated for ligaments that tightly bound the jugal to the maxilla. The postorbital process is best preserved (albeit poorly) in BMNH R4911. Beneath this process, the body of the jugal is dorsoventrally narrow, giving a very gracile form to the bone when compared to other hadrosaurids. The caudal portion of the jugal is unknown.

*Quadrate.* The quadrate of *T. transsylvanicus* is known from a number of specimens (FGGUB 1005, 1006; BMNH R3386, R4911; Text-fig. 3D). The head of the quadrate is relatively narrow transversely and shallowly curved in lateral view. The caudal aspect of the quadrate head bears a buttress that lies against the rostrolateral surface of the paroccipital process. More ventrally, the shaft is relatively straight. Above the mandibular condyle, the cranial margin of the shaft is excavated for reception of the quadratojugal. However, there appears to be no paraquadratic foramen. Directly beneath this excavation, there is again a slight buttress similar to that found in the hadrosaurid *Gilmoreosaurus mongoliensis*. The transversely broad mandibular condyle resembles the condition in *Camptosaurus dispar*, species of *Iguanodon*, *Ouranosaurus nigeriensis*, and *Gilmoreosaurus mongoliensis*, but differs from the more rounded and narrow condition found in all remaining hadrosaurids.

*Supraoccipital.* The supraoccipital (Text-fig. 1C) is lodged between the squamosals, the parietal, and the exoccipitals within the dorsal region of the occiput (BMNH R3386, R3387, R3401). Lateral facets on the supraoccipital articulate with the medial process of the squamosal. Immediately ventral to each facet is the relatively large post-temporal foramen which transmitted the dorsal head vein between the supraoccipital, opisthotic, and squamosal.

*Exoccipital.* In caudal view (Text-fig. 1C), the exoccipital forms the dorsal margin of the foramen magnum as well as the majority of the occipital table (i.e. BMNH R3386, R3387, R3401). Ventrally, the well-developed



TEXT-FIG. 2. *Telmatosaurus transsylvanicus*. Braincase in right lateral view. Reconstructed after BMNH R3386, R3401, R3387, R4915. Scale = 50 mm. Abbreviations: AF = auditory foramen; CC = carotid canal; MCV = foramen for the median cerebral vein; V, VII, X, XI, XII: foramina for cranial nerves.

exoccipital condyloids supplement the basioccipital condyle where it forms the craniovertebral joint with the atlas.

In the centre of the caudal surface of the exoccipital is a scar for *m. obliquus capitis magnus*. The base of the paroccipital process is found immediately lateral to this scar, but the extreme lateral aspect of the exoccipital is not preserved in any existing material. Hence, it is unclear how well developed the paroccipital processes were in life. Furthermore, the sutures with the opisthotic are entirely obliterated in both caudal and lateral views, so it is unclear as to the extent that either the exoccipital or opisthotic form the paroccipital process.

The lateral wall of the exoccipital is exposed in lateral view (Text-fig. 2). Here the base of the exoccipital makes an undulatory contact with the basioccipital. The exoccipital appears to meet the basisphenoid immediately caudal and ventral to the auditory foramen. Based on BMNH R4915, the lateral wall of the exoccipital contains the foramina for several cranial nerves. The exit for the hypoglossal nerve (c.n. XII) is unclear, but may be found approximately two-thirds along the length of the exoccipital. Whether there is a single exit or two is not known (two are reconstructed in Text-figure 2). Immediately rostral, the foramen that transmitted the spinal accessory and vagus nerves (c.nn. X, XI) is separated by a prominent pillar from the auditory foramen. This pattern of cranial foramina through the body of the exoccipital is also seen in other hadrosaurids (Horner 1992), but differs from that of *Iguanodon atherfieldensis*, *I. lakotaensis* (Norman 1986; Norman and Weishampel 1990), and possibly *Ouranosaurus nigeriensis* (Taquet 1976), where these same foramina are found along the suture between the exoccipital and opisthotic.

*Opisthotic*. As indicated above, the boundaries of the opisthotic are not easily demonstrated, but presumably the element comprises the caudal portion of the otic (i.e. caudal to the metotic fissure) and the extreme portion of the paroccipital process.

The lateral wall of the opisthotic is marked by the caudal half of the crista otosphenoidale as it extends into the rostrolateral surface of the paroccipital process (Text-fig. 2). At the base of the crista otosphenoidale, where it continues onto the prootic, the opisthotic is pierced by the auditory foramen at the level of the metotic fissure. Dorsally, this foramen accommodates the foot plate of the stapes, while ventrally, the glossopharyngeal nerve (c.n. IX) and the jugular vein exit the braincase. A shallow groove for the jugular vein extends ventrally from the auditory foramen across the lateral surface of the basisphenoid. Both groove and foramen are shrouded rostrally by a pillar that separates both from the foramen accommodating the facial nerve (c.n. VII).

*Prootic.* As indicated above, the crista otosphenoidale terminates rostrally in the caudoventral corner of the prootic (Text-fig. 2). The foramen for the facial nerve (c.n. VII) is probably positioned above the foramen for c.n. VI and caudal to the foramen for c.n. V. It is likely that the middle cerebral vein pierces the lower body of the prootic or the junction between the prootic and laterosphenoid immediately dorsal to the exit of c.n. VII. Finally, the rostoventral margin of the prootic forms the dorsal and caudal margins of the exit for the trigeminal nerve (c.n. V).

*Laterosphenoid.* The pillar-like laterosphenoid extends rostrolaterally from the front of the braincase (Text-fig. 2) to abut the undersurface of the postorbital and frontal in what appears to be a synovial joint (Weishampel 1984). The olfactory tract (c.n. I) exits between the paired laterosphenoids.

*Orbitosphenoid.* The orbitosphenoid (Text-fig. 2) is extremely poorly preserved and provides no information on the foramina for the trochlear nerve (c.n. IV) or the palatine artery, two structures expected to be found in this region of the braincase.

*Basioccipital.* The basisphenoid contributes the largest portion of the occipital condyle and forms as much as a sixth of the (ventral) rim of the foramen magnum (Text-fig. 1c). The occipital condyle is supported rostrally by a modest neck. The most rostral portion of the basioccipital forms the caudal third of the rugose basal tuber (the remainder is formed by the basisphenoid; see below). At the ventral limit of the suture between the basioccipital and basisphenoid is a small, shallow fossa that appears to be shared by both the basioccipital and basisphenoid. This fossa may mark the attachment site of *m. rectus capitis rostralis.*

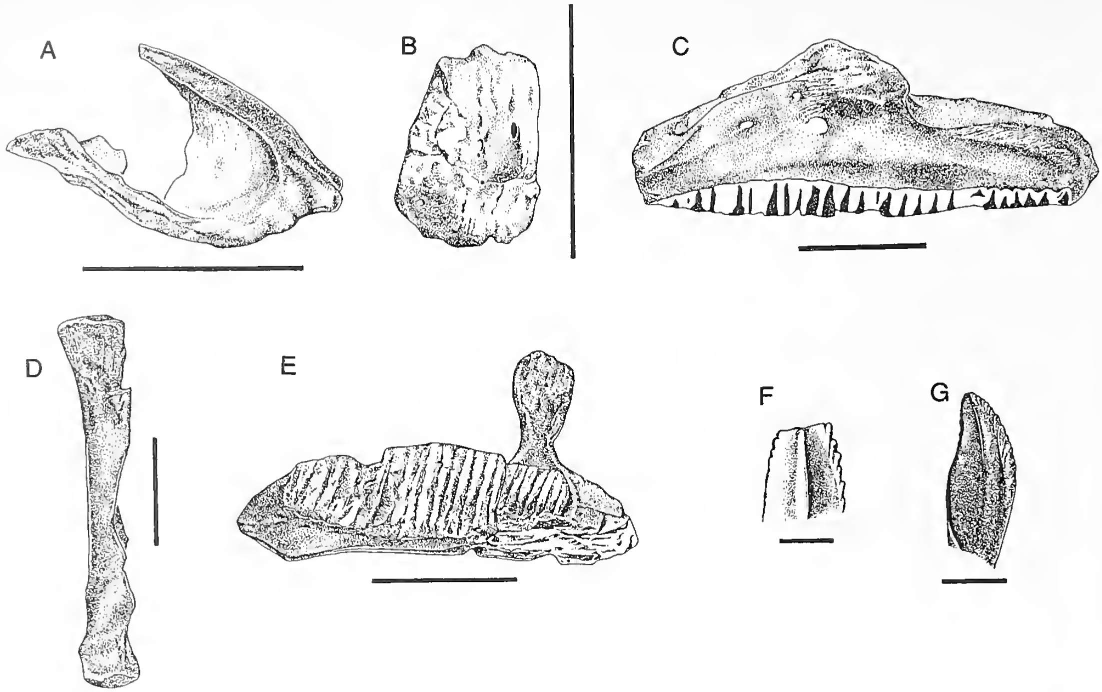
*Basisphenoid.* The basisphenoid (Text-fig. 2) forms the rostral two-thirds of the large basal tuber, which projects ventrally approximately 40° from the midline. Likewise, the basipterygoid processes are relatively large, although incompletely preserved. At the base of each process is the opening of the carotid canal. This opening also marks the terminus of a channel descending from the facial nerve foramen. This wide and slightly sinuous channel presumably contained the palatine branch for the facial nerve and probably also the median cerebral vein prior to its union with the lateral head vein.

As noted earlier, the foramina for the median cerebral vein and trigeminal nerve are poorly preserved in existing *T. transsylvanicus* material. However, a large gap between the laterosphenoid, prootic, and basisphenoid (see BMNH R3386, R4915) assuredly accommodated both structures as indicated in Text-figure 2. Extending ventrally from the trigeminal foramen, immediately rostral to the channel for the palatine branch of the facial nerve, is a moderately-developed groove for the maxillary and mandibular branches of the trigeminal nerve (c.n. $V_{2,3}$). Another groove extending rostrally from the trigeminal foramen accommodated the ophthalmic branch of the trigeminal nerve. Both sets of grooves for branches of the trigeminal nerve flank the relatively large scar for *m. protractor pterygoideus.*

*Pterygoid.* Of the palate, only the pterygoids are at all easily identifiable (although extremely crushed) in BMNH R3386. The strongly developed caudoventral projection of the quadrate ramus extends laterally to contact the medial aspect of the quadrate shaft, while the caudal alar projection is typically thin and high (Text-fig. 1c). The remainder of the pterygoid, including the articulation with the basipterygoid process of the basisphenoid, are very fragmentary due to crushing.

*Dentary.* The dentary is known from a number of specimens (MAFI Ob. 1943; BMNH R2967, R3386, R3401, R3844, R4910; Text-figs 1, 3e). In the region where it contacts the predentary, the rostral end of the dentary bends ventrally and medially to form the mandibular symphysis. There appears to be no more than a small diastema between the predentary (estimated from the predentary articular surface on the dentary) and the first dentary tooth.

In lateral view, the body of the dentary is roughly rectangular, with parallel dorsal and ventral margins. The dentition is emarginated from the lateral surface. In the largest dentary (BMNH R3386), there are approximately 30 tooth positions. Replacement teeth are arranged in a dental battery, typical of hadrosaurid dinosaurs. A series of foramina is irregularly placed in nearly a longitudinal row beneath the tooth row. These



TEXT-FIG. 3. *Telmatosaurus transsylvanicus*. A–B, right premaxilla (FGGUB 1015) in lateral and ventral views. C, left maxilla (FGGUB 1010) in lateral view. D, right quadrate (FGGUB 1005) in lateral view. E, right dentary (BMNH R3401) in medial view. F, tooth (BMNH R4966) from the left maxilla in buccal view. G, tooth (FGGUB [5]) from the right dentary in lingual view. Scales for A–E = 50 mm; scale for F = 5 mm; scale for G = 10 mm. (G after Weishampel *et al.* 1991).

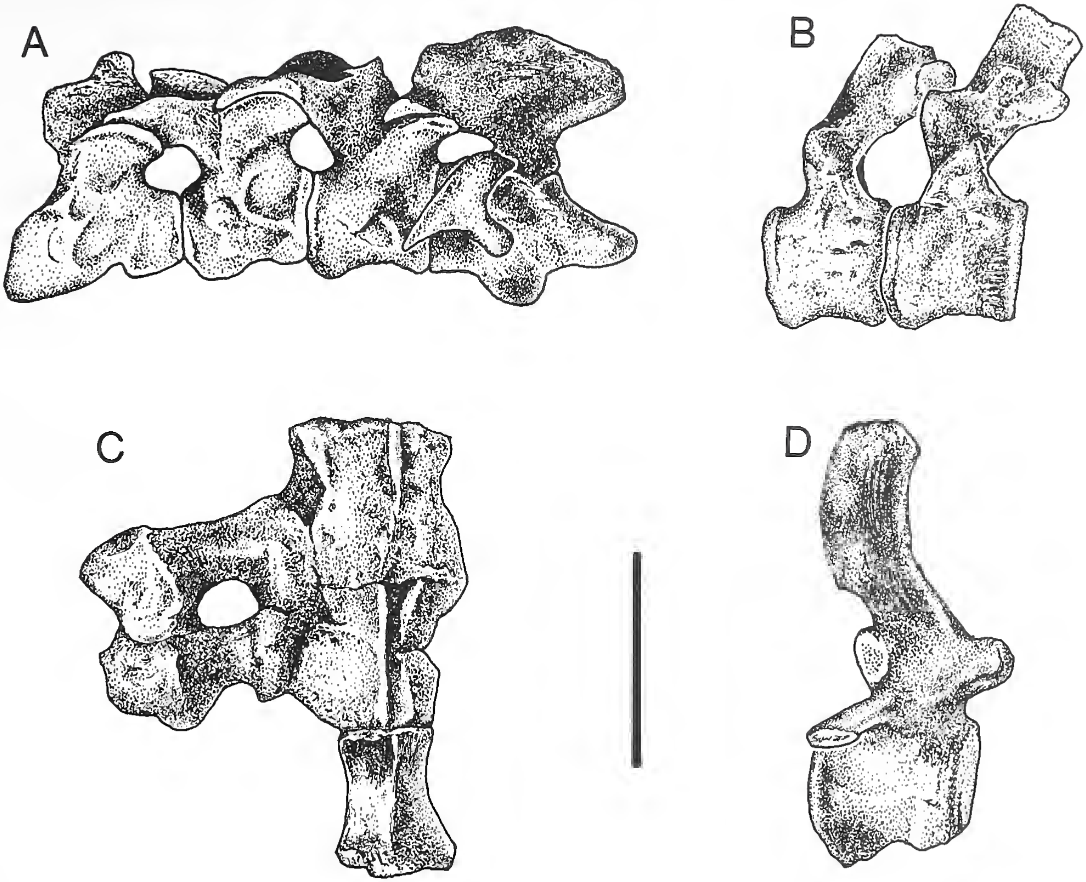
foramina attest to neurovascular supply to the lower regions of the buccal cavity and cheek via the mandibular branch of the trigeminal nerve (c.n. $V_3$). The largest of these foramina is found near the articular surface for the lateral process of the predentary. Such a position indicates a particularly important neurovascular supply to the predentary portion of the oral margin.

Immediately lateral to the distal limit of the dentary dentition, the coronoid process rises 35 per cent higher than the height of the body of the dentary. The coronoid process forms a 105° angle with the long axis of the dentary. Dorsally, the coronoid process flares into a marked coronal margin. Caudally, the base of the coronoid process is excavated to form the mandibular fossa, which continues rostrally as the mandibular canal (seen in medial view). The surangular comprises the caudal continuation of the lateral wall of the mandibular fossa.

The medial wall of the dentary bears a series of special foramina (*sensu* Edmund 1957) at the base of the alveolar chambers. Immediately caudal to the dental battery and these special foramina, the dentary forms a squamous, rostrally crescentic suture with the splenial. Beneath this position, the dentary contacts the angular ventral to the mandibular canal.

*Surangular*. The large surangular (Text-fig. 1A; see BMNH R3386, R4911; MAFA Ob.3123, v.13497) forms the caudal part of the coronoid process, the large, lateral aspect of the mandibular glenoid, and a portion of the retroarticular process. The glenoid is a shallow, cup-shaped depression. A prominent lateral lip forms the lateral margin of the glenoid. There is no surangular foramen. Beneath the glenoid, the ventral surface of the surangular is undulatory. More caudal, the retroarticular process of the surangular is upturned and lobate. The caudoventral margin of the angular fits into a groove on the ventral surface of the surangular.

*Splenial*. The splenial forms the medial wall of the mandibular fossa beginning at the caudal limit of the dentary



TEXT-FIG. 4. *Telmatosaurus transsylvanicus*. A, axis and next three cervical vertebrae (BMNH R3841) in right lateral view. B, last cervical and first dorsal vertebrae (BMNH 3841) in left lateral view. C, sacrum (BMNH R4911) in ventral view; D, isolated proximal caudal vertebra (BMNH R4973) in right lateral view. Scale = 50 mm.

dentition. Further posteriorly, the junction between the splenial and the articular is indistinct, suggesting that both elements may fuse.

*Angular*. The angular is a long, narrow mandibular element that forms the floor of the mandibular fossa and the mandibular canal. Medially, it forms a long, linear suture with the splenial, while laterally, it develops a similar articulation with the dentary and surangular.

*Articular*. The articular forms a broad squamous joint with the surangular, thereby contributing the smaller, more medial aspect of the mandibular glenoid. The portion of the glenoid is also enclosed medially by a rounded lip. The articular also contributes the inner surface of the retroarticular process.

*Dentition*. Both maxillary and dentary dentitions are organized into dental batteries. Maxillary batteries consist of one to two functional teeth and up to three replacement teeth per tooth position, while two to three functional teeth and an estimated four to five replacement teeth per tooth position occupy the dentary. Maxillary teeth are high and relatively narrow in cross-sectional dimensions (Text-fig. 3F). Mean tooth width is 4·0 mm. The enamelled buccal face of each tooth is ornamented by a strong median carina. The margins of the crown are highly denticulate, but the denticles are not supported by marginal (i.e. secondary) ridges.

By contrast, teeth within the dentary are considerably wider than those within the maxilla (Text-fig. 3G).

They are also relatively wider than dentary teeth in other hadrosaurids. Mean tooth width is 8·0 mm. Unlike other hadrosaurids (with the possible exception of *Gilmoreosaurus mongoliensis* [PIN 2949/1] and *Claosaurus agilis* [YPM 1190; Carpenter *et al.* in press]), dentary teeth of *T. transsylvanicus* are slightly recurved distally. The apex is acutely pointed. The lingual surface of the crown bears only a low primary ridge offset somewhat mesially and sometimes a very slight, mesially-placed secondary ridge. The margins of the crown are denticulate. For mesial denticles, each is supported by a ridge on the enamelled lingual face of the crown; distal denticles are not supported by ridges.

### *Axial skeleton*

The axial skeleton of *T. transsylvanicus* is incompletely known. The best material includes three sections of the cervical series (BMNH R3841) and two partial sacra (BMNH R4911, R4915) that Nopcsa (1928) referred to this species. Additional isolated vertebral material is also known. Those that have been described include BMNH R3809, R3842, and R4973 (Nopcsa 1928). All vertebrae are preserved with the neural arches securely fused to the centra. No ossified tendons or haemal spines that might have come from these axial specimens appear to be preserved at any of the Hateg localities.

*Cervical vertebrae and ribs.* No atlantal material is known for *T. transsylvanicus*. The axis, however, is present (BMNH R3809, R3811; Text-fig. 4A). This vertebra bears a prominent, conical dens that extends from the well-buttressed cranial surface of the axial centrum. Likewise, the centrum is expanded and opisthocoelous. The neural spine is long, arched, and blade-like. The neural arch is well developed, surrounding an ovate (higher than wide) vertebral canal. Cranially, the dorsolaterally facing prezygapophysis is virtually flush with the sides of the neural spine. In contrast, the postzygapophysis overhangs the caudal end of the centrum. In between, the diminutive transverse process supports a small cervical rib (see below).

The next three cervicals are strongly opisthocoelous (Text-fig. 4A). In cranial view, the centrum is ovate (wider than high). The neural spines are short and diminish in size caudally within this series. The prezygapophyses progressively lengthen and project laterally down the cervical series, while the postzygapophyses lengthen and sweep caudolaterally at a very wide angle. In both these conditions, *T. transsylvanicus* resembles other hadrosaurids. The parapophysis is small and oriented horizontally. Ventrally, a sagittal ridge begins faintly with the third cervical and becomes most accentuated on the undersurface of the fifth cervical. Laterally-positioned ridges lie parallel to the sagittal ridge.

The cervical–dorsal transition appears to be very gradual (Text-fig. 4B). The last cervical centrum is rather stout and subcircular in cranial view. The parapophysis, found on the lateral aspect of the neural arch, is slightly developed. Only the base of the transverse process, toward the top of the neural arch, is preserved. The postzygapophysis is elevated well above the vertebral canal and the neural spine (preserved only at its base) appears to be relatively stout.

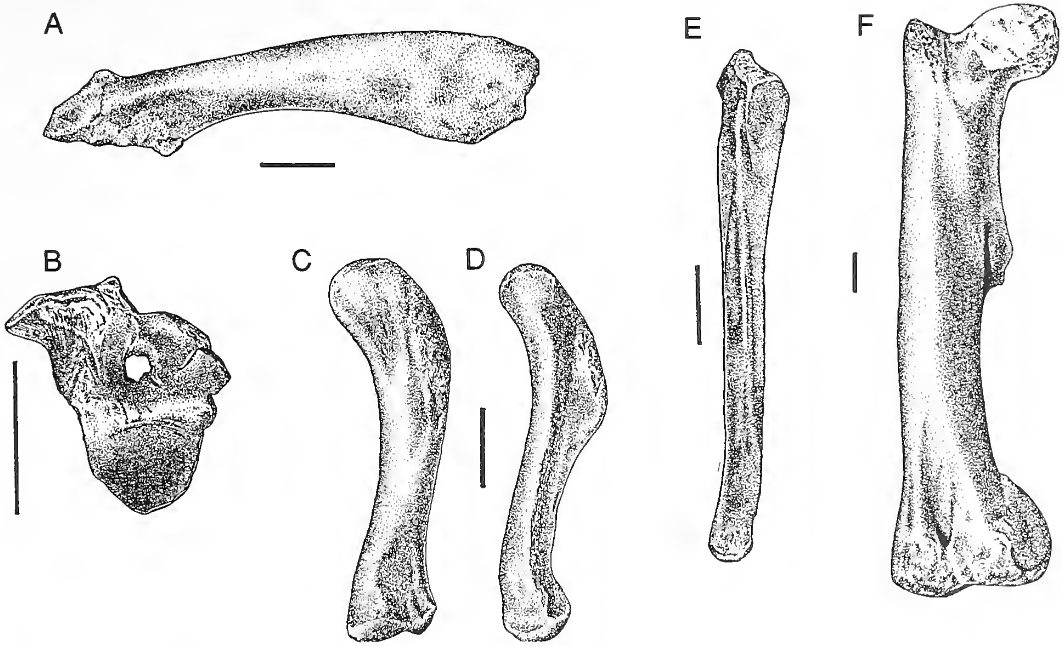
Very few cervical ribs are preserved. The atlantal rib has a single head, modestly elongate neck, and short shafts (see BMNH R3841). Successive ribs have approximately the same morphology.

*Dorsal vertebrae and ribs.* The number of dorsal vertebrae is unknown in *T. transsylvanicus*. The first dorsal (BMNH R3842) is very similar to the last cervical (Text-fig. 4B). The centrum is slightly opisthocoelous cranially to virtually platycoelous caudally. The parapophysis is strongly developed at the base of the neural arch. Like the last cervical, the transverse process extends from near the top of the neural arch, immediately beneath the prezygapophysis. Although dorsally incomplete, the neural spine appears to be of modest size, comparable to that in some hadrosaurids (e.g. *Gryposaurus notabilis*, *Edmontosaurus regalis*).

Dorsal ribs are unremarkable in their morphology (see BMNH R4911). The head is small and single, the neck is relatively long, the tubercle is large, and the shaft is shallowly curved, with a well-developed costal groove.

*Sacrum and sacral ribs.* Partial sacra referred to *T. transsylvanicus* (BMNH R4911, R4915) indicate that the sacrum was composed of at least four vertebrae (Text-fig. 4C). Eight or nine were probably present in life. The ventral surface of these sacrals bears a prominent longitudinal ridge.

Accompanying BMNH R4911 are two sacral ribs. The more cranial articulates principally with the first preserved centrum, as well as with the cranial surface of the base of the second rib. The latter articulates solely with the side of the second centrum. Both articulate with each other at their lateral extremities. The space between these sacral ribs forms one of the sacral foramina. Isolated sacral ribs that probably pertain to *T. transsylvanicus* are in the FGGUB collections (FGGUB [24], 1051).



TEXT-FIG. 5. *Telmatosaurus transsylvanicus*. A, left scapula (FGGUB [4]) in lateral view. B, fragmentary right coracoid (BMNH R3843) in lateral view. C–D, left humerus (MAFI Ob.3126) in medial and cranial views (after Weishampel *et al.* 1991). E, right ulna (MAFA Ob.3124) in lateral view. F, right femur (MAFI v.10338) in cranial view (after Weishampel *et al.* 1991). Scale = 50 mm.

*Caudal vertebrae*. The full complement of caudals of *T. transsylvanicus* is not presently known, but probably ranged upwards of fifty vertebrae. Isolated caudals are known from several regions of the tail (BMNH R3841, R3842, R4915, R4973; Text-fig. 4D). Proximal vertebrae are short and cylindrical, with circular intervertebral articulations. Each vertebra bears a modest neural spine that is caudodorsally upturned, much as in *Gryposaurus notabilis* and species of *Iguanodon*. The zygapophyses are oriented nearly vertically. The transverse process extends from the base of the neural arch. Ventrally, the proximal and distal aspects of the centrum bear facets for the haemal spines.

More distally, caudal vertebrae are spindle-shaped, with reduced zygapophyses and short neural spines. The ventral surface is dominated by proximal and distal facets for haemal spines and a groove that extends longitudinally between these facets.

## *Appendicular skeleton*

The appendicular skeleton of *T. transsylvanicus* is partly known. Of the forelimb, the scapula, coracoid, humerus, and ulna are best preserved. Sternal bones, radius, and elements of the manus have not so far been recovered from the Haţeg Basin. Of the hindlimb, only the femur, tibia, and isolated metatarsals and phalanges are known (MAFI records indicate the presence of an ischium in their collections (MAFA 3125), but this specimen was destroyed in 1938]. An ischium referred to *Telmatosaurus* sp. by Brinkmann (1984) is known from Upper Cretaceous beds of northeastern Spain, but, because of its provenance, will not be part of the present description. The appendicular material from the Haţeg Basin is sufficiently well preserved not only for good morphological description (including myologic interpretation; see Norman 1986) but also appropriate phylogenetic assessment.

*Scapula*. Known only from FGGUB [4] (Text-fig. 5A), the scapula of *T. transsylvanicus* is long and curved caudodorsally. Immediately above the glenoid region (not preserved), the blade expands slightly so that the craniodorsal and caudoventral borders diverge toward the vertebral border. Along the craniodorsal border, a rounded acromial process is found in front of the glenoid region. The rostral side of the glenoid may accommodate the insertion of *m. trapezius*, while the caudal aspect is the origin of *m. deltoides clavicularis*.

*Coracoid*. A single, partial coracoid (BMNH R3843; Text-fig. 5B) preserves the glenoid facet and a large coracoid foramen that is removed from the scapular junction by approximately 30 mm. Immediately ventral to the glenoid facet, there is a striated scar for the insertion of *m. costocoracoideus*. More ventral yet to this position, another scar marks the origins of *mm. coracobrachialis ventralis* and *triceps longus caudalis*.

*Humerus*. The humerus (MAFI Ob.3126; BMNH R3842, R3845, R3847) is somewhat gracile in form (Text-fig. 5C–D). The relatively large humeral head is slightly medially and caudally displaced relative to the longitudinal axis of the element. The flattened shoulder medial to the humeral head bears a prominent scar for *m. deltoides scapularis*. The low, rounded deltopectoral crest merges imperceptibly with the main body of the humerus at midshaft level, similar to the condition found in *Camptosaurus dispar*, species of *Iguanodon*, and *Ouranosaurus nigeriensis*. The cranial margin of the deltopectoral process is not medially reflected as in such hypsilophodontids as *Orodromeus makelai* and *Hypsilophodon foxii*. The *m. deltoides clavicularis* scar is strongly developed on the lateral surface of the deltopectoral crest, while the *m. pectoralis* scar is found on the medial surface. On the caudal aspect of the humerus, at the level of the deltopectoral crest, is an ovate scar for *mm. latissimus dorsi* and *teres major*. Beneath this region, the shaft is relatively narrow and straight. The distal humerus consists of a tear-drop-shaped ulnar condyle and a somewhat narrower radial condyle. The ulnar condyle is much larger and more ventrally placed than the radial condyle. Above the ulnar condyle, the medial epicondyle bears a supracondylar ridge that continues half-way up the humeral shaft and presumably served for the origin of the lower fibres of *m. triceps brevis intermedius*.

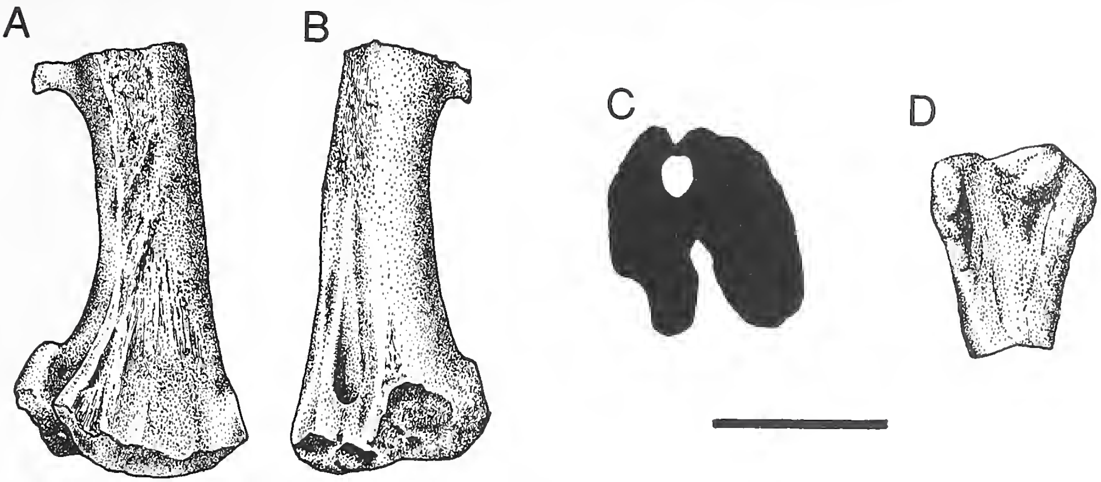
*Ulna*. The ulna (MAFI Ob.3124, Ob.4212; FGGUB 1078; Text-fig. 5E) is long, narrow, and relatively straight in craniocaudal views. Only in lateral view is there a slight caudal deviation of the distal ulna. The proximal head is formed into a triangular articular surface for the ulnar condyle of the humerus. The radial fossa is large and the olecranon process is moderately developed,

The lateral aspect of the ulna is raised into a relatively narrow interosseus border. Muscle scars are not particularly well developed. There appears to be a *m. pronator quadratus* scar on the proximal half and a scar for the ulnar head of *m. flexor digitorum longus* more distally on the lateral aspect of the ulnar shaft. Finally, the insertion of *m. flexor ulnaris* extends the length of the shaft on the medial aspect of the ulna. Distally, the ulna ends in a bluntly rounded articular surface. Laterally, it is flattened to accommodate the distal radius.

*Femur*. The femur (MJH 66; MAFI Ob.3128, v.10338; BMNH R3846, R4914, R11539; Text-fig. 5F) is slightly laterally bowed. The head is large, globose, and set on a stout neck angled approximately 145° to the long axis of the femoral shaft. More lateral, the greater and lesser trochanters are separated by a vertical cleft. The craniomedial surface of the greater trochanter probably marks the insertion of *mm. iliotrochantericus II et III*, while a rugose area on the caudal aspect marks the insertion of *mm. ischiotrochantericus* and *iliotrochantericus I*. On the lateral aspect of the lesser trochanter and possibly continuing down the shaft to the level of the lateral condyle is a scar for the insertion of *m. iliofemoralis*.

The well-developed fourth trochanter crosses the caudomedial aspect of the shaft. In this position, it is situated 45 per cent of the length of the femur from the top of the greater trochanter. A moderately developed fossa on the medial surface of the fourth trochanter probably marks the insertion of *m. caudifemoralis longus*, with the cranial margin of the fossa forming the insertion site of *m. puboischiofemoralis internus I*. The caudomedial edge of the fourth trochanter marks the insertion of *m. caudifemoralis brevis*. The remainder of the femoral shaft bears several additional muscle scars, among them the origin of *m. femorotibialis internus* on the craniomedial aspect of the femoral shaft adjacent and ventral to the fourth trochanter. This site may reach as high as the femoral neck and as ventral as a few centimetres above the medial epicondyle. More lateral, the long and narrow scar for *m. femorotibialis externus* is found between the fourth trochanter and the scar for *m. iliofemoralis*. Finally, the indistinct scar for *m. adductores* can be plausible identified as an ovate region on the caudal aspect of the femur distal to the fourth trochanter and proximal to the femoral condyles.

The distal condyles are large and face slightly medially. The medial condyle is the larger of the two, while the lateral condyle bears a narrow condylid process (*sensu* Forster 1990). Presumably the insertion tendon of *m. iliofibularis* ran in the large groove that forms the lateral face of this condylid. Each distal condyle is shallowly convex, although both extend caudally for a considerable distance. In caudal view, there is a wide intercondylar groove between them. Cranially, the distal condyles meet to form an extensor 'tunnel' that surrounds the insertion tendon of *mm. iliotibiales* on its way to the cnemial crest of the tibia.



TEXT-FIG. 6. *Telmatosaurus transsylvanicus*. A–C, right distal femur of a hatchling (FGGUB 248) in lateral, cranial, and ventral views respectively. D, left proximal tibia of a hatchling (FGGUB 250) in lateral view. Scale = 10 mm.

In addition to these adult femora, two partial hatchling femora referable to *T. transsylvanicus* have been recently discovered in association with relatively complete eggs (Grigorescu *et al.* 1990; Weishampel *et al.* 1991). Both specimens, comprising distal ends, have a very porous, striated surface texture. FGGUB 248 (Text-fig. 6A–C), a 26·5 mm long fragment of the right femur, preserves the majority of the distal shaft from the base of the fourth trochanter to the distal condyles. From what can be seen, the fourth trochanter extends 3·5 mm from the shaft and is slightly pendent at its tip. Like adult femora, the distal condyles extend cranially beyond the shaft to enclose the cranial intercondylar groove. The caudal intercondylar groove is very deep and there is a moderately-developed condylid on the lateral condyle. It is very likely that the incomplete nature of the distal end is due to the immaturity of the element; embryonic and hatchling hadrosaurids have a very spongy endochondral femoral metaphysis (Horner and Weishampel 1988). FGGUB 249, a smaller femoral fragment, is less well preserved than FGGUB 248. It includes the distal shaft as well as proximal portions of the condyles. Both cranial and caudal intercondylar grooves are relatively deep.

*Tibia*. The tibia of *T. transsylvanicus* is known only from isolated fragments (MAFI Ob.3129; MNMB v.60/1708, v.60/1709). Proximally, the head is expanded, presenting a transversely flat and slightly convex craniocaudally condylar surface for the femur. The cnemial crest is relatively small and faces slightly laterally, where it surrounds the proximal fibula. More distally, the tibial shaft is relatively straight and typically twisted about its long axis.

The lateral malleolus is missing in MAFI Ob.3129, but it apparently articulated with the fibula, much like the condition in *Iguanodon atherfieldensis* and other ornithopods (Norman 1986). Ventrally, the articular surface for the astragalus is transversely expanded and rounded. The medial limit of the distal tibia is formed into a well-developed malleolus that projects well beyond the shaft.

Like the femora, hatchling-size tibial material (again associated with eggs) is also known for *T. transsylvanicus* (FGGUB 250; Text-fig. 6D). Surface texture of the specimen is striated. The relatively flat proximal end of the tibia is craniocaudally expanded. The subequal medial and lateral condyles are well developed, overhanging slightly the caudal aspect of the tibial shaft. The fibula facet is set in from the lateral surface of the cnemial crest. The latter would have wrapped slightly around the cranial aspect of the fibula.

*Metatarsus and phalanges*. Several isolated metatarsals (BMNH R4913, R4914; MAFI Ob.3120, Ob.3121, Ob.3122; FGGUB [11], [15]) are represented among *T. transsylvanicus* material. These pertain to metatarsals II, III, and IV. Metatarsal II (MAFI Ob.3121) is a relatively stout element, with a transversely compressed, flat proximal end. Proximally, the cranial margin of metatarsal II overhangs the more distal shaft. The shaft itself is relatively robust and laterally compressed, curving forward and slightly lateral to form the expanded distal articulation. The lateral surface of the shaft presents a broad flat surface for articulation with the medial surface of metatarsal III. The distal condyles are separated by a modest ginglymus. The slightly more distally positioned medial condyle gives a medial deviation to the long axis of digit II.

Metatarsal III is the largest and most symmetrical of the metatarsals (MAFI Ob.3120, Ob.3122; FGGUB [15]; BMNH R4913). The proximal end is flat and expanded craniocaudally. The broad, flat surface dominating the medial aspect of metatarsal III forms the articulation with metatarsal II. The rugose lateral surface articulates with metatarsal IV. The shaft is relatively narrow throughout its length, culminating in expanded distal condyles, again separated by a ginglymus. The medial condyle is slightly smaller and less distally prolongated than the lateral condyle.

The rounded proximal end of metatarsal IV (FGGUB [11]; MAFI Ob.3120) is the least expanded of the *T. transsylvanicus* metatarsal elements. The slightly excavated medial aspect of the proximal end articulates with metatarsal III. The distal half of the round shaft curves laterally to form an expanded condyle that is only slightly separated into medial and lateral halves by a faint ginglymus.

The few phalanges referred to *T. transsylvanicus* consist only of isolated material. FGGUB 1033 comprises several phalanges. One, a stout element with an expanded distal condylar region, appears to be the first phalanx of digit III. Another, probably the first phalanx of digit II, is relatively long, with a modest, asymmetrically expanded distal end.

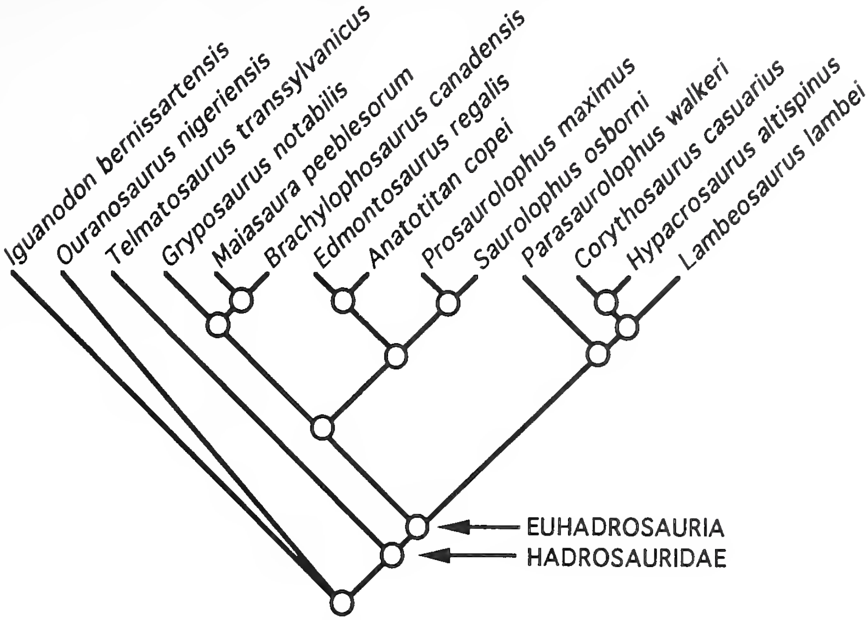
## SYSTEMATIC ANALYSIS

Hadrosauridae presently comprises nearly twenty-five genera and forty species, mostly from the Western Interior of North America and central and eastern Asia, with other, rarer forms from Europe and South America (Weishampel 1990; Weishampel and Horner 1990). In order to understand their phylogenetic relationships (particularly with regard to *T. transsylvanicus*), we undertook a preliminary numerical cladistic analysis of these taxa using Phylogenetic Analysis Using Parsimony (PAUP-2·4; Swofford 1985). This analysis is based on 12 hadrosaurid species and 37 cranial, dental, and postcranial characters. *Ouranosaurus nigeriensis*, *Iguanodon atherfieldensis*, *I. bernissartensis*, and *I. lakotaensis* were used for outgroup comparisons.

The character/taxon matrix for these iguanodontians was compiled from a variety of sources, among them original observations, as well as literature sources (Sereno 1986; Horner 1990; Norman 1990; Norman and Weishampel 1990; Weishampel and Horner 1990). Those characters used in the present analyses were chosen to best reflect the relative completeness of *T. transsylvanicus*. In addition, autapomorphic features were excluded from these analyses. The resulting character/taxon matrix is largely complete (Table 1; only 1·7 per cent missing). These data were analysed using the Branch-and-Bound option of PAUP to retrieve the most parsimonious tree from the data at hand. In addition, the Accelerated Transformation and Delayed Transformation

TABLE 1. Character taxon data matrix.

| | | | | |
|---|---|---|---|---|
| OUTGROUP | 0000000000 | 0000000000 | 0000000000 | 0000000 |
| *Iguanodon* | 0000000000 | 0000000000 | 0000000000 | 1000000 |
| *Ouranosaurus* | 1000000010 | 0000100000 | 0010000000 | 0001000 |
| *Telmatosaurus* | 0000000000 | 0001100001 | 1000011100 | 1110100 |
| *Gryposaurus* | 1110101000 | 0000101001 | 1100111111 | 1110101 |
| *Maiasaura* | 1110001010 | 0001101101 | 1100111111 | 1110101 |
| *Brachylophosaurus* | 1110101010 | 0001101101 | 1100111111 | 1110101 |
| *Edmontosaurus* | 1110101000 | 0010100001 | 1100111111 | 1110101 |
| *Anatosaurus* | 1110101000 | 0010100001 | 1100111111 | 1110101 |
| *Prosaurolophus* | 1110101100 | 0000100001 | 1100111111 | 1110101 |
| *Saurolophus* | 1110101100 | 0000100001 | 1100111111 | 1110101 |
| *Parasaurolophus* | 1101019001 | 0000110011 | 1111111111 | 0111111 |
| *Corythosaurus* | 1101019001 | 1100110011 | 1111111111 | 0111111 |
| *Hypacrosaurus* | 1101019001 | 1100110011 | 1111111111 | 0111111 |
| *Lambeosaurus* | 1101019001 | 0100110011 | 1111111111 | 0111111 |



TEXT-FIG. 7. Cladogram of iguanodontoidean iguanodontian taxa indicating the relationship of *Telmatosaurus transsylvanicus*, based on a single 44-step most-parsimonious tree with a consistency index of 0·841.

options were separately used to evaluate the level at which reversals and convergences accrued within the tree.

Analyses of the complete data matrix result in a single 44-step tree with a consistency index of 0·841 (Text-fig. 7).

On the basis of this analysis, Hadrosauridae constitutes a monophyletic clade, diagnosed on the following synapomorphies (numbers appearing in square brackets refer to characters in Appendix 1).

1. Elevation of the dorsal process of the maxilla, with concomitant migration of the antorbital fenestra onto the dorsal surface of the maxilla [20]
2. Absence of a paraquadratic foramen [21]
3. Angular positioned on the medial surface of the mandible [26]
4. Absence of surangular foramen [27]
5. Narrow maxillary teeth [28]
6. Three or more dentary teeth per tooth position [32]
7. Reduced dorsal margin of the scapular blade [35]

*T. transsylvanicus* possesses all of these characters and is thus an unambiguous member of the hadrosaurid clade (Weishampel and Horner 1990). However, this species lacks a number of synapomorphies that diagnose remaining members of Hadrosauridae, as follows.

1. Absence of a denticulate oral margin of the premaxilla [2]
2. Narrow mandibular condyle of the quadrate [22]
3. Narrow dentary teeth [29]
4. Large single carina on dentary teeth [30]
5. Angular deltopectoral crest [37]

A transversely expanded rostrum (character 1) and a mandibular diastema (character 25) may constitute further synapomorphies of this clade using the DELTRAN option of PAUP (convergently evolved in *Ouranosaurus nigeriensis*). However, when synapomorphies are accelerated (ACCTRAN option), these features are positioned as a synapomorphy of Hadrosauroidea (*sensu* Sereno 1986), with a reversal in *T. transsylvanicus*. As a consequence of this conflict, it is at present impossible to assess the significance of rostral expansion and mandibular diastema among these taxa.

The hadrosaurid clade united by these synapomorphies, here termed Euhadrosauria, consists of the traditional grouping of lambeosaurines and hadrosaurines (Weishampel and Horner 1990).

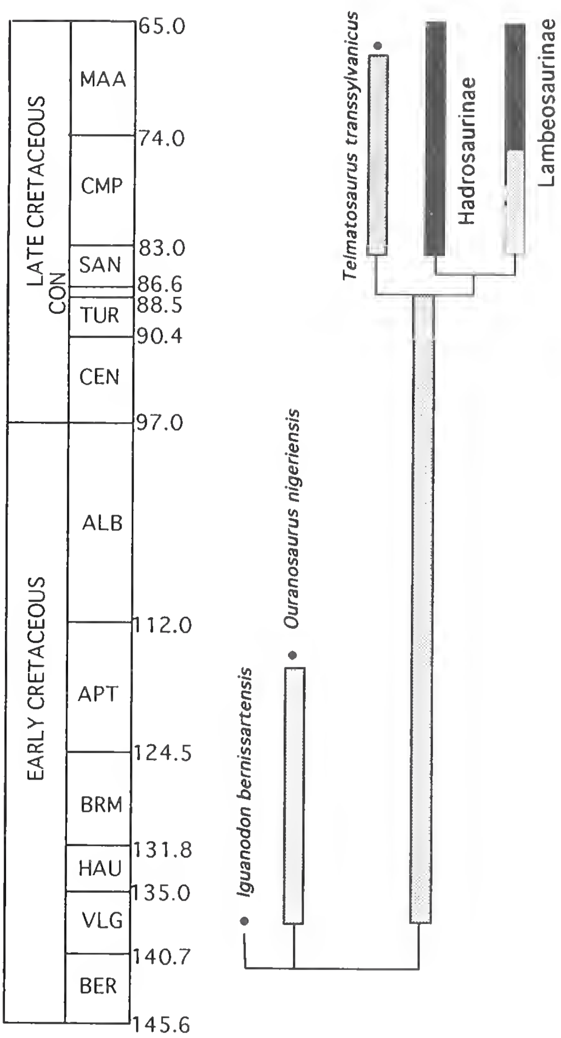
*T. transsylvanicus* itself possesses a number of autapomorphies: reduced body size, large caudal ectopterygoidal shelf, isosceles triangle-shaped rostral process of the jugal, relatively long post-metotic braincase, relatively large basipterygoid processes, large scar for *m. protractor pterygoideus* on the lateral aspect of the basisphenoid, well-developed channel for the palatine branch of the facial nerve that also accommodated the median cerebral vein, and bowed femur. Reversal of rostral expansion and absence of a diastema between the predentary and dentary dentition may also constitute autapomorphies of *T. transsylvanicus*.

## DISCUSSION

As originally noted by Nopcsa (1934; see also Weishampel *et al.* 1991), virtually all of the animals from the Upper Cretaceous sites of Transylvania, including *T. transsylvanicus*, were considerably smaller than their relatives elsewhere. That they were not juveniles or subadults at the time of their death is indicated by the degree of fusion of the braincase and vertebrae. As an adult, *T. transsylvanicus* was probably no more than approximately 5 m in length and weighed in excess of 500 kg, which is at most 10 per cent of an average adult of other hadrosaurid species. Other less well known dinosaur taxa from the Haţeg region are equally small compared to relatives elsewhere. Of relevance here is Nopcsa's (1923, 1934) identification of the Haţeg region as one of many islands comprising a trans-European archipelago in the Late Cretaceous. Armed with this knowledge, Nopcsa regarded small body size among these Transylvanian dinosaurs as examples of dwarfing on islands. Dwarfism is relatively common on islands (Case 1978; Heany 1978; Marshall and Corruccini 1978; Ford 1980; Pregill 1986) and it probably should not be unexpected among taxa found on the 'Haţeg island'. Such dwarfism in *T. transsylvanicus* may involve heterochronic alterations of growth processes. Accordingly, the miniaturization of the maxillary dentition and the evolution of a dental battery in *T. transsylvanicus*, and perhaps all hadrosaurids, may owe their development to progenetic paedomorphosis (see McKinney 1988 for use of terms).

Despite the possibility of dwarfism, *T. transsylvanicus* appears to be little different ecologically from other, larger iguanodontoidean iguanodontians. For example, the serrate oral margin, large adductor muscle mass, and pleurokinetic construction of the skull are all plesiomorphic within this nexus of iguanodontian history and hence suggest that *T. transsylvanicus* had feeding habits similar to more basal iguanodontians such as *Ouranosaurus nigeriensis* and species of *Iguanodon*. In this way, *T. transsylvanicus* was probably little different from these animals in either procuring or processing food. Transverse chewing motion between upper and lower teeth appears to have been achieved by slight lateral rotation of the maxillae (Norman 1984; see also Weishampel 1984; Norman and Weishampel 1985).

In contrast, other features found in *T. transsylvanicus* appear to have their evolutionary origin (i.e. are apomorphic) basally in Hadrosauridae. These include elevation of the dorsal process of the maxilla, miniaturization of the maxillary dentition, and the development of a battery of dentary teeth. That these features appear to have evolved together suggests a shift in feeding among hadrosaurids relative to outgroup taxa. Such changes involve altering the behaviour of some of the links within the kinematic framework of the skull, increasing the complexity of the maxillary occlusal surface, and creating an entirely new organization of tooth replacement, ultimately producing a new construction for the masticatory system.



TEXT-FIG. 8. Stratigraphical distribution of iguanodontoidean iguanodontians. Solid symbols indicate stratigraphical occurrence of a taxon, while hatched symbols indicate minimal divergence times. Stratigraphical data from Weishampel (1990) with geochronological calibration based on Harland *et al.* (1990).

For *T. transsylvanicus* itself, several unique features suggest that its feeding mechanics may have been different from those of other iguanodontoideans. For example, the size of the scar for *m. protractor pterygoideus*, coupled with the relatively large basipterygoid processes in *T. transsylvanicus* may indicate that the basicranial-constrictor dorsalis musculoskeletal system (the maxillary-return mechanism in pleurokinesis; Norman 1984; Weishampel 1984) was emphasized to a greater degree than in other taxa.

It is very difficult to assess the locomotor organization of *T. transsylvanicus*, principally because of the lack of appropriate portions of the limbs. However, there is very little to suggest that these regions differed much from those of other iguanodontoideans. The fore and hindlimb are very similar to those of *Iguanodon* and *Ouranosaurus*. Where they differ – in the reduced nature of the dorsal scapular margin, and the parallel borders of the scapular blade (both apomorphic for Hadrosauridae) – these features are difficult to interpret functionally. The slightly bowed femur of *T. transsylvanicus* may indicate different hindlimb kinematics from that in other hadrosaurids, both young and adult. Conversely, it may be due to reduced peak stresses operating during locomotion in a relatively small animal; bone curvature of the kind seen in *T. transsylvanicus* is less constrained at smaller body size, particularly when the predictability of loads is considered (Biewener 1983; Bertram and Biewener 1988). Should the latter be true, *T. transsylvanicus* may have walked and run no differently from larger hadrosaurid species.

Whatever the functional qualities of *T. transsylvanicus* relative to other iguanodontians, the basal phylogenetic position of this species within Hadrosauridae (Text-fig. 7) and late stratigraphical distribution of this species (Text-fig. 8) appear at face value to be highly discordant (see Weishampel *et al.* 1991). The discordance implied by basal species known only from late within the history of a clade can be studied through the use of minimal divergence times (MDTs; see Norell 1987, 1992; Gauthier *et al.* 1989; Benton 1990; Sereno 1991; Weishampel 1991; Weishampel and Heinrich 1992). MDTs are based initially on the sibling relationships among taxa. These relationships establish phylogenetic continuity from common ancestor to each terminal taxon. Because the common ancestor of two sister taxa can be no younger than each sister taxon, the oldest stratigraphical occurrence of each terminal taxon – and subsequently each node – sets the youngest limit for the other sister taxon. The difference in ages between sister taxa is thus a measure of the minimal divergence time of the younger of the two taxa. Consequently, species-level MDTs are a measure of the completeness of the fossil record from a phylogenetic perspective.

Using MDTs to understand the evolutionary and temporal distribution of *T. transsylvanicus* requires an understanding of the biostratigraphy of remaining hadrosaurids. The oldest age for diagnosable euhadrosaurian taxa is at least ?Early Campanian (the age of *Lophorhothon atopus*). However, this earliest appearance of Euhadrosauria may extend to the Turonian, if Rozhdestvensky (1968) is correct in his assessment of the stratigraphic distribution of Kazakhstan hadrosaurids. The sister-group relationship between *T. transsylvanicus* and Euhadrosauria thus requires that the common ancestor of both taxa is no younger than the older of the two taxa. This relationship implies MDTs of at least 18 million years (and possibly as much as 23 million years) between the first appearance of euhadrosaurian taxa and the appearance of *T. transsylvanicus*. These MDT values are the highest for Hadrosauridae, but near the mean for those available for Dinosauria (Weishampel unpublished data).

High MDT values assuredly mean that some number of species-level taxa yet to be discovered are required to maintain this MDT-based phylogenetic continuity (Weishampel 1991). For *T. transsylvanicus*, the reason that this portion of hadrosaurid history is so poorly known may be a combination of the geographical and depositional setting of these same undiscovered taxa. Given the trans-European archipelago of the Late Cretaceous, we previously suggested that the restricted distribution of *T. transsylvanicus* may have been the result of island hopping, itself a consequence of the dispersal abilities of the animal (Weishampel *et al.* 1991). Our conclusions were based on the geographical distribution of iguanodontoidean iguanodontians as indicated here (i.e. species of *Iguanodon*, *Ouranosaurus nigeriensis*, Hadrosauridae including *T. transsylvanicus*) and the geological history of Europe throughout the Cretaceous. It is clear, however, that whatever the explanation (e.g. vicariance, dispersal) for the geographical distribution of *T. transsylvanicus*, such explanations ultimately depend on an adequate sampling – perhaps as expressed as MDTs – of taxa from the fossil record. In this case, it is very likely that the patchiness of islands in time and space limit our ability to sample much of the line culminating in *T. transsylvanicus*.

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## APPENDIX 1

### *Cranial characters*

1. Lateral expansion of the rostrum. In Ornithopoda ancestrally, the rostrum is relatively narrow. This primitive condition is retained among hadrosaurids in *Telmatosaurus* and Lambeosaurinae. By contrast, the rostrum is considerably more expanded in *Gryposaurus*, *Maiasaura*, *Brachylophosaurus*, *Edmontosaurus*, *Anatotitan*, *Prosaurolophus*, and *Saurolophus* among hadrosaurids, and *Ouranosaurus*. Such a distribution renders character 1 ambiguous with respect to the taxa under consideration. It may either be a synapomorphy of Hadrosaurinae, convergently evolved in *Ouranosaurus* when using the DELTRAN option, or it may constitute a synapomorphy of Hadrosauroidea (i.e. *Ouranosaurus* + Hadrosauridae; Sereno 1986) using the ACCTRAN option.
2. Absence of a denticulate oral margin of the premaxilla and predentary. Primitively for Ankylopollexia, the oral margin of the premaxilla and predentary is strongly denticulate (see *Camptosaurus*, *Iguanodon*, *Ouranosaurus*; Weishampel and Heinrich 1992). *Telmatosaurus* also retains this denticulate oral margin, at least for the premaxilla (predentary is unknown). In contrast, the oral margins of the premaxilla and predentary are not overtly denticulate in lambeosaurine and hadrosaurine taxa (Weishampel and Horner 1990). Given such a character distribution, character 2 is best interpreted as a synapomorphy of Euhadrosauria.
3. Reflected premaxillary lip. Primitively in *Iguanodon*, *Ouranosaurus*, and *Telmatosaurus*, the premaxilla extends laterally without other alterations to the margins of the narial fossa. This primitive condition is also retained in lambeosaurine taxa. In contrast, the lateral margins of the premaxilla fold dorsally to form a prominent lip that mark the ventral wall of the narial fossa in *Gryposaurus*, *Maiasaura*, *Brachylophosaurus*, *Edmontosaurus*, *Anatotitan*, *Saurolophus*, and *Prosaurolophus*. Horner (1990) argued that this feature constitutes a synapomorphy of Hadrosauria (*Iguanodon* + non-lambeosaurine hadrosaurs). However, given that the lateral margin of the premaxilla does not form an appreciable reflected lip in *Iguanodon* and given that *Telmatosaurus* (also without a lip) is interposed between this more basal form and other hadrosaurid taxa, character 3 is best interpreted as a synapomorphy for Hadrosaurinae.
4. Absence of premaxillary foramina. Premaxillary foramina, which form the openings for a canal between the narial fossa and palatal surface of the premaxilla, are present ancestrally in Euornithopoda (Weishampel and Heinrich 1992). Compared with this primitive condition, the premaxilla lacks these basally in *Corythosaurus*, *Lambeosaurus*, *Parasaurolophus*, and *Hypacrosaurus*. Loss of premaxillary foramina is consequently identified as a synapomorphy of Lambeosaurinae. Thus, this evaluation supports the interpretation of Horner (1990; *sensu* Lambeosauridae).

5. Enlarged external naris. Primitively for Ankylopollexia, the external naris is little more than 20 per cent basal skull length. This ancestral condition is retained in *Iguanodon*, *Ouranosaurus*, *Telmatosaurus*, *Maiasaura*, and lambeosaurine taxa. In contrast, the external naris is relatively large (up to 40 per cent basal skull length) in *Gryposaurus*, *Brachylophosaurus*, *Prosaurolophus*, *Saurolophus*, *Edmontosaurus*, and *Anatotitan*. In contrast to Sereno (1986), who regarded enlarged external nares as a synapomorphy of Iguanodontoidea (= *Iguanodon* + *Ouranosaurus* + Hadrosauridae), our analyses place character 5 as a synapomorphy of Hadrosaurinae, in agreement with Horner (1990; *sensu* Hadrosauridae). The relatively small external naris in *Maiasaura* then constitutes a reversal within Hadrosaurinae.
6. External naris surrounded by the premaxilla. In Iguanodontia ancestrally, the external naris is surrounded on its rostral, and ventral sides by the premaxilla, while its dorsal and caudal margins are formed by the nasal. This primitive condition is retained in *Iguanodon*, *Ouranosaurus*, *Telmatosaurus*, and Hadrosaurinae. In contrast, the external naris of *Parasaurolophus*, *Corythosaurus*, *Hypacrosaurus*, and *Lambeosaurus* is completely surrounded by the premaxilla. Although hierarchical levels differ, the present study supports Horner's (1990) identification of this character as a synapomorphy for Lambeosaurinae.
7. Circumnarial depression extending onto the nasal. The external surface of the nasal is relatively flat (i.e. not marked by a fossa or excavation) primitively in Ornithischia. The feature is retained in *Iguanodon*, *Ouranosaurus*, *Telmatosaurus*, and Lambeosaurinae. *Gryposaurus*, *Brachylophosaurus*, *Maiasaura*, *Prosaurolophus*, *Saurolophus*, *Anatotitan*, and *Edmontosaurus* differ from this ancestral condition; the nasal bears a faint to well-developed circumnarial depression immediately caudal to the external nares. Because of the migration of the nasal cavity in lambeosaurines to a supracranial position, a circumnarial depression is considered missing in this taxon. With such a character distribution (see also Horner 1990), the hadrosaurine clade is united by character 7.
8. Narrow solid crest. Ancestrally in Ornithischia (and beyond), the skull roof is relatively flat, unadorned by any cranial excrescence. This condition is retained through *Iguanodon* and basally in Hadrosauridae (see *Telmatosaurus*). In contrast, the caudal aspect of the nasals and adjacent frontals are raised into a relatively narrow, low-lying crest in *Prosaurolophus* and *Saurolophus*. Consequently, character 8 is interpreted as a synapomorphy uniting these two taxa (i.e. saurolophs; Weishampel and Horner 1990).
9. Broad solid crest. As indicated above, the supraorbital region among iguanodontians is primitively flat. In contrast, the broad, solid crest, seen in *Maiasaura* and *Brachylophosaurus* is considered derived, thus constituting a synapomorphy of this small clade of maiasaurs (Weishampel and Horner 1990). The crest of *Ouranosaurus* then constitutes a case of convergence.
10. Modified nasal cavity. In at least Ornithischia ancestrally, the nasal cavity (vestibule, cavum nasi proprium, nasopharyngeal duct) is formed rostral to the orbital region by the facial skeleton. This condition is found throughout Iguanodontia, including *Iguanodon*, *Ouranosaurus*, *Telmatosaurus*, and Hadrosaurinae. The derived condition, in which the cavum nasi proprium is positioned above the orbit and skull roof, is found in *Lambeosaurus*, *Corythosaurus*, *Parasaurolophus*, and *Hypacrosaurus*. As has long been known, modification of the nasal cavity to a supraorbital position uniquely unites Lambeosaurinae.
11. Nasal forming half of the crest. Polarizing features of the crest in Lambeosaurinae is somewhat difficult, given that the sister taxon to the group lacks a hollow crest. However, given what is known about the ontogenetic development of the crest (Dodson 1975; Hopson 1975; Weishampel 1981), it may be possible to infer some aspects of crest polarity. Thus ancestrally the crest of lambeosaurines appears to be formed principally from bones surrounding the vestibule (premaxillae), with the nasals contributing only a small portion of the crest base. A crest bearing large contributions from the nasal, especially around the cavum nasi proprium is thus considered the derived condition, seen in *Hypacrosaurus*, *Lambeosaurus*, and *Corythosaurus*. Character 11 thus constitutes a synapomorphy for the small clade consisting of these three taxa (Weishampel and Horner 1990).
12. Enlargement of the common median chamber. Using the same ontogenetic argument outlined above, the cavum nasi proprium of Lambeosaurinae is relatively small primitively within the clade. In contrast, the chamber is much enlarged in *Lambeosaurus*, *Corythosaurus*, and *Hypacrosaurus*. In our analyses, character 12 stands as a synapomorphy of the clade consisting of these three taxa (Weishampel and Horner 1990).
13. Massive jugal. A relatively gracile jugal is present ancestrally in Iguanodontia, a condition retained in nearly all of the taxa under consideration here. A striking enlargement of the jugal is apomorphically present in *Edmontosaurus* and *Anatotitan*. In our analyses, character 13 constitutes a synapomorphy for the small clade of edmontosaurs (Weishampel and Horner 1990).

14. Isosceles-triangle-shaped rostral process of the jugal. In at least Iguanodontia ancestrally, the rostral end of the jugal, where it articulates with the maxilla, is roughly triangular, but asymmetric. Among the taxa under consideration here, this condition is retained in *Iguanodon*, *Ouranosaurus*, and nearly all Hadrosaurinae. In Lambeosaurinae, the rostral portion of the jugal is truncated and broadly curved (see character 16). In contrast to these conditions, the rostral end of the jugal in *Telmatosaurus*, *Maiasaura*, and *Brachylophosaurus* is nearly shaped like an isosceles triangle. This condition independently diagnoses the small clade of *Maiasaura* and *Brachylophosaurus* (maiasaurs; Weishampel and Horner 1990), while its presence in *Telmatosaurus* is considered convergent.
15. Dorsoventral expansion of the rostral end of the jugal. Primitively for at least Ornithischia, the rostral region of the jugal is relatively narrow, little larger than the area beneath the orbital rim. Among the animals under consideration here, *Iguanodon* retains this ancestral condition. The derived condition, in which the rostral aspect of the jugal is dorsoventrally expanded, is seen in *Ouranosaurus* and all hadrosaurid taxa. As Sereno (1986) originally noted, this character constitutes a synapomorphy for the clade of *Ouranosaurus* + Hadrosauridae (Hadrosauroidea *sensu* Sereno 1986).
16. Truncated, rounded rostral process of the jugal. Ancestrally for Iguanodontia, the articular relationships among the jugal, maxilla, and lacrimal are such that the rostral extreme of the jugal is distinctly angular. This primitive condition is retained in *Iguanodon*, *Ouranosaurus*, *Telmatosaurus*, and Hadrosaurinae. The development of a truncated, rounded rostral aspect of the jugal is apomorphically found in *Parasaurolophus*, *Hypacrosaurus*, *Corythosaurus*, and *Lambeosaurus*. In our analyses, character 16 forms a synapomorphy for Lambeosaurinae.
17. Shallow caudal jugal process. Primitively, the caudal process of the jugal is relatively dorsoventrally broad among ornithischians, a condition retained throughout much of Iguanodontia (i.e. *Iguanodon*, *Ouranosaurus*, Lambeosaurinae, and the majority of Hadrosaurinae). The apomorphic acquisition of a shallow caudal process occurs in *Gryposaurus*, *Brachylophosaurus*, and *Maiasaura*. This feature thus constitutes a synapomorphy for the small clade of these taxa.
18. Scalloped ventral margin of caudal process of the jugal. Ancestrally for Iguanodontia, the caudal process of the jugal is ventrally straight to slightly convex in lateral view. Retention of this feature is found in *Iguanodon*, *Ouranosaurus*, Lambeosaurinae, and virtually all Hadrosaurinae. In contrast, a jugal with a caudal process that is ventrally concave, yielding a scalloped silhouette in lateral view, is found in *Gryposaurus*, *Brachylophosaurus*, and *Maiasaura*. Character 18 stands as a synapomorphy for this small hadrosaurine clade.
19. Maxillary shelf. Ancestrally in Iguanodontoidea (see Sereno 1986), the articulation between the maxilla and premaxilla is marked by a broadening of the contact surface and the development of a rostrolateral maxillary process that aids the rostromedial maxillary process in supporting the more dorsal premaxilla. Within Hadrosauridae, this condition is retained in *Telmatosaurus* and Hadrosaurinae. Unlike these animals, *Corythosaurus*, *Hypacrosaurus*, *Parasaurolophus*, and *Lambeosaurus* are known to lack the rostromedial process, instead having a medial maxillary shelf that supports the inner aspect of the maxilla–premaxilla contact. We do not believe that *Ouranosaurus* had a maxillary shelf, as did Horner (1990) who used this feature as a synapomorphy of *Ouranosaurus* + Lambeosaurinae (his Lambeosauria). Our analyses instead position character 19 as a synapomorphy for the more restricted taxon, Lambeosaurinae.
20. Elevation of the dorsal process of the maxilla. In Ornithischia primitively, the dorsal process of the maxilla is only slightly elevated. This condition is retained in *Iguanodon* and *Ouranosaurus*, among the taxa under consideration here. In contrast, the dorsal maxillary process is considerably elevated in *Telmatosaurus*, Lambeosaurinae, and Hadrosaurinae. A morphological consequence of the elevation of the dorsal maxillary process is the migration of the antorbital fenestra to take a position along the upper reaches of the premaxillary articular surface (Weishampel and Horner 1990). Given its distribution, character 20 constitutes a synapomorphy for Hadrosauridae.
21. Absence of a paraquadratic foramen. In at least Ankylopollexia ancestrally, the quadratojugal articulates with the quadrate in such a way that there is a gap between the two (paraquadratic foramen; see *Camptosaurus*, *Iguanodon*, *Ouranosaurus*). In contrast to these taxa, virtually all Hadrosaurinae, all Lambeosaurinae, and probably also *Telmatosaurus*, appear to lack a paraquadratic foramen. Character 21 consequently stands as a synapomorphy for Hadrosauridae.
22. Narrow mandibular condyle. In at least Dinosauria ancestrally, the mandibular condyle of the quadrate is transversely expanded, forming a well-developed roller joint with the mandibular glenoid. In Iguanodontia, this condition is retained in *Tenontosaurus*, *Dryosaurus*, *Camptosaurus*, *Iguanodon*, *Ouranosaurus*, and *Telmatosaurus*. In contrast, all hadrosaurine and lambeosaurine taxa under

consideration have a relatively narrow and subhemispheric mandibular condyle. Character 22 is consequently apomorphically acquired in Euhadrosauria.

23. Short parietal. In *Iguanodon*, *Telmatosaurus*, and Hadrosaurinae, the parietal is relatively long. This condition appears to be ancestral not only for these taxa, but also for Iguanodontia in general, as it is primitively present in *Camptosaurus* and *Tenontosaurus*. In contrast, *Ouranosaurus*, *Corythosaurus*, *Lambeosaurus*, *Parasaurolophus*, and *Hypacrosaurus* have a relatively short parietal. Shortening of the parietal is seen as independent acquisitions of *Ouranosaurus* and Lambeosaurinae.
24. Ventral margin of the foramen magnum formed of the basioccipital. Primitively in Iguanodontia, the exoccipital condyloids nearly or completely exclude the basioccipital from the margins of the foramen magnum. This condition is encountered in *Iguanodon*, *Telmatosaurus*, and Hadrosaurinae, but contrasts with that found in *Ouranosaurus* and Lambeosaurinae, in which the exoccipital condyloids are well separated medially, allowing the basioccipital to form the ventral margin of the foramen magnum. Horner (1990) interpreted the well-separated condyloid condition as primitive, which suggests that condyloid closure is apomorphic at least for Hadrosauridae. However, such polarity appears to be incorrect, rendering character 24 a synapomorphy of Lambeosaurinae, convergently attained in *Ouranosaurus*.
25. Diastema in mandible. Ancestrally in Ornithischia, the dentary dentition begins immediately behind the caudal limits of the lateral processes of predentary. *Iguanodon* and *Telmatosaurus* retain this condition. In contrast, *Ouranosaurus*, Hadrosaurinae and Lambeosaurinae have caudally displaced dentary dentitions in which a pronounced diastema is formed between the predentary and mesialmost tooth position. Given this distribution, character 25 is ambiguous with respect to tree topology. The ACCTRAN option identifies the acquisition of a mandibular diastema as a synapomorphy of Hadrosauroidea (*sensu* Sereno 1986). This feature is then independently reversed in *Telmatosaurus*. With the DELTRAN option, character 25 becomes an autapomorphy for *Ouranosaurus* and a synapomorphy for Euhadrosauria. Without additional characters and/or taxa, it is presently impossible to discriminate among these possibilities. Thus the phylogenetic significance of a mandibular diastema remains unclear.
26. Angular positioned on the medial surface of the mandible. The angular has a ventral and slightly lateral position ancestrally in Ornithopoda. Those taxa under consideration that retain this plesiomorphic condition include *Iguanodon* and *Ouranosaurus*. In contrast, the angular has a more medial disposition in *Telmatosaurus*, Hadrosaurinae, and Lambeosaurine. This medial angular condition is therefore considered derived for Hadrosauridae.
27. Absence of surangular foramen. A foramen is primitively present in the body of the surangular near the mandibular glenoid in Hypsilophodontidae and basal Iguanodontia (*Tenontosaurus*, *Dryosaurus*, *Iguanodon*, *Ouranosaurus*). In contrast, *Telmatosaurus*, Hadrosaurinae, and Lambeosaurinae lack a surangular foramen. Our analysis indicate that character 27 is apomorphically lost in Hadrosauridae.

### *Dental characters*

28. Miniaturization of maxillary teeth. Primitively in Iguanodontia, maxillary teeth are relatively broad and few in number. For the taxa under consideration, *Iguanodon* and *Ouranosaurus* retain this plesiomorphy. However, in *Telmatosaurus*, Lambeosaurinae, and Hadrosaurinae, maxillary teeth are much reduced in size and packed into a mosaic of replacement. This miniaturization of the maxillary dentition constitutes a synapomorphy for Hadrosauridae.
29. Miniaturization of the dentary teeth. A dentary dentition composed of relatively broad teeth has a primitive distribution in Iguanodontia, a condition also retained in *Iguanodon*, *Ouranosaurus*, and *Telmatosaurus*. The apomorphic state, a reduction in dentary tooth size and an increase in number of dentary teeth, is seen in hadrosaurine and lambeosaurine taxa. This miniaturization of dentary teeth apomorphically diagnoses Euhadrosauria.
30. Large single carina on dentary teeth. Ancestrally in Ankylopollexia, the crowns of dentary teeth have a number of ridges that adorn their lingual surfaces, but none of these ridges is strikingly more prominent than another. This plesiomorphy is retained in *Iguanodon*, *Ouranosaurus*, and *Telmatosaurus*. In contrast, a strongly developed, single carina is found in lambeosaurine and hadrosaurine taxa. This distribution for character 30 allots it as a synapomorphy of Euhadrosauria.
31. Angle between the crown and root of dentary teeth less than 130°. Primitively, the angle between the crown and root of dentary teeth is relatively high, a condition retained in *Camptosaurus*, *Ouranosaurus*, *Telmatosaurus*, and Lambeosaurinae, among ankylopollexian iguanodontians. In Hadrosaurinae,

however, the angle is less than 130°. In our analyses, character 31 constitutes a synapomorphy for Hadrosaurinae, convergently evolved in *Iguanodon*.

32. Three or more dentary teeth per tooth position. Ancestrally for Ornithischia, the dentary dentition is formed of a single functional tooth and a single replacement. This condition is also seen in basal iguanodontians, among them *Tenontosaurus*, *Dryosaurus*, *Camptosaurus*, *Iguanodon*, and *Ouranosaurus*. In contrast, the dentary dentition of *Telmatosaurus*, Lambeosaurinae, and Hadrosaurinae consist in from three to five teeth per tooth position. Character 32 has long been identified as a synapomorphy for Hadrosauridae (Lull and Wright 1942; Ostrom 1961).

## *Postcranial characters*

33. Groove on the ventral surface of the sacrum. In Euornithopoda, the ventral surface of the sacrum plesiomorphically bears a longitudinal ridge. This condition is retained not only in *Camptosaurus* and *Iguanodon*, but also all hadrosaurine taxa under consideration. In contrast, in *Ouranosaurus*, *Corythosaurus*, *Lambeosaurus*, *Hypacrosaurus*, and *Parasaurolophus*, the ventral surface of the sacrum is longitudinally grooved. In our analyses, character 33 stands as an autapomorphy for *Ouranosaurus* and as a synapomorphy for Lambeosaurinae (*contra* Horner 1990 who identified a ventrally ridged sacrum as a synapomorphy for his Hadrosauria).
34. Very tall neural spines. Primitively in Iguanodontia, the neural spines of the dorsal, sacral, and caudal series are of modest height. This condition is plesiomorphically retained in *Iguanodon*, *Telmatosaurus*, and Hadrosaurinae. In contrast, the neural spines are very tall in *Ouranosaurus* and Lambeosaurinae. Given this distribution, character 34 is apomorphic for Lambeosaurinae, convergently acquired in *Ouranosaurus*.
35. Reduced dorsal margin of the scapular blade. In at least Iguanodontia ancestrally, the dorsal margin of the scapular blade is expanded. This primitive condition is known to be retained in *Iguanodon* (*contra* Horner 1990) and *Ouranosaurus*. By contrast, the dorsal scapular margin is reduced relative to the midsection of the blade in *Telmatosaurus* and all hadrosaurine and lambeosaurine taxa under consideration. Thus, this character constitutes a synapomorphy for Hadrosauridae.
36. Robust humerus. Primitively in Iguanodontia, the humerus is relatively gracile, with a relatively small midshaft diameter relative to humeral length and a modestly developed deltopectoral crest. This humeral condition is found in *Iguanodon*, *Ouranosaurus*, *Telmatosaurus*, and hadrosaurine taxa. Compared to this ancestral condition, the humerus is much more robust (greater relative humeral diameter, larger and deeper deltopectoral crest) in *Parasaurolophus*, *Hypacrosaurus*, *Lambeosaurus*, and *Corythosaurus*. Given its taxonomic distribution, character 36 is apomorphic for Lambeosaurinae.
37. Angular deltopectoral crest. The humerus bears a well-rounded deltopectoral crest primitively in *Iguanodon*, *Ouranosaurus*, and *Telmatosaurus*. Compared to this ancestral condition, the ventral margin of the deltopectoral crest extends much more abruptly from the humeral shaft to give a distinctly angular profile to the crest in all known hadrosaurines and lambeosaurines. Given this distribution, our analyses mark character 37 as a synapomorphy of Euhadrosauria.

# BIOSTRATIGRAPHICAL IMPLICATIONS OF A *CHUARIA–TAWUIA* ASSEMBLAGE AND ASSOCIATED ACRITARCHS FROM THE NEOPROTEROZOIC OF YAKUTIA

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ABSTRACT. A new occurrence of the carbonaceous fossils *Chuaria circularis* and *Tawuia dalensis* is reported from subsurface Neoproterozoic in the Khastakh 930 Borehole in the Lena-Anabar Depression, northern Yakutia. Neoproterozoic deposits in this region are regarded as belonging largely to the Yudomian Stage. There have been no faunal records from this site and the strata directly underlying fossiliferous Permian deposits are, on lithostratigraphical grounds alone, regarded as Cambrian. Preliminary palynological results here can be compared with other Neoproterozoic (late Riphean) occurrences of large and morphologically complex acanthomorph acritarch taxa such as *Trachyhystrichosphaera vidalii*. This biostratigraphically diagnostic taxon is associated with vase-shaped fossil protists and other diagnostic acritarchs also known from Upper Riphean strata elsewhere, placing this *Chuaria circularis–Tawuia dalensis* assemblage within the time interval of around 840–700 Ma. By comparison with other regions, the recovered fossils appear to indicate that the investigated succession is of Neoproterozoic (Late Riphean) age, thus preceding the Varanger glacial event.

PROTEROZOIC organic-walled microfossils have been reported from various regions of Siberia (Timofeev 1959, 1966, 1969; Rudavskaya 1971, 1973, 1980; Rudavskaya and Frolov 1974; Ogurtsova 1975; Timofeev *et al.* 1976; Volkova *et al.* 1980; Volkova 1981; Faizulina *et al.* 1982; Rudavskaya and Vasileva 1984; Sokolov and Fedonkin 1985; Sokolov and Ivanovsky 1985; Pjatiletov 1986). The vast majority of these finds are acritarchs (organic-walled envelopes of predominantly encysted life stages of taxonomically problematic single-celled algae: Downie 1973). In this paper, we report on a biostratigraphically significant occurrence of macroscopic, possibly algal, fossils identified as *Chuaria circularis* (Walcott) Vidal and Ford, 1985 and *Tawuia dalensis* Hofmann, 1979, from Proterozoic subsurface units in Yakutia, eastern Siberia.

## GEOLOGICAL BACKGROUND

Proterozoic rocks dealt with in this report are known to occupy a vast area in the Olenek region of northern Yakutia (Text-fig. 1; Sokolov and Fedonkin 1985). Neoproterozoic (Vendian) deposits in the region belong to the Yudomian Stage (Sokolov and Fedonkin 1985) and are generally overlain by detrital rocks of the Kessyusa Formation (partly referred to the Cambrian). The Kessyusa Formation rests with erosional contact on the Turkut Formation (Text-fig. 2). At the investigated Khastakh drilling site, no faunal record is presently known from rock units underlying fossiliferous Permian deposits. On lithostratigraphical grounds alone, the immediately sub-Permian rocks were considered to contain the entire Cambrian System, whereas the lower 120 m of the 230 m thick Kessyusa Formation were regarded as Vendian in age. On a regional scale, the Yudomian is considered roughly time-equivalent to the Vendian. However, correlations were constructed on rather circular arguments, using 'phytolite' assemblages (Sokolov and Fedonkin 1985, p. 181).

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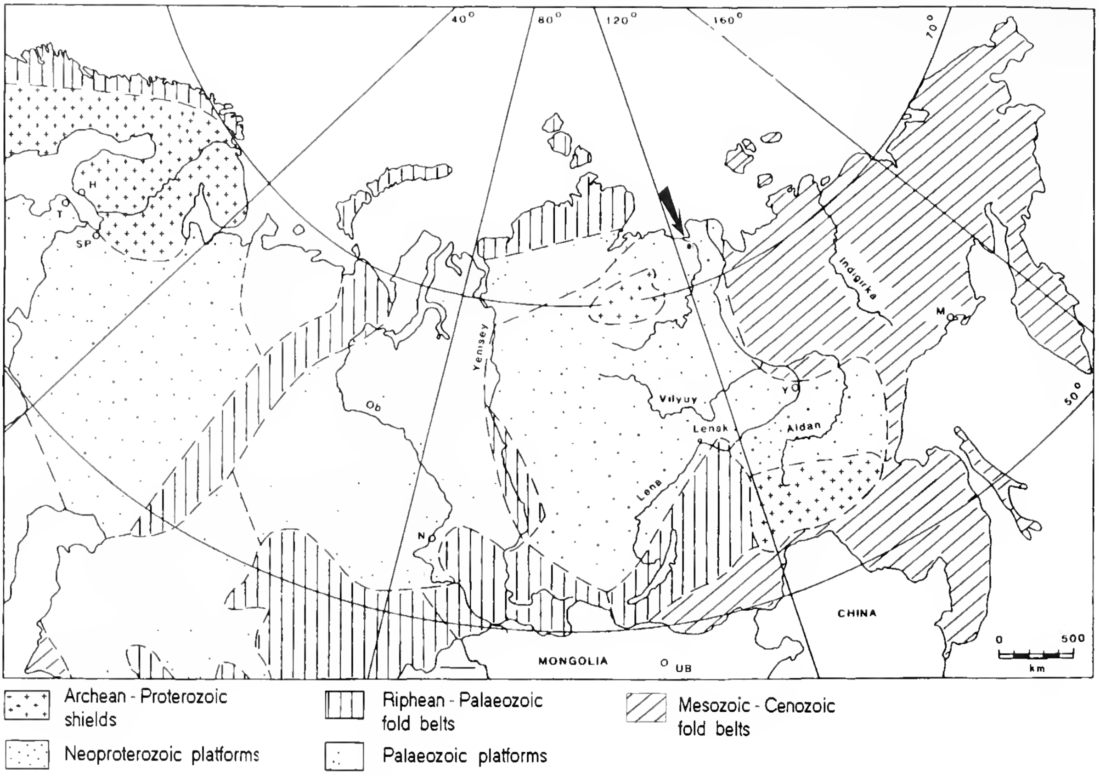
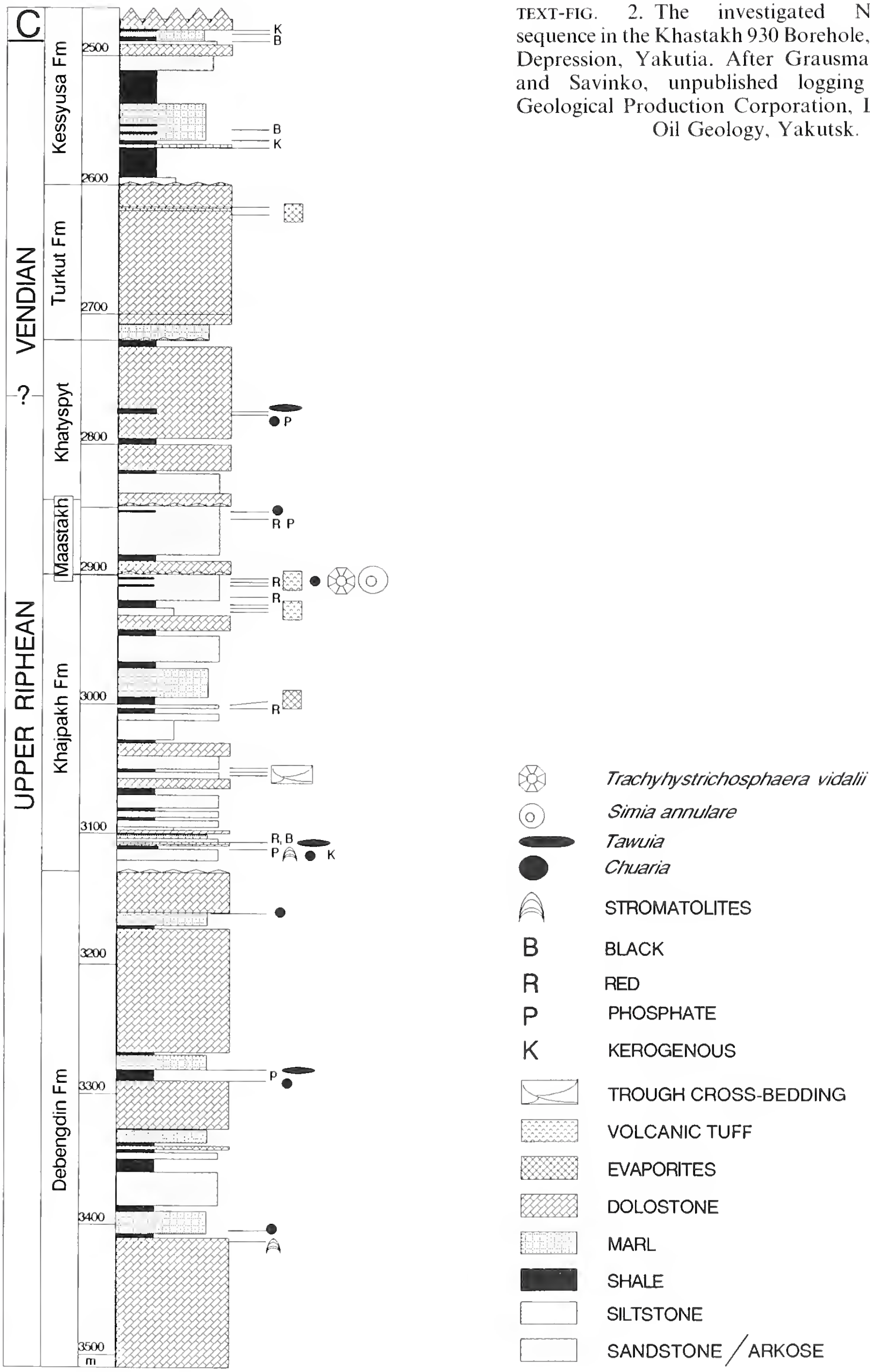


TEXT-FIG. 1. Main structural units and location of the Khastakh 930 Borehole (arrow) in the Lena-Anabar Depression, Yakutia. H, Helsinki; T, Tallinn; SP, St Petersburg; N, Novosibirsk; Y, Yakutsk; M, Magadan; UB, Ulan Bator.

In the North Atlantic region, the East European Platform and elsewhere, the Varanger glacial deposits are used to define the Varanger glacial episode, which is generally considered to mark the base of the Vendian (Sokolov and Fedonkin 1985; Harland *et al.* 1990). Despite poor isotopic and palaeontological dating, they are generally regarded as being the result of virtually contemporaneous glacial events (Chumakov 1981; Chumakov and Semikhatov 1981). The recognition of the Lower Vendian is mainly a matter of recognizing these predominantly glacigenic deposits (Chumakov 1981). However, the absence of Neoproterozoic glacigenic deposits in the part of the Anabar Slope of Yakutia involved in this study presents major obstacles for the unequivocal recognition of the Lower Vendian (Sokolov and Fedonkin 1985).

In areas outside Siberia, the Upper Vendian is normally recognized by the presence of distinctive non-skeletal metazoans and/or vendozoans (Seilacher 1989), and belongs to the Ediacara Series (Glaessner 1982; Cloud and Glaessner 1982; Harland *et al.* 1990). However, the strength of this argument is weakened by recent finds of Ediacaran fossils in intertillite beds in northwestern Canada (Hofmann *et al.* 1990). Interestingly, components of the Ediacaran fauna were reported from outcrops of the Khatyspyt Formation along the River Khorbusuonka and River Olenek, thus roughly suggesting time equivalence with Redkino 'Horizon' rocks of the Upper Vendian Valdai 'Series' in the East European Platform (Sokolov and Fedonkin 1985, p. 134). No such faunal components were ever observed in the rock succession dealt with in this report.

The sub-Permian sequence penetrated by the Khastakh 930 Borehole (Text-Fig. 2) is dominated by carbonate rocks largely consisting of dolostones with (as far as visible in examined cored intervals) a general lack of primary sedimentary structures. On the whole, the carbonates are



TEXT-FIG. 2. The investigated Neoproterozoic sequence in the Khastakh 930 Borehole, Lena-Anabar Depression, Yakutia. After Grausman, Vinokurov and Savinko, unpublished logging data, 1989, Geological Production Corporation, Lena Gas and Oil Geology, Yakutsk.

beige, buff and red, and thus have very low content of organic carbon. But there are remarkable exceptions in the form of bituminous, thinly laminated limestones at depths of 3108·0–3111·9 m, 2576·9–2572·4 m, 2482·1–2487·6 m and 2425·0–2433·0 m.

The presence of red beds consisting of feldspathic sandstones and red and crimson mudstones was noted at various levels in the sequence (Text-fig. 2). Conglomerates, arkoses (often cross-bedded) and tuffaceous beds occur at various levels. Haematite-rich, laminated mudstones occur in close stratigraphical proximity at 2903·9–2910·0 m and 2910·0–2916·7 m. This, and the occurrence of gypsum casts, at least at two levels, suggests sedimentation in a periodically nearly closed depositional setting. There were periods of sediment starvation, that resulted in the accumulation throughout the sequence of organic-rich, phosphoritic and strongly fossiliferous levels. This succession is similar to other known Neoproterozoic (Riphean and Vendian) sequences in intracratonic settings, that accumulated as a comparable set of facies associations.

## MATERIAL AND METHODS

Only small intervals of the Khastakh 930 Borehole were cored. The succession shown in Text-figure 2 was compiled from unpublished logging information provided by the Geological Production Corporation, Lena Gas and Oil Geology, Yakutsk (V. V. Grausman, B. N. Vinokurov and N. A. Savinko, pers. comm.). Cored intervals were examined and in some instances samples were collected. The detailed examination of bedding surfaces revealed numerous organic films and preliminary results from study in progress of HF-resistant organic residues indicate the presence of very abundant acritarchs.

Specimens of *Chuaria circularis* and *Tawuia dalensis* were found at eight levels within the borehole, in dark-grey and black, often phosphatic mudstones and shales (Text-fig. 2). At one of these levels, in the upper Khajpakh Formation, abundant acritarchs were also recovered.

Generally, bedding surfaces in fossiliferous shales from the Debengdin, Khajpakh, Maastakh and Khatyspyt Formations, display an extraordinary abundance of irregularly shaped organic films. Only a minority of the organic remains can be definitely identified as fossils. However, most of the filmy fragments are probably fragmented fossils, as suggested by the fact that rather large fragments of *Chuaria* and *Tawuia* were also observed.

Specimens with the prefix PMU-Sib are in the collections of the Institute of Palaeontology, Uppsala University, Uppsala; those with the prefix VNIGRI followed by a number are deposited at the All-Union Scientific Research Geological Prospecting Institute in St Petersburg. In relevant cases, the location of specimens in microscopic slides is given by England Finder coordinates (specimens in Plate 1, figs 1–4; Text-figures 5A–B, 6A–C). Micrographs of figured specimens of *Chuaria* and *Tawuia* were taken using a Wild Photomakroskop M 400 and incident light sources. Acritarchs were concentrated in permanent mounts using standard palynological techniques and micrographs were taken under an interference contrast microscope.

## SYSTEMATIC PALAEONTOLOGY

### Group ACRITARCHA Evitt, 1963

### Genus CHUARIA (Walcott) Vidal and Ford, 1985

*Type species*. *Chuaria circularis* (Walcott) Vidal and Ford, 1985, from the Neoproterozoic Chuar Group in northern Arizona, U.S.A.

### *Chuaria circularis* (Walcott) Vidal and Ford, 1985

Text-figs 3A–D; 4B, D

1894 Unnamed, Wiman p. 109, pl. 5, figs 1–5.

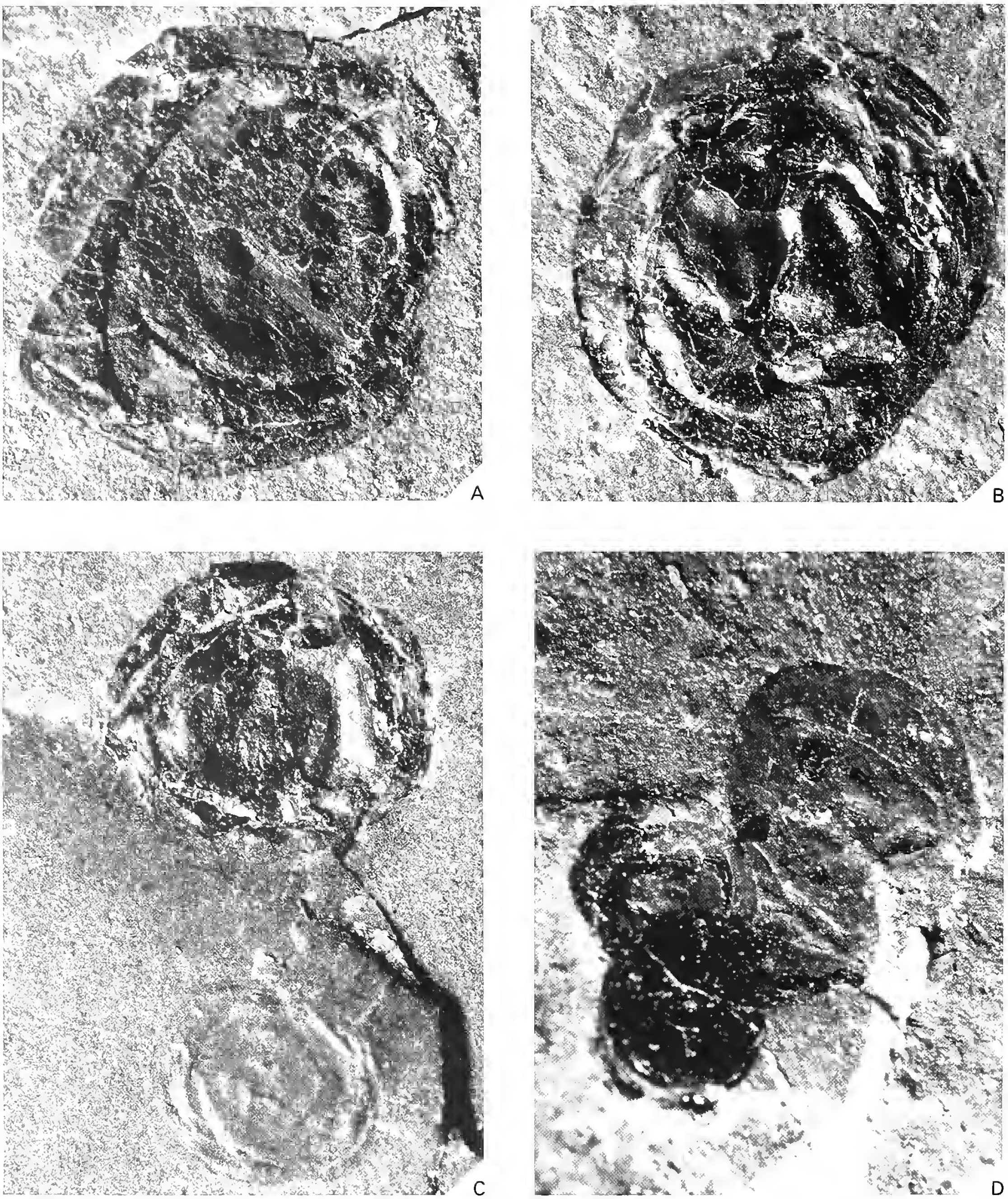
1899 *Chuaria circularis* Walcott p. 234, pl. 27, figs 12–13.
1966 *Chuaria wimani* Brotzen; Eisenack, p. 52, figs 1–2.
1969 *Trachysphaeridium vetterni*, Timofeev, p. 21, pl. 4, fig. 3.
1970 *Kildinella magna* Timofeev; Timofeev, p. 158, pl. 1, fig. D.
1973 *Chuaria circularis* Walcott; Ford and Breed, p. 539, pl. 61, figs 1–7, pl. 62, figs 1–6, pl. 63, figs 1–4.
1974 *Chuaria circularis* Walcott; Vidal, p. 6, pl. 1, figs 3–6.
1976 *Chuaria circularis* Walcott; Vidal, p. 18, fig. 8A–H.
1979 *Chuaria circularis* Walcott; Vidal, p. 19, pl. 4, figs *a–b*.
1981 *Chuaria circularis* Walcott; Vidal, p. 23, fig. 11J–K.
1985 *Chuaria circularis* Walcott; emend. Vidal and Ford, p. 355, fig. 3A.
1987 *Chuaria circularis* Walcott; Sun, p. 115, pl. 1, figs 1–8, pl. 4, figs 1–2.
1990*a* *Chuaria circularis* (Walcott) Vidal and Ford; Vidal, p. 488, fig. 1.
1992 *Chuaria circularis* (Walcott) Vidal and Ford; Amard, p. 121, pl. 1, figs 1–8; pl. 2, figs 1–8.

*Description*. Specimens consist of compressed discoidal structures (Text-fig. 3A–C) preserved as slightly convex carbonaceous vesicles, ranging from 500 to 3000 μm across and displaying sets of irregular and sharp compression folds. The specimens are identical to discoid fossils attributed to *C. circularis* from, for example, the Neoproterozoic (late Riphean, > 700 Ma; Text-fig. 7) Visingsö Group in Sweden. As with occurrences elsewhere (e.g. Vidal 1976; Vidal and Siedlecka 1983; Vidal and Ford 1985; but see Sun 1987 for a different standpoint) the present material can be liberated by careful HF maceration.

*Remarks*. Undoubtedly, the very simple morphology of the near-macroscopic, flattened, spheroidal alga presents significant problems for a sound taxonomic treatment (see for example discussions in Vidal and Ford 1985 and Sun 1987). From this lack of clearly diagnostic characters emanates the suspicion that *C. circularis* may in fact be a taxonomic waste-basket containing true biogenic, as well as various non-biogenic objects such as films of organic sapropel and carbonaceous intraclasts (Horodyski 1980). The true biotic category may include accumulations of bacterial (Moczydlowska and Vidal 1988, p. 6) or cyanobacterial filaments (Horodyski 1980), the latter perhaps including objects explained as possible *Nostoc* balls by Sun (1987, p. 118). However, the variably degraded, discoid fossils attributed to *C. circularis* (Vidal 1974, 1976) have thick sturdy 'sporopollenin-like' (Eisenack 1966) organic walls, very different from the thin outer layer of true *Nostoc* balls (whose likelihood of surviving into the fossil record must be regarded as extremely low). Nevertheless, mechanical and chemical degradation introduce into the fossil record features (Vidal 1974; 1976, fig. 8E–H) that are prone to inflate the flora with superfluous taxonomic combinations. The same degradationally introduced features are observable in nearly macroscopic (*c*. 600 μm in diameter) specimens of *Tasmanites* (G. Vidal, unpublished data). Contrary to suggestions by Sun (1987), specimens of *C. circularis* from the Neoproterozoic Visingsö Group displaying degradational features resulting from intensive pyrite growth and sapropelitization, have no traces of trichomes. In addition, specimens from the Upper Proterozoic Chuar Group (Vidal and Ford 1985) display a visible level of chemical degradation (Vidal 1990*a*) higher than that of some of the rather 'fresh' material from the Visingsö Group in Sweden.

In conclusion, the problematic status of these fossils is due to the variety of possibly unrelated objects included under the common umbrella of the name *C. circularis*. In this connection, it is worth mentioning that fossils tentatively attributed to *Chuaria* from the Upper Proterozoic (Vendian) Pusa Formation in central Spain (Palacios 1989) may, as suggested by Sun (1987), have little to do with both the Upper Riphean and the clearly pre-Varangerian occurrences of *Chuaria*. This Spanish material consists of thin-walled specimens that are one degree of magnitude larger than any specimens of *Chuaria* recorded from older units. The age of the Spanish material is quite certainly late Vendian (Palacios 1989; Palacios and Vidal 1992) as clearly indicated by the association with vendotaenids, ichnofossils, the early skeletal fossil *Cloudina* (Grant 1990) and the immediately overlying Lower Cambrian strata.

As it stands, it seems that various clearly biogenic objects are involved in the concept of *C. circularis* as currently in use. This concept prevents proper evaluation of its biostratigraphical



TEXT-FIG. 3. *Chuaria circularis*. Khastakh 930 Borehole; Upper Riphean; specimens showing various stages of preservation (A, D from the Debengdin Formation; B–C from the Khajpakh Formation). A, PMU-Sib.7; specimen slightly convex with concentric compaction folds and partly preserved carbonaceous wall; depth 3280·2–3286·6 m. B, PMU-Sib.8; convex specimen with organic wall only partly preserved (left side); at the bare areas the imprint is observable on the rock surface; depth 3108·2–3111·9 m. C, PMU-Sib.9; two specimens preserved as flattened carbonaceous vesicles (upper) and as the vesicle imprint (lower) on the rock surface; depth 3108·2–3111·9 m. D, PMU-Sib.10; group of four specimens preserved with organic wall (lower portion) and as imprints (upper portion); depth 3158·0–3165·0 m. All specimens × 30.

usefulness. A more useful approach for establishing the taxonomic status of *Chuaria* may be through ultrastructural studies (e.g. Amard 1992). Nevertheless, despite a generalized morphology, it is clear that the sub-Varangeran smaller discoid fossils, ranging into the microscopic realm (Vidal and Ford 1985) or only considered at the sub- or macroscopic level (Sun 1987), appear restricted to a broad interval of strata pre-dating the Varanger glacial deposits (marking the base of the Vendian; Harland *et al.* 1990). These deposits also yield other probable algal fossils (such as *Tawuia* Hofmann and Aitken, 1979; Hofmann 1985; Sun 1987) and a distinctive assemblage of ornamented spheromorphic and acanthomorphic acritarchs (Vidal and Knoll 1983, Jankauskas *et al.*, 1989).

### INCERTAE SEDIS

### Genus TAWUIA hofmann, 1979

*Type species*. *Tawuia dalensis* Hofmann, 1979; from the Neproterozoic Little Dal Group, Mackenzie Mountains, Canada.

### *Tawuia dalensis* Hofmann, 1979

Text-fig. 4A, C

1979 *Tawuia dalensis* Hofmann *in* Hofmann and Aitken, p. 158, fig. 13A–I.
1985 *Tawuia dalensis* Hofmann; Hofmann, p. 334, pl. 35, figs 1–3, 6; pl. 36, figs 1–5, 7–11.
1982 *Tawuia dalensis* Hofmann; Knoll, p. 3, figs 12–14.
1987 *Tawuia dalensis* Hofmann; Sun, p. 123.

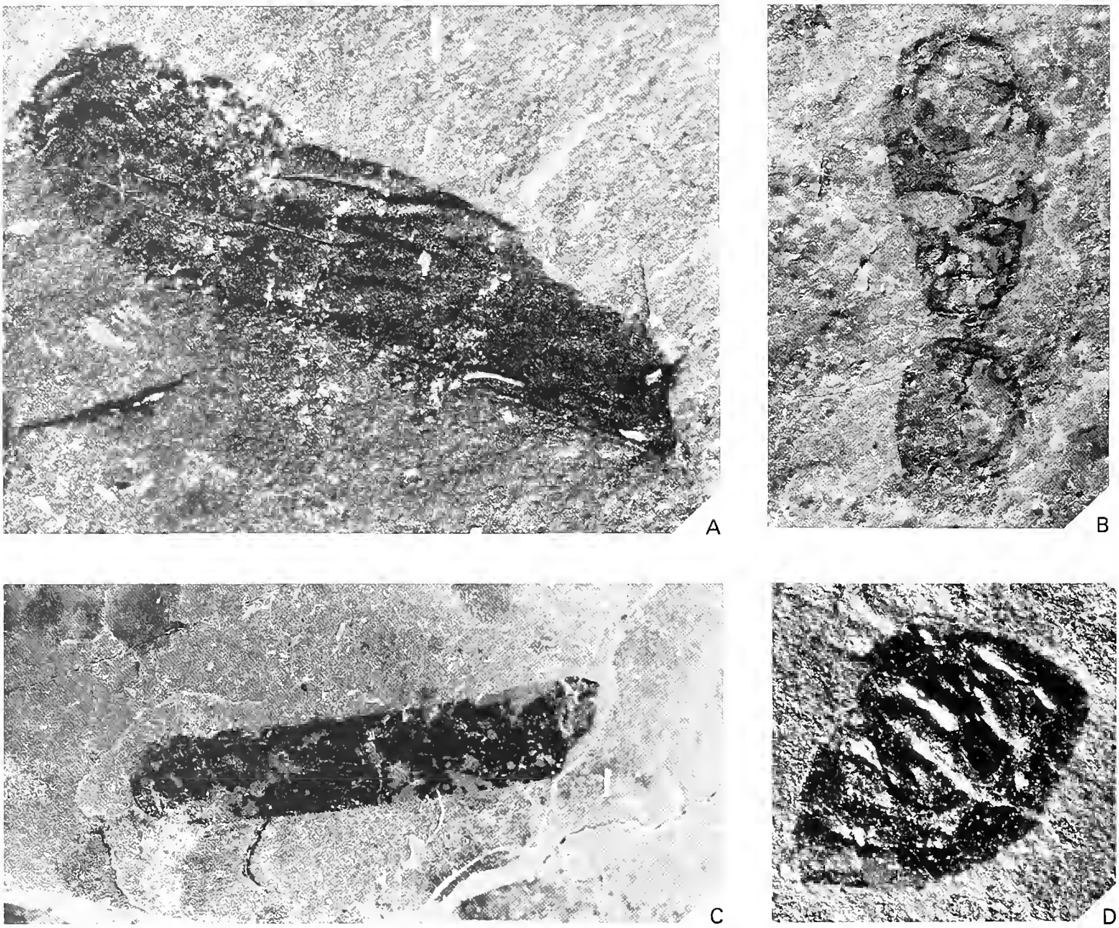
*Description*. Fossils attributed to this species include one almost complete specimen 1 mm wide and 5 mm long with rounded ends, from the Debengdin Formation (Text-fig. 4C), and three fragmentary specimens from the Khajpakh and Khatyspyt Formation (Text-fig. 4A). They consist of flattened, organic, carbonaceous ribbons. One specimen (Text-fig. 4A) displays clear compaction wrinkles. The specimens are in the lower size-range indicated by Hofmann and Aitken (1979) and Hofmann (1985) for material from the Little Dal Group.

*Remarks*. The present material adds little to the problematic biological affinity of *Tawuia*. Sun (1987) put *Morania*? *antiqua* Fenton and Fenton, 1937 (*sensu* Hofmann and Aitken 1979) in synonymy with *T. dalensis*. Organic films comparable to *M.*? *antiqua* occur in the present material, and we consider *M.*? *antiqua* as probably part of *T. dalensis*; not having examined the original material of *M.*? *antiqua* we refrain from placing the latter in synonymy.

The two most extensively investigated collections of *T. dalensis* derive from the Little Dal Group (Hofmann 1985; 146 specimens) and the Kapp Lord Formation in Nordaustlandet, Svalbard (125 specimens attributed to *T. dalensis*; Knoll 1982). From the point of view of morphological variability these collections constitute formidable assemblages. To these should be added more than 20 specimens from North China (Sun 1987, p. 113, who pointed out that the bivariate plot for specimens of *T. dalensis* from the Kapp Lord Formation may include specimens of *C. circularis*; this assumption may be correct for at least the smallest specimens reported by Knoll, 1982, p. 275).

The biological nature of *T. dalensis* could perhaps be inferred from an analysis of their possible habitat, as deduced from a study of the encompassing sediments. Nevertheless, little is known about the depositional setting and environmental constraints of the material from the North China Platform. Apart from general statements indicating the shallow marine nature of the strata, this is also true of the whole Franklinsundet Group in Nordaustlandet (e.g. Flood *et al.* 1969). The occurrence in the Kapp Lord Formation was considered to have been preserved in a coastal mud-flat (Knoll 1982, p. 275), whereas the original occurrence from the Little Dal Group is in deep-water carbonate-clastic rhythmites (Hofmann and Aitken 1979, p. 153).

Environmental constraints on the present occurrences of *T. dalensis* are imposed by facies associations and sedimentary structures (see above). Dominated by carbonates (Text-fig. 2), the Khastakh succession includes deposits that probably formed in braided-plain and coastal

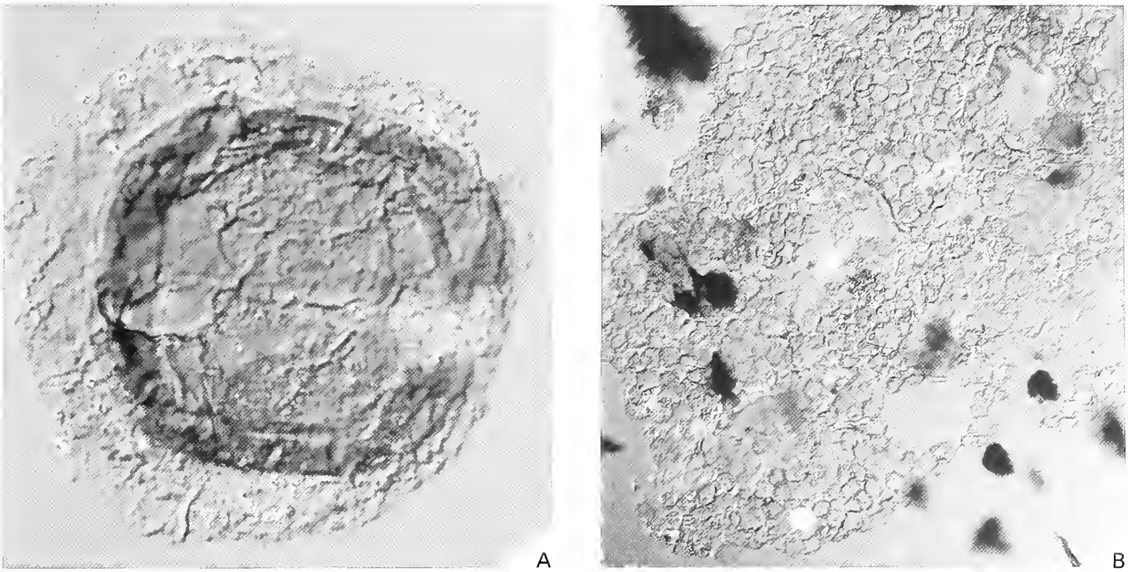


TEXT-FIG. 4. A, C, *Tawuia dalensis*; Khastakh 930 Borehole; Upper Riphean (A from the Khajpakh Formation, C from the Debengdin Formation); A, PMU-Sib.15; specimen deformed by lateral compaction resulting in elongated folds and fracturing, end partly broken; depth 3108·2–3111·9 m, ×30; C, PMU-Sib.17; specimen with rounded end (left) and partly broken right end; depth 3280·2–3286·6 m, ×12. B, D, *Chuaria circularis*; Borehole Khastakh 930; Upper Riphean (from the Debengdin Formation). B, PMU-Sib.16; imprints of two specimens; depth 3403·5–3410·0 m, ×10; D, PMU-Sib.18; complete compressed organic vesicle; depth 3158·0–3165·0 m, ×30.

environments that seem to pass gradually into cycles of carbonate and evaporite deposition. These features suggest deposition in a periodically restricted shallow basin, which is significantly different from the environment inferred for the Little Dal occurrence. At the least, the final burial sites of the *Chuaria–Tawuia* assemblages represent different depositional settings. The biological affinity of *Chuaria* and *Tawuia* cannot be certainly established on the basis of the available evidence. However, it seems reasonable to assume that *Tawuia* represents a thallophytic level of organization that possessed considerable environmental and geographical dispersal.

## BIOSTRATIGRAPHY

Samples collected at various cored intervals are the subject of an investigation in progress, to recover organic-walled microfossils. Some significant results can be already advanced at this stage, in particular that acritarchs, together with possible algal tissues or cell aggregates (Plate 1, figs 1–4; Text-figs 5A–B, 6A–C) are quite abundant.



TEXT-FIG. 5. A, *Simia annulare*; specimen PMU-Sib.6-M/40/1; Khastakh 930 Borehole; Upper Riphean (from the Khajpakh Formation); depth 2903·9–2910·0 m, × 1320. B, fragment of possible algal tissue; specimen PMU-Sib.6-G/56/3; Khastakh 930 Borehole; Upper Riphean (from the Khajpakh Formation); depth 2903·9–2910·0 m, × 240.

Stratigraphically significant acritarchs have thus far been recovered at the depth of 2903·9–2910·0 m. Among them are abundant specimens of *Simia annulare* (Timofeev) Mikhailova and Jankauskas (Text-fig. 5A), rare specimens of *C. circularis* (including fragments of macroscopic and smaller specimens), various *Leiosphaeridia*, unnamed cell aggregates possibly comparable to *Ostiana microcystis* Herman (Text-fig. 5B) and three specimens of *Trachyhystrichosphaera vidalii* Knoll (Plate 1, figs 1–4; Text-fig. 6A–C). The latter is in our view a synonym of *T. stricta* Hermann, 1989 (*in* Jankauskas *et al.* 1989, p. 47) from the Upper Riphean Miroedikha Formation in Siberia.

*T. vidalii* (Plate 1, figs 1–4; Text-fig. 6A–C) possesses tubular processes that communicate with the cavity of the vesicle. The processes appear to have open distal portions and are enclosed by a thin organic membrane that is substantially thinner than the central vesicle. *T. vidalii* was interpreted as possibly representing various growth stages of a prasinophycean green alga (Knoll *et al.* 1991). While this is plausible, it is also possible that, as discussed below for *C. circularis*, large Neoproterozoic acritarchs such as *T. vidalii* could represent reproductive stages of thallophytic algae (Vidal 1990*b*, p. 290).

## SIGNIFICANCE OF THE BIOTA

Most previous occurrences of *Chuaria–Tawuia* assemblages are not associated with identifiable acritarchs. They thus cannot be placed in the acritarch biostratigraphy, which is only occasionally linked to isotopic ages. To evaluate the relative age of the Khastakh assemblage consideration of various previously investigated sequences in Baltica, Svalbard, North America and China is required (Text-fig. 7).

The geographically closest comparable assemblage is in the supposedly Upper Riphean Miroedikha Formation, in the River Miroedikha area of central Siberia, from which Timofeev (1969) reported a later synonym of *C. circularis* (*sensu* Vidal and Ford 1985). This unit also yielded *T. stricta* ( = *T. vidalii*; see above). However, the age of the Miroedikha Formation is poorly constrained. A late Riphean age attributed to the *Chuaria–Tawuia* assemblage from the Kapp Lord Formation in Nordaustlandet (Svalbard) is inferred from rare acritarchs (Knoll 1982, p. 275) and from comparisons with biotas from the late Riphean Eleonore Bay Group in East Greenland (Vidal 1979). A late Riphean age is attributed to the Little Dal Group also based on palaeontological evidence (Vidal and Ford 1985, p. 380). The discovery in Yakutia of *Chuaria* and *Tawuia* with *T. vidalii* provides further support to the age of the assemblage.

A co-occurrence of *Chuaria* with *S. annulare* and several taxa attributed to *Trachyhystrichosphaera* (most likely conspecific with *T. vidalii*) was reported from the Neoproterozoic Kildin Group in Kildin Island, Russia (Lyubtsov *et al.* 1989). The absolute age of the Kildin Group, poorly constrained by K/Ar isotopic dating of glauconite from the lower part of the group, is at Sredniy Peninsula 1059–762 Ma and at Kildin Island 1015–849 Ma (Lyubtsov *et al.* 1989). Additional dating according to Polkanov and Gerling (1961) is between 1655 and 920 Ma for rocks at Sredniy and 887–715 Ma for rocks in Ribachiy Peninsula.

An interesting co-occurrence of vase-shaped microfossils with *T. vidalii* was reported by Knoll and Calder (1983) from the Ryssö Formation at the top of the Murchisonfjorden Group in Svalbard. While no isotopic ages are available for these beds, their relatively lower stratigraphical position with respect to the Varangerian correlative glacial deposits of the Gothia Group (Knoll 1982) and their biostratigraphical correlation with strata of the pre-Varangerian Eleonore Bay Group, suggest a late Riphean age around a broad estimate of 800–700 Ma (Knoll and Calder 1983, p. 469). According to Knoll *et al.* (1991, p. 53) the age estimates are also supported by comparisons with other rock units that were investigated using stable and radiogenic isotopes. As an interesting parallel, *C. circularis* and vase-shaped microfossils co-occur in the isotopically dated Visingsö Group (*c.* 800–700 Ma according to Rb–Sr datings of whole-rock shale and clay minerals by Bonhome and Welin 1983). Isotopically dated groups of strata underlying the Varanger glacial deposits in northern Norway (Beckinsale *et al.* 1975) are particularly important for determining the age of acritarch assemblages that include *C. circularis* (Vidal and Siedlecka 1983).

Although not associated with *C. circularis*, a reported occurrence of *Trachyhystrichosphaera vidalii* and *T. magna* (most likely a junior synonym of the former), vase-shaped microfossils, e.g. *Hyalocyrillium clardy* Allison (Allison and Awramik 1989), spheromorphic acritarchs and cyanobacterial and possibly fungal microfossils in the upper Tindir Group, Northwest Canada, has an indirect bearing on the age bracketing of the *Chuaria–Tawuia* assemblage. The Upper Tindir Group was originally considered as possibly latest Proterozoic or early Cambrian (Allison and Awramik 1989). Recent biostratigraphical and chemostratigraphical evidence is consistent with a late Riphean age for the Upper Tindir microfossil association (Kaufman *et al.* 1992).

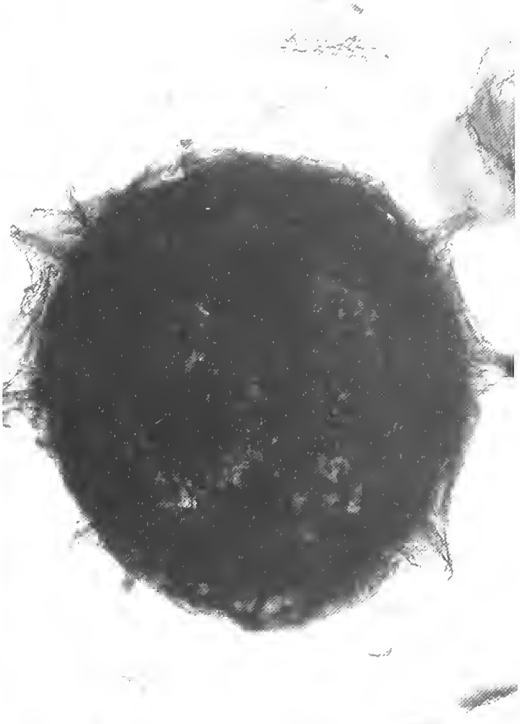
In North China, *C. circularis* and *T. dalensis* occur in the Liulaobei and Jiuliqiao Formations of the Huainan and Feishui Groups, dated respectively as 840 Ma (Rb–Sr on whole-rock shale) and 740 Ma (K–Ar on glauconite; Sun 1987, p. 113). The stratigraphically most significant occurrences of *Chuaria–Tawuia* and associated time-diagnostic microfossils are shown in Text-figure 7.

## EXPLANATION OF PLATE 1

Figs 1–4. *Trachyhystrichosphaera vidalii* Knoll. Specimen PMU-Sib.6-N/43/3; Khastakh 930 Borehole; Upper Riphean (Khajpakh Formation); depth 2903·9–2910·0 m. 1, 3–4, detail portions of the vesicle showing tubular processes with free communication with the vesicle cavity and enclosed by transparent organic membrane, × 960. 2, complete specimen, × 380.

PLATE 1

1



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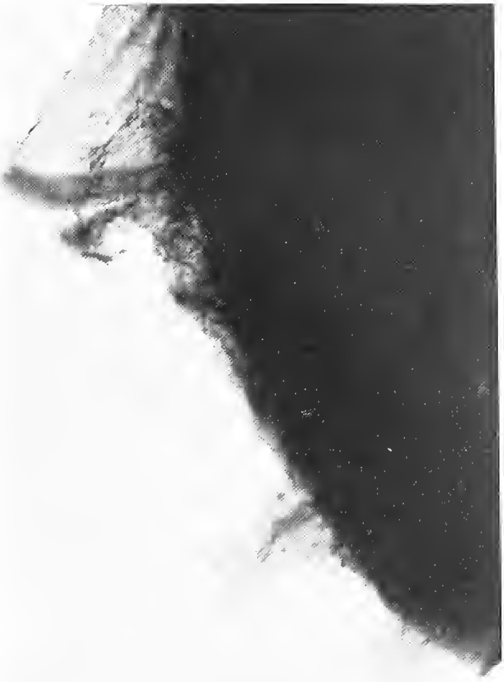

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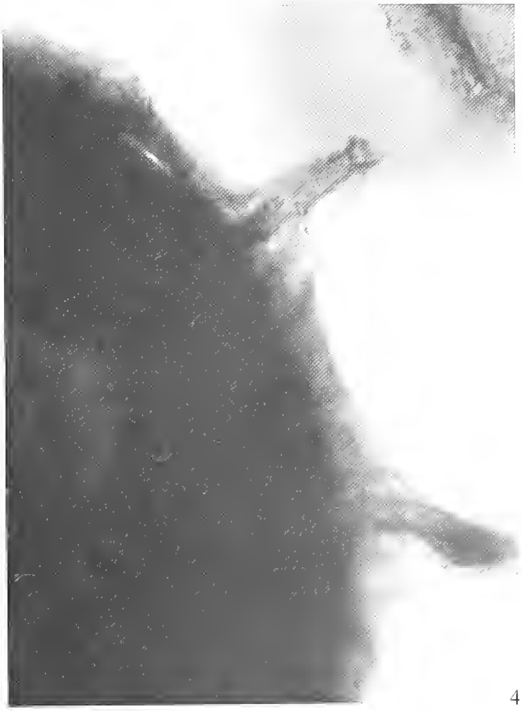

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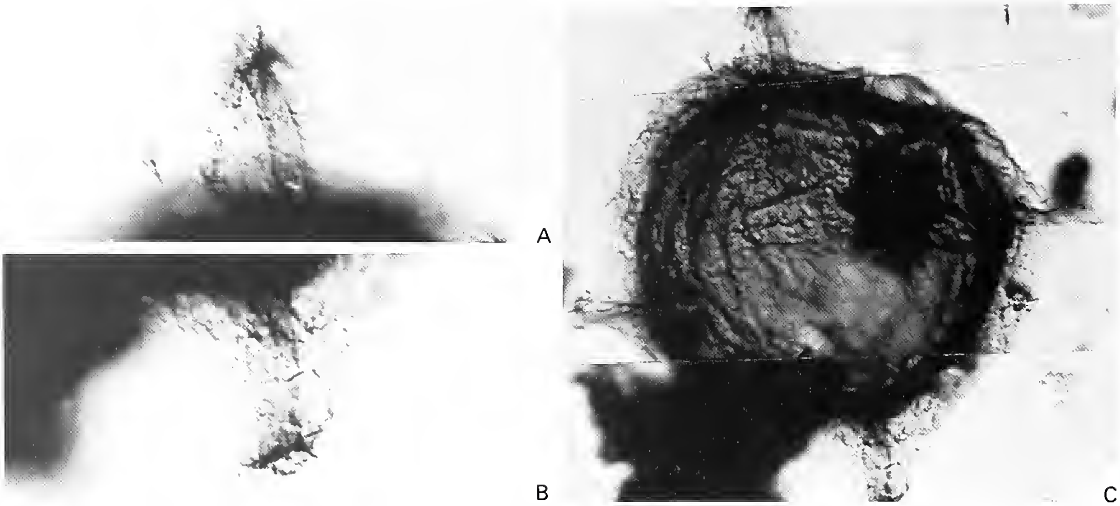
VIDAL *et al.*, *Trachyhystrichosphaera*



TEXT-FIG. 6. *Trachyhystrichosphaera vidalii*. Specimen VNIGRI. 3559/2-u/63; Khastakh 930 Borehole; Upper Riphean (from the Khajpakh Formation); depth 2903·9–2910·0 m. A–B, detailed views of processes and membrane, ×960. C, complete specimen, ×550.

## CONCLUSIONS

Despite repeated study, the biological affinities of the acritarch *C. circularis* and the possibly algal fossil *Tawuia* remain uncertain. A number of hypotheses have been advanced concerning the nature of *C. circularis* and various other related palaeontological and possibly non-biogenic objects. The hypothesis favoured here is that *C. circularis* represents the compressed envelope of a planktic algal protist, possibly a prasinophycean green alga, often reaching macroscopic dimensions (Vidal and Ford 1985). However, the alternative hypothesis of *C. circularis* representing compressed *Nostoc* colonies (Sun 1987) is probably equally plausible. Whether *C. circularis* is in some way (more than by occurrence) related to *T. dalensis* remains uncertain. However, as with other Neoproterozoic acritarchs (Vidal 1990*b*), the possibility remains that *C. circularis* is the reproductive stage (e.g. cyst, aplanospore or zygote) of a thallophyte. While this possibility can neither be proved nor disproved, there is compelling evidence suggesting that metaphytic green and red algae were extant in Neoproterozoic times (Butterfield *et al.* 1988; Zhang 1989; Grant *et al.* 1991; Zhang and Yuan 1992).

The present record of the association of *Chuaria* and *Tawuia* is accompanied by diagnostic acritarchs including the large acanthomorph *T. vidalii*, a time-diagnostic species linking the present assemblage to other dated assemblages in Baltoscandia, the Scandinavian, Greenland and Svalbard Caledonides, China and western North America. The inferred age is Neoproterozoic (late Riphean) and bracketed around 840–700 Ma, which thus predates the Varanger glacial event in all areas of discovery.

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| FOSSIL TAXA | | | | | INFERRED AGE | | ROCK UNIT | AREA |
|---|---|---|---|---|---|---|---|---|
| *Chuaria circularis* | *Tawuia dalensis* | *Trachyhystrichosphaera vidalii* | *Simia annulare* | Vase-shaped microfossils | ISOTOPIC AGE | AGE | | |
| ■ | | | | ■ | 700-800 | L. Riphean | VISINGSÖ GROUP | BALTOSCANDIA |
| | | ■ | | ■ | | L. Riphean | RYSSÖ FORMATION | SVALBARD |
| | ■ | ■ | | | | L. Riphean | KAPP LORD FORMATION | |
| ■ | ■ | | | | | L. Riphean | LITTLE DAL GROUP | N. AMERICA |
| ■ | | | | ■ | 790-845 | L. Riphean | CHUAR GROUP | |
| ■ | | ● | | | | L. Riphean | MIROEDIKHA FORMATION | SIBERIA |
| ■ | ■ | | | | | L. Riphean | KHATYSPYT FORMATION | |
| ■ | | | | | | L. Riphean | MASTAKH FORMATION | |
| ■ | ■ | ■ | ■ | | | L. Riphean | KHAJPAKH FORMATION | |
| ■ | ■ | | | | | L. Riphean | DEBENGDIN FORMATION | |
| ■ | ■ | | | | ~ 740 | L. Riphean | FEISHUI GROUP | N. CHINA |
| ■ | ■ | | | | ~ 840 | L. Riphean | HUINAN GROUP | |
| ■ | | ● | ■ | | > 849 | L. Riphean | KILDIN GROUP | RUSSIA |

TEXT-FIG. 7. Geographical occurrence and stratigraphical range of organic-walled fossils recovered in the investigated Khastakh 930 sequence. Rectangular bars indicate established occurrences. Black circles indicate the occurrence of species probably conspecific with *T. vidalii* in the Kildin Group and the occurrence of *Trachyhystrichosphaera stricta* (probably a junior synonym of *T. vidalii*) in the Miroedikha Formation. Isotopic dates indicate bracketed ages in million years.

our initial manuscript was substantially improved by the constructive criticisms of anonymous reviewers and by suggestions provided by Dr Christopher J. Cleal.

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# CONULARIID MICROFOSSILS FROM THE SILURIAN LOWER VISBY BEDS OF GOTLAND, SWEDEN

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Abstract. A conulariid fauna from the Lower Visby Beds (uppermost Llandovery–lowermost Wenlock) is described, based on microscopic exoskeletal parts found in limestones and marls prepared using standard laboratory techniques for phosphatic fossils. Although not a single complete conulariid specimen has ever been found in the unit, conulariids were evidently abundant during the deposition of the Lower Visby Beds, as inferred from the microscopic fragments. So far, five species have been identified: *Conularia sarae* sp. nov., *C. wimani* sp. nov., *C.* sp. a, *Metaconularia aspersa*, and *Pseudoconularia* aff. *scalaris*. The microscopic fragments exhibit considerable external morphological variation. They can be sorted into four discernible morphological groups, and their position in the exoskeleton can be identified. Thus, more or less complete reconstructions of the exoskeletons have been made on species unknown prior to this investigation. Characters used in species descriptions based on intact specimens are summarized and compared with characters used for microscopic fragments. The conclusion is that the general ornamentation of the exoskeleton is the most useful character in species descriptions. Moreover, microscopic fragments are not only as easily identifiable as intact specimens, but due to the fact that a larger quantity of material is obtainable, the study of microscopic fragments also gives a far better picture of the individual variation, ontogenetic development, geographical range and the stratigraphical range of conulariid species. Finally, some existing morphological terminology is modified and some new terms are introduced.

Conulariids are an extinct group of marine invertebrates with a four-sided, apatitic, steeply pyramidal exoskeleton. The group has been assigned to a range of different phyla, e.g. Mollusca (e.g. Lindström 1884; Holm 1893; Slater 1907), Cnidaria (e.g. Kiderlen 1937; Moore and Harrington 1956*a*; Werner 1966, 1967, 1973; Bischoff 1978; Van Iten 1991*a*) and Chordata (Steul 1984). Babcock and Feldmann (1986*a*, 1986*b*) proposed placing conulariids in an independent phylum. This general inconsistency of conulariid systematic placement depends mainly on the morphological uniqueness of the conulariid exoskeleton which lacks distinct common characters with other groups.

Though many important papers have been published on conulariids, the group has been largely neglected compared with other Palaeozoic invertebrates. Their range is somewhat uncertain but was previously regarded as Middle Cambrian to Lower Triassic (Moore and Harrington 1956*b*). A better-supported stratigraphical range, Lower Ordovician to Lower Triassic, was presented by Babcock (1991). Conulariid-like fossils have also been reported from the earliest Cambrian of Yunnan Province, South China (Qian Yi and Bengtson 1989). Only a few papers, including Lindström (1884), Holm (1893), Wiman (1895), Slater (1907), Bouček (1928) and Bischoff (1978), have dealt with Silurian conulariids.

The general opinion that conulariids are rare fossils is mainly because nearly all studies are based on intact specimens. Except for a few localities e.g. in the Devonian of Bolivia (Babcock *et al.* 1987*a*, 1987*b*), and in some late Ordovician beds in the USA (Van Iten 1991*b*), intact specimens are often a curiosity. Accordingly, it has been very difficult to map the stratigraphical and geographical occurrences of most taxa. The rarity of intact conulariids is caused by the extremely fragile nature of their exoskeletons which broke down shortly after the death of the animal (Babcock and

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Feldmann 1986*c*; Feldmann and Babcock 1986). The exoskeletal fragments were then scattered over the bottom by currents, wave oscillation and bioturbation. Thus, intact conulariid exoskeletons are, with a few known exceptions (see, for example, Van Iten 1991*b*), normally found only in units that record exceptional preservational circumstances (Babcock and Feldmann 1986*a*; Feldmann and Babcock 1986). Furthermore, collections of intact specimens are strongly biased towards those genera and species that had the most robust exoskeletons. However, microscopical exoskeletal fragments are preserved in many strata, often in very large numbers. For example, in the Lower Visby Beds on Gotland no complete conulariid specimens have ever been recorded, although conulariid fragments are abundant in the microfossil fauna. The present study is based on about 10000 microscopic exoskeletal fragments.

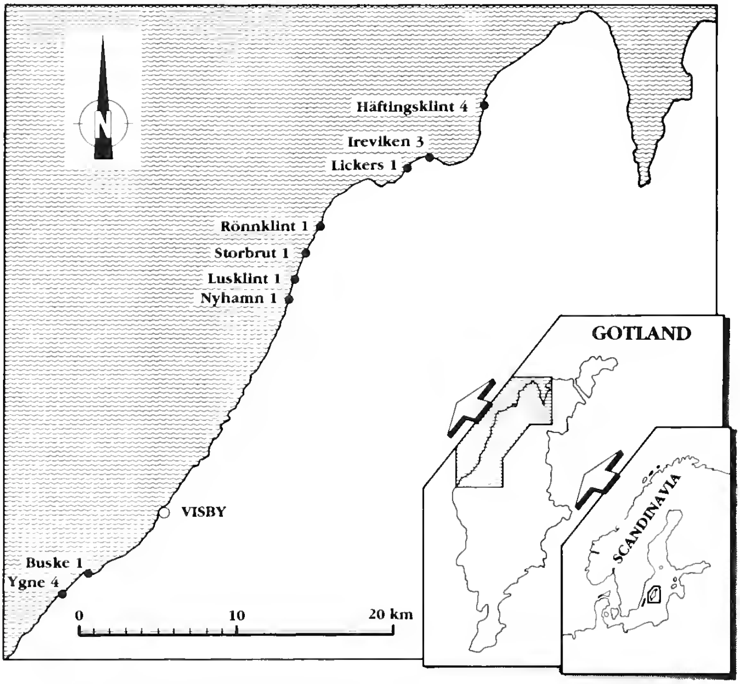
Conulariids were extracted from marls and various limestones using the same laboratory techniques as for conodonts, fish scales, polychaetes, secondarily phosphatized fossils, etc. These methods have also been applied in the study of conulariids by Bischoff (1973, 1978) and Brood (1979).

In this paper, no attempt is made to solve higher taxonomic relationships, nor are the biological affinities of conulariids discussed. Such discussions may be found in works by, among others, Slater (1907), Kiderlen (1937), Moore and Harrington (1956*a*), Werner (1966, 1967, 1973), Kozłowski (1968), Bischoff (1978), Steul (1984), Babcock and Feldmann (1986*a*), Babcock (1991) and Van Iten (1991*a*).

## GEOLOGICAL SETTING

The Silurian of Gotland exhibits a complex variety of shallow marine, mainly carbonate, deposits formed in a tropical environment. The strata were mapped by Hede (for a brief English summary, see Hede 1960), who recognized thirteen major units. The various lithologies found on the island include biohermal limestone, stratified limestone, marlstone, oolite and siltstone (see Hede 1921, 1925, 1940; Laufeld 1974*a*).

The Lower Visby Beds are the oldest exposed unit found on Gotland, outcropping along the northwest coast in a 55 km long narrow strip (Text-fig. 1). The lithologies consist of alternating calcareous marlstones and



TEXT-FIG. 1. Map of the north-western part of Gotland showing the sampled localities.

argillaceous limestones (Hede 1921, 1925, 1940, 1960; Laufeld 1974*a*; Sandford and Moscher 1985). The thickness of the sampled sequence is about 20 m at Ireviken 3, including samples collected in submarine exposures (L. Jeppsson, pers. comm.).

A detailed conodont stratigraphy has made it possible to subdivide the Lower Visby Beds into units *a* to *e*, where unit *a* reaches above sea level in a small area only (L. Jeppsson, pers. comm.). Three well-defined bentonite horizons are present in the formation (Spjeldnaes 1959). The uppermost bentonite (about 10 cm thick) has been dated using K-Ar at 430,5 ± 3,0 Ma (Odin *et al.* 1986). The Lower Visby Beds belong to the *Pterospathodus amorphognathoides* conodont zone (Jeppsson 1983, 1987*a*; Odin *et al.* 1984). At the type locality for the base of the Wenlock, this zone spans the Llandovery–Wenlock boundary (Aldridge 1975). Thus, the boundary between Llandovery and Wenlock is to be drawn within the Lower Visby Beds, probably in the upper part (Jeppsson 1983; Odin *et al.* 1984).

The boundary between the Lower Visby Beds and the Upper Visby Beds was defined by differences in the macrofauna by Hede (1925). According to Laufeld (1974*a*) the boundary cannot be defined on lithology because the changes are gradual. However, Jeppsson (1983) has noted that the marls in the units weather differently: the Lower Visby Beds produce a sticky clay whereas the Upper Visby Beds weather to dust.

## LOCALITIES AND METHODS

### *Localities*

A total of 43 samples, weighing 291·8 kg, were collected from nine localities (Text-fig. 1). Three additional samples (25·5 kg) from the Upper Visby Beds were also briefly studied. All samples have been productive, i.e. no sample has been found to be barren of conulariids.

In addition to the Lower Visby Beds, many of the following localities expose the Upper Visby Beds and Högklint Beds. Only the studied Lower Visby Beds (abbreviated L.V.B.) are mentioned. References marked with an asterisk (*) contain a more complete description of the locality. After each sample number the total weight of dissolved rock, and the exact sample-level is listed. The sample-levels are given 'above reference level' (a.r.l.) or 'below reference level' (b.r.l.). All samples are listed in stratigraphical order. The conodont faunas in the samples will be described in a forthcoming paper by Lennart Jeppsson. The sampled localities are shown in Text-figure 1.

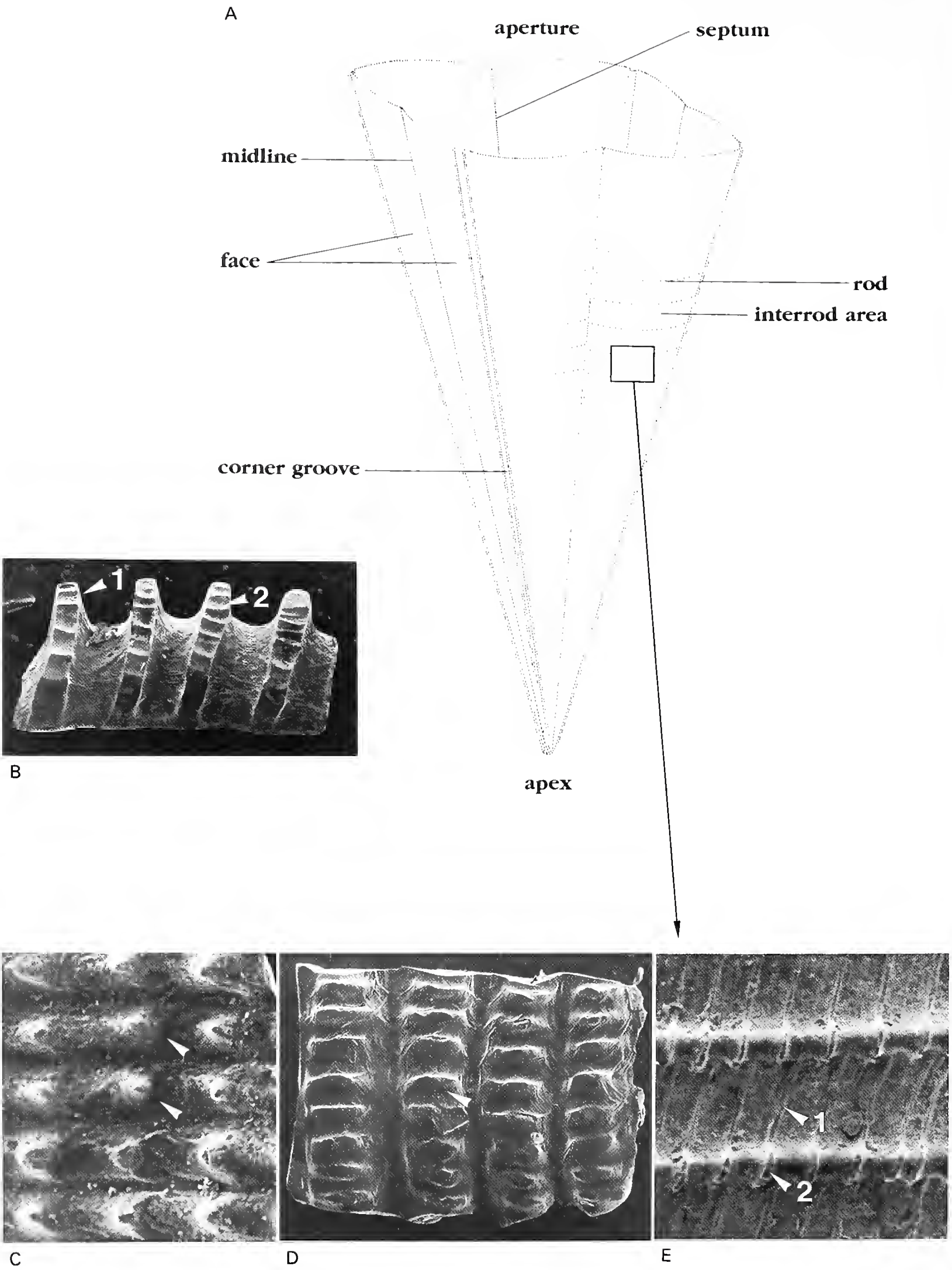
BUSKE 1. L.V.B. unit *e* (and unit *d* in the submarine part of the exposure). References: Laufeld 1974*a*, 1974*b**; Larsson 1979; Odin *et al.* 1984. The reference level described by Laufeld (1974*b*) is imprecise, therefore an auxiliary reference level has been selected: the best visible bentonite horizon about 1·2 m below the level abundant in large, solitary rugose corals. Sample: Unit *d*: G88-804FJ (12·5 kg), 2·36–2·31 m below auxiliary reference level.

HÄFTINGSKLINT 4. L.V.B. unit *d*–*e* (unit *c* in submarine exposure). References: Hede 1933; Bergman 1989; Fredholm 1990; Jeppsson in prep.* Samples: Unit *c*: G84-38LJ (4·2 kg), 0·75 m below sea level. Unit *d*: G84-39LJ (8·5 kg), 0·05–0·00 m below sea level, G88-625LJ (6·7 kg), 0·58–0·62 m above sea level.

IREVIKEN 3. L.V.B. unit *b*–*e* (unit *a* in submarine exposure). References: Laufeld 1974*a*, 1974*b**; Larsson 1979; Odin *et al.* 1984*, 1986; Bergman 1989. Samples: Unit *a*: G86-129LJ (5·3 kg), 15·38 m b.r.l. Unit *b*: G85-37LJ (3·7 kg), 1·95–2·05 b.r.l.; G82-1LJ (0·6 kg), 0·15–0·08 m b.r.l.; G88-802FJ (20·3 kg), 0–0·12 m b.r.l.; G82-2LJ (0·5 kg), 0·02–0·15 m a.r.l.; G88-803FJ (13·4 kg), 0·69–0·87 m a.r.l.; G82-3LJ (0·5 kg), 0·85–0·90 m a.r.l. Unit *c*: G81-5LJ (0·6 kg), 1·10 m a.r.l.; G82-6LJ (0·6 kg), 2·16–2·26 m a.r.l.; G82-6LJ (4·3 kg), 2·36–2·46 m a.r.l.; G85-36aLJ (10·7 kg), 2·36–2·46 m a.r.l. Unit *d*: G89-723LJ (16·2 kg), 2·89–2·94 m a.r.l.; G89-725LJ (13·8 kg), 3·53–3·61 m a.r.l.; G89-722LJ (11·0 kg), 4·11–4·15 m a.r.l. Unit *e*: G86-145LJ (5.0 kg), 4·27 m a.r.l.

LICKERS 1. L.V.B. unit *b*–*c*. Reference: Bergman 1989*. Sample: Unit *b*: G81-10LJ (0·5 kg), 0·1 m above sea level.

LUSKLINT 1. L.V.B. unit *b*–*e* (unit *a* in submarine exposure). Reference: Jeppsson in prep.* Samples: Unit *a*: G88-613LJ (9·4 kg), 8·98–8·83 m b.r.l.; G89-715LJ (5·4 kg), 8·56 m b.r.l.; G89-716LJ (4·4 kg), 8·28 m b.r.l. Unit *b*: G89-701LJ (7·7 kg), 7·68–7·58 m b.r.l.; G89-702LJ (6·2 kg), 7·18–7·13 m b.r.l.; G89-703LJ (4·8 kg), 6·48–6·33 m b.r.l.; G89-704LJ (7·4 kg), 5·91–5·76 m b.r.l.; G89-705LJ (6·3 kg), 5·26–5·09 m b.r.l.; G89-706LJ (6·2 kg), 4·67–4·63 m b.r.l.; G89-707LJ (6·1 kg), 3·97–3·82 m b.r.l.; G89-708LJ (6·8 kg), 3·45–3·33 m b.r.l.; G89-709LJ (11·7 kg), 2·75–2·70 m b.r.l.; G89-710LJ (5·6 kg), 2·10–1·97 m b.r.l.; G89-711LJ (2·8 kg), 1·50–1·35 m b.r.l.; G89-712LJ (4·3 kg), 1·08–0·97 m b.r.l.; G89-713LJ (9·6 kg), 0·53–0·43 m b.r.l.; G89-714LJ (6·5 kg), 0·26–0·15 m b.r.l.


A
aperture
septum
midline
face
rod
interrod area
corner groove
apex
B
1
2
C
D
E
1
2

NYHAMN 1. L.V.B. unit *b*. References: Hede 1940; Martinsson 1962; Laufeld 1974*a*, 1974*b**; Larsson 1979; Bergman 1989. Sample: unit *b*: G81-28LJ (0·5 kg), 1·4 m above sea level.

RÖNNKLINT 1. L.V.B. unit *b–e*. References: Jeppsson 1983*; Ramsköld 1984; Fredholm 1990. Sample: Unit *b*: G81-11LJ (0·5 kg), at sea level.

STORBRUT 1. L.V.B. unit *b–e*. Reference: Jeppsson in prep.* Samples: Unit *b*: G88-810FJ (9·8 kg), 0·00–0·12 m b.r.l. Unit *c*: G88-633LJ (14·0 kg), 1·42–1·54 m a.r.l. Unit *d*: G88-632LJ (11·2 kg), 2·62–2·65 m a.r.l.

YGNE 4. L.V.B. unit *d–e* (unit *c* in submarine exposure). Reference: Jeppsson in prep.* Sample: Unit *e*: G85-6bLJ (5·7 kg), 1·58–1·60 m a.r.l.

### *Methods*

Samples of between 0·5 and 20 kg were dissolved in buffered acid generally following the recommendations given by Jeppsson *et al.* (1985), although the methods have been modified and improved and new methods have been developed since the publication of that article. Petroleum–ether treatment and other methods were used to disintegrate the clay (see Pokorny 1963; Swift 1987). Other methods to reduce the residues included magnetic separation to remove iron-rich minerals as pyrite, and treatment with high density solutions to concentrate the phosphatic material. In pyrite-rich samples it is often necessary to oxidize the $Fe^{2+}$ in the pyrite to $Fe^{3+}$ prior to magnetic separation to attain satisfactory results. This was done by soaking the sample residue in natriumhypoklorite for a maximum of one week, although it is desirable to expose the sample in the solution for as short a time as possible to avoid damage of the fossil surfaces and to avoid undesirable red staining of the fossils. The insoluble residues were washed through a 1·0 mm and a 63 $\mu$m sieve. All fractions above 63 $\mu$m were stored for future reference. The samples were originally prepared to obtain conodonts; the only technique used specifically to obtain the conulariid material was picking fragments from dried residues. The picking-technique was described by Barnes *et al.* (1987). The identifiable parts of the conulariid fragments are generally larger than 125 $\mu$m. In those cases where conulariids were not extracted at the same time as conodonts, a sieve with a 125 $\mu$m mesh was used to reduce picking time.

For a more detailed description of methodology see Jeppsson *et al.* (1985), Jeppsson and Fredholm (1987), Jeppsson (1987*b*), Fredholm (1988), Bergman (1989) and references given in these papers.

## TERMINOLOGY

An understanding of conulariid morphology has often been confounded by the use of poorly-defined terms or multiple meanings for the same term. A modern morphological terminology has recently been introduced by Babcock and Feldmann (1986*a*, 1986*b*). The terminology presented by these authors is based on the assumption that the conulariid exoskeleton is made of two discrete components: rods and integument. There is insufficient evidence either presented by these authors or present in my material to verify this construction. The terms introduced by Babcock and Feldmann are, however, in most cases well chosen and function well as purely descriptive terms. Therefore the terms used here are to a large extent the same as those defined by Babcock and Feldmann.

The definitions of some of the terms listed below have been slightly modified based on more complete information from the study of microscopic exoskeletal parts. It has also been necessary to introduce some new terms for features found on microscopic parts. These, and other mentioned terms, are illustrated in Text-figure 2.

*corner groove* — longitudinal invagination of exoskeleton connecting points where pairs of rods from adjacent faces cross near the marginal terminations of these rods

TEXT-FIG. 2. Schematic drawing of a conulariid to illustrate terms mentioned in the text. A, previously described terms used on intact specimens (see Babcock and Feldmann 1986*a*, 1986*b*). B, rod from *Conularia sarae*; LO 4575t, sample G88-708LJ; in adapical view possessing four rod-crests with serration (arrow 1 points to a rod-crest; arrow 2 points to the serration). C, exoskeletal fragment from *Metaconularia aspersa* with nodes (same specimen as in Pl. 4, fig. 7); LO 4576t. D, exoskeletal fragment from *Pseudoconularia* aff. *scalaris*; LO 4930t; possessing four parallel ridges with tightly spaced, elongate nodes (one is arrowed). E, details from a larger exoskeletal fragment from *C. sarae*; the holotype, LO 4931T (same specimen as in Pl. 2, figs 3–5); with two rods, rod-crests and adapertural crests (arrow 1 points to an adapertural crest; arrow 2 points to a rod-crest); the aperture is upwards in the picture; note the serration on the adapical sides of the rod-crests.

*face* — one of four sides of the exoskeleton crossed by rods; a face is delimited by the aperture, the apex and two corner grooves
*interrod area* — open region located between two rods
*midline* — longitudinal line connecting points where either two adjacent rods on a face meet, or central to the facial terminations of each pair of adjacent rods if they do not meet; the midline can be expressed as either a thin groove, a raised line or simply a narrow, unornamented longitudinal line
*node* (modified term) — minute, subcircular to elongated, raised surface on a rod, ridge or directly on the mineralized, exoskeletal surface
*ridge* (modified term) — coarse, raised line crossing a face from corner groove to the midline; the cross section is rectangular to circular (see Pl. 4, fig. 3), sometimes also more or less triangular; differs from a rod in being a more massive structure, and in lacking rod crests.
*rod* — narrow, elongated structure that is semicircular in cross section; it is thickened near the marginal termination, and tapers very gradually to a blunt point at the facial termination

*New or replaced terms.* Terms that should be abandoned were summarized by Babcock and Feldmann (1986*b*). However, there are two terms defined by Babcock and Feldmann (1986*a*, 1986*b*) that should be changed to avoid unnecessary confusion — the terms are adapertural spine and adapical spine. The structures in question are not consistent with what is generally understood by the word spine. Instead, they are more like short ridges, or crests, pointing in an adapical or adapertural direction. Accordingly, it is proposed that these terms be replaced as follows: adapertural spine is changed to adapertural crest, and adapical spine to adapical crest.

The term septum was also abandoned by Babcock and Feldmann (1986*b*) because of its previous application for at least three different structures. It has been used for longitudinal walls interior of the midlines and the corner grooves (Wiman 1895; Kiderlen 1937), and for a convex wall found on the apical point of the exoskeleton (Slater 1907). Later, Babcock *et al.* (1987*a*) used the term carina for a longitudinal wall on the interior side of the midline. The term carina was also used by Bischoff (1978), but he restricted the term to longitudinal walls interior of the corner grooves. Septa was applied to longitudinal walls interior of the midline. Accordingly, it is recommended that carina is restricted to longitudinal walls interior of the corner grooves and septum to longitudinal walls of different shape and structure (see Bischoff 1978, p. 284) interior of the midline.
*adapertural crest* — crest projecting from, or near, the adapertural side of a rod, in the direction of the aperture
*adapical crest* — crest projecting from the side of a rod, in the direction of the apex
*carinae* — longitudinal wall extending inward from the corner groove, crossing the interior side of a corner from apex to aperture
*node-width* — the width of a node measured at its base; the diameter measured on a subcircular node
*ridge-width* — the width of a ridge measured at its base
*rod-crest* — raised line crossing a rod, usually at a right angle; continuing into the interrod areas as an adapertural or adapical crest
*rod-width* — the width of a rod measured at its base
*septum* — longitudinal wall of different shape and structure (see Bischoff 1978, p. 284), extending inward from the midline, crossing the interior side of a face from apex towards the aperture
*serra* — serration found on the adapical side of a rod-crest

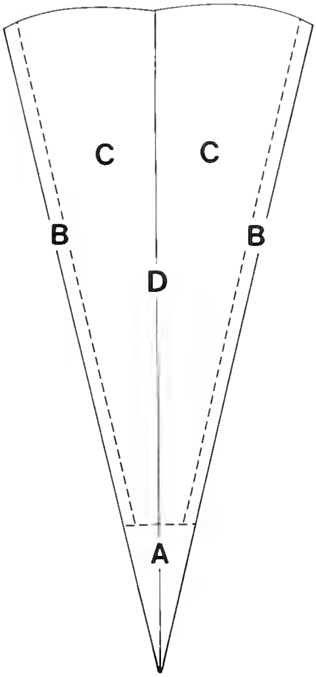
## CONULARIIDS AS MICROFOSSILS

Many fossil groups are difficult or nearly impossible to find as complete specimens. One reason is the lack of preserved soft parts in combination with poorly mineralized endo- and/or exoskeletons such as in conodonts, polychaetes and neoselachians. Another reason is the fragility of the exoskeletons of such animals as crinoids, echinoderms, fish and conulariids. All of these groups require extreme sedimentary environments, with the proper taphonomic conditions, to be preserved as intact fossils. Many species associated with high, or even moderate, energy environments will probably never be found as complete specimens. Thus, it is often necessary to include fragmentary specimens in a study in order to get a complete picture of the fauna.

As noted by previous authors (Kozłowski 1968; Bischoff 1973, 1978; Brood 1979; Babcock and Feldmann 1986*b*; Feldmann and Babcock 1986), conulariid fragments are usually found in rock units sampled for microfossils by insoluble residue techniques. I am convinced that most samples collected for conodonts, or other phosphatic or phosphatized fossils, and treated accordingly, contain conulariid fragments. Diagnostic features can be obtained from these fragmentary specimens alone, although restudy of taxa based on intact specimens usually is needed to supplement the descriptions of these taxa. This must be done in order to avoid the introduction of a parallel nomenclature, or parataxonomy, based only on microscopic characters. A total of seventy-four intact specimens (housed in the Swedish Museum of Natural History, Stockholm) from younger strata on Gotland have been studied and compared with the microscopic fragments. The exoskeletal surfaces on these more or less intact specimens are mostly in a poor state of preservation, leaving only limited information on the original ornamentation. The poor preservation could be the result of taphonomic processes, although I suspect rough preparation techniques. Consequently, the material on which this study is based reveals details of the morphology which are possibly overlooked in studies based on intact specimens only.

The Lower Visby Beds represent a moderately bioturbated (Riding and Watts 1991) sedimentary sequence unfavourable for preserving fragile conulariids intact. Though no complete conulariid specimen has yet been found in the formation, conulariids were evidently abundant during the deposition of the Lower Visby Beds. Studied samples have revealed conulariid fragments at an average of about 30 identifiable pieces per kg of dissolved rock. The lower part of the collected section (unit *a*) contains even higher frequencies, up to about 200 identifiable pieces per kg. The material consists of single rods of different lengths and larger exoskeletal pieces containing several parallel rods attached to the mineralized interrod areas. The exoskeletal pieces found represent all parts of an intact specimen, except for the apex, the reasons for which are unknown. Such fragments occur, however, in my collections from younger strata on Gotland.

There are roughly four morphologically distinguishable types of exoskeletal fragments located in different positions on a face (Text-fig. 3). These fragments are as follows:



TEXT-FIG. 3. Schematic drawing of a single conulariid face. See text for explanation.

A. larger exoskeletal parts with rods connected vertically by mineralized interrod areas. These large mineralized exoskeletal fragments were probably located near the apex, reaching an unknown distance adaperaturally (Text-fig. 3). The position of the dotted line in Text-figure 3, which delimits the area where fragments of this kind are found, probably depends both on ontogeny and species. The drawing is based on *Conularia sarae* sp. nov.

B. coarse, slightly curved rods. These rods are sometimes found connected with mineralized interrod areas, but these are generally broken and not preserved. Rods in this position form the longitudinal 'channel' of the corner groove. The morphological characters found on these rods are mostly poor species indicators, and should not be used alone for species-level identification. Species within a genus often possess strikingly similar rods in this position (compare Pl. 1, figs 2, 5 with Pl. 3, figs 5–6).

C. exoskeletal fragments in this position are mostly found as single rods with no longitudinal connection between them in the interrod areas. In a few pieces where small parts of mineralized interrod areas occur, the interrod areas are connected with the rods on the adapertural side only.

D. exoskeletal fragments formed on or in connection with the midline. The material generally consists of exoskeletal fragments with adjacent rods meeting along either a thin groove, or simply a narrow, unornamented longitudinal line. These fragments usually occur in low frequencies in the samples but are of great value when comparing microscopic fragments with complete specimens. The manner in which rods 'articulate' along the midline has been used as a diagnostic feature at the species level (Babcock and Feldmann 1986*a*, 1986*b*).

Together these four different 'types' of exoskeletal pieces represent most of the characters found on a complete conulariid specimen. Intermediate forms between these types are often found. Samples usually contain fairly large numbers of intermediate rods in the transition between positions B and C. Typically in these rods, the rod-crests are incompletely developed in shape and height close to position B, whereas in position C they are mostly well developed and long. Also obvious is the transition, when moving from corner groove horizontally towards the midline, from short rod-crests to rods that gradually possess long rod-crests. It is most likely that intermediate forms also occur between positions A and D, represented by pieces formed in connection with the midline. Thus the dotted line in Text-figure 3 should probably consist of two convex (adapically) lines connected with the midline and ending in the corner grooves.

There are also conulariids that lack rods in their exoskeletons (conulariids with nodes in the ornamentation) and these cannot be placed within the morphological types described above; they are described in detail below.

*Diagnostic characters.* Through the history of conulariid research, different morphological characters have been considered important in characterizing species. In early publications, authors often used the relative number of rods and ridges together with rod characteristics, as distinguishing features (e.g. Holm 1893). Holm (1893) partly based his four groups of conulariid species on rod construction. Sinclair (1952) described new species and genera using the structure of the corner grooves in addition to previously used characters. He stated that the ornamented surface of the exoskeleton was a diagnostic feature of minor use. The way in which rods articulate along the midline was used as an important character by Babcock and Feldmann (1986*a*, 1986*b*). They found four different rod articulation styles useful for species-level determinations. Babcock and Feldmann (1986*a*, 1986*b*) and Babcock *et al.* (1987*a*, 1987*b*) used the following characters to distinguish different conulariid genera and species: (1) relative spacing of rods; (2) relative proportion of rods that abut at the midline to those that alternate; (3) apical angles; (4) presence or absence of nodes and spines; and (5) spacing of nodes and spines. The relative spacing of rods should not be interpreted as a measure of the number of rods on a fixed length interval, but as the rod-width in proportion to the length of the interrod areas. This is important to remember because close to the apex the number of rods per cm is often greater than close to the aperture.

The lengths of the adapertural crests or the adapical crests are usually useful characters for specific identification. To recognize and separate these characters in fragmented material, the direction of the aperture must be identified. This is generally possible if large exoskeletal pieces (with at least four parallel rods) are available, because rods generally become wider in the apertural direction and thinner near the apex. If only single rods, or even single rod-crests, are present, their symmetry can be used. Rods with nodes and rod-crests are together regularly asymmetrical in cross-section. The species of *Conularia* studied have rods with cross-sections shaped roughly like a breaking oscillatory wave, with the rod-crests forming the wave crest. The 'wave crest' points in the direction of the apex (Pl. 2, fig. 5). In *Metaconularia* the exoskeletal ornamentation sometimes includes almost symmetrical transverse and longitudinal rows of regularly arranged nodes. It is thus difficult to determine the apertural direction, from the four different directions that are possible, based on exoskeletal fragments only. Sometimes, however, the transverse rows can be identified because the nodes may occur with a regular spacing whereas longitudinal rows lack any regularity in spacing of the nodes. Thus, two of the four hypothetical directions of the aperture can be excluded.

When using microscopic exoskeletal fragments, all characters mentioned above were used. In addition, many other characters are present which often are neglected, or at least rarely mentioned, in the study of macroscopic specimens. I have found that the following observations preferably should be included in species-level identifications: (1) presence of rods and ridges on the exoskeleton; (2) general shape of rods and ridges; (3) presence of rod-crests and nodes; (4) general shape of rod-crests and nodes; (5) structures found on the interrod areas (mainly adapertural and adapical crests); (6) length of adapertural crests; (7) character of the midline; and (8) rod articulation along the midline. Additional characters that could be useful for identification are: the width of rod-crest, the relative spacing of rod-crests and nodes, rod- and ridge-width, and the relative spacing of rods and ridges.

Apical angle is a character of minor use when identifying species on fragmented material because most conulariids show allometric growth. The apices represent the juvenile parts of the conulariid and the apical angle of a juvenile can differ substantially from that of an adult.

It is desirable, though not always possible, for a full description to have most of these characters represented for each species. However, it is possible to identify species on as little as a single rod-crest. This is especially important when conulariids are abundant but fragmented, which is commonly the case.

## COMMENTS ON QUANTIFICATION AND STRATIGRAPHICAL DISTRIBUTION

*Quantification.* Quantifying material of this kind presents problems. The easiest thing to count would be the number of pieces. However, the number of exoskeletal pieces per kg sample does not give accurate information on the actual number of whole conulariids represented in the sample. The number of pieces will depend on various taphonomic factors, including the degree of bioturbation, the rate of sedimentation and current strength.

The minimum number of conulariid specimens per kg of sample could be theoretically estimated by calculating the total area of hardpart-surface on a complete conulariid. This value could then be compared with the total area of hardpart-surface obtained from the exoskeletal pieces. However, this method is unreliable since the area of the hardpart-surface varies among different species, and among specimens of various ontogenetic stages and those that lived in different environments.

Because of the many difficulties inherent in the calculation described above, only rough estimates of the conulariid frequency per kg are recorded here. The intervals used to express this relative frequency are: very common, common, rare, and absent. This calculation is not a measure of the number of pieces per kg of sample but an estimate of how frequent a species is in relation to other species in the fauna.

*Stratigraphical distribution.* Conulariids are abundant throughout the Lower Visby Beds but their frequency generally diminishes upward.

Unit *a*, uppermost 8 m collected, 4 samples from 2 localities, together 24·5 kg produced over 2000 pieces.
Unit *b*, thickness about 9 m, 25 samples from 6 localities, together 142·3 kg produced about 5000 pieces.
Unit *c*, thickness about 1·4 m, 6 samples from 3 localities, together 34·4 kg produced about 1000 pieces.
Unit *d*, thickness about 1·8 m, 6 samples from 4 localities, together 67·5 kg produced about 1000 pieces.
Unit *e*, thickness about 1·3 m, 3 samples from 2 localities, together 23·2 kg produced about 500 pieces.

Three samples from the overlying Upper Visby Beds have also been briefly examined to confirm if some of the species cross the boundary between Lower and Upper Visby Beds. The samples are from Ireviken 3. Together the samples have a weight of 25·5 kg and contained about 100 pieces.

*Conularia sarae* is very common in unit *a*, common in the other units, and also continues into the Upper Visby Beds. All 44 studied samples contained this species. *Conularia wimani* is rare in units *a*, *b* and *e*; absent in units *c* and *d* and unknown from the Upper Visby Beds. *Conularia* sp. a is common in unit *a* and rare in the other units. This species has not been found in the Upper Visby Beds. *Metaconularia aspersa* is rare throughout the Lower Visby Beds and crosses the boundary with the Upper Visby Beds. *Pseudoconularia* aff. *scalaris* has only been found in one sample in unit *d*.

## SYSTEMATIC PALAEONTOLOGY

Holotypes have been selected which show the maximum number of species-specific characters. In practice this generally means that the holotypes are disarticulated specimens with ornamentation representing the adult part of the exoskeleton.

### Genus CONULARIA Sowerby, 1821

*Type species. Conularia quadrisulcata* Sowerby, 1821.

*Remarks.* The most recent description on the generic concept is by Babcock (*in* Babcock *et al.* 1990) and is as follows: The genus is characterized by a thick exoskeleton with coarse, often closely spaced (9–84 per cm), transverse rods. Fewer than 60 per cent of the rods alternate at the midline; more than 40 per cent abut. Nodes, rod-crest, and often wide adapertural crest, with or without adapical crests, may be present and closely spaced (usually 1–10 per mm).

In addition, the midline is not marked by a raised line or groove and, according to, for example, Babcock (1991) and Van Iten (1991*a*), some species have low septa, a character that has not been observed among the *Conularia* present in my material.

### *Conularia sarae* sp. nov.

Plate 1, figs 1–8; Plate 2, figs 1–5; Text-fig. 2B

?1978 Conodont supporting elements, Bischoff, pp. 149–151, pl. 1, fig. 8.

*Derivation of name.* Named in honour of my daughter Sara.

*Types.* Holotype: LO 4931T. Paratypes: LO 6410t, and LO 6415t.

*Type locality.* Lusklint 1. Lower Visby Beds unit *a*. The holotype is from sample G88-613LJ, 8·98–8·83 m b.r.l.

*Material.* More than 5000 exoskeletal fragments.

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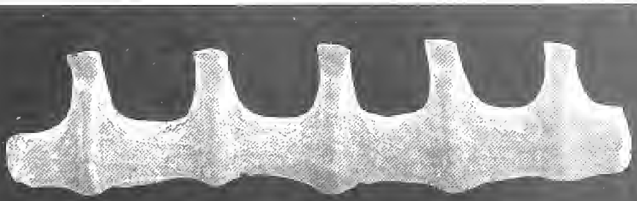
EXPLANATION OF PLATE 1

Figs 1–8, *Conularia sarae* sp. nov. 1–2, paratype, LO 6410t; Lusklint 1, sample G88-708LJ; 1, rod with rod-crests in adapertural view formed in position C, × 75; 2, detail of the middle rod-crest, × 150. 3, rod with rod-crests in adapertural view, formed in position B; LO 6411t; Ireviken 3, sample G85-36aLJ, × 75. 4, rod and rod-crest in cross-section, formed in position B; LO 6412t; Häftingsklint 4, sample G88-625LJ, × 150. 5, rod and rod-crest in cross-section, formed in position C; LO 6412t; Lusklint 1, sample G88-613LJ, × 150. 6, rod with serrated rod-crests in adapical view, formed in position B; LO 6413t; Lusklint 1, sample G88-613LJ, × 120. 7–8, LO 6414t; Lusklint 1; 7, rod with rod-crests in adapical view, formed in position C, × 75; 8, detail of the middle rod-crest; note the striation on the left side of the rod-crest, × 150.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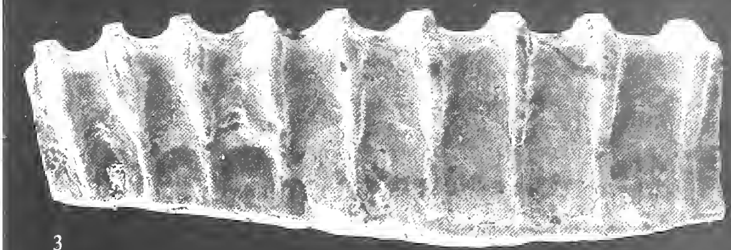
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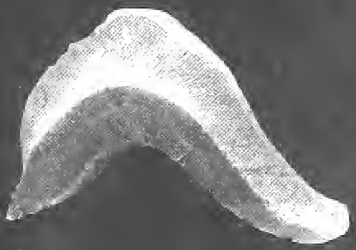
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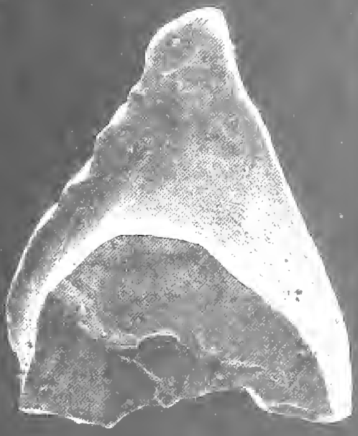
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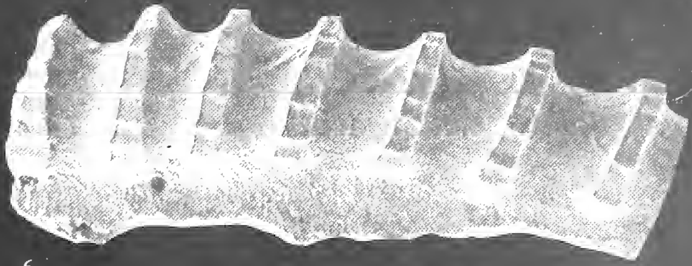
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JERRE, *Conularia*

*Diagnosis. Conularia* with rods possessing long rod-crests in the upper part of the exoskeleton and short ones in the lower part and near the corner grooves. Rods alternate at midline (90%). Rods and rod-crests tightly spaced. Rod-crests are serrated on the adapical sides. Adapertural crests are connected to the rod-crests, crossing the interrod areas, connecting rods longitudinally.

*Description.* The exoskeleton is fairly coarse with distinct rods crossing the face transversally. When the exoskeleton is seen in longitudinal cross section, the rods form a high relief, wave-like pattern (Pl. 2, fig. 5). The rods are more or less symmetrical with a roughly semicircular cross-section (Pl. 1, figs 4–5). Rod spacing is about 80 rods per cm near the apex and wider adaperturally (about 50(?) rods per cm). Both long and short rod-crests are present. The rod-crests have a more or less distinct serration on the adapical side (Pl. 1, figs 6–8; Pl. 2, fig. 4). There are an average of 2–4 crest-widths in the space between two rod-crests. The rod-crests are tightly spaced (8–18 per mm). Adapertural crests are present and they run completely across the interrod areas (Pl. 2, figs 2–5). The rod-crests are fused with the adapertural crests, forming a continuous structure. The midline is visible as an interruption of the rods and sometimes also as a shallow groove or channel (Pl. 2, figs 1–2). The rods alternate irregularly at the midline and the blunt rod-ends sometimes cross the middle. Rods that abut at the midline have also been found, but this is rare (less than 10 per cent?). Rod pattern along the midline cannot with certainty be assigned to any of those described by Babcock and Feldmann (1986*a*, 1986*b*).

Four different types of exoskeletal fragments are present (see explanation above). Pieces that have been formed in position A (i.e. the apical part) are present in most samples. These are found as larger exoskeletal fragments with rods connected by mineralized interrod areas, and reveal a gradual development from short rod-crests near the corner groove, to longer more or less blunt ones towards the midline (see Pl. 2, figs 2–5).

Rods from position B (i.e. fragments of the corner grooves) are represented by coarser and strongly curved rods present in fairly large amounts in the samples (these coarser rods could probably better withstand physical breakdown) (Pl. 1, figs 3–4, 6). These rods have been formed in connection with the corner grooves. Their shape indicates that the corner grooves were rather deep. On the rods are coarse, short rod-crests with distinct serrations on the adapical side (Pl. 1, fig. 6). Interrod areas are generally broken away, leaving irregular fractures along the rod margins.

Material from position C (i.e. upper central face part, midline excluded) consists of single rods only. These rods possess long, blunt to sharp, rod-crests with well marked serrations (2–5 serrae on each rod-crest) on the adapical side (Pl. 1, figs 7–8). The adapertural side of the rod-crests are more or less smooth with a ridge-like structure running towards the interrod area adaperturally (Pl. 1, figs 1–2). The rods have not been found connected with mineralized interrod areas. There are, however, thin pieces attached to the rods on the adapertural side but this is rare. This suggests that the upper central part of the face-halves was not completely mineralized. Intermediate forms (single rods) between positions B and C occur frequently in the samples. These rods are similar to the rods found in position C but the rod-crests are shorter and closer together (see Text-fig. 2B).

Fragments from position D (i.e. fragments from the midline) consist mostly of larger exoskeletal parts with rods connected by mineralized interrod areas (Pl. 2, fig. 1). The mineralized interrod areas indicate that these have been formed in the transition between positions A and D. The rods end bluntly along the shallow groove

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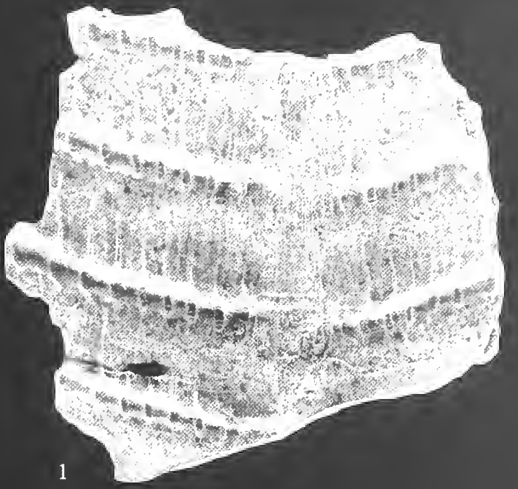
## EXPLANATION OF PLATE 2

Figs 1–5, *Conularia sarae* sp. nov. 1, exoskeletal piece showing alternated rods along the midline, formed in position D, possibly near position A; the aperture is upwards in the picture; LO 6415t, paratype; Häftingsklint 4, sample G88-625LJ, × 75. 2, exoskeletal piece showing the midline formed in position A in the centre part; note the rods that abut in the lower part of the specimen; aperture is upwards; LO 6416t; Lusklint 1, sample G88-613LJ, × 75. 3–5, LO 4931T, the holotype; Lusklint 1, sample G88-613LJ; 3, exoskeletal piece with rods possessing rod-crests formed in position A; note the adapertural crests, fused with the rod-crests adaperturally, and connected on the adapical side with the upper rod, × 75; 4, detail of rod in adapical view; note the incompletely developed serration and the contact between the adapertural crest and the rod, × 500; 5, sideview with the aperture upwards; the fracture forming the right side, exposing the cross-section, is probably close to the midline; note how the rod-crests gradually increase in height towards the midline and the wave-like pattern formed by the rod-crests seen in cross-section, × 75.

PLATE 2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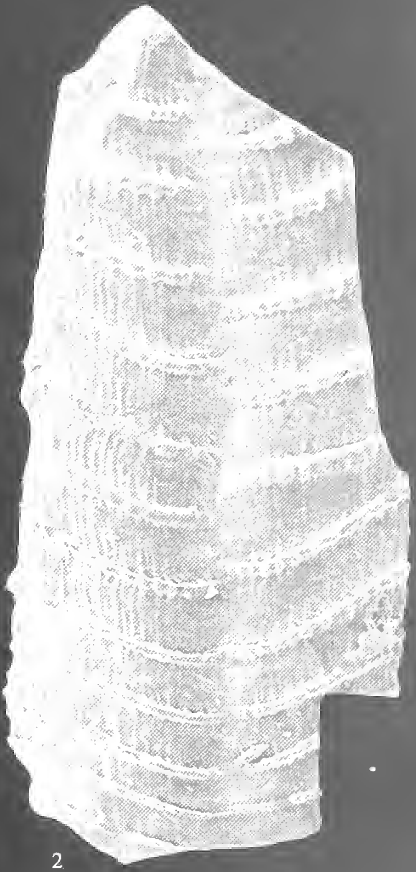
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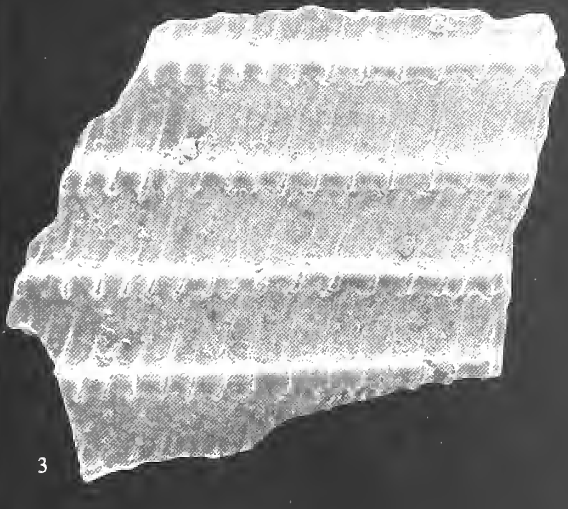
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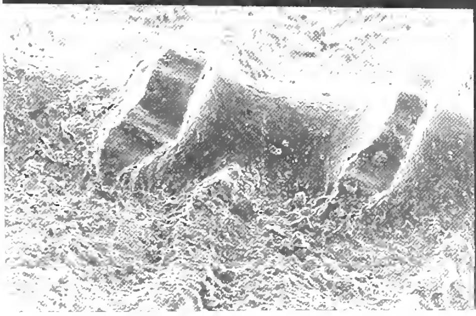
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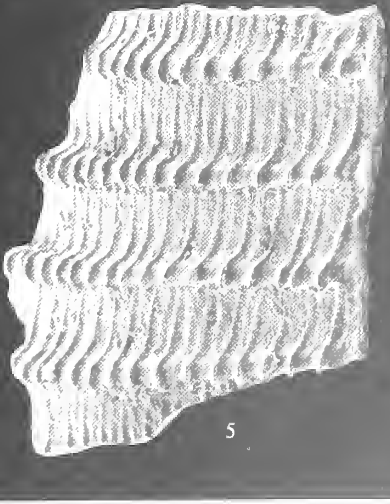
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JERRE, *Conularia*

which constitutes the midline. Single rods are also found that have been formed in connection with the midline. These are identified on their blunt, rounded 'rod-ends'.

*Remarks.* This species, and the two described below, have most characters in common with the genus *Conularia* but also have characters that separate them from that genus. When there is more information available, *C. sarae*, *C. wimani* and possibly also *C.* sp. a could turn out to represent a hitherto undescribed genus.

A specimen illustrated by Bischoff (1978, pl. 1, fig. 8) from the *Pterospathodus amorphognathoides* conodont zone (the Llandovery–Wenlock boundary) of New South Wales, Australia, has a striking resemblance, judging from the illustration only, with rods formed in position C from *C. sarae*.

*Comparisons. Conularia sarae* could perhaps be confused with both *C. wimani* and *C.* sp. a. *C.* sp. a is separated from *C. sarae* in having rod-crests of a different shape and lacking serration.

*Conularia sarae* differs from *C. wimani* which has coarser rods and rod-crests, rod-crests with irregular serration on the adapical sides, and conspicuously smooth adapertural sides. *C. sarae* has 8–18 rod-crests per mm whereas *C. wimani* has 5 rod-crests per mm. *C. sarae* differs from *Ctenoconularia monile* (Lindström, 1884), found in Upper Visby and Högklint beds, in that: (1) the rods in *C. monile* abut along the midline (nearly 100 per cent), whereas most of the rods alternate in *C. sarae*; (2) the midline has the shape of a raised line in *C. monile* whereas in *C. sarae* it has the shape of a shallow groove; and (3) the distance between rod-crests is different, with *C. monile* having 5–6 rod-crests per mm, whereas *C. sarae* has 8–18 rod-crests per mm.

### *Conularia wimani* sp. nov.

Plate 3, figs 1–7

*Derivation of name.* Named in honour of the Swedish palaeontologist Carl Wiman.

*Holotype.* LO 6417T.

*Type locality.* Ireviken 3. Lower Visby Beds unit *e*. The holotype is from sample G86-145LJ, 4·27 m a.r.l.

*Material.* About 100 exoskeletal fragments.

*Diagnosis. Conularia* with coarse rods possessing closely spaced, broad, rectangular rod-crests. The rod-crests have distinct but irregular serration on the adapical side and are smooth on the adapertural side.

*Description.* Material of this species consists mainly of single rods. The rods in position C are asymmetrical but roughly subcircular in cross section (Pl. 3, fig. 5). Coarse, rectangular rod-crests occur at frequent intervals;

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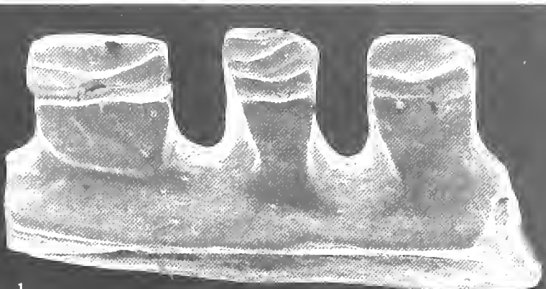
EXPLANATION OF PLATE 3

Figs 1–7. *Conularia wimani* sp. nov. 1–2, LO 6417T, holotype; Ireviken 3, sample G86-145LJ; 1, rod with rod-crests in adapical view formed in position C, ×75; 2, detail of the middle rod-crest; note the irregular serration, ×150. 3, rod with rod-crests in adapertural view formed in position C; LO 6418t; Ireviken 3, sample G86-145LJ, ×75. 4, exoskeletal piece showing rod adjacent to the midline, formed in position D probably in the lower part; the right rod has been worn off; aperture is upwards; LO 6419t; Ireviken 3, sample G86-145LJ, ×75. 5, rod and rod-crest in cross-section, formed in position C; LO 6420t; Ireviken 3, sample G86-145LJ, ×150. 6, rod with serrated rod-crests in adapical view, formed in position B; the corner groove is to the left of the rod; LO 6421t; Ireviken 3, sample G86-145LJ, ×75. 7, coarse rod with rod-crests in adapertural view, formed in position B; the corner groove is to the left of the rod; LO 6422t; Ireviken 3, sample G86-145LJ, ×75.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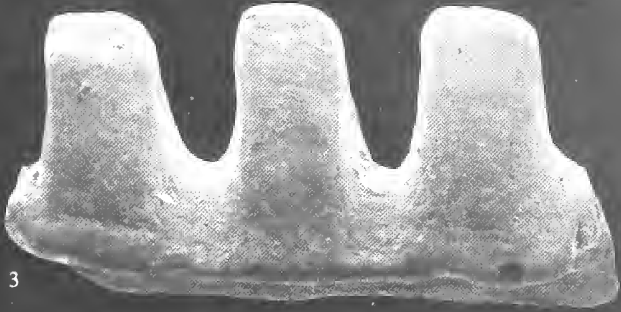
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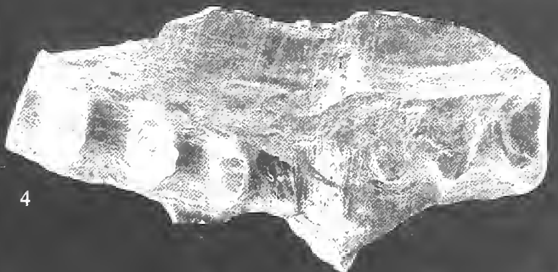
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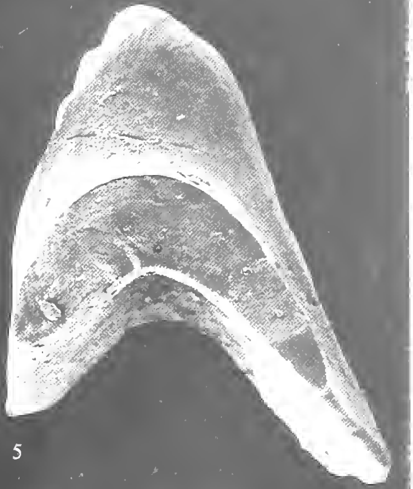
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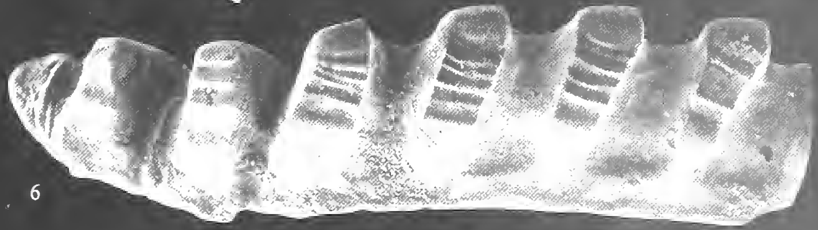
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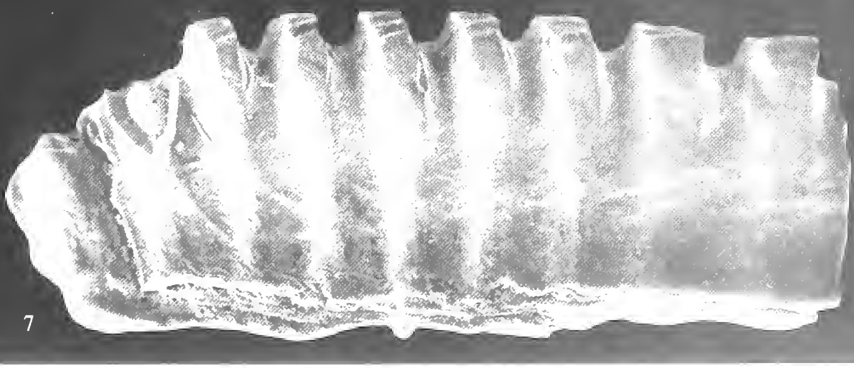
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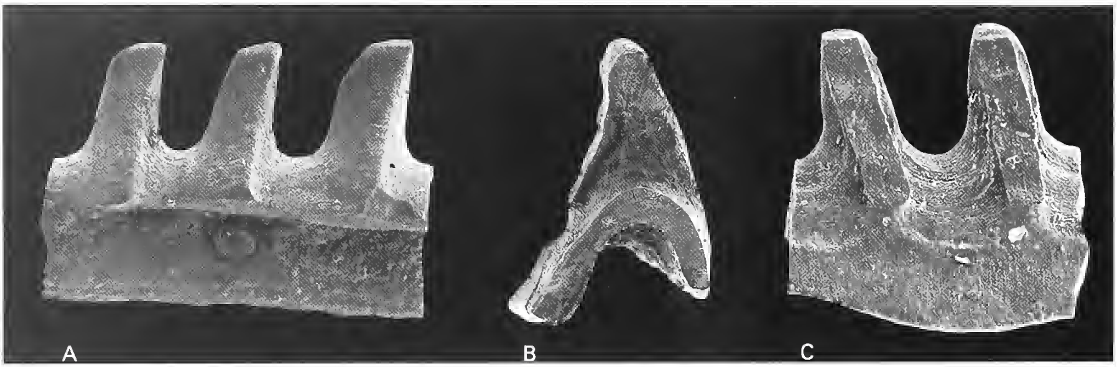
JERRE, *Conularia*



TEXT-FIG. 4. *Conularia* sp. a. SEM photographs of specimens from Lusklint 1, sample G88-613LJ. A, rod in adapertural view, formed in position C; LO 4932t, × 75. B, cross-section of a rod with a rod-crest, LO 4933t, × 100. C, rod in adapical view, formed in position C; note the lack of serration; LO 6409t, × 75.

5 rod-crests per mm (Pl. 3, figs 1, 3, 6–7). The rod-crests are remarkably broad at the top. The adapical side is characterized by a more or less rectangular, sometimes quadratic, area crossed by a distinct but irregular serration (Pl. 3, fig. 2). The margins of the rods are smooth and no pieces of the interrod areas have been found. This could indicate that there were no mineralized interrod areas present. One would expect to find fractures along the rod margins if such mineralized areas had been broken away.

Coarse rods formed near the corner grooves (i.e. in position B) are not as curved as those found on *C. sarae* (see above), which suggests that the corner grooves were more shallow. The rod-crests are more closely spaced and reduced in size towards the corner grooves (Pl. 3, figs 6–7). Mineralized interrod areas have as yet not been found. However, these rods are fractured along the rod margins, unlike rods in position C, indicating that thin mineralized interrod areas were originally present but are now broken away. One single piece has been found that exposes the midline (Pl. 3, fig. 4). The specimen is difficult to place in correct position (either position A or D) but is most likely from a position closer to the apex than to the aperture. This piece is poorly preserved with only one distinct rod present. The rod on the opposite side of the midline has been broken away. The rods seem to have abutted at the midline. There is a small piece of the interrod area connected to the rod adaperturally but the ornamentation, if there was any present originally, has been lost.

*Comparison*. See *C. sarae*, above.

### *Conularia* sp. a

Text-fig. 4A–C

*Material*. Over 1000 exoskeletal fragments.

*Description*. The material consists of rods and single rod-crests only, presumably formed in position C, i.e. upper central face part (see Text-fig. 3). The rods are roughly semicircular in cross-section, possessing relatively long, broad rod-crests (Text-fig. 4B). These rod-crests are slightly tilted longitudinally. The adapertural side of the rod-crests is smooth with a distinct ridge reaching up to the top of the rod-crest (Text-fig. 4A). The adapical side is characterized by a flat, more or less rectangular, area lacking serration (Text-fig. 4C). There are no mineralized interrod areas attached to the rods. As described for *C. wimani*, the rod margins are smooth and lacking fractures from mineralized interrod areas that, if ever present, have been broken away.

*Remarks*. Only fragments from the upper central face part (position C) have been identified. Despite the fact that the amount of identified rods is so high (over 1000), parts from the other positions have not been recognized. These parts are probably present in the samples but could turn out to be almost indistinguishable from those found of *C. sarae*.

*Conularia* sp. a may represent a new species, but available material is inadequate for a complete diagnosis of the taxon.

*Comparison.* See *C. sarae*, above.

## Genus METACONULARIA Foerste, 1928

*Type species. Conularia aspersa* Lindström, 1884.

*Remarks.* The following morphological features are of generic importance: thin, often large exoskeleton; two midlines flanked by a pair of narrow septa; ornamentation with minute nodes often arranged in transverse rows and longitudinal files; and rows arched adaperturally and crossing the corner grooves and midlines without interruption.

According to Sinclair (1940) specimens of the genus are extremely uncommon. The genus is, however, not uncommon either in the Lower Visby Beds or in other formations on Gotland. Roughly 50 per cent of the samples investigated have produced specimens of *Metaconularia*. Considering that the fragments mostly are fairly small, often less than 100 $\mu$m, and that the ornamentation within a specimen can show some variation (Sinclair 1940), a proper identification depends strongly on the size and numbers of the fragments recovered.

### *Metaconularia aspersa* (Lindström, 1884)

Plate 4, figs 4–7; Text-fig. 2c

v* 1884 *Conularia aspersa* Lindström, p. 46, pl. 7, figs 1–3; pl. 19, fig. 1.
v. 1893 *Conularia aspersa* Lindström; Holm, p. 134, pl. 6, figs 43–46.
1907 *Conularia aspersa* Lindström; Slater, p. 19, pl. 1, figs 5–9.
1928 *Metaconularia aspersa* (Lindström); Foerste, p. 107.
1940 *Metaconularia aspersa* (Lindström); Sinclair, p. 101.

*Material.* Over 100 exoskeletal fragments from 23 samples from the Lower Visby Beds, the holotype and 6 other more or less complete specimens from younger strata (Högklint and Hemse Beds) on Gotland.

*Description.* The exoskeleton is thin with rows of fine conical nodes crossing each face transversally (Text-fig. 2c; Pl. 4, figs 6–7). The distance both between rows and between individual nodes varies considerably within the same face. Nodes may be equally spaced transversely and longitudinally, forming seemingly longitudinal rows. In some cases nodes within a single transverse row are so tightly packed that they form a knobbly ridge. In complete specimens there are two conspicuous dark lines (septa) running from apex to aperture in the middle of each face. The lines do not interrupt the ornamentation at the midline. The distance between these lines, measured on the holotype (a 50 mm long specimen), is approximately 0·5 mm near the apex, and 2 mm near the aperture where the width of the face is about 30 mm. The lines correspond with two thin septa, triangular in cross-section, on the internal surface of the exoskeleton. Pieces of these septa with attached external exoskeletal fragments are often found in the samples (see Pl. 4, fig. 5). Septa are approximately 0·3–0·5 mm in width (Pl. 4, figs 4–5).

*Remarks.* Ornamentation varies considerably from piece to piece: the distance between transverse rows, the distance between nodes within a single row, and the coarseness of the nodes all vary within a single sample. Such a degree of morphological variation has not been found among the studied intact specimens. It is thus possible, when more material is available and more detailed analysis is possible, that the material now included in *Metaconularia aspersa* may in the future turn out to consist of two or more species.

*Comparison. Metaconularia aspersa* differs from *M. biliniata* (Lindström, 1884) (found in the Slite Beds) essentially in having conical or round nodes, whereas *M. biliniata* generally has smaller and more or less elliptical nodes.

### Genus PSEUDOCONULARIA Bouček, 1939

*Type species. Conularia grandissima* Barrande, 1867.

*Remarks.* This genus, called 'Grupp Longitudinales' by Holm (1893, p. 131) and 'Groupe der *Conularia grandissima*' by Bouček (1928, p. 92), is a conulariid with a unique ornamentation characterized by knobbly, longitudinal ridges, or rows of elongate, irregular nodes which also are often arranged in transverse rows (Sinclair 1941). The midline is defined by a low, often broad ridge. Apical angles are large, from 22° to 23° in *P. grandissima* and up to 40° in *P. klouceki* (Bouček, 1928). Septa are unknown.

Many of the conulariids referable to *Pseudoconularia* are of large size, as is apparent from the specific names *grandissima* (which can reach a height of 30 cm), *magnifica* and *megista* (Hessland 1949). *Pseudoconularia* is a mainly Ordovician genus but its stratigraphical range evidently extends into the Lower Silurian.

### *Pseudoconularia* aff. *scalaris* (Holm, 1893)

Plate 4, figs 1–3; Text-fig. 2D

*Material.* 12 exoskeletal fragments.

*Description.* The exoskeleton is covered with tightly packed, smooth rounded ridges (Pl. 4, fig. 1). The ridges are often linked together (i.e. there is hardly any interridge area visible between the ridges). However, in those places where a narrow but distinct interridge area is visible, the distance between the ridges is generally less than 0·5 ridge-widths. Numerous (15–20 per mm) depressions cut about halfway through the ridges forming elongated nodes with sharp crests on the top (Pl. 4, fig. 2). The nodes are tightly spaced with approximately one, or less than one, node-width between two nodes. In cross-section, the ridges form a sinusoidal-like pattern (Pl. 4, fig. 3). Determining the direction of the aperture and apex from this material is impossible.

*Comparison. Pseudoconularia* aff. *scalaris* has few morphological characters in common with the other species. Based on this fairly meagre material, the species cannot be formally named. The holotype of *P. scalaris* (Holm, 1893) has not yet been studied and a comparison with Liljevall's drawings (see Holm 1893, pl. 4, figs 49–52), is inadequate to identify *P.* aff. *scalaris* as a new species.

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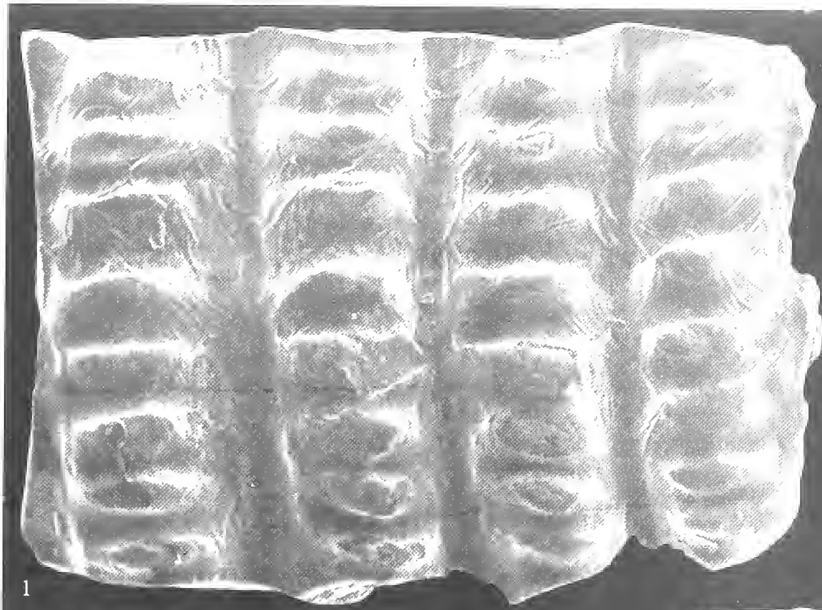
#### EXPLANATION OF PLATE 4

Figs 1–3, *Pseudoconularia* aff. *scalaris*. 1–2, LO 6423t; Storbrut 1, sample G85-16LJ; 1, large exoskeletal piece showing four parallel ridges with tightly spaced, elongated nodes; direction of the aperture is unknown, × 150; 2, sideview showing elongated nodes; note the typical striation on the sides, × 200. 3, cross-section of a specimen with two preserved ridges; LO 6424t; Storbrut 1, sample G85-16LJ, × 150. 4–7, *Metaconularia aspersa* (Lindström). 4–5, LO 6425t; Ireviken 3, sample G86-129LJ; 4, anterior side of an exoskeletal piece exposing one of the septa, × 150; 5, cross section; note the triangular shape of the septum and the ornamentation with nodes on the external surface of the exoskeleton, lowermost in the picture, × 300. 6, exoskeletal part with nodes; orientation unsure; LO 6426t; Lusklint 1, G89-715LJ, × 190. 7, nodes arranged in a symmetric pattern forming rows in both longitudinal and transverse directions; direction of the aperture is either up or down; LO 4576t; Ireviken 3, G86-129LJ, × 200.

PLATE 4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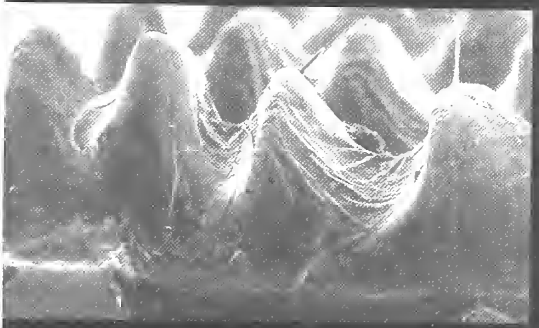
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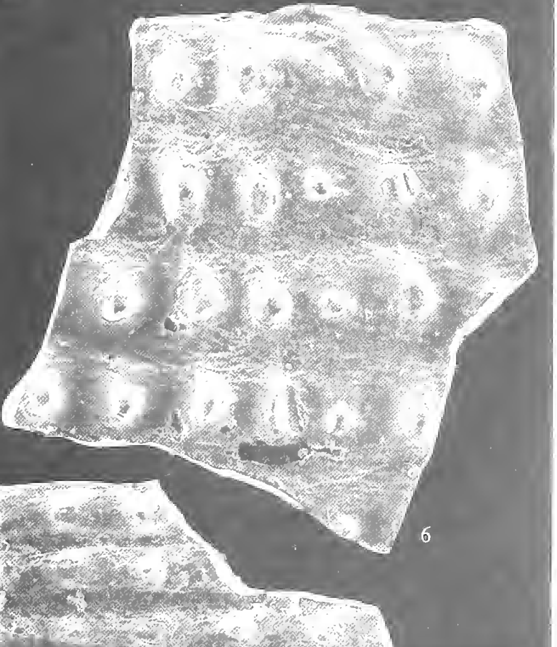
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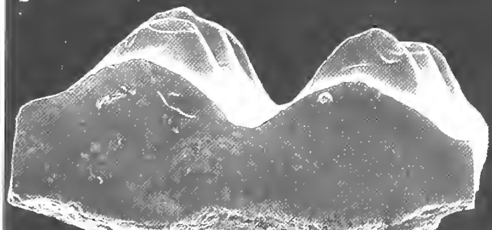
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JERRE, *Pseudoconularia*, *Metaconularia*

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# *ORNITHODESMUS* – A MANIRAPTORAN THEROPOD DINOSAUR FROM THE LOWER CRETACEOUS OF THE ISLE OF WIGHT, ENGLAND

*by* STAFFORD C. B. HOWSE *and* ANDREW R. MILNER

ABSTRACT. The holotype and only specimen of *Ornithodesmus cluniculus*, a sacrum from the late Wealden (= Barremian) of the Isle of Wight, is redescribed and is shown not to be pterodactyloid as previously described. Comparison with sacral vertebrae of pterodactyloids and of advanced theropod dinosaurs shows it to resemble most closely those of the small theropod *Saurornithoides*. Because *O. cluniculus* is the type species of *Ornithodesmus*, the genus is transferred to the Theropoda. It is assigned to the Troodontidae with uncertainty, because of the limited nature of the holotype. *Ornithodesmus cluniculus* cannot be diagnozed within the Troodontidae and is a *nomen vanum* within the family. If it is a troodontid, it represents the first record of a troodontid from the Wealden of Europe, and also the earliest record of this family. The undoubted pterodactyloid material from the Barremian of the Isle of Wight, '*Ornithodesmus*' *latidens*, requires a new generic name.

THE holotype of *Ornithodesmus cluniculus* from the Wealden of the Isle of Wight is a set of six co-ossified vertebrae (BMNH R187) described by Seeley (1887), who concluded that it was the sacrum of a bird. This identification was based on the presence of two features: (1) the co-ossification of successive neural spines resulting in a continuous neural blade; and (2) the presence of a 'neural platform' made up of horizontal laminar extensions of the bases of the neural arches. Three further characteristics which he noted to be shared with both birds and pterosaurs were: (1) fusion of sacral vertebrae through ankylosis; (2) the sacrum comprising at least five vertebrae; and (3) the presence of pneumatic foramina. However, as no pterosaurs were known to possess the neural blade or neural platform, Seeley argued that the specimen was an avian sacrum, even though it differed from those of modern birds in the small number (six) of vertebrae, the absence of recesses for the reception of mid-renal lobes, and the structure of the anterior articulation of the sacrum. Lydekker (1888, p. 42) catalogued the specimen as a reptile, indeterminate at ordinal level, noting that it could be dinosaurian or pterosaurian in origin.

Seeley (1901) attributed a greater part of a pterodactyloid skeleton (BMNH R176) from the Wealden of the Isle of Wight to *Ornithodesmus*, as the new species *O. latidens*. He associated the two specimens on the basis of supposed similarities in the sacrum, and hence *Ornithodesmus*, now comprising two species, was transferred to the Pterodactyloidea. Hooley (1913) described two more specimens ofv *O. latidens* (BMNH R3877 and R3878), also from the Wealden of the Isle of Wight, and was able to provide a detailed osteology of this species. However, he made no mention of the sacrum of *O. cluniculus* and very little reference to that of *O. latidens*. As a result of Seeley's (1901) and Hooley's (1913) descriptions, *O. latidens* has been treated as the effective type of the genus *Ornithodesmus* for the purposes of diagnosis (e.g. Wellnhofer 1978, p. 54), while Plieninger (1930) even reduced the senior *cluniculus* in synonymy with the junior *latidens*. Apart from a general assertion of similarity by Seeley (1901), no attempt has been made to compare the sacrum of *O. cluniculus* directly with those of pterosaurs, despite the differences noted by Seeley in his original (1887) description.

Independent reexamination of *O. cluniculus* by the senior author and by Christopher Bennett (University of Kansas) led both to the conclusion that it did not resemble the sacrum of

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pterodactyloids as now known. The ensuing attempt to place this specimen systematically has resulted in this paper. The sacral vertebrae associated with the undoubted pterodactyloid '*Ornithodesmus*' *latidens* are quite distinct from those of *O. cluniculus* and are redescribed later in this work.

Interpretation of BMNH R187 necessitated comparative reference to two other specimens. One is the sacrum of *Saurornithoides junior* (Barsbold 1974, pl. 3, fig. 1; pl. 4, fig. 2) which comprises six ankylosed vertebrae and is about twice as long as that of BMNH R187, having a length of 199 mm. The other specimen is BMNH R4463, an undescribed small theropod sacrum (Pl. 1, figs 4–6; Text-fig. 2A–B) from the Late Cretaceous of Mexico Ranch, Red Deer River, Alberta, Canada. This specimen includes sacrals 2–6 and is about one-and-a-half times as long as BMNH R187 (110 mm for sacrals 2–6, as against 79 mm in BMNH R187). The anterior face of the centrum of sacral 2 appears to be clean and flat, implying that sacral 1 was not ankylosed to the rest of the sacrum. This specimen was catalogued as an ornithomimid, but bears a close resemblance to the sacrum of *Saurornithoides*. Although undetermined, it is sufficiently similar to BMNH R187 in size and configuration to be useful in interpreting damaged features on that specimen, and also for demonstrating the presence of a neural platform in the troodontid sacrum.

The following institutional abbreviations are used in this work: BMNH, Department of Palaeontology, The Natural History Museum, London, UK; GI, Geological Institute, Ulan Bator, Mongolia; TMP, Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; Z.PAL, Institute of Palaeobiology, Warsaw, Poland.

## SYSTEMATIC PALAEONTOLOGY

Subclass DIAPSIDA Osborn, 1903
Superorder ARCHOSAURIA Cope, 1891
Order SAURISCHIA Seeley, 1888
Suborder THEROPODA Marsh, 1881
?Family TROODONTIDAE Gilmore, 1924
(= SAURORNITHOIDIDAE Barsbold, 1974; ? = ORNITHODESMIDAE Hooley, 1913)

*Diagnosis*. As given by Currie (1987, p. 73) with the following additional diagnostic characteristics of the sacrum: all six sacral vertebrae fully ankylosed; pneumatic foramina present on the first two sacrals; ventral surface of sacrals flattened with medial groove developing shallowly on sacral 2 and very pronounced on sacrals 3–6; neural platform present.

*Component genera*. *Troodon* (= *Stenonychosaurus*, *Pectinodon*), *Saurornithoides*, *Borogovia*, *Heptasteornis* and ?*Ornithodesmus*.

*Remarks*. In attributing *Ornithodesmus*, with caution, to the same family as *Saurornithoides* and *Troodon*, we must note that the senior family-level name derived from any of these genera is Ornithodesmidae Hooley, 1913, a name previously associated with the Pterodactyloidea. The very

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### EXPLANATION OF PLATE 1

Figs 1–3. *Ornithodesmus cluniculus* Seeley, 1887. Holotype sacrum BMNH R187; Barremian; Isle of Wight, England; in 1, left lateral view; 2, right lateral view; 3, ventral view. All ×0·7.

Figs 4–6. Troodontid sacrum BMNH R4463; Late Cretaceous, Red Deer River, Alberta, Canada; in 4, left lateral view; 5, right lateral view; 6, ventral view. All ×0·63.

PLATE 1


1


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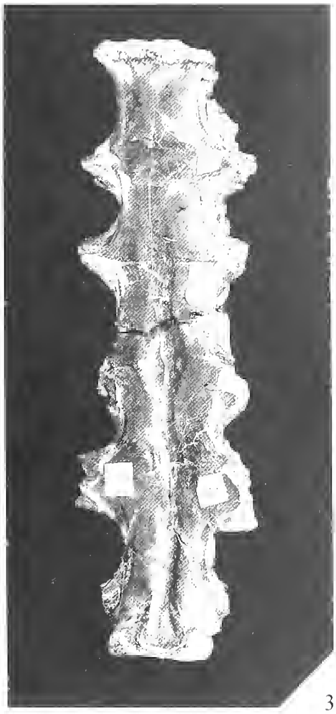
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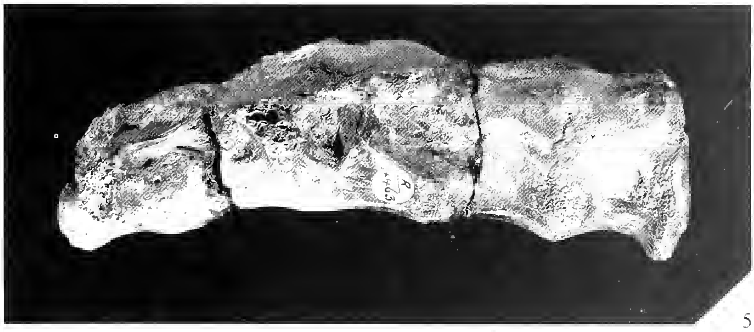

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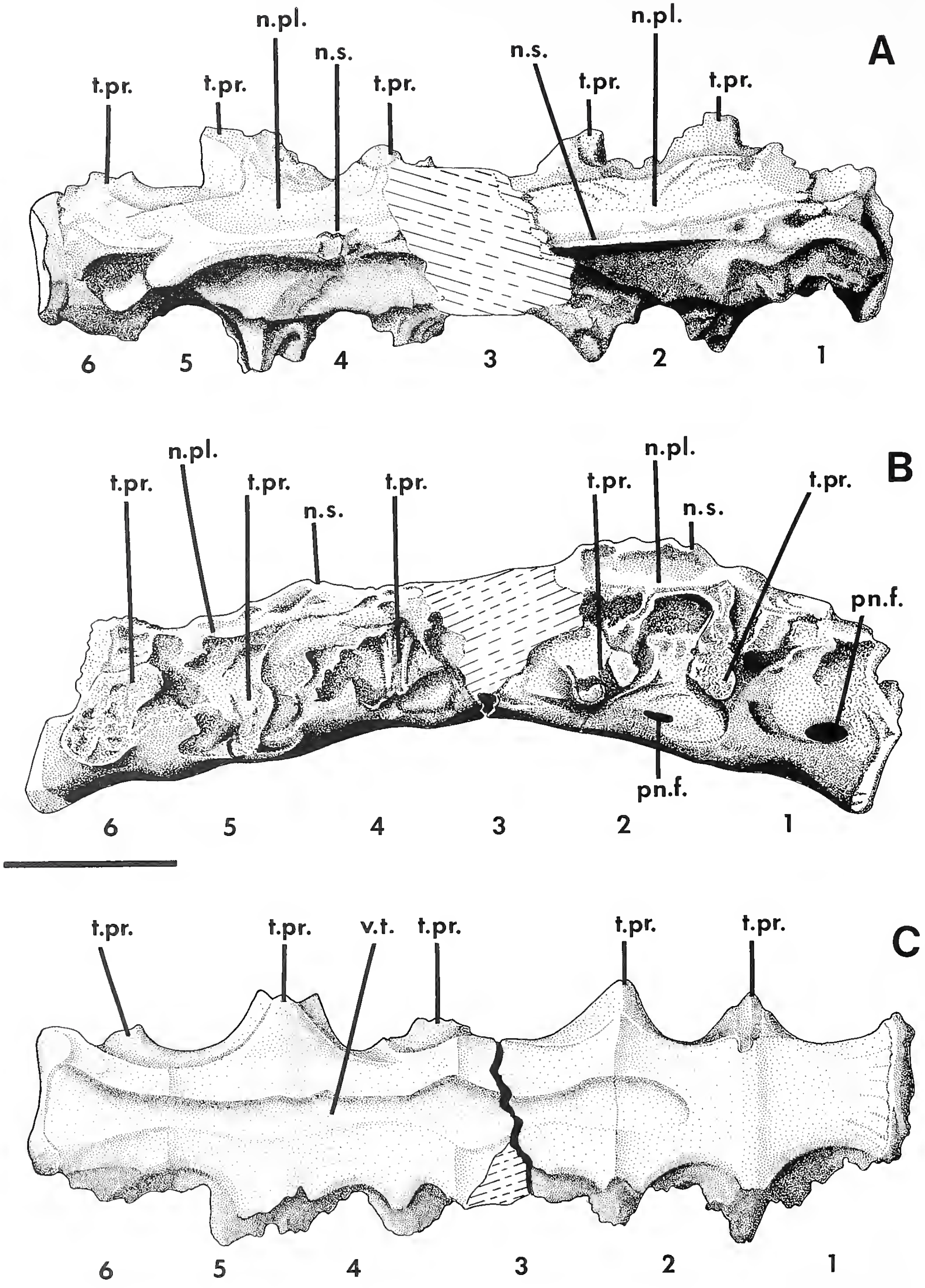
HOWSE and MILNER, *Ornithodesmus cluniculus*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limited nature of the *Ornithodesmus* material means that it can only be attributed, with caution, to any family-level unit. For this reason, and in the interests of stability, the name Troodontidae Gilmore, 1924 is retained for the family.

### Genus ORNITHODESMUS Seeley, 1887

*Type species. O. cluniculus* Seeley, 1887.

*Diagnosis.* As for the only species.

### *Ornithodesmus cluniculus* Seeley, 1887

Plate 1, figs 1–3; Text-fig. 1A–C

1887 *Ornithodesmus cluniculus* Seeley, p. 206, pl. 12, figs 1–5.
1888 *Ornithodesmus cluniculus* Seeley; Lydekker, p. 42.
1901 *Ornithodesmus* Seeley, p. 174.
1930 *Ornithodesmus latidens* Seeley; Plieninger, p. 44 [*non* Seeley 1901].
1978 *Ornithodesmus cluniculus* Seeley; Wellnhofer, p. 54.

*Holotype and only specimen.* BMNH R187, a poorly preserved sacrum, 96 mm in length and comprising six ankylosed vertebrae.

*Locality and horizon.* Given as 'Brook' (probably Compton Bay), Isle of Wight, England; Wealden Marls = Wessex Formation (Daley and Stewart 1979), Barremian, Lower Cretaceous.

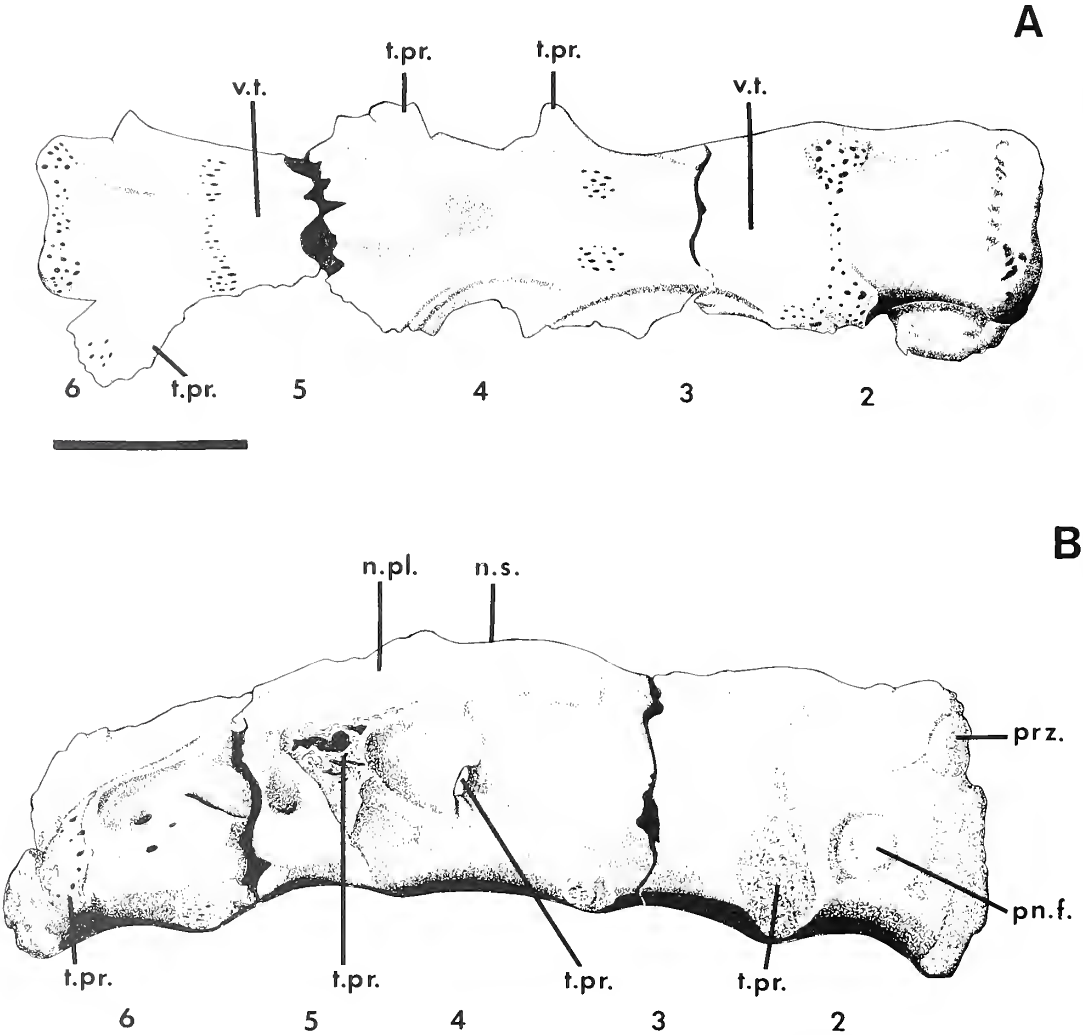
*Diagnosis.* All six sacral vertebrae fully ankylosed at a sacrum length of under 100 mm; sacral 6 shorter than sacral 5.

*Discussion.* The relative lengths of sacrals 5 and 6 serve to distinguish this sacrum from that of *Saurornithoides*, in which sacral 6 is the same length as sacral 5. It is impossible to diagnose *Ornithodesmus cluniculus* with respect to any other troodontids, as no other genera are represented by sacral material. *Ornithodesmus cluniculus* must be considered to be a *nomen vanum* (*sensu* Simpson 1945, p. 27; Simpson 1948, p. 31; Mones 1989) within the family Troodontidae, as the holotype and only specimen is insufficient for comprehensive comparative diagnosis.

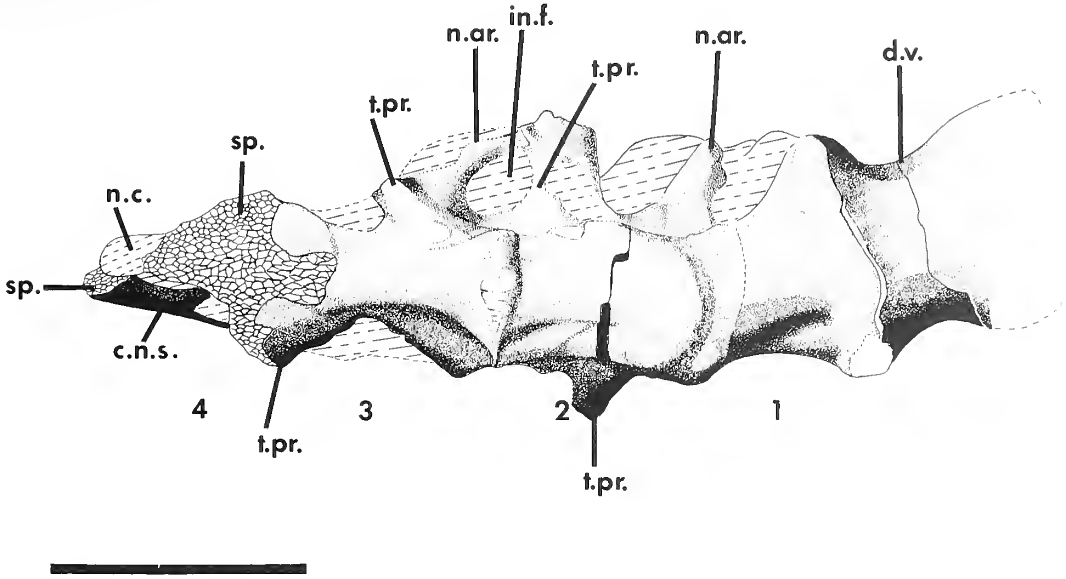
*Description with comparisons.* The sacrum BMNH R187 (Pl. 1, figs 1–3; Text-fig. 1A–C) is 96 mm long and all six vertebrae are present. Most of the matrix has been removed and the ventral face of the specimen is well preserved, the dorsal and lateral surfaces being abraded to varying extents. It is slightly arched along its length (Text-fig. 1B) and is composed of six completely ankylosed vertebrae with strongly waisted centra. The first centrum is relatively deep, and succeeding centra are progressively shallower. The junctions between centrum 3 and adjacent centra are relatively conspicuous ridges, but the other junctions are poorly discriminated lines. In BMNH R4463 (Pl. 1, fig. 6), the corresponding ankylosed sutures are more clearly visible. The centra of BMNH R187 are roughly equal in length apart from the sixth centrum which is conspicuously shorter. The ventral midline lengths of the centra of BMNH R187 and other theropod sacra are presented in Table 1. BMNH R4463 resembles BMNH R187 closely in that the sixth sacral is shorter than the preceding vertebrae and also that sacrals 3 and 5 are slightly longer than 3 and 4. In the otherwise almost identical *Saurornithoides* sacrum, sacrals 5 and 6 are similar in length.

TEXT-FIG. 1. *Ornithodesmus cluniculus* Seeley, 1887. Holotype sacrum BMNH R187; Barremian; Isle of Wight, England; A, dorsal, B, right lateral, and C, ventral views. Abbreviations for all text-figures: c.n.s., coossified neural spine; d.v., dorsal vertebra; in.f., intervertebral fenestra; n.ar., neural arch; n.c., neural canal; n.pl., neural platform; n.s., neural spine; pn.f., pneumatic foramen; prz, prezygapophysis; sp., spongiosa; t.pr., transverse process; v.t., ventral trough. Scale bar = 20 mm.

The ventral surface of the first sacral vertebra of BMNH R187 is transversely rounded and anteroposteriorly concave. Succeeding centra have flattened ventral faces and show neither transverse convexity nor anteroposterior concavity (Text-fig. 1c). A most conspicuous and characteristic feature of the ventral surface is a medial groove which arises shallowly in the mid-central region of the second sacral centrum, and runs posteromedially to terminate as an expansion at the ventral rim of the posterior edge of the sixth sacral centrum (Text-fig. 1c). The groove is a pronounced narrow trough with smooth rounded edges throughout. It widens over the line of ankylosis at the boundary between each pair of vertebrae. BMNH R4463 shows the same flattened underside to the centra and has an extremely similar but slightly less extensive ventral groove which appears to develop on the third sacral centrum, to be pronounced on sacrals 3–5 but to be weakly developed on sacral 6 (Text-fig. 2A). *Saurornithoides* also has very flattened undersides to the centra and has a pronounced ventral groove (described as a furrow by Barsbold 1974) on sacrals 3–5 but again weakly developed on sacral 6 (Barsbold 1974, pl. 3, fig. 1).



TEXT-FIG. 2. Troodontid sacrum BMNH R4463; Late Cretaceous, Red Deer River, Alberta, Canada; A, ventral, and B, right lateral views. For abbreviations see Text-figure 1. Scale bar = 20 mm.



TEXT-FIG. 3. '*Ornithodesmus*' *latidens* Seeley, 1901. Pterodactyloid sacrum BMNH R176; Barremian; Isle of Wight, England; in ventral aspect. For abbreviations see Text-figure 1. Scale bar = 20 mm.

The first and second sacral vertebrae of BMNH R187 each possess a pair of pneumatic foramina on the lateral walls of the centrum (pn. f. in Text-fig. 1B). Each foramen consists of a single perforation set in a deep excavation which accounts for much of the pronounced waisting of these two vertebrae. The sides of the posterior sacrals are too poorly preserved for the presence or absence of pneumatic foramina to be determined. In BMNH R4463, the second sacral has pneumatic foramina but none is visible on sacrals 3–6.

Transverse processes arise close to the junctions between adjacent vertebrae and have a characteristic configuration in BMNH R187, BMNH R4463 and *Saurornithoides*. The structure of the transverse processes in BMNH R187 (Text-fig. 1A–C) is as follows, with comparative comments on the other specimens where relevant.

Sacral 1 has only the stumps of transverse processes situated near the anterior end of the vertebra (sacral 1 absent or heavily damaged in the other specimens).

Sacral 2 has posterolaterally directed transverse processes situated very close to the anterior edge of the vertebra and with a slight contribution from the posterior end of sacral 1 (similar posterolaterally directed processes occur in BMNH R4463, close to the border with sacral 1 but apparently not so close as to have any structural contribution from that vertebra).

Sacral 3 has laterally directed transverse processes overlapping the junction with sacral 2 (in BMNH R4463, only stumps are present).

Sacral 4 has stumps of transverse processes just posterior to the junction with sacral 3 (in BMNH R4463, posterolaterally directed transverse processes are situated just behind the junction with sacral 3).

Sacral 5 has very wide, laterally directed, transverse processes overlapping the junction with sacral 4 (likewise in BMNH R4463).

Sacral 6 has posterolaterally directed transverse processes situated in the middle of the centrum (likewise in BMNH R4463).

Buttress-like diapophyses arise perpendicularly to the long axis of the sacrum above the transverse processes and fuse with horizontal laminae extending from the bases of the neural spines to give a neural platform, i.e. a continuous sheet of bone extended laterally on each side of the bases of the sacral neural spines (n. pl. in Text-fig. 1A–B). Where the diapophyses fuse with the neural platform, the latter is expanded in width and consequently bears an undulating margin with the expansions corresponding to the lines of fusion between the vertebrae. A similar neural platform is present in BMNH R4463 (Text-fig. 2B), but the *Saurornithoides* sacrum is too poorly preserved for the presence of a neural platform to be established.

The neural arches are relatively rounded structures surrounding the neural canal. The leading edge of the neural arch of the first sacral extends forward as prezygapophyseal processes terminating in dorsomedially directed facets. The damaged neural spines are represented only by bases and broken stumps, but were clearly co-ossified to give a continuous blade-like structure (n.s. in Text-fig. 1A). The neural spines are thickened where they meet the laminae of the neural platform. In conclusion, not only are all six centra ankylosed in this sacrum but all the supra-central components (neural spines, neural arches, transverse processes) are co-ossified to give an entirely rigid structure.

The anterior articular surface of the centrum of the first sacral vertebra is very slightly concave and is a flattened oval shape. The posterior articular surface of the centrum of the sixth sacral vertebra is also slightly concave and is curved down at each side. This posterior articular surface is slightly upwardly directed in relation to the long axis of the sacrum. At each ventrolateral corner is a worn tubercle apparently bearing a ventrally directed oval facet (Text-fig. 1C), which presumably represents a secondary surface of articulation with the first caudal vertebra.

## *Systematic position of* Ornithodesmus cluniculus

The only sacra that are significantly similar to that of *Ornithodesmus cluniculus* are those attributed to the theropod genera *Saurornithoides*, *Ornithomimus*, *Gallimimus* and *Chirostenotes*. The following material was used as the basis for systematic comparison.

*Saurornithoides.* Only one troodontid sacrum has been described and figured, namely that of *Saurornithoides junior* Barsbold, from the Upper Nemegt Beds of Mongolia (Barsbold 1974, pl. III, fig. 1; pl. IV, fig. 2). This comprises six ankylosed vertebrae and has a length of about 200 mm.

*Ornithomimus* and *Gallimimus.* Ornithomimids appear to have possessed five (Osmólska *et al.* 1972) or six (Russell 1972) sacral vertebrae. Where six are present they seem to be directly homologous to the six in BMNH R187. Where five are present as in *Gallimimus*, they are homologous to sacrals 2–6 in BMNH R187 with dorsal 13 being homologous to sacral 1. Throughout this discussion, we have standardized on a homology based on six fused sacrals and refer to dorsal 13 + sacrals 1–5 of *Gallimimus* as sacrals 1–6. The sacrum of *Ornithomimus* is represented by USNM 4736, the type specimen of *O. sedens* Marsh, 1892, from the Lance Formation of Niobrara County, Wyoming, USA, as figured by Gilmore (1920, fig. 67). This sacrum is almost five times as large in linear dimensions as BMNH R187 and includes only sacrals 3–6 which are 305 mm long as against 62 mm for the equivalent vertebrae in R187. Gilmore described these as sacrals 1–4, but it is now clear that one or two more vertebrae are incorporated into the anterior sacral series in ornithomimids, and that these were missing in Gilmore's specimen (Russell 1972, p. 377). The sacrum of the type specimen of *Gallimimus bullatus* Osmólska, Roniewicz and Barsbold, 1972 (pl. 45; fig. 9) was described as having five sacrals but, as noted above, the last 'dorsal' appears to be homologous with the first sacral as identified by Russell (1972). This sacrum is eight times as long as BMNH R187 and sacrals 3–6 (2–5 of Osmólska *et al.*) are 510 mm in length. The dimensions of the sacral vertebrae of a second smaller specimen of *Gallimimus* have also been taken from Osmólska *et al.* (1972) and are incorporated in Table 1.

*Chirostenotes.* The infraorder Oviraptorosauria comprises two families of small toothless theropods, the Caenagnathidae and the Oviraptoridae, all from the Late Cretaceous of North America and Mongolia. The Caenagnathidae is now believed to include the genus *Chirostenotes*, which possesses a sacrum comprising six ankylosed vertebrae (Currie and Russell 1988, fig. 1). The Oviraptoridae are reported to possess six (*Oviraptor*) or seven (*Ingenia*) presacral vertebrae (Barsbold 1983), but these have not been figured, and the sacrum of *Chirostenotes* of necessity is taken as representative of the oviraptorosaurs.

When *Ornithodesmus cluniculus* was first described as a primitive bird (Seeley 1887), troodontid, ornithomimid and oviraptorosaur dinosaurs had not been recognized as such, although a few ornithomimid fragments had been named. Shortly after the description of recognizable ornithomimids by Marsh (1890), *Ornithodesmus* was erroneously associated with pterodactyloid material, without precise comparisons with bird-like dinosaurs ever being made.

The above redescription has shown that *Ornithodesmus cluniculus* may be placed systematically by means of the following morphological features.

1. Pneumatic foramina present in the first two sacral vertebrae. The first sacral is a modified dorsal implying the presence of such foramina and pleurocoels in the posterior dorsal series. This is a characteristic of the Theropoda *sensu* Gauthier (1986, p. 19) although Upper Cretaceous Troodontidae lack pleurocoels in the posterior dorsals (Currie 1987). The *Saurornithoides* sacrum is too poorly preserved for such foramina to be visible, but they are present in sacrals 1–4 in *Gallimimus* (dorsal 13 and sacrals 1–3 of Osmólska *et al.* 1972). In *Chirostenots*, sacrals 1–6 all bear pleurocoels, but they are very small in 4–6 and might well be missed in a poorly preserved specimen.
2. Sacrum comprising at least four ankylosed vertebrae. The presence of at least four sacrals is a characteristic of the Theropoda (Currie and Russell 1988, p. 974). Most theropods have at least five presacrals, but *Dilophosaurus* and *Compsognathus* retain four.
3. Extensions of the sacral diapophyses form a neural platform. Similar neural platforms are present in BMNH R4463 (Text-fig. 2B), *Ornithomimus* and *Chirostenotes*, but not in *Gallimimus* where the diapophyses remain unconnected. The *Saurornithoides* sacrum is too poorly preserved for the presence of a neural platform to be established.
4. Sacrals 2, 4 and 6 have posterolaterally directed transverse processes, while sacrals 3 and 5 have laterally directed transverse processes. This also characterizes troodontids, ornithomimids (if the posterior dorsal is homologized with the first sacral in R187) and *Chirostenotes*.
5. Sacrum comprising six ankylosed vertebrae. The presence of six sacrals appears to be restricted to the Troodontidae (Barsbold 1974), the Oviraptorosauria (Barsbold 1983; Currie and Russell 1988) and some Ornithomimidae (Russell 1972), although most of the latter have only five co-ossified sacrals (Osmólska *et al.* 1972). In *Saurornithoides*, such preserved fragments of neural spine that are present show evidence of co-ossification of the spines. However, in *Gallimimus* the spines are closely appressed but not co-ossified.
6. Sacral centra 2–5 have broad flattened undersides with a medial groove present throughout their length. *Saurornithoides* also has very flattened undersides to the centra and has a pronounced ventral groove on sacrals 3–5 (Barsbold 1974, pl. 3, fig. 1). Gilmore (1920) described the corresponding groove in *Ornithomimus* (USNM 4736) as prominent on sacrals 3–5 (his 1–3). Osmólska *et al.* (1972, p. 119) referred to a medial depression on sacrals 2–5 (their 1–4) in *Gallimimus*. This feature characterizes the *Saurornithoides* and the Ornithomimidae, but not *Chirostenotes*.
7. The ventral surface of the centrum of sacral 6 is broadly flattened with a medial groove. This occurs in *Saurornithoides* and BMNH R4463, but not in ornithomimids (*Ornithomimus*) or *Chirostenotes*. In both of the latter, sacral is 6 narrower with a convexly curved underside which is not flattened and has only a slight groove.
8. All six sacrals co-ossified, indicating maturity, in a sacrum slightly less than 100 mm long. Scaled against small theropods, this suggests a total length of no more than one-and-a-half metres for an adult animal, considerably less than known ornithomimids, which had adult sizes of 3 metres or more, but of similar size to troodontids.
9. Sixth sacral centrum shorter than fifth sacral centrum. This is also the condition in BMNH R4463. In *Saurornithoides*, the two centra are approximately the same length. In *Ornithomimus* and *Gallimimus*, the sixth sacral is longer (Table 1).

Characters 1 and 2 serve to identify this specimen as a theropod sacrum. Characters 3 to 5 identify

TABLE 1. Ventral midline lengths (mm) of centra of sacral vertebrae. * = approximation. Information from Gilmore 1920, p. 133 (*Ornithomimus*); Osmólska *et al.* 1972, p. 120 (*Gallimimus*); Barsbold 1974, p. 15 (*Saurornithoides*).

| Sacral vertebra | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| Troodontidae | | | | | | |
| *Ornithodesmus* (BMNH R187) | 17 | 16 | 18 | 15 | 16 | 13 |
| Indeterminate troodontid (BMNH R4463) | — | 21·4 | 23·5 | 22·3 | 25·6 | 17·6 |
| *Saurornithoides* (GI no. SPS 100/1) | 34* | 31* | 31·0 | 31·0 | 36·0 | 36·2 |
| Ornithomimidae | | | | | | |
| *Ornithomimus* (USNM 4736) | — | — | 71 | 71 | 79 | 84 |
| *Gallimimus* (GI no. DPS 100/11) | 98 | 95 | 92 | 85 | 115 | 118 |
| Z.Pal Mg.D-1/94 | 41 | 40 | 40 | 39 | 41 | 44 |

it as a sacrum of a maniraptoran theropod and a member of either the Troodontidae, the Ornithomimidae or the Oviraptorosauria. Character 6 identifies it as either a troodontid or an ornithomimid. Characters 7 and 8 identify it as a troodontid. The significance of this identification will be considered in the discussion below. As noted in the discussion following the diagnosis, there is little basis for comparative diagnosis of *Ornithodesmus* within the Troodontidae, because only *Saurornithoides* has an associated sacrum. Character 9 is a notional distinguishing character, but *Ornithodesmus cluniculus* is, to all intents and purposes, a *nomen vanum* within the Troodontidae.

## THE SACRUM OF '*ORNITHODESMUS*' *LATIDENS*

The holotype of '*Ornithodesmus*' *latidens*, (BMNH R176) is a set of associated pterodactyloid elements. The sacrum associated with this material is certainly pterodactyloid as it forms part of an articulated vertebral column, the anterior region of which is a notarium of pterodactyloid type. This needs to be emphasized, because one major non-pterodactyloid fragment was originally incorporated in BMNH R176, namely a skull-table of the crocodile *Theriosuchus* (Buffetaut 1983). Seeley (1901) regarded the holotype of *O. cluniculus* and the sacrum of BMNH R176 as sufficiently morphologically similar to be considered congeneric, although he did not specify the similarities. Hooley (1913) made only brief mention of the sacrum of BMNH R176, noting that it was impossible to determine its overall form because of its fragmentary condition. However, there is sufficient structure preserved to demonstrate that the sacrum of the pterosaur '*O*'. *latidens* is a typical pterodactyloid sacrum and hence distinct from that of *O. cluniculus*. This sacrum will be described and illustrated more fully by the senior author as part of a complete redescription of '*O*' *latidens*. The following short description is provided simply to demonstrate the distinct nature of these two sacra.

*Description*. The sacrum of BMNH R176 (Text-fig. 3) is incomplete and comprises the first three sacral vertebrae, visible in ventral and lateral aspect, together with the anterior region of the fourth sacral. Most of the dorsal and dorsolateral regions of the sacrum are obscured by matrix and by overlying metacarpal elements which have distorted the neural spines of the third and fourth sacrals. For each of the first three sacral centra, the length (measured along the ventral midline) and width (across the mid-ventral surface) are as follows: (1) 15 mm, 11·25 mm; (2) 13 mm, 11·50 mm; (3) 12 mm, 9·25 mm. Thus there is a gradual decrease both in length and width along the anterior sacral series. The centra are waisted and become shallower posteriorly.

The sacral vertebrae are fully ankylosed as a synsacrum. The zones of fusion between the centra are thickened ventrally as smooth ridges which disappear ventrolaterally (Text-fig. 3). The ventral surfaces of the centra are not flattened and there is no medial trough. Instead, the ventral surface of each centrum is concave anteroposteriorly and smoothly convex transversely. The transverse processes (t. pr. in Text-fig. 3) are represented by abraded bases. They originate immediately behind the anterior margins of the vertebrae at progressively lower levels from the first to the third sacral, with that of the fourth originating at the same level as the third. The transverse processes of the first sacral originate high on the laminae of the neural arches and immediately behind the vertical plane of the anterior margin of the centrum. On the right side, the broken transverse process is represented by a horizontally elongate triangular cross-section. The transverse processes of the second, third and fourth sacrals are stouter, broad-based structures originating on the centra. The bases of these processes are angled obliquely backwards at about 50° to the axis of the sacrum. From each transverse process base, an anterodorsal and posterodorsal ridge extend up to become confluent with the neural arch.

The laminae of the neural arches of adjacent sacrals are fused, obliterating the zygapophyses. Between the neural arches of the third and fourth sacrals, the zone of fusion can be seen as a thin line with thickening of the bone on either side of it. The laminae rise and curve steeply towards the apex of the neural arch. On the left side, the neural arches are sufficiently exposed that it is clear that no neural platform is present.

The neural spines of sacrals 1–3 are fragmentary but can be seen to be discrete structures ankylosed at their dorsal extremities to form a continuous dorsal bar of bone. At the level of the fourth sacral vertebra, this bar is subrectangular in cross-section and is 5 mm deep, 3·5 mm wide across its upper margin and 2 mm wide across its ventral margin. A similar bar was described in *Pteranodon* by Eaton (1910). The neural spine of the fourth sacral (c.n.s. in Text-fig. 3) is relatively intact and is thickened anteriorly, narrowing to a slender blade posteriorly.

*Systematic position.* BMNH R176 is a pterodactyloid sacrum, characterized by the presence of progressive narrowing of centra posteriorly, transverse processes orientated obliquely backwards, and neural spines united by a bar of bone along their dorsal edges, combined with the absence of ventral flattening of the centra, absence of ventral groove and absence of neural platform. In all these features it differs from the troodontid sacrum BMNH R187 described above. It is similar in size to BMNH R187 and both comprise at least four ankylosed vertebrae with some fusion of the neural spines, but these are the only significant resemblances.

## DISCUSSION

The Troodontidae were small maniraptoran theropod dinosaurs growing to 2 m in total length. They had relatively large brains, widely spaced eyes, slender jaws with coarsely serrated teeth, long arms and retractable second digits on the feet. All previously described troodontid genera, namely *Troodon* (= *Stenonychosaurus*, *Pectinodon*), *Saurornithoides*, *Borogovia* and *Heptasteornis*, derive from the Campanian to Maastrichtian of North America and Eurasia. A literal interpretation of this chronological range might suggest that the troodontids were a late-appearing group of theropods. However Currie (1987) has argued that the troodontids are the closest relatives of birds. If the Troodontidae were the sister-group of the Avialae of Gauthier (1986) (i.e. the avian clade from *Archaeopteryx* upwards), then troodontids could be expected to be present from at least the Tithonian onwards when their sister-taxon first appears in the record. Milner and Evans (1991) redescribed *Lisboasaurus estesi* from the Oxfordian of Guimarota, Portugal, as fragments of a small maniraptoran theropod which could be either a troodontid or an avialan. The presence of Lower Cretaceous troodontids might therefore be predicted on cladistic grounds. There are sufficiently few rich Lower Cretaceous microvertebrate assemblages that the previous absence of early Cretaceous troodontids can be argued to be based on negative evidence.

Although its limited nature and stratigraphical separation from other troodontids necessitates caution in attribution, the sacrum of *Ornithodesmus cluniculus* does appear to represent the first record of a troodontid dinosaur from the Wealden of Europe and the earliest record of a troodontid. In view of the apparent closeness of troodontids to birds, it is ironical to note that *Ornithodesmus cluniculus* was originally identified as the sacrum of a primitive bird by Seeley (1887), before being reassigned to the ptserosaurs.

With the transfer of *Ornithodesmus cluniculus* to the Theropoda, a change in the nomenclature of the Isle of Wight Wealden pterosaur material is necessary. Seeley's species *latidens*, with the holotype BMNH R176, continues to be the valid name for the remaining described Isle of Wight pterosaur material. The unity of this material is clear and will be established by the senior author when work in progress is completed. This material now lacks a valid generic name and, as no similar form has been described from elsewhere, a new generic name is required. Pending the redescription and renaming of this material by the senior author, we suggest that it be referred to as '*Ornithodesmus*' *latidens*.

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# LATE TRIASSIC BRACHIOPODS FROM THE LUNING FORMATION, NEVADA, AND THEIR PALAEOBIOGEOGRAPHICAL SIGNIFICANCE

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ABSTRACT. Brachiopods from the Late Triassic Luning Formation are described from localities in the Pilot and Shoshone Mountains, Nevada. The spiriferids *Balatonospira*? cf. *B. lipoldi*, *Zugmayerella uncinata*, ?*Z.* sp., *Spondylospira lewesensis*, and the terebratulids *Plectoconcha aequiplicata*, *P. newbyi* sp. nov., *Rhaetina gregaria*, *R.* cf. *R. gregaria* and *Zeilleria* cf. *Z. elliptica* are described. This Luning fauna contains species known from western Europe (*Z. uncinata* and *R. gregaria*) and forms closely comparable to species known from western Europe are also present (*B.*? cf. *B. lipoldi* and *Z.* cf. *Z. elliptica*). Other species are only known from the Americas, *S. lewesensis* from displaced terranes in the cordilleran region of North America and from Peru, *P. aequiplicata* and *P. newbyi* sp. nov. from the displaced Paradise terrane of Nevada. Some of the brachiopods and associated corals, bivalves and foraminifers are conspecific with latest Triassic forms from central Europe. Ammonoids indicate the age of the fauna to be early Norian. The palaeobiogeographical distribution indicates existence of the Hispanic Corridor possibly as early as the Late Triassic which cannot be discounted as a possible migratory passage between Nevada and Tethys.

BRACHIOPODS were important benthic elements in shallow-water marine faunas during Late Triassic time. They are well known in Late Triassic sections of the former Tethys region in southern Germany, Austria and other Alpine regions farther east (e.g. Suess 1854; Zugmayer 1880; Bittner 1890; Dagys 1974). Along with sponges, foraminifers, corals, molluscs, and echinoderms, brachiopods are a common constituent of Late Triassic rocks in western North America. Many brachiopods occur in carbonate rocks, representing deposition in warm, relatively shallow-water environments of tropical to subtropical latitudes (Stanley 1979). Despite their local abundance, few monographic studies have been devoted to Late Triassic brachiopods of North America, although the works of Logan (1964, 1967) and Hoover (1991) are exceptions. Mostly they have been described in some of the pioneering studies on the western part of the continent (Gabb 1864; Hall and Whitfield 1877; Whiteaves 1889; Clapp and Shimer 1911; Smith 1914, 1927; Lees 1934). Brachiopods mentioned by the above authors included spiriferids, rhynchonellids and terebratulids, some of which were endemic to North America, while others have European and Japanese affinities (Ager and Westermann 1963). Late Triassic and Early Jurassic rhynchonellids from British Columbia were described by Ager and Westermann (1963), including a revision of some species originally described by Smith (1927).

Brachiopods in western North America frequently occur in reef-like buildups (Stanley 1979), few of which are comparable in terms of size and facies development to those of the Tethys region of western Europe (Stanley 1980, 1982). In North America, Late Triassic examples occur in rocks belonging to various displaced terranes, many of which have geological histories independent of the craton of North America (Coney *et al.* 1980; Nur and Ben-Avraham 1982). The significance of Triassic to Jurassic faunas in assessing the former positions of displaced terranes has been highlighted during the past decade (e.g. Tozer 1982; Hallam 1986; Smith and Tipper 1986; Stanley 1987; Newton 1988); ammonoids, bivalves and corals have been emphasized, excluding other commonly occurring faunal elements. Triassic brachiopods appear to be a group offering excellent possibilities for such studies but have so far been neglected; the group is among those that are being

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used to investigate Permian palaeogeography of terranes from the American Cordillera (e.g. Stevens *et al.* 1990).

The Triassic brachiopod fauna described here (Text-figs 1–3) is the most taxonomically diverse known for the Mesozoic of North America probably because so little detailed collecting and systematic study has been done. The brachiopod fauna contains only spiriferids and terebratulids. The following have been identified from the Lower Member of the Luning Formation, in Dunlap and Cinnabar Canyons, Pilot Mountains (Text-figs 1, 3), *Balatonospira*? cf. *B. lipoldi*, *Zugmayerella uncinata*, ?*Z.* sp., *Spondylospira lewesensis*, rare *Plectoconcha aequiplicata*, *P. newbyi* sp. nov., *Rhaetina gregaria*, *R.* cf. *R. gregaria*, and *Zeilleria* cf. *Z. elliptica*. From West Union Canyon, Union District, Shoshone Mountains, *Spondylospira lewesensis*, *Plectoconcha aequiplicata*, small specimens of *Rhaetina gregaria*, and *Zeilleria* cf. *Z. elliptica* have been identified. Specimens collected from the Pilot Mountains by S. W. Muller in 1934 and by D. E. Cornwall in 1979 were also studied. Of the brachiopods described herein, *B*? cf. *B. lipoldi*, *Z. uncinata*, *R. gregaria*, and *Z.* cf. *Z. elliptica* have Tethyan affinities.

Muller and Ferguson (1936, 1939) recorded *Spiriferina gregaria* Suess, *Spiriferina peneckei* Bittner, *Terebratula debilis* Bittner, *Terebratula julica* Bittner and *Terebratula suborbicularis* Munster var. *typica* Bittner from the Luning of Dunlap Canyon, Pilot Mountains. The brachiopods listed by Muller and Ferguson are most likely referable to the following taxa described herein (followed by original designation): *Spondylospira lewesensis* (Lees), (*Spiriferina gregaria* Suess); *Zugmayerella uncinata* (Schafhaeutl), (*Spiriferina peneckei* Bittner); *Zeilleria* cf. *Z. elliptica* (Zugmayer), (*Terebratula debilis* Bittner); *Rhaetina gregaria* (Suess), (*Terebratula julica* Bittner, although Cooper (1983, pp. 51–52) has referred fifteen Late Triassic specimens from Table Mountain, Hawthorne quadrangle, Nevada, lacking dental lamellae, to 'Triassic genus and species undetermined'. The specimens of Muller and Ferguson (1939, p. 1599) were from Dunlap Canyon. *Rhaetina gregaria* lacks dental lamellae); *Plectoconcha newbyi* sp. nov., (*Terebratula suborbicularis* Munster var. *typica* Bittner).

In a broad overview of Tethyan faunas in North America Kristan-Tollmann and Tollmann (1983) recorded '*Spiriferina*' aff. *munsteri* Davidson, *Zugmayerella* aff. *uncinata* (Schafhaeutl), '*Rhynchonella*' cf. *austriaca* Suess, '*Rhynchonella*' sp. and '*Terebratula*' sp. from the Luning Formation of Dunlap Canyon, Pilot Mountains. The papers by Muller and Ferguson (1936, 1939) and Kristan-Tollmann and Tollmann (1983) lacked serial sections of the brachiopods.

## TECHNIQUES AND CONVENTIONS

For this study transverse serial sections were taken to investigate the internal structures of a number of specimens. A full description of the technique and equipment used in the preparation of serial sections in the Palaeontology Laboratory, Department of Geology, University of Dayton was given by Sandy (1989), wherein additional references can be found. Images from acetate peels were drawn using a Nikon SMZ-10 binocular microscope and drawing tube. All serial sections are drawn with the brachial valve lowermost.

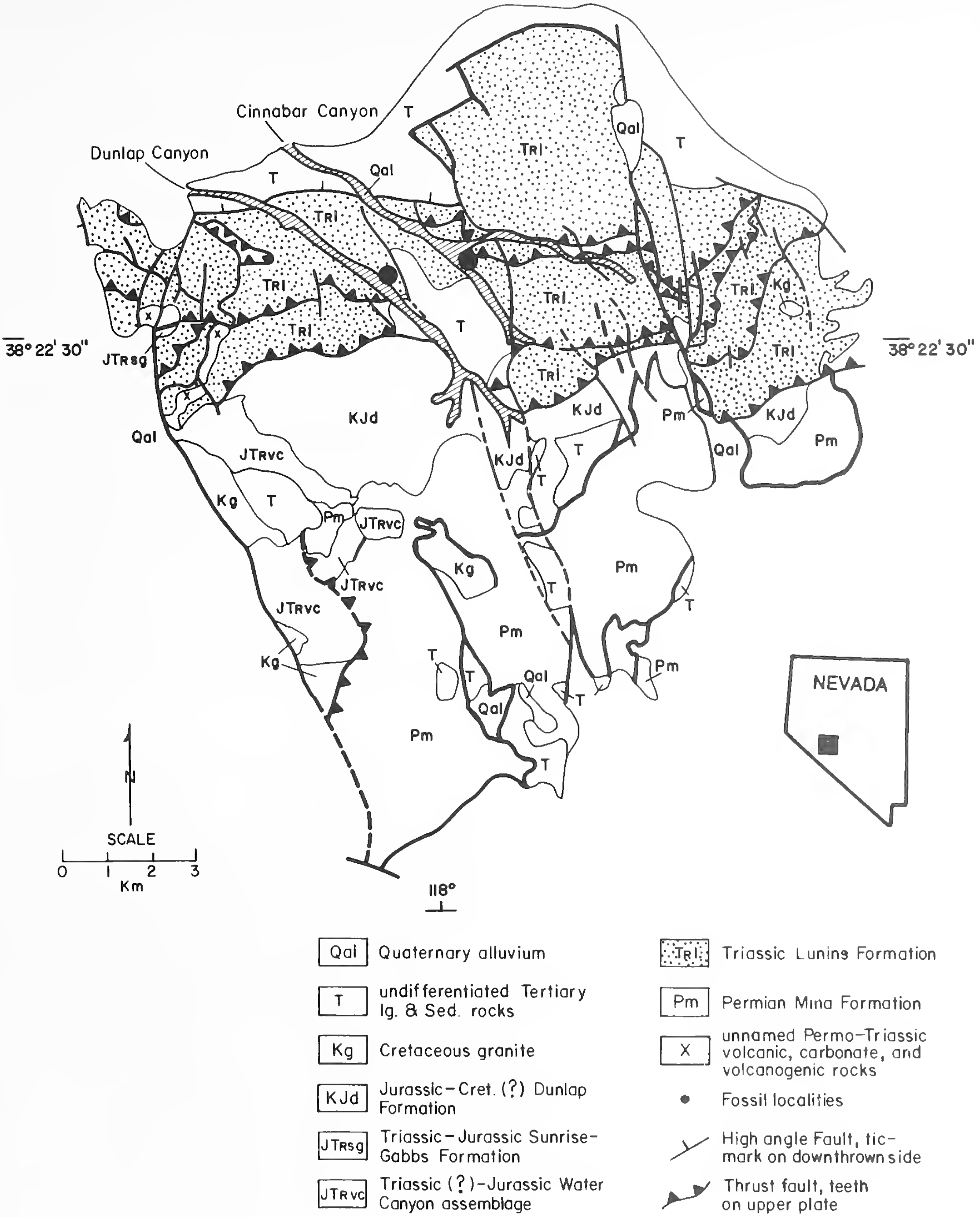
Annotations for synonymy lists and open nomenclature follow those proposed by Richter (see Matthews 1973).

The following dimensions are used: L = length; Lbv = length of the brachial valve; W = width; T = thickness; + = damage in that orientation. All dimensions are given in mm.

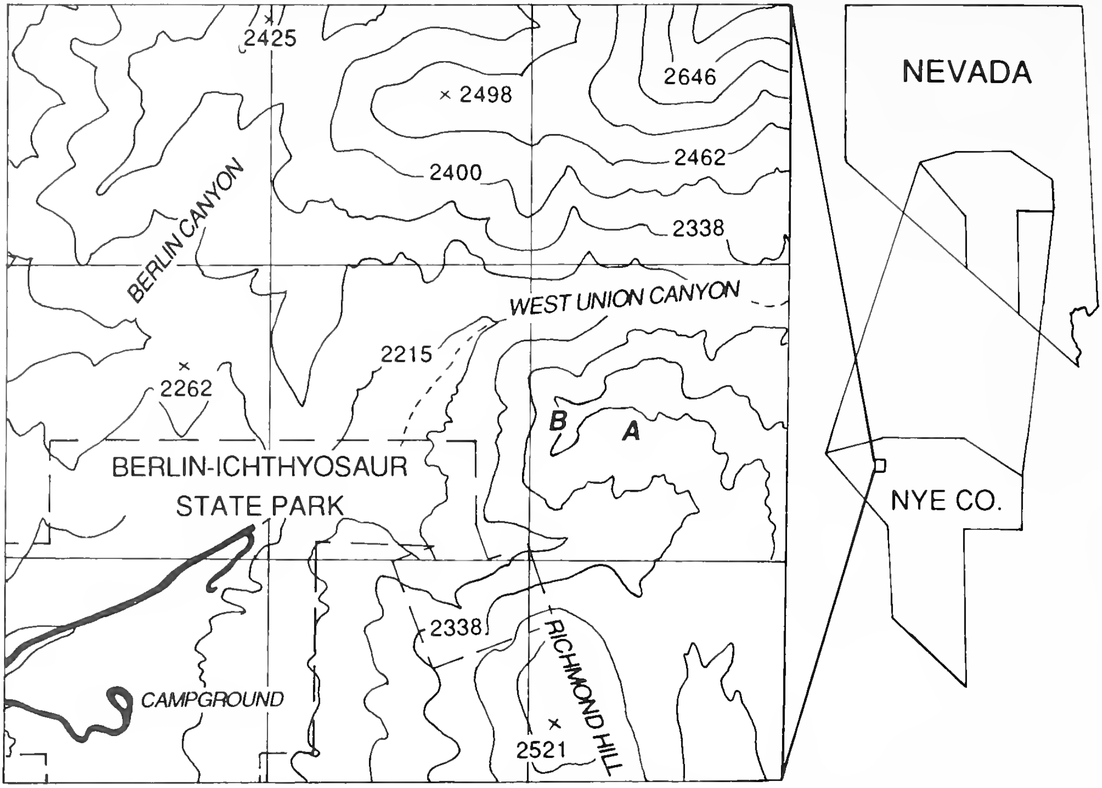
## STRATIGRAPHY

### *Lithostratigraphy*

The Luning Formation is widely exposed within numerous thrust sheets in the Pilot Mountains, east of the town of Mina, as well as in the Garfield and Royston Hills, Shoshone and Cedar Mountains and Paradise Mountain Range to the north, west and east of the Pilot Mountains. In its type locality



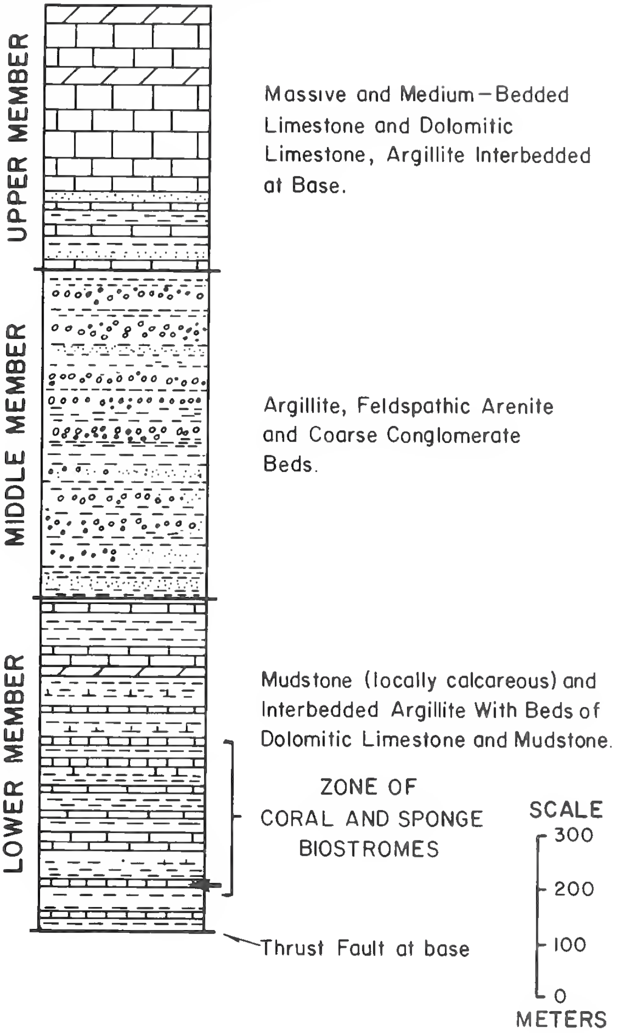
TEXT-FIG. 1. Geological map of a portion of the Pilot Mountains showing structural relations and approximate location of fossil localities in Dunlap and Cinnabar Canyons (black dots). Map from Oldow (1981). Outline of State of Nevada shown to bottom right of map, black square indicates location of Pilot Mountains.



TEXT-FIG. 2. Location of collecting sites in West Union Canyon, Berlin-Ichthyosaur State Park, Nye County, Nevada. A = locality with large *Plectoconcha aequiplicata* (Gabb); B = 'Brachiopod Ledge' with small *Plectoconcha aequiplicata* (Gabb). Both localities in the limestone and secondary dolomite member of Silberling and John (1989), Luning Formation. Roads represented by solid black line, tracks by short dashed line, State Park boundary by long dashed line. Map based on Ione 15′ quadrangle map, Township 12 North, Range 39 East. Contour interval 60·96 m (200 feet). All elevations converted to metres.

the Luning Formation is more than 2·5 km thick, with lithologies ranging from limestone and dolomite to argillite, sandstone, and conglomerate. The type Luning is part of the Luning Allochthon (Oldow 1981) which includes a series of nappe thrusts moved considerable distances to the southeast as part of the Paradise terrane (Silberling 1990).

The brachiopods from the Pilot Mountains come from the so-called 'coral reef' facies in the Lower Member of the Luning (Text-fig. 3). According to Muller and Ferguson (1939), this facies occurs in a consistent stratigraphical position within the 775 m thick member and is therefore of value in correlating between different thrust blocks. Muller (1936) discussed the occurrence of 'coral reefs' in the Luning Formation from this area based on well-exposed outcrops in Dunlap Canyon. Here the facies is about 60 m thick, traceable as far as 130 km to the north. The rock and fossil associations within this interval in the Pilot Mountains were studied by Stanley (1979) who considered them not to be reefs but, small, bedded biostromal buildups of impure limestone which alternate with thin argillite and mudstone beds. Some of these limestones are dominated by abundant corals and sponges, while others are characterized almost entirely by a very large mytilid bivalve *Trichites* sp. and '*Ostrea*' *montiscaprilis*. Individual limestone beds of corals and sponges can be traced along strike for up to 1·5 km. They range from 1·5 m to 10·0 m thick, and pinch and thicken laterally along their outcrop (Stanley 1979, p. 10). At the top of one measured section



TEXT-FIG. 3. Generalized stratigraphy of the Luning Formation, Pilot Mountains, showing the subdivision into three informal members. The brachiopods described herein occur near the base of the Lower Member, within an interval of coral and sponge biostromes (horizons indicated by solid arrow). Stratigraphy generalized from unpublished field notes of J. S. Oldow.

(loc. MC, Stanley 1979, Appendix A) a massive limestone and dolomite interval 23 m thick contains bioclastic debris and cross-bedded oolitic zones. The Pilot Mountain fauna of Stanley (1979) consists of rare foraminifers, five species of chambered sponges, five species of spongiomorphs, twenty-three species of corals, and numerous and diverse bivalves; indeterminate gastropods, a nautiloid, ostracodes, echinoids, crinoids and brachiopods also occur. Notably absent from thin sections or sieved material in the argillites is any kind of involutinid foraminifer or calcareous algae which might be diagnostic of age or environment. From interbedded argillites, skeletal remains of large ichthyosaurs are common (Camp 1980). The sponges previously investigated by Seilacher (1962) have been revised (Senowbari-Daryan and Stanley 1992). Benthic foraminifers, sponges, corals, an ammonite, brachiopods and crinoid columnals were illustrated by Kristan-Tollmann and Tollmann (1983).

In Berlin-Ichthyosaur State Park the Luning Formation consists of four members – clastic, shaly limestone, calcareous shale and carbonate (Silberling 1959). Silberling and John (1989) redescribed four members of the Luning Formation in the Berlin Allochthon of the Paradise Range as 'clastic rock member', 'shaly limestone and calcareous shale member', 'phyllite, grit and conglomerate member' and 'limestone and secondary dolomite member'. Hogler (1990) identified three biofacies in the formation, the 'benthic bivalve', 'ammonite/ichthyosaur/thin-shelled bivalve', and 'brachiopod/gastropod' biofacies. A velellid medusoid hydrozoan was reported from the Luning Formation of the Shoshone Mountains by Hogler and Hanger (1989). The brachiopods described here were collected from the 'limestone and secondary dolomite member' of Silberling and John (1989) ('carbonate member' of Silberling 1959, 'brachiopod/gastropod biofacies' of Hogler 1990) in West Union Canyon (Text-fig. 2). Large specimens of *Plectoconcha aequiplicata* were obtained loose from talus, while small specimens of the same species were obtained *in situ* from an exposure informally named 'Brachiopod Ledge' (Hogler, personal communication; Text-fig. 2). The diverse ammonoid fauna from Union Canyon (Muller and Ferguson 1939; Silberling 1959; Kristan-Tollmann and Tollmann 1983) occurs at stratigraphical levels below that of the 'limestone and secondary dolomite member'. Kristan-Tollmann and Tollmann (1983) also recorded four bivalves, a crinoid, and seven taxa of foraminifers.

### *Biostratigraphy*

Corals from limestones of the Luning Formation in Dunlap Canyon were originally identified as of Jurassic age, but subsequently as Late Triassic (Norian) (Smith 1927, p. 9). Muller and Ferguson (1939) assigned the entire Luning Formation to the Carnian. Silberling and Roberts (1962) and Silberling and Tozer (1968) established the formation as a transgressive unit ranging from the latest Carnian into the mid and possibly late Norian. Silberling (personal communication) places the coral biostromes of the Lower Member of the Luning in the Pilot Mountains in the Kerri ammonite Zone (early Norian) based on the occurrence of *Mojsisovicsites kerri*; the brachiopod-bearing beds in the Shoshone Mountains range from the Kerri to Magnus ammonite Zones (early Norian). According to previous work, none of the Luning in the Pilot Mountains is any younger than the mid Norian. Ammonites are not common in the sections studied, but the association of spiriferid and terebratulid brachiopod species identified herein could be useful in identifying early Norian strata elsewhere.

Kristan-Tollmann and Tollmann (1983) illustrated ammonites from the Luning Formation at Union Canyon and the Pilot Mountains. At the latter locality, their discovery of *Pararcestes*, a genus also known from Austria in the Early Norian Kerri Zone, and in Union Canyon the occurrence of many species of ammonoid and halobiid bivalves, confirm previous assertions of a range from late Carnian into the early and mid Norian Stages. The presence, for example, of *Klamathites macrolobatus*, *Klamathites schucherti*, *Stikinoceras kerri* and *Guembelites jandianus* in the Union Canyon section (Silberling 1959) records the passage from the late Carnian to the early Norian in strata just below those of the brachiopod localities (Text-fig. 2).

Ager (1987, 1990) defended the Rhaetian as the last stage in the Triassic, contrary to Tozer (1980, 1988, 1990) and Silberling and Nichols (1988). There are similarities between the brachiopods described herein with those of the European Rhaetian, but the brachiopod-bearing part of the Luning can be assigned an early Norian age based on the ammonites. Some of the brachiopod taxa are long-ranging forms which were geographically widely dispersed. Mesozoic brachiopods are of use in biostratigraphy when conventional stratigraphically useful fossil groups such as ammonites and microfossils are absent. Ager (1979) suggested that rhynchonellids are the most useful brachiopods in Mesozoic stratigraphy.

Ager (1987, p. 10) considered that the brachiopods from the Pilot Mountains support a Rhaetian age for the Luning Formation. Ager reiterated this (1990, p. 9), with *Rhaetina* cf. *gregaria*, *Zugmayerella uncinata* and *Austrirhynchia*? sp. being named as characteristic Rhaetian forms. Of these, only the last named is restricted to the Rhaetian, *R. gregaria* and *Z. uncinata* are longer-ranging species of genera that also range beyond the Rhaetian. *Rhaetina gregaria* 'is without doubt the commonest and most widely distributed of the Rhaetian brachiopods' (Pearson 1977, p. 38) and it has been identified as a guide fossil for the Alpine Rhaetian, although it is probably not restricted to the Rhaetian. Therefore, its presence in the Luning Formation of Nevada does not support a Rhaetian age (*sensu* Ager 1990) for the Lower Member of the Luning Formation in the Pilot

Mountains. The identification of *Austrirhynchia*? sp. in the Late Triassic of Nevada was based on a few brachiopods collected by Stanley in 1975. Subsequent collections from the Luning in 1990 have allowed detailed taxonomic study of the brachiopods, including serial sections, and Ager's (1990) *Austrirhynchia*? sp. is now referred to *Balatonospira*? cf. *B. lipoldi* (Bittner) herein. *Balatonospira lipoldi* has been recorded from the Ladinian?–Carnian (Dagys 1974; Siblik 1988). *Balatonospira*? cf. *B. lipoldi* appears to be a closely related form from the early Norian. *Zeilleria* cf. *Z. elliptica* does not provide specific stratigraphical information, other than it has a resemblance to some Norian species.

Ager (1990) stated that the absence of *Halorella* in the Nevada brachiopod fauna was evidence for a Rhaetian age because this genus is typical of the Norian elsewhere. It is thought unlikely that this absence indicates a Rhaetian age. Of the other brachiopods, *Plectoconcha aequiplicata* was originally described by Gabb (1864) from the East Range, Nevada. It was recorded from the Dun Glen Formation, Magnus Zone, which is late early Norian (Silberling, personal communication). *P. aequiplicata* has also been collected from the Luning of Union Canyon and a few specimens from the Pilot Mountains, where *P. newbyi* sp. nov. also occurs. The genus may be indicative of the early Norian. Hoover (1990) suggested that *Spondylospira* was not restricted to the Norian and ranged into the earliest Jurassic of Central Peru.

## PALAEOECOLOGY

According to Muller and Ferguson (1939), rocks of the Luning Formation in the Pilot Mountains can be divided into three distinct biofacies, each characterized by a distinctive faunal association. The first is a nearshore facies represented by bivalves, especially the large oyster '*Ostrea*', which locally forms thin 'banks'. The second facies was termed a 'coral reef' by these authors because of the predominance of abundant scleractinian corals and sponges. Brachiopods flourished during clearwater phases; they are closely associated with invertebrates that inhabited small-scale biostromes which existed in lagoonal environments offshore from areas of active deltaic and carbonate shelf sedimentation. The small-scale biostromes attained at best only a few metres of relief above the surrounding sea floor. Lack of algae and a predominance of low-energy (micritic mud) matrices indicate that the biostromes may have inhabited settings within deeper or turbid waters. Depths of up to 60–70 m were estimated. Ammonoids are rare from the biostromes and their associated sediments. The third facies type is argillaceous, bearing an ammonoid fauna and representing offshore, deeper water environments.

Palaeoecological zonation is apparent among the corals, sponges and other invertebrates in the biostromes, as indicated by vertical succession and quantitative point-count studies on bedding surfaces (Stanley 1979). Other palaeoecological relationships, including overgrowth encrustations by corals and sponges, substrate stabilization by thalamid sponges, boring by lithophagous bivalves, and cryptic niche habitats have been recognized. Episodic influxes of fine-grained (clay and silt-size) siliciclastic sediment were deleterious to the corals and other invertebrate organisms, periodically engulfing them. As outlined by Stanley (1979), frequent extermination is clearly evident in measured sections with at least five or six thin coral biostromes occurring within a 115 m interval. The top of each biostrome is draped by unfossiliferous mudstone and argillites, preserving *in situ* the invertebrate fauna.

The presence of pockets or cavities formed by overgrowth of encrusting and laminar corals was reported within some of the biostromes by Stanley (1979). Many of these cavities contained abundant spiriferid brachiopods, *Zugmayerella uncinata*, in gregarious 'nestled' associations. Presumably, therefore, these brachiopods had functional pedicles into adulthood (cf. Hoover 1983). Such 'nestled' associations within reef cavities seem good evidence for cryptic habitats and gregarious lifestyles for this brachiopod. One specimen of this species has an example of the trace fossil *Oichnus* Bromley (1981) towards the posterior end of the pedicle valve sulcus. It probably originated from predation on the living brachiopod and indicates that the pedicle valve was accessible for attack; the interarea of the pedicle valve may have been protected by being close to a substrate. A few specimens of this brachiopod were collected from thin shale interbeds (*c.* 0·1 m thick) within unit 35 of Stanley (1979, p. 53). Three specimens were observed with their pedicle valve lowermost. If they were preserved in life positions, this may represent an alternative strategy for exploitation of a fine-grained clastic substrate. The terebratulids and other spiriferid brachiopods do not appear to show much in the way of life associations within the lower member of the Luning. Brachiopod-rich 'pockets' are apparent in the field, although life position is not suggested by the orientation of the specimens. They may represent little-transported, post-mortem accumulations within depressions on the substrate. However, one specimen of *Plectoconcha newbyi* sp. nov. was observed in Dunlap Canyon with its pedicle umbo and brachial valve resting directly on a flat, horizontal sponge, this may represent burial of a brachiopod while still attached to its substrate.

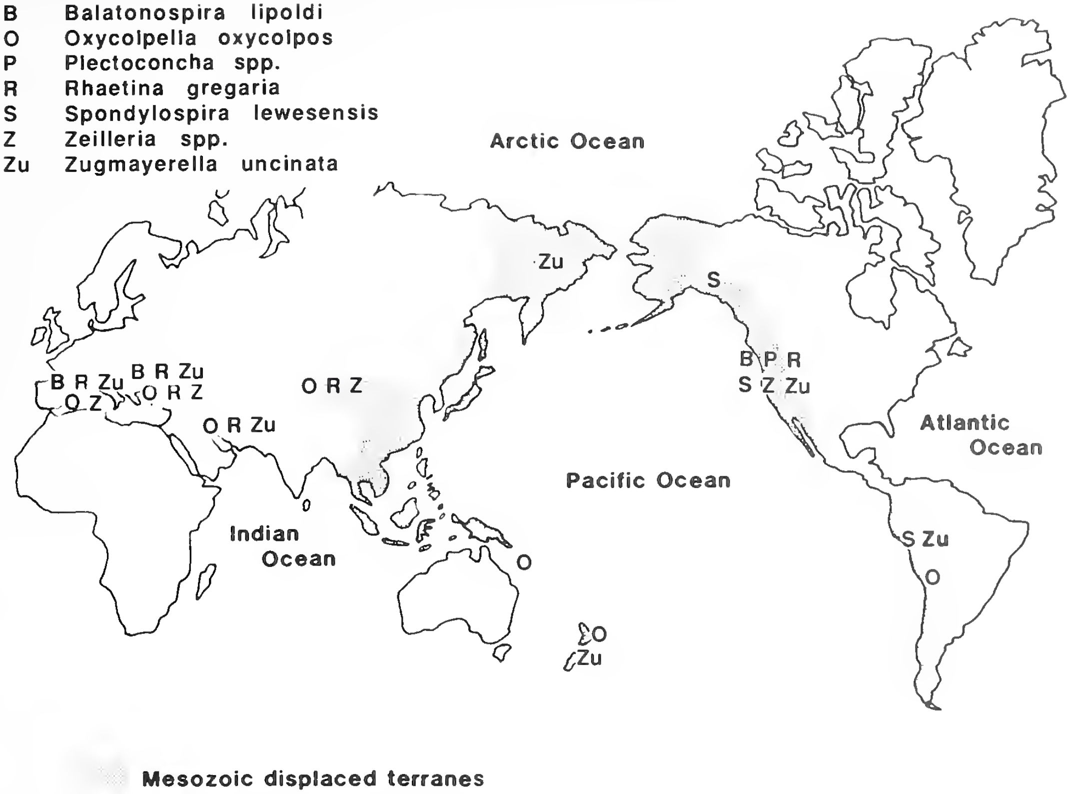
Rhynchonellids appear absent in the collections studied herein. *Plectoconcha aequiplicata* initially may be mistaken for a rhynchonellid, as did Gabb (1864) in his original description. Kristan-Tollmann and Tollmann (1983) recorded '*Rhynchonella*' cf. *austriaca* Suess (possibly *Balatonospira*? cf. *B. lipoldi* herein) and '*Rhynchonella*' sp. from the Pilot Mountains localities. The scarcity of rhynchonellids may be related to environment. The small, costate spiriferid *Balatonospira*? cf. *B. lipoldi* may be occupying the role of a rhynchonellid generalist in the fauna.

The three successive biofacies identified by Hogler (1990) in the Luning formation of the Shoshone Mountains were interpreted as indicating 1) a relatively shallow, normal marine, current-washed setting, 2) deeper, less well ventilated bottom waters, and 3) a return to shallower, more turbulent, and better oxygenated conditions.

## PALAEOBIOGEOGRAPHICAL DISCUSSION

Dagys (1974) provided the most comprehensive evaluation of Triassic brachiopod biogeography. He identified three regions, the Boreal, Tethyan and Maori, for latest Triassic brachiopods (Dagys 1974), and pointed out that these had been established earlier in the Triassic. The Tethyan region is characterized by the greatest faunal diversity; about 80 per cent of the species belong to families not known outside this region, and two distinct faunas are identifiable. One is in the Alps, Carpathians, Crimea, Caucasus, Pamirs and Indochina; the other in Oman, the Himalayas and Indonesia, the latter characterized by less diversity. Endemism was high enough for Dagys to consider these regions as the Alpine and Indian subregions which equate with the northern and southern shores of the Mesozoic Tethys (Ager and Sun 1989). The Boreal region includes the northeastern area of Asia and Primor'ye and only the northeastern former USSR in the latest Triassic; rhynchonellids and spiriferinids predominate in this fauna. The brachiopod fauna of the Maori region (New Zealand and New Caledonia) differs from that of the Tethyan region by its sharply reduced diversity (Dagys 1974). Campbell (1985) reviewed the status of the Maori province.

The occurrence of some Triassic brachiopod species both in North America and European Tethys has been remarked upon. Smith (1927) commented on the very close resemblance of some species he described from the Triassic of the Western Cordillera of North America to species described from Europe. A number of the new brachiopod species he described probably represent taxonomic over-splitting and might obscure palaeobiogeographic relationships, and he incorrectly referred some rhynchonellids to the terebratulid *Dielasma* (Ager and Westermann 1963). Logan (1964) in describing *Spiriferina abichi* (Oppel 1865) from Ladinian to Carnian cratonal rocks of northeastern British Columbia provided an interesting species-level link between the North American craton and the Oman and the Himalayas. *Zugmayerella uncinata* has been recorded from the Late Triassic of Nevada and Europe (Stanley 1979; Text-fig. 4), and the rhynchonellid *Halorella amphitoma* Bronn var. *rarecostata* Bittner, 1890 from Oregon is con-subspecific with material from the Alps (Schenk 1934; Ager 1968; Ager and Sun 1989). In western North America *Halorella* has been recorded from east-central Oregon and north-west Nevada. The Oregon material is from the Fields Creek Formation and Rail Cabin Argillite in the Izee terrane (Schenk 1934; Dickinson and Vigrass 1965; Silberling, personal communication). However, Brown and Thayer (1977) interpreted this *Halorella* to come from limestone slide blocks probably derived from mélange areas to the northeast and



TEXT-FIG. 4. Map showing present-day geography and the distributions of brachiopod genera and species recorded from the Luning Formation, Nevada, and *Oxycolpella* (from Kristan-Tollmann 1987). Key to letters given in top left corner of figure. B = *Balatonospira*? cf. *B. lipoldi* in Nevada. Sources of summaries of occurrence: *Balatonospira lipoldi*, Siblik 1988; *Rhaetina gregaria*, Pearson 1977; *Spondylospira lewesensis*, Hoover 1983, the genus has also been identified in the Koryak Range, north east former USSR; *Zeilleria* spp., Delance 1974; Ching *et al.* 1979; *Zugmayerella uncinata*, Pearson 1977; and *Oxycolpella oxycolpos*, as interpreted by Kristan-Tollmann 1987. Map adapted from Stanley 1988.

hence from the Baker terrane. *Halorella* also has been collected from the Jungo terrane in the vicinity of Muttlebury Pass, West Humboldt Range, north-west Nevada (Silberling, personal communication). In a recent study of cyrtinoid spiriferinacean brachiopods from western North America, Hoover (1991) considered that there were no species in common with Tethys. Our study, considering spiriferinaceans and other articulate brachiopods, reaches different conclusions.

*Plectoconcha* and *Spondylospira* have been interpreted as endemic respectively to western North America and North and South America (Text-fig. 4), although the latter genus has been identified in the Koryak Range (northeastern former USSR) by Bychkov and Dagys (see Hoover 1991, pp. 68, 81). The only genus that Cooper (1983) considered similar enough in its internal structures to belong in the same subfamily as *Plectoconcha* is the plicate *Merophricus*, from the Early Jurassic of the Middle and High Atlas, Morocco.

The circumtropic distribution of the Upper Triassic athyrid brachiopod *Oxycolpella oxycolpos* (Suess) has been emphasized by Kristan-Tollmann (1987). She recorded the species from the northern Calcareous Alps of Austria and Bavaria, the eastern Mediterranean (Turkey to Iran), the Himalayas, China, New Caledonia and New Zealand. It is interpreted as a species with a very variable external morphology over its broad geographical range. A detailed taxonomic investigation including information on the internal structures of this species as interpreted by Kristan-Tollmann (1987) would be very useful to reduce the possibility of external homoeomorphy. If the distribution of *O. oxycolpos* considered by Kristan-Tollmann (1987, fig. 2) is plotted on a Late Triassic palaeogeographic base-map (e.g. Norian map in Scotese *et al.* 1987, cf. Text-fig. 4) representing present-day geography), then the distribution of this species falls mainly between the palaeolatitudes of 30° N and 30° S. Its occurrence in New Zealand gives a questionable southern high latitude record that could imply a circum-Gondwanaland distribution. However, displaced terranes of possible Tethyan origin are present in New Zealand (e.g. Bishop *et al.* 1985). *Halorella* is another Tethyan brachiopod recorded from New Zealand. It is known from the Torlesse terrane (Milne and Campbell 1969; Campbell 1985; Ager 1986). *Canadospira* appears to be a temperate or cool water form, known from the Canadian Arctic and the northeastern part of the former USSR (Dagys 1974).

The presence of a number of Triassic invertebrate species from a variety of fossil groups in both the Tethys of Europe and a number of displaced terranes from North America presents something of a palaeobiogeographical and palaeogeographical enigma. For example, many of the coral species from the Luning Formation are characteristic of the latest Triassic Rhaetian Reef Limestone, Koessen Beds and Dachstein Limestone of Austria and southern Germany (Stanley 1979). The same could also be said for some of the bivalve, brachiopod and spongiomorph species. These occurrences are not only possibly facies related, but also record earlier occurrences of some species in North America. A number of theories have been put forward to explain these occurrences (summarized from Stanley 1991): (1) beached funeral Viking ships, referring to tectonically transported fossil faunas across the Mesozoic Pacific (Panthalassa); (2) steady-state dispersal, where invertebrate larvae are transported across the Panthalassa by favourable currents and terranes do not need to be far travelled (Kristan-Tollmann and Tollmann 1981 suggested a North American–Tethyan dispersal; Newton 1988 favoured a Tethys–American dispersal); (3) stepping stones, a dispersalist approach, whereby a series of small volcanic terranes may have enabled steady state dispersal; (4) Staging Posts and Noah's Arks, a vicariance approach, with terrane dispersal by plate-tectonic processes with concomitant evolution of faunas and ultimately extension of biogeographical ranges (Flügel *et al.* 1989; Smith *et al.* 1990; Stanley 1988); and (5) Hispanic Corridor, an embryonic seaway thought to have been in existence between western Tethys and eastern Panthalassa, allowing exchange of faunas since the Early Jurassic (Smith 1983; Smith *et al.* 1990), but possibly operating since the Triassic. Palaeobiogeographical information for Late Triassic brachiopods of North America is as yet limited, but is discussed below in the light of the present study. A major consideration has to be the location of the Nevadan Paradise terrane during the Late Triassic and whether the biogeography of the fauna can assist in interpreting geography. The Paradise terrane is the most inboard terrane and during the Triassic probably was closer to North America than others.

Brachiopods are limited in their dispersal potential by their sessile, benthic mode of life and it has been suggested that like extant taxa, post-Palaeozoic articulate brachiopods possessed non-planktotrophic larvae (Valentine and Jablonski 1983). Similar limitations on dispersal were presented for Late Triassic dasycladacean algae from Oregon which show close taxonomic affinities with examples in Italy (Flügel *et al.* 1989). This would contrast with dispersal among other Triassic invertebrates such as ammonoids and bivalves which possessed planktotrophic larvae. Such differences in larval development would therefore make brachiopods suitable for palaeobiogeographical investigation, as they would be likely to develop endemism should gene-flow become severed. Of the 'European' Tethyan spiriferid and terebratulid species occurring in Nevada, none is closely related to living brachiopods and it would be speculative to say they had non-planktotrophic larvae.

Until more is known about the taxonomic composition of North American brachiopod faunas through at least the Triassic it is not possible to comment in any detail on the role of the beached funeral Viking ships model as a post-mortem dispersal mechanism. It is thought unlikely that if articulate brachiopods possessed non-planktotrophic larvae, they dispersed solely by ocean currents across the Triassic Pacific. However, it is clear that some Mesozoic articulate brachiopod genera were geographically widespread at times, through the low-latitudes of Tethys (e.g. Ager 1986; Sandy 1990), or from low to high latitudes (Sandy 1990, 1991*a*, 1991*b*). Ager and Sun (1989) suggested that some Mesozoic Tethyan taxa from southern Europe and North America were widespread at low latitudes, possibly crossing the Pacific by sea-mount hopping (also Ager 1986). By the Cretaceous, trans-Atlantic and trans-Arctic dispersal routes were established by more broadly latitudinally distributed genera (Sandy 1990, 1991*b*). A vicariance mode of dispersal utilizing island-hopping (which could include exotic terranes – newly formed seamounts and volcanic islands) aided by favourable currents could account for the occurrence of the Triassic 'European' species and endemic taxa in Nevada. Alternatively if accretion occurred during post-Triassic time in Nevada as suggested by Coney (1989), then the Paradise terrane could have acted as a beached funeral Viking ship.

The incipient central Atlantic Ocean began in the late Permian and during the Triassic tectonic activity resulted in crustal extension, volcanism and fault-controlled sedimentation, followed by the formation of a marine seaway (Hispanic Corridor) in the Triassic(?)–Jurassic which connected the western Tethys to the eastern Pacific. Sea-floor spreading started in the Middle Jurassic. The Hispanic Corridor (Smith 1983) was used to account for the distributions and dispersal directions of the earliest Jurassic molluscan taxa in the western Americas and Europe (Damborenea 1987; Damborenea and Manceñido 1979; Westermann 1981; Smith and Tipper 1986; Smith *et al.* 1990). The existence of marine basins west of southern Spain, open to the west and closed off from the Tethys to the east indicates an embryonic central Atlantic seaway during the Late Triassic. This is supported in part by stratigraphical and faunal occurrences (Martin and Braga 1987). The existence of an Atlantic seaway during Triassic time could explain some of the biogeographical relationships amongst the Nevadan faunas. While the presence of a Triassic marine connection between western Tethys and the eastern Pacific via the Gulf of Mexico region does not appear to be supported by stratigraphical data in central Mexico (Salvador 1987), the Late Triassic Barranca Group farther north in Sonora, has been interpreted as having been deposited in a rift-basin developed on the craton (Stewart *et al.* 1990). Undescribed marine invertebrates occurring at certain horizons show the existence of an east–west trending basin. Whether this basin connected eastward to other series of rift basins and eventually the Tethys is still open to discussion.

The relative timings of brachiopod occurrences is relevant to discussion of the Hispanic Corridor versus Panthalassa-bound dispersal. Both *Zugmayerella uncinata* and *Rhaetina gregaria* are known from the Norian of Europe (mainly western Tethys) and Nevada although they are typically Rhaetian in Europe. Delance (1974) recorded *Zeilleria elliptica* from the latest Triassic of Europe. *Zeilleria* cf. *Z. elliptica* is recorded here from Nevada. The Norian terebratulid *Plectoconcha* predates the probably-related *Merophricus* (Cooper 1983) from the Jurassic of the Middle and High Atlas, Morocco. These records of *Z. uncinata*, *R. gregaria*, *Z.* cf. *Z. elliptica* and *Plectoconcha* may indicate American–Tethyan dispersal. *Balatonospira lipoldi* is first known from the Ladinian?–Carnian of Europe and *B*? cf. *B. lipoldi* from the Norian of Nevada. The nature and timing of occurrences of these faunas might suggest a western Tethys–American migration. These indications of two-way exchange between faunas are not inconsistent with the operation of the Hispanic Corridor in the Norian to Early Jurassic. Other faunal elements from the Luning of Nevada (Pilot Mountains and Union Canyon) clearly indicate that Tethyan species are present (Kristan-Tollmann and Tollmann 1983): two halobiid bivalves, both Tethyan; seven sponges, mostly endemic (one known from the Stikinia terrane, two from Sonora and one from Tethys; Senowbari-Daryan and Stanley 1992); seven foraminifers, all Tethyan; seven corals, all Tethyan. Tethyan cephalopods are also present.

## MUSEUM ABBREVIATIONS

The following repository abbreviations are used: GBV, Geologische Bundesanstalt, Vienna, Austria; MSM, Mackay School of Mines Geological Museum, University of Nevada, Reno, USA; UMIP, University of Montana, Missoula, Invertebrate Palaeontology Collections, USA; USNM, former United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

## SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA Duméril, 1806
Class ARTICULATA Huxley, 1869
Order SPIRIFERIDA Waagen, 1883
Superfamily SPIRIFERINACEA Davidson, 1884
Family SPIRIFERINIDAE Davidson, 1884
Subfamily BALATONOSPIRINAE Dagys, 1974

*Diagnosis.* Small shells with ribbed sulcus and fold. Septum high, dental plates reduced. Jugum complete. Spinate microsculpture absent.

*Discussion.* (After Dagys 1974.) This monotypic subfamily differs from the Spiriferininae in the absence of both spinate microsculpture and dental plates. Discrimination from the Punctospirellinae which is similar in the nature of its microsculpture, is quite clearly made on the nature of the jugal structure and apical apparatus. Also lacking in spinate microsculpture is the Pennospiriferininae, from which the Balatonospirinae differ sharply in external appearance (shell form, character of area, ribbing, etc.), structure of the apical apparatus, as well as in the complete jugum.

### Genus BALATONOSPIRA Dagys, 1974

*Type species. Spiriferina lipoldi* Bittner, 1890, p. 139, pl. 28, figs 20–21, from the *Cardita* horizon, Carnian, of Hoch-Obir, Austria.

*Diagnosis.* (After Dagys 1974.) Slightly inequivalved shells of small size with a short hinge line and rounded hinge angles. Beak curved, area low, apsacline. Deltidial and chilidial plates disconnected. Lateral portions of valves, as well as fold and sulcus, are ribbed.

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### EXPLANATION OF PLATE 1

Figs 1–5. *Spondylospira lewesensis.* UMIP 6716; Lower Member, Luning Formation; from the low hills between Cinnabar and Dunlap Canyons, Nevada, north of the prominent andesite rhyolite hill (type locality of *Platyplateon nevadensis*); collected by Muller in 1934; brachial, pedicle, lateral, anterior and posterior views respectively. All × 1·5.

Figs 6–10. *Spondylospira lewesensis.* UMIP 20314 (sectioned, Text-fig. 10B); Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral, anterior and posterior views respectively. All × 1·5.

Figs 11–15. *Zugmayerella* cf. *uncinata.* UMIP 20348; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral, posterior and anterior views respectively. All × 1·5.

Figs 16–20. *Zugmayerella uncinata.* UMIP 20365; Lower Member, Luning Formation; Cinnabar Canyon, Nevada; brachial, pedicle, lateral, anterior and posterior views respectively. All × 2.

Figs 21–24. *Balatonospira*? cf. *B. lipoldi.* UMIP 20416 (sectioned, Text-fig. 7), Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1·5.

Fig. 25. *Balatonospira*? cf. *B. lipoldi.* UMIP 20328; Lower Member, Luning Formation; Dunlap Canyon, Nevada; anterior view. × 1·5.

Figs 26–30. *Balatonospira*? cf. *B. lipoldi.* UMIP 20350; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral, anterior and posterior views respectively. All × 1·25.

PLATE 1


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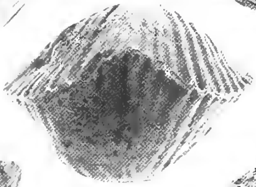
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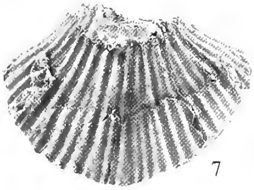
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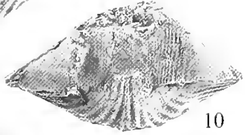
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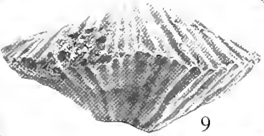
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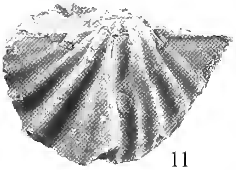
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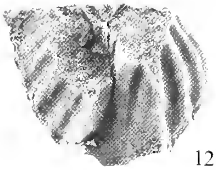
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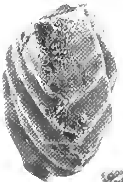
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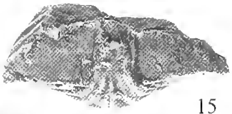
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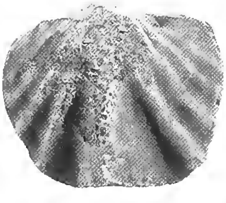
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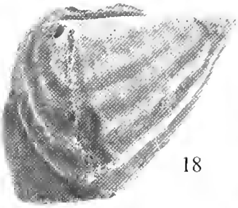
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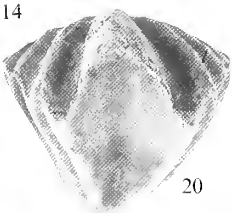
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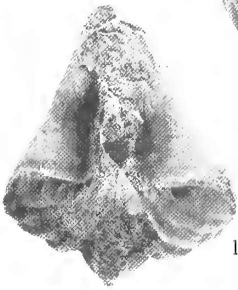
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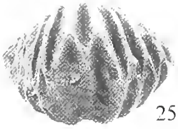
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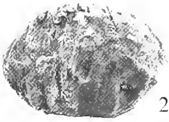
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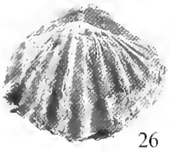
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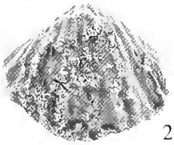
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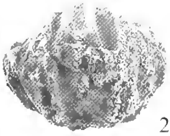
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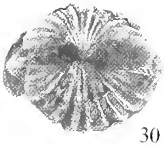
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SANDY and STANLEY, *Spondylospira*, *Zugmayerella*, *Balatonospira*?

*Discussion.* It is possible that *Balatonospira* is a junior synonym of *Sinucosta* (see discussion for *B*? cf. *B. lipoldi*).

*Occurrence.* Ladinian?–Carnian stage of the Alps; Carpathians and Caucasus (Austria, Hungary, Bulgaria, Yugoslavia, Italy and Israel).

### *Balatonospira*? cf. *B. lipoldi* (Bittner, 1890)

Plate 1, figs 21–30; Text-figs 5–7

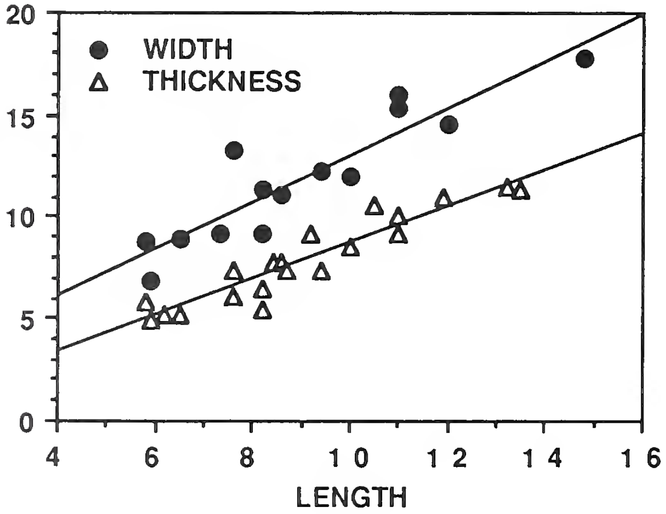
| | |
|---|---|
| cf. 1890 | *Spiriferina lipoldi* Bittner, p. 139, pl. 28, figs 20–21. |
| ? 1972 | *Balatonospira lipoldi* (Bittner); Detre, p. 89, pl. 1, fig. 2. |
| cf. 1974 | *Balatonospira lipoldi* (Bittner); Dagys, p. 137, pl. 39, fig. 1. |
| ? 1977 | *Pseudospiriferina leopoldi* (Bittner) [*sic*]; Ching and Feng, p. 49, pl. 2, figs 16–21. |
| v cf. 1978 | *Spiriferina* (= *Balatonospira*) *lipoldi* Bittner; Sieber, p. 170. |
| cf. 1988 | *Balatonospira lipoldi* (Bittner); Siblik, p. 62. |
| v 1990 | *Austrirhynchia*? sp.; Ager, p. 9. |

*Type material.* The holotype is lost (Siblik 1988).

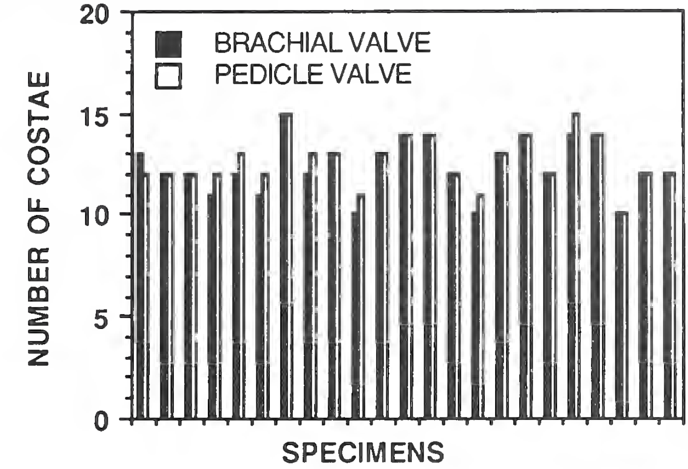
*Material.* Numerous specimens from the Luning Formation (beds 35 and 37 of Stanley, 1979, p. 53; Text-figs 1, 3), Dunlap Canyon; also common at Cinnabar Canyon. UMIP 6857, 20316, 20318, 20328–20331, 20335, 20341, 20345, 20350, 20361, 20371, 20379, 20384, 20386, 20396, 20400, 20404, 20415–20416 (sectioned), 20424, 20436.

*Diagnosis.* Medium sized spiriferinids, transversely oval, truncated outline, biconvex profile. Width greater than length; length greater than thickness. Incurved pedicle umbo, concave unornamented interarea. Triangular delthyrium with incipient deltidial plates. Ten to fifteen costae on each valve, two on brachial fold, one in pedicle sulcus. Punctate shell. Dental lamellae of brachial valve small, median septum persistent in pedicle valve. Dorsally directed crura.

*Description.* Small to medium sized spiriferids, up to 15 mm long, 18 mm wide and 12 mm thick (Text-fig. 5). Oval outline truncated by straight hinge line. Larger specimens have a strongly biconvex profile with an incurved pedicle umbo and an incurved, catacline pedicle valve interarea (see Logan 1967, text-fig. 6). Triangular delthyrium, incipient deltidial plates. Costae radiate from the umbos of each valve. Ten to fifteen costae on both valves (Text-fig. 6). Costate do not branch but are inserted laterally as the hingeline width



TEXT-FIG. 5. Plot of length versus width and thickness for *Balatonospira*? cf. *B. lipoldi* (Bittner); Pilot Mountains, Nevada. The correlation coefficient for length versus width is 0·830, and length versus thickness 0·883.



TEXT-FIG. 6. Bar graph of number of costae on brachial and pedicle valves of *Balatonospira*? cf. *B. lipoldi* (Bittner); Pilot Mountains, Nevada.

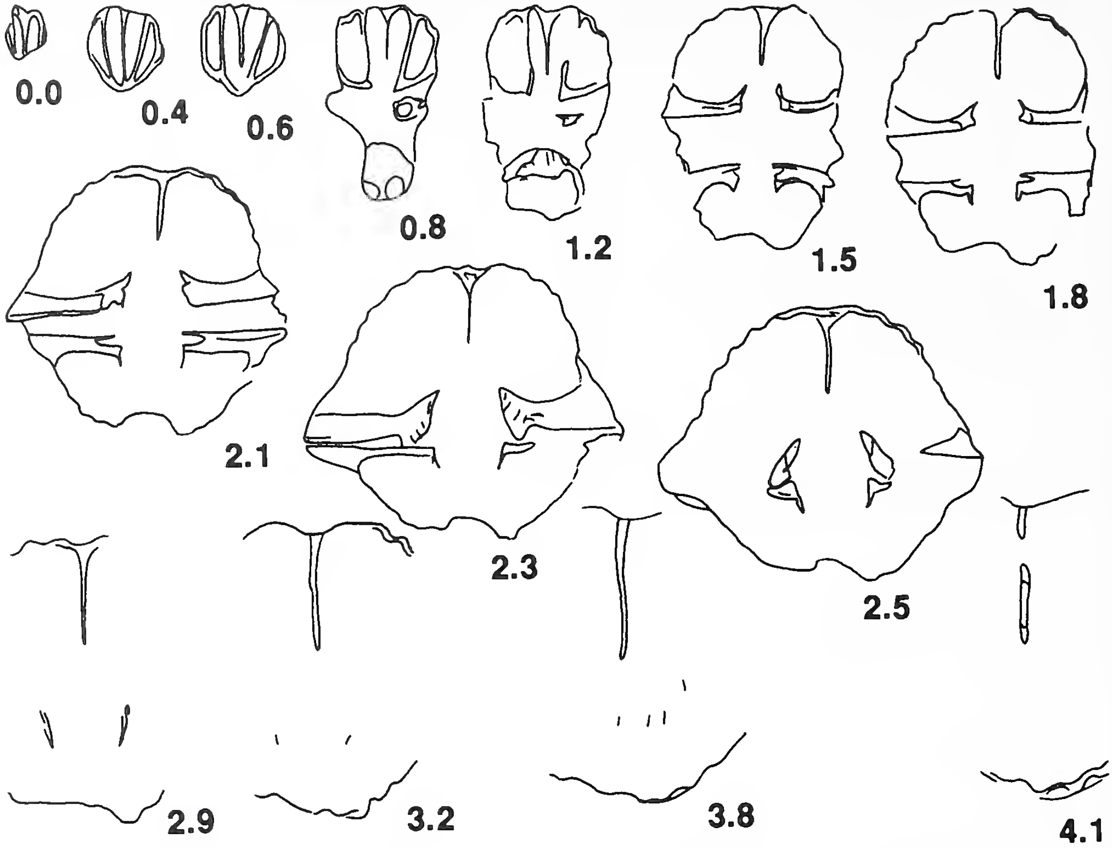
increases. Generally straight lateral commissure although may be some asymmetry. Anterior commissure gently uniplicate, costate. Punctae present.

Transverse serial sections (Text-fig. 7) show the pedicle valve contains sub-parallel dental lamellae and a persistent median septum, traced to section 4.1 mm, after which it is a diminutive structure. Dorsally directed crura are attached to horizontal hinge plates (sections 1.8, 2.1). The spiralium is broken, traces of it may be present in section 3.8.

*Discussion*. The material of equivalent size from Nevada agrees very closely with the illustrations given by Bittner (1890), though our material reaches a larger size. Compared to *B. lipoldi* of Dagys (1974) our material tends to have a more incurved pedicle umbo and more marked pedicle sulcus; little significance is attached to these differences. The material from the former USSR is similar in size to Bittner's originals. Topotype material of *B. lipoldi* has been examined, in a block of pale yellowish brown (10 YR 6/2; Goddard *et al.* 1984) to pale yellowish orange (10 YR 8/6) weathering wackestone (GBV, number 1978/12/1); it also contained specimens of *Rhaetina* sp. Isolation of specimens for serial sectioning was not possible due to the friable nature of the fossils. However, it has been possible to grind the umbos of a few of them. In the brachial valve of one specimen a U-shaped hinge-trough or septalium was observed, but no additional details. The pedicle valve possesses a median septum, but no dental lamellae were seen. The shell is punctate. As dental lamellae have not been observed in topotype material of the species, the Nevadan specimens are referred to as *B*? cf. *B. lipoldi*. It may prove more appropriate to refer the Nevadan material to *Spiriferina*.

Pearson (1977) referred *Spiriferina lipoldi* Bittner, 1890 to *Sinucosta* Dagys, 1963. Dagys (1974) had previously referred the species to *Balatonospira*, in a monotypic subfamily. Pearson wrote his monograph prior to that of Dagys, although it was not published until after the latter appeared (see comment by Ager *in* Pearson 1977, p. 65). Dagys (1974, fig. 81) and Pearson (1977, fig. 1) both gave serial sections of specimens they referred to *Sinucosta emmrichi* (Suess). Both sets of sections show dental lamellae and a median septum in the pedicle valve. In his diagnosis of *Sinucosta*, Pearson (1977, p. 16) noted that the hinge line is shorter than maximum width. This is not the case with *lipoldi* where the maximum width is at or close to the hinge line.

The lack of a detailed description or serial sections of the material illustrated by Detre (1972) from the Carnian of the Bakony Mountains, Hungary, makes comparison with the Nevada specimens difficult. Similarly *Pseudospiriferina leopoldi* [*sic*] of Ching and Feng (1977) lacks serial sections. Two specimens of *B*? cf. *B. lipoldi* from Nevada were serially sectioned; the results from one specimen are given (Text-fig. 7). There are some differences between *B*? cf. *B. lipoldi* (Text-fig. 7) and *B. lipoldi* of Dagys (1974, fig. 92). Dental lamellae are not seen in the sections given by Dagys, the



TEXT-FIG. 7. Transverse serial sections through a specimen of *Balatonospira*? cf. *B. lipoldi* (Bittner); UMIP 20416; Lower Member, Luning Formation; Dunlap Canyon. Sections taken perpendicular to right lateral commissure and central costae on brachial valve. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Dental lamellae and median pedicle septum visible from 0.0, horizontal hinge plates (2.1–2.5) give rise to crura directed towards the floor of the brachial valve (2.1–2.9) and traces of the damaged spiralium (3.8). Last section taken through the median septum of the pedicle valve at 4·4 mm; last section taken at 4·7 mm. Magnification of sections, ×4. Dimensions of sectioned specimen: L = 12·4; W = 14·5; T = 10·9+ mm.

hinge plates are dorsally directed rather than horizontal and well-developed inner socket ridges are present. A ventrally arching cardinal process was observed in the other sectioned Nevadan specimen. The form of the median septum and crura are comparable in both series of sections from the Nevadan material. *Balatonospira* has punctae but no spinate microsculpture or dental plates, while *Sinucosta* has an impunctate shell with a micro-ornament of fine spines and divergent dental plates (Pearson 1977). In some of the Nevadan specimens where shell material has been partially lost, infilled punctae could be mistaken for a micro-ornament of fine spines. Type material of *S. emmrichi* (Suess, 1854) from Austria has not been investigated to examine the nature of shell ornament or structure in relation to that of *B. lipoldi* from Austria, or *B*? cf. *B. lipoldi* from Nevada. Yang and Yin (in Ching *et al.* 1979, p. 174, fig. 108) described *Balatonospira lipoldiformis* from China. The serial sections indicate the presence of well-developed dental lamellae and a ventrally arching cardinal process. There is therefore some doubt that the Chinese specimens belong to *Balatonospira*.

*Occurrence.* Lower Member, Luning Formation, Pilot Mountains, Nevada.

### Family LABALLIDAE Dagys, 1962
### Subfamily LABALLINAE Dagys, 1962
### Genus ZUGMAYERELLA Dagys, 1963

*Type species. Spiriferina koessenensis* Zugmayer, 1880, p. 28, pl. 3, figs 2–3, 13, from the Rhaetian of Kitzberg, near Neusiedl, Piesting-Tal, Austria. Lectotype in the Palaeontological Institute of the University of Vienna (Pearson 1977).

*Diagnosis.* (From Pearson 1977, p. 23.) Medium sized pyramidal species. Beak tall; hinge line shorter than maximum width; lateral margins rounded. Sulcus and fold distinct, unribbed. Lateral slopes bear several ribs. Cardinal margin wholly or partially denticulate, area concomitantly ornamented with denticular ridges. Delthyrium open. Shell surface pustulose, possibly spinose. Dental lamellae fused with medium septum forming a spondylium-like structure. Cardinal process low, striate. Jugum as simple arch; descending lamellae of spiralia supported by plates. Punctate.

*Discussion.* Judging from the generic diagnoses for *Spondylospira* Cooper, 1944 and *Zugmayerella* given in Pitrat (1965) these genera are similar. *Zugmayerella* has a smooth fold and sulcus, i.e. only one costa forms the brachial fold, and no costa is present in the corresponding sulcus of the pedicle valve. Species of *Spondylospira* have more costae than those of *Zugmayerella*. The calcareous net supporting the descending lamellae of the spiralia in *Spondylospira* also appears to be present in *Zugmayerella*; 'the primary plates of the spiral are supported by net-like plates which, in turn, rest on low ridges in the valve bottom' (Dagys 1963, p. 99). A single pedicle valve from the Luning Formation, referred to ?*Zugmayerella* sp. (Plate 3, figs 5–6), appears intermediate between *Zugmayerella* and *Spondylospira*. It has strong costae and two costae in the sulcus. It casts some uncertainty on the validity of *Zugmayerella*.

*Occurrence.* Pearson (1977) recorded the genus from the Norian of Slovakia, east Bulgarian Balkan Mountains, Caucasus, Crimea and north east former USSR, and from the Rhaetian of the Northern Alps, Slovakia and north west Romania and probably the Carnian of Spitzbergen. Stanley (1979) recorded and figured *Z. uncinata* from Nevada. Newton (*in* Smith *et al.* 1990) recorded two species of *Zugmayerella* from the Late Triassic of Cordilleran America.

### *Zugmayerella uncinata* (Schafhaeutl, 1851)

Plate 1, figs 11–20; Plate 3, figs 1–4; Text-figs 8–10A

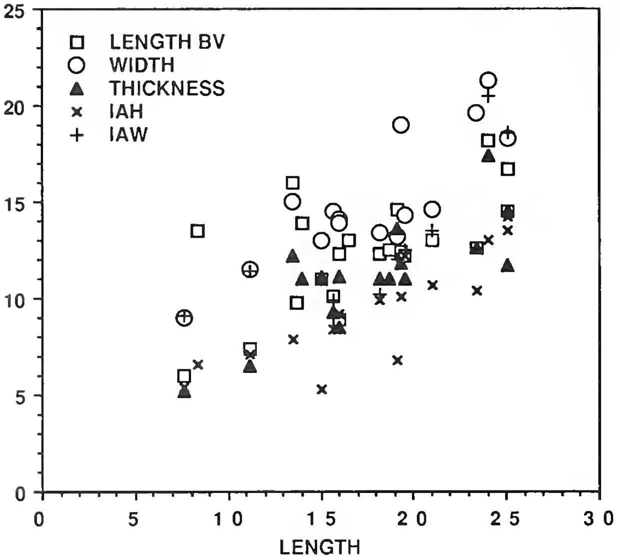
*1851 *Spirifer uncinatus* Schafhaeutl, p. 135, pl. 24, fig. 33.
1880 *Spiriferina uncinata* Schafhaeutl; Zugmayer, p. 27, pl. 3, fig. 1.
1963 *Zugmayerella uncinata* (Schafhaeutl); Dagys, p. 99.
1977 *Zugmayerella uncinata* (Schafhaeutl); Pearson, p. 23, pl. 2, figs 6–10; text-figs 3–5.
1979 *Zugmayerella uncinata* (Schafhaeutl); Stanley, p. 57, pl. 8, figs 10–12.
1988 *Zugmayerella uncinata* (Schafhaeutl); Siblik, p. 75.
1991 *Phenacozugmayerella minuncinata* Hoover, p. 90, pl. 12, figs 6–24.

*Type material.* From 'Gervillien Schichten' of 'Hirschbühl hinter dem hohen Kramer bei Garmisch'; presumed lost (Pearson 1977, p. 23).

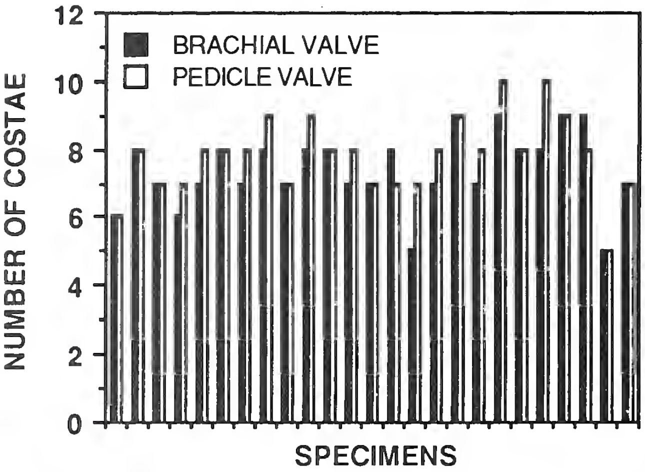
*Material.* Numerous specimens from Dunlap Canyon (Bed 35, Stanley 1979) and Cinnabar Canyon, Nevada (Text-figs 1, 3). Also from unnamed canyon 14·5 km east of Mina and from the Sonomia Quadrangle, south of Rose Creek, east of Auld Lang Syne Peak at approximately 2120 m, 23 m below top of the Dry Canyon Formation, East Range Mountains, Nevada. UMIP 6845, 6847, 6849, 6855–6856, 6858, 6861–6862, 6945, 20319–20321, 20334, 20338, 20343–20344, 20346, 20348, 20357, 20365–20366, 20368–20369, 20375, 20387, 20395, 20402, 20409, 20418, 20421, 20427.

*Diagnosis*. (From Pearson 1977, p. 23.) Ribs angular, three to five on lateral slopes of brachial valve. Cardinal margin partially denticulate; portion of area adjacent to delthyrium bears denticular ridges. Diagnosis otherwise as for genus.

*Description*. Pearson (1977, p. 23) gave a description of the species. Additional comments regarding the Nevada material are made here. Length is generally greater than width, which is greater than thickness. Brachial valve width is often greater than brachial valve length. The interarea width is generally greater than interarea height (Text-fig. 8). Interarea measurements are estimated in many cases and no account has been taken of the curvature of the interarea in the anterior–posterior plane. This results in a general underestimate of interarea heights, which may in fact be similar to interarea widths in more instances than indicated (Text-fig. 8). Five to nine costae were counted on brachial valves and five to ten on pedicle valves (Text-fig. 9). The brachial valve has one prominent costa marking the brachial fold, and no costae in the pedicle sulcus. A few specimens show fine capillae and many growth lines where the outer shell layer is preserved. Transverse serial sections have been



TEXT-FIG. 8. Plot of length versus width, thickness, length of brachial valve; interarea height; and interarea width for *Zugmayerella uncinata* (Schafhaeutl); Pilot Mountains, Nevada.



TEXT-FIG. 9. Bar graph of number of costae on brachial and pedicle valves of *Zugmayerella uncinata* (Schafhaeutl); Pilot Mountains, Nevada.

taken through one specimen (Text-fig. 10A). These show the dental lamellae fused to the median septum in the pedicle valve to form a spondylium-like structure (sections 1.5, 1.9, 3.0) with a median septum. Serial sections were taken for 3 mm from the initial section. The brachidium was not preserved in the sectioned specimen.

*Discussion.* In discussing the morphology of *Zugmayerella koessenensis* (Zugmayer), Pearson (1977, pp. 28–29) commented that this species is somewhat laterally compressed, both valves are characteristically elongate in outline, the prominent fold and sulcus are medianly flattened in all but the youngest specimens and rare adults and that the costae are narrow and rounded. At least four costae are present on the lateral slopes of the brachial valve of the smallest specimens with up to six in adult specimens (Pearson 1977). These characters have been used to distinguish *Z. koessenensis* from *Z. uncinata*. The number of costae counted on the Nevada specimens ranges up to nine on the brachial valve and ten on the pedicle valve (Text-fig. 9). However, using the number of costate present on a specimen to identify it has to be done with consideration of other characters because costation is a variable character. Only the dental lamellae, median septum and spondylium-like structure of the pedicle valve were seen in a series of transverse serial sections (Text-fig. 10A). Damage to the brachial valve umbo is the probable reason for the absence of the cardinal process (cf. Pearson 1977, fig. 4). Other details of the brachial valve's internal structures were not preserved.

Recently, Hoover (1991) described a new genus and species, *Phenacozugmayerella minuncinata*. He commented that it is easily confused with *Zugmayerella uncinata*, differing from it by its capillate-cancellate surface micrornament, and in lacking the duplex interarea that is characteristic of the latter species. Many of the spiriferinacean brachiopods described by Hoover (1991) from western North America typically are silicified. Brachiopods collected from localities in the Pilot Mountains still retain calcitic shell material. It may be that the capillate-cancellate micrornament noted by Hoover as a distinguishing feature of *Phenacozugmayerella minuncinata* is seen on these specimens because of their detailed preservation; perhaps cruder silicification does not preserve this fine surface ornament.

*Occurrence.* Lower Member, Luning Formation, Pilot Mountains, Nevada. Pearson (1977, p. 24) noted the characteristic occurrence of *Z. uncinata* with *Rhaetina gregaria* (recorded by earlier authors). Pearson (1977, p. 24) reported it from the Norian–Lower Lias of the French and Italian Alps, Slovakia, Polish sub-Tatra, northwest Iran, Romania and east Iran. He also noted its occurrence in the Lower Lias of northeast Turkey and the Pamirs and he thought that this species persisted into the Lower Lias of the German Alps.

### ?*Zugmayerella* sp.

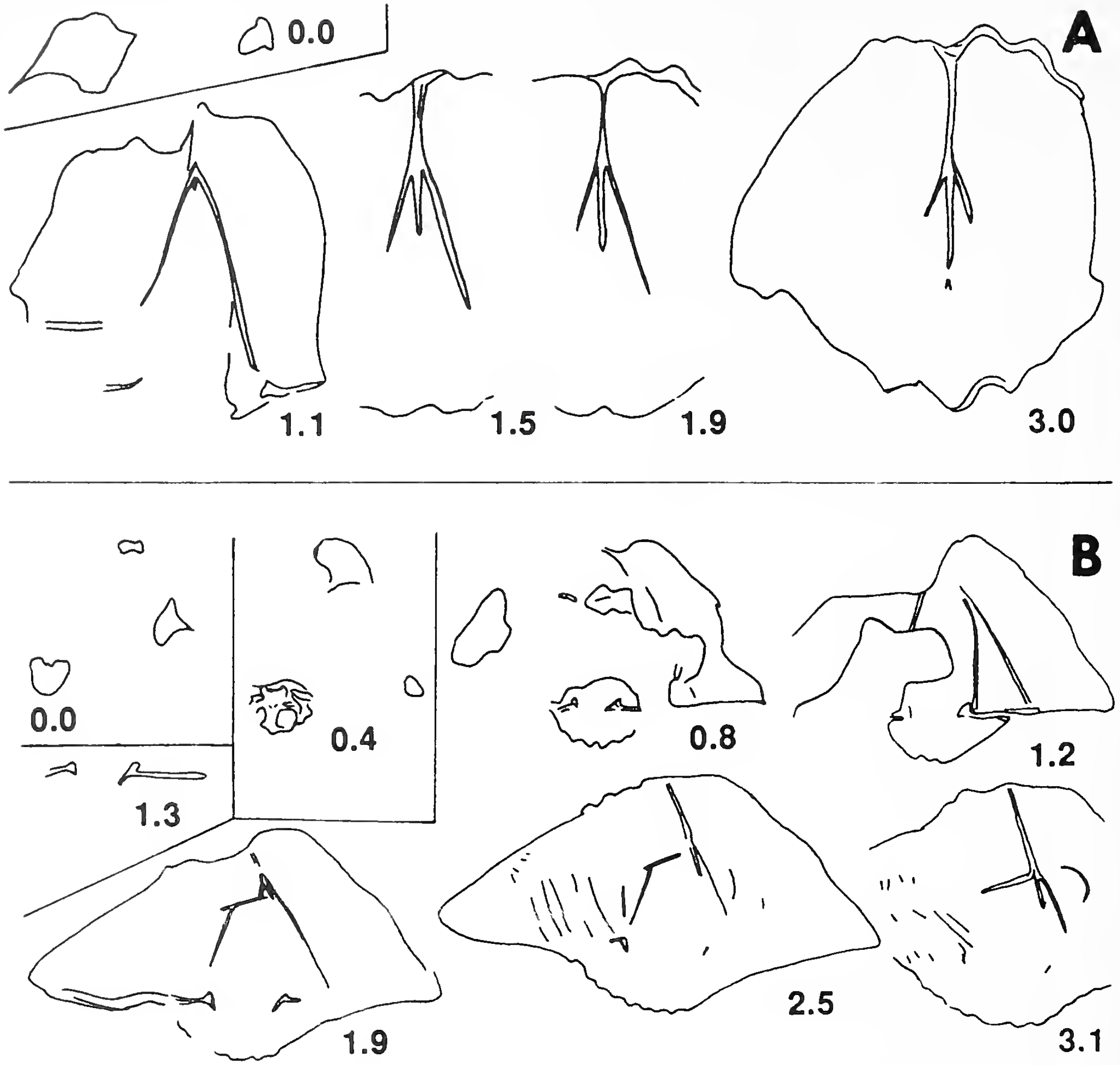
Plate 3, figs 5–6

*Material.* One pedicle valve, UMIP 6952.

*Dimensions.* L = 22·0+; W = 17·8+.

*Description.* The single pedicle valve has an incurved umbo and twelve costae. Many of the costae are strong. The sulcus contains two costae. The interarea appears smooth. In the pedicle valve dental lamellae unite with a median septum to form a spondylium.

*Discussion.* This single pedicle valve is distinguished from other brachiopods from Nevada by the strength of the costae and the smooth interarea. The strong costae and presence of a spondylium suggest affinities with *Zugmayerella*. The presence of costae in the pedicle sulcus distinguish it from *Z. uncinata* which possesses no costae in the sulcus. *Spondylospira lewesensis* has more numerous and finer costae than species referred to *Zugmayerella*. The interarea in ?*Zugmayerella* sp. appears smooth, lacking the vertical striations typically found in *Zugmayerella* and *Spondylospira*. However, this may be due to poor preservation. A spondylium is present in the pedicle valve showing that the specimen is a homoeomorph of *Neoretzia superba* (Suess, 1856). The presence of strong costae on the pedicle valve and two in the sulcus of ?*Zugmayerella* sp. suggests it may be intermediate between



TEXT-FIG. 10. A. Transverse serial sections through a specimen of *Zugmayerella uncinata* (Schafhaeutl); UMIP 20320; Lower Member, Luning Formation; Dunlap Canyon. Sections taken perpendicular to posterior part of right-lateral commissure and central costae on brachial valve. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Spondylium-like structure (dental lamellae and extended median septum of pedicle valve) seen in sections 1.1–3.0. Last section taken through specimen at 3·0 mm. Magnification of sections, ×4. Dimensions of sectioned specimen: L = 17·9+; Lbv = 11·8; W = 13·6; T = 10·3 mm. B, Transverse serial sections through a specimen of *Spondylospira lewesensis* (Lees); UMIP 20314; Lower Member; Luning Formation; Dunlap Canyon, Nevada. Sections taken perpendicular to lateral commissure and brachial valve length. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Detail of hinge plates only shown at 1.3, damaged spondylium-like structure seen in sections 1.9–3.1, traces of damaged spiralium seen in sections 2.5–3.1. Last section taken through specimen at 3·6 mm. Magnification of sections, ×2.5. Dimensions of sectioned specimen: L = 18·3+; Lbv = 16·1; W = 25·1; T = 13·0+ mm.

*Zugmayerella* and *Spondylospira*. Alternatively, it may be derived independently from *Zugmayerella* (or *Spondylospira*). It casts some uncertainty on the validity of the genus *Zugmayerella*.

*Occurrence*. Luning Formation (probably Lower Member), unnamed canyon 14·5 km east of Mina, Nevada (locality MC of Stanley 1979).

### Genus SPONDYLOSPIRA Cooper, 1942

*Type species*. *Spondylospira reesidei* Cooper, 1942, p. 232; 1944, p. 359, pl. 140, figs 43–47, from the Seven Devils Formation, Triassic, east side of Mission Creek, 1·5 miles (2·4 km) above Mission, 4·5 miles (7·3 km) above Jacques, about Section 15, Township 36 N, Range 3 W, Nez Perce County, Idaho.

*Occurrence*. Hoover (1983) recorded the genus from the Carnian to late Norian (Suessi Zone) of North and South America. In Central Peru it may also extend into the lowermost Jurassic (Hoover 1990).

### *Spondylospira lewesensis* (Lees, 1934)

Plate 1, figs 1–10; Text-fig. 10B

*1934 *Cyrtina lewesensis* Lees, p. 35, pl. 1, figs 14–16.
1937 *Spiriferina acrotamboensis* Körner, p. 168, pl. 11, figs 5–8.
1942 *Spondylospira reesidei* Cooper, p. 232.
1944 *Spondylospira reesidei* Cooper, p. 359, pl. 140, figs 44–47.
1944 *Spondylospira alia* Cooper, p. 359, pl. 140, figs 48–51.
1962 *Spondylospira lewesensis* (Lees); Tozer, p. 26, pl. 12, figs 11–13.
1972 *Spondylospira lewesensis* (Lees); Tozer, p. 638, pl. 18, fig. 15*a–c*.
1974 *Spondylospira reesidei* Cooper; Dagys, p. 145, pl. 41, figs 5–8.
1974 *Spondylospira lewesensis* (Lees); Dagys, pl. 41, fig. 9*a–b*.
1983 *Spondylospira lewesensis* (Lees); Hoover, p. 1026, figs 3G–S, fig. 5.
1991 *Spondylospira lewesensis* (Lees); Hoover, p. 81, pl. 9, figs 10–38; pl. 10, figs 1–3.

*Holotype*. USNM 10346*a*.

*Diagnosis*. (From Hoover 1983, p. 1027.) *Spondylospira* with strong costae on dorsal fold that increase initially by equal bifurcation, subsequently by equal or unequal bifurcation; fold and sulcus moderately to strongly developed; deltidial plates and bipartite cooperculum rarely preserved.

*Material*. Three complete specimens (UMIP 6716, 20314, 20428), one brachial (UMIP 6909) and two pedicle valves (UMIP 20389, 20420). UMIP 6716 and 6909 were collected from the low hills between Cinnabar and Dunlap Canyons, north of the prominent andesite rhyolite hill (type locality of *Platyplateon nevadensis*) by S. W. Muller in 1934. UMIP 20314, 20389, 20420 and 20428 were collected from Dunlap Canyon. One specimen from 'Brachiopod Ledge' (Text-fig. 2, locality B), Berlin-Ichthyosaur State Park (Hogler Collection). All specimens are from the Luning Formation.

*Description*. Dimensions of specimens: UMIP 6176: L = 27·9+; Lbv = 19·8; W = 23·9; T = 15·9; UMIP 20314: L = 18·6+, Lbv = 16·3, W = 25·1; T = 11·6; UMIP 20420: L = 25·0; W = 21·3. Counts were made of the number of costae on each valve. The counts are estimates, made at the commissure of each specimen. UMIP 6716: brachial valve costae (BVC) 29; brachial fold costae (BFC) 7; pedicle valve costae (PVC) 31; pedicle sulcus (PVS) 7. UMIP 20314: BVC 24; BFC 5; PVC 28; PVS 5. UMIP 20389: PVC 18. Neither the deltidial plates nor the cooperculum have been observed in any of the specimens from Nevada.

*Discussion*. *Spondylospira lewesensis* is highly variable in its external morphology (see Hoover 1983 for a recent discussion). It is externally homoeomorphic with *Sinucosta emmrichi* (Suess, 1854) figured by Pearson (1977, pl. 1, figs 9–14, and especially that of Zugmayer 1880, figured by Pearson 1977, pl. 1, fig. 9). *Spondylospira lewesensis* differs in its external morphology from *Sinucosta* *emmrichi* by lacking the dense network of fine spines noted by Pearson for the latter species and in possessing a vertically striated interarea. The internal structures of one specimen have been investigated (Text-fig. 10B). They show the presence of dental lamellae (section 1.2) and a median septum (section 1.9) in the pedicle valve which are fused into a spondylium-like structure (sections 1.9, 2.5, 3.1). A small, flat cardinal process is present in the brachial valve (section 0.4). Crura are directed dorsally (sections 0.8, 1.2, 1.3, 1.9, 2.5) from horizontal hinge plates (section 1.3). The spondylium-like structure and the brachidium were damaged (sections 1.9, 2.5, 3.1).

*Occurrence*. Lower Member, Luning Formation, Pilot Mountains, Nevada. *Spondylospira lewesensis* was recorded from the late Carnian to late Norian (Suessi Zone) by Hoover (1983), from North America (Alaska, California, Idaho, Nevada, Oregon, Yukon Territory) and South America (Peru).

## Order TEREBRATULIDA Waagen, 1883
## Suborder TEREBRATULIDINA Waagen, 1883
## Superfamily TEREBRATULACEA Gray, 1840
## Family TEREBRATULIDAE Gray, 1840
## Subfamily PLECTOCONCHINAE Dagys, 1974 (emended Cooper 1983)
## Genus PLECTOCONCHA Cooper, 1942

*Type species*. *Rhynchonella aequiplicata* Gabb, 1864, p. 35, pl. 6, fig. 37, from the Cinnabar District, Humboldt Mountains, Nevada.

*Diagnosis*. (Modified from Cooper 1983, p. 38.) Medium to large, semicostate. Beak labiate. Anterior commissure rectimarginate to uniplicate. Outer hinge plates dorsally attached to crural bases. Loop short, wide.

*Discussion*. Despite records of *Plectoconcha* from China (Sun *et al. in* Ching *et al.* 1979) and the Soviet Union (Dagys 1974), our study confirms *Plectoconcha* as endemic to Nevada, USA. The only genus that Cooper (1983) considered similar enough to *Plectoconcha* to place it in the same subfamily is the plicate *Merophricus* from the Lower Jurassic of the Middle and High Atlas, Morocco. This is particularly interesting for palaeogeographical interpretation.

*Occurrence*. Luning Formation, Shoshone and Pilot Mountains and Dun Glen Formation, East Range, Nevada.

### *Plectoconcha aequiplicata* (Gabb, 1864)

Plate 2, figs 1–8, 21–28; Text-figs 11–12

| | |
|---|---|
| *1864 | *Rhynchonella aequiplicata* Gabb, p. 35, pl. 6, fig. 37. |
| 1914 | *Rhynchonella aequiplicata* Gabb; Smith, p. 146, pl. 44, figs 9–11. |
| 1959 | *Plectoconcha* cf. *Plectoconcha aequiplicata* (Gabb); Silberling, p. 22, pl. 11. |
| 1979 | *Plectoconcha aequiplicata* (Gabb); Hoover, p. 10, pl. 2, figs 6–7. |
| 1983 | *Plectoconcha aequiplicata* (Gabb); Cooper, p. 48, pl. 59, figs 11–14. |

*Type material*. Gabb's original figured specimen could not be located in the collections of the USNM (Thompson personal communication).

*Diagnosis*. (Modified from Cooper 1942, p. 233.) Terebratuloid, generally rotund and longer than wide; uniplicate with superimposed alternate multiplication. Foramen large, permesothyrid, labiate. Deltidial plates not exposed. Pedicle valve interior with large strong teeth not supported by dental plates. Pedicle collar strong. Cardinalia with strong inner socket plate and deep sockets. Broad cardinal process. Crural bases directed ventrally, crural processes close to end of hinge plates.

Crural processes high, subparallel. Loop short and wide, descending lamellae short and flaring laterally; transverse band high arched.

*Material.* Numerous specimens from red-weathering massive limestone beds, limestone and secondary dolomite member of the Luning Formation. Collected loose from the south facing slope, north of the Union Canyon Fault (Silberling 1959, p. 22, pl. 10) at the eastern end of West Union Canyon, at an altitude of approximately 2400 m above sea level, latitude 38° 52′ 30″ N, longitude 117° 34′ 00″ W, Nye County, Nevada (Text-fig. 2, locality A); UMIP 20447–20453. Numerous small specimens were collected from an exposure on the west facing slope to the north of the Union Canyon Fault (Silberling 1959, p. 22, pl. 10) at an altitude of approximately 2400 m above sea level. This exposure has been informally named Brachiopod Ledge by Hogler (Text-fig. 2, locality B); UMIP 20437–20442.

In addition there are approximately 140 specimens in the collection of the United States Geological Survey, Denver, Colorado from Berlin-Ichthyosaur State Park, locality LSJU 800-b (also labelled LSJU 2778, 2940, 2948). These were collected from the Luning Formation by S. W. Muller and N. J. Silberling on the east side of Union Canyon, about 1·6 km from the mouth of the canyon (Ione 15′ quadrangle map, Township 12 North, Range 39 East); this approximates to locality A (Text-fig. 2). In addition, a few specimens referable to *Plectoconcha aequiplicata* have been identified from the Luning Formation of the Pilot Mountains.

*Description.* Large terebratulids with round outline and evenly biconvex profile. Approximate maximum dimensions, length 35 mm, width 27 mm, thickness 28 mm. Length is greater than width and thickness. The pedicle umbo is suberect to erect, with a large rounded, labiate pedicle foramen. Both valves bear coarse costae (approximately 14) that run most of the length of the valves, although the number of costae is variable. The plicate anterior commissure may be broadly uniplicate. The specimens are generally poorly preserved, infilled with a dark grey (N 3, Goddard *et al.* 1984) micrite. Many valves are partly coated by a light brown to moderate reddish orange (5 YR 6/4 to 10 R 6/6, Goddard *et al.* 1984) layer of calcite, probably originating from recent surficial weathering. Internal structures show a cardinal process that has overgrown concave juvenile hinge plates (Text-fig. 11, section 3.2 mm). Anteriorly hinge plates are subhorizontal (sections 4.8, 5.2). Crural processes develop rapidly from free crural bases (sections 6.1–7.3). Transverse band high-arched (section 9.5).

*Discussion.* The species is represented by large and small forms collected from two different horizons. The large specimens from West Union Canyon agree well with material originally described and figured by Gabb (1864, pl. 6, fig. 37, reprinted in Smith 1914, pl. 44, figs 9–11) from the Cinnabar District, East Range, Nevada. Both show a rounded outline, biconvex profile, large, round pedicle foramen and a similar number of strong costae covering the valves. Cooper (1983, pl. 59, figs 11–12) figured a hypotype of *Plectoconcha aequiplicata* collected from the Luning Formation, 610 m ENE of Richmond Mine, 1·6 km from the mouth of Union Canyon, East side, Nye County. (A hypotype is a specimen described and/or illustrated after the establishment of the type lot; G. A. Cooper, personal communication). This specimen is certainly from the same locality and horizon from which the material described herein was collected. Cooper also figured an imperfect brachidium of a specimen of *P. aequiplicata* from Pershing County, Nevada (1983, pl. 59, figs 13–14, previously figured by Hoover 1979, pl. 2, figs 6–7), and a reconstruction (1983, pl. 66, figs 14–15). Comparing the serial sections of the Early to Middle Triassic species *P. variabilis* (Dagys, 1974) with the brachidium of the type species, Cooper (1983, p. 48) considered the Soviet species to belong to a different stock. '*P.*' *variabilis* possesses dorsally directed 'prefalcifer' crura and a centronellid stage in its loop development (translation from Dagys 1974, p. 197, *in* Cooper 1983, p. 38). These features, in addition to others considered by Cooper (1983), distinguish it at the genus and species level from the type species. The species from the former USSR is smaller and has a more elongate outline than *P. aequiplicata.*

Transverse serial sections have been taken through one large specimen of *P. aequiplicata* from Nevada (Text-fig. 11; described above). These confirm Cooper's observations on the differences between the American material and that from the former USSR. The sections also show that Chinese material referred to *Plectoconcha* by Sun *et al.* (*in* Ching *et al.* 1979, p. 196) does not belong in this genus. Sun *et al.* recorded a new species, '*P.*' *delicata* from the Triassic of China. It appears to be smaller in size and with fewer costae than the type species, *P. aequiplicata*. The crura are falcifer-type (Sun *et al. in* Ching *et al.* 1979, fig. 132) and bear a similarity to the crura shown by Dagys (1974, fig. 143). Compared with the Soviet species the transverse band is low-arched in the Chinese species. Therefore, the genus *Plectoconcha* has only been substantiated in Nevada, USA.

Silberling (1959, p. 17) recorded abundant terebratuloid and rhynchonelloid brachiopods approximately 160 m above the base of the limestone and secondary dolomite member of the Luning Formation in the massive limestone bluffs near the crest of the ridge forming the southeast wall of West Union Canyon. On his plate 11 Silberling (1959) recorded abundant terebratuloid brachiopods from the carbonate member. The specimens of *Plectoconcha* were collected from these horizons, the smaller specimens from a ledge ('Brachiopod Ledge'; Text-fig. 2, locality B) in the massive limestone bluffs. The small forms are interpreted as juveniles of *P. aequiplicata*. It is interesting that the large and small specimens occur at different horizons (Silberling 1959; Hogler personal communication) and were therefore not synchronous. If the large and small forms are representatives of the same species, current-sorting or palaeoecological and palaeoenvironmental differences are indicated to account for the absence of small and large forms at the same horizon. The outline of the small forms ranges from subtriangular to rounded. Their profile is markedly biconvex. The costae are coarse and well developed. It has proved difficult to obtain many measurements for both large and small forms as they are often broken and the removal of adhering matrix from the small specimens is also a problem. The internal structures of one small specimen have been investigated (Text-fig. 12). These show a flat cardinal process (section 1.9 mm), hinge plates that are flat (section 2.0), to gently ventrally convex (section 2.6) and crural bases that project ventrally (section 3.2) and rapidly to the crural processes (section 4.6). The crural processes are incurved (section 5.0). This may reflect the form of the crural processes in juvenile *Plectoconcha*. It does not appear to be due to damage to the brachidium. A moderately arched transverse band was seen in another damaged specimen that was partially ground on a diamond wheel. These characters, both external and internal, support the assignation of these small forms to *Plectoconcha*, and indicate that they may be juveniles of *P. aequiplicata*.

Hoover (1979) created the new genus *Vex*, for '*Terebratula*' *semisimplex* White, 1880. The species is probably from the Portneuf Limestone Member of the Thaynes Formation, southeastern Idaho.

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EXPLANATION OF PLATE 2

Figs 1–4. *Plectoconcha aequiplicata*. UMIP 20449; limestone and secondary dolomite member, Luning Formation; West Union Canyon, Berlin-Ichthyosaur State Park, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1.

Figs 5–8. *Plectoconcha aequiplicata*. UMIP 20448 (sectioned, Text-fig. 11); limestone and secondary dolomite member, Luning Formation; West Union Canyon, Berlin-Ichthyosaur State Park, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1.

Figs 9–12. *Plectoconcha newbyi* sp. nov. UMIP 20410, holotype; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1·3.

Figs 13–16. *Plectoconcha newbyi* sp. nov. UMIP 20322, paratype; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1·3.

Figs 17–20. *Plectoconcha newbyi* sp. nov. UMIP 20412 (sectioned, Text-fig. 14), paratype; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1·3.

Figs 21–24. *Plectoconcha aequiplicata*. UMIP 20441, juvenile; limestone and secondary dolomite member, Luning Formation; West Union Canyon, Berlin-Ichthyosaur State Park, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1·5.

Figs 25–28. *Plectoconcha aequiplicata*. UMIP 20439 (sectioned, Text-fig. 12), juvenile; limestone and secondary dolomite member, Luning Formation; West Union Canyon, Berlin-Ichthyosaur State Park, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1·5.


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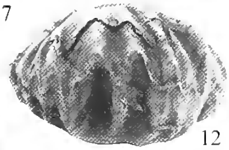
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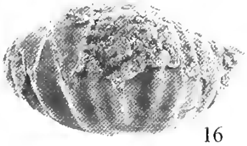
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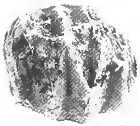
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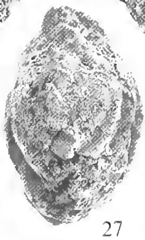
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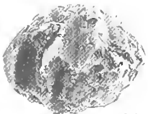
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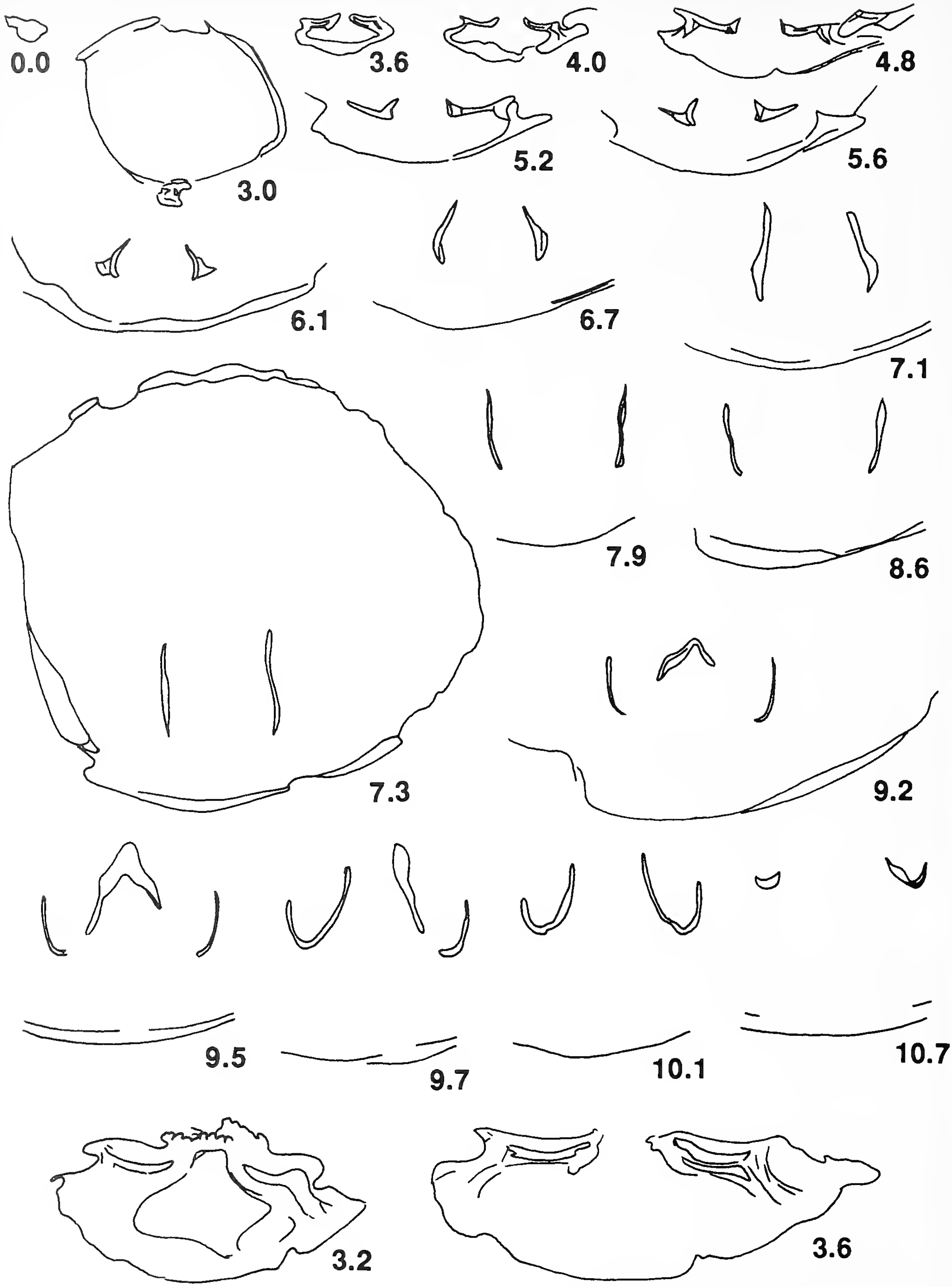
SANDY and STANLEY, *Plectoconcha*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Hoover (1979, p. 10) commented on the similarities between *Vex* and *Plectoconcha*. He noted that the loops of both genera are not well known but that they are similar externally, with *Plectoconcha* commonly larger. Hoover (1979) referred *Vex* to the subfamily Plectoconchiinae (*sic*), but Cooper (1983) considered that it was not a terebratulid, and that there was no established family for the genus. Cooper commented (1983, p. 51) that the long loop of *Vex* was suggestive of *Zeilleria*, but that it lacked a median septum and dental lamellae found in the latter genus.

In the original description of *Plectoconcha aequiplicata*, Gabb (1864) figured a specimen from the Cinnabar district, East Range, Nevada. It was considered a Middle Triassic species (Smith 1914). Whilst the material described herein from the Shoshone Mountains is not topotypic (i.e. it is not from the East Range), it is probably from strata of a similar age. The material described by Gabb is from the Magnus Zone (late early Norian, Dun Glen Formation; Silberling, personal communication).

*Occurrence*. Limestone and secondary dolomite member, Luning Formation, West Union Canyon, Berlin-Ichthyosaur State Park, Union district, Nye County, Shoshone Mountains; Lower Member, Luning Formation, Pilot Mountains; Dun Glen Formation, Cinnabar district, East Range, Nevada.

### *Plectoconcha newbyi* sp. nov.

Plate 2, figs 9–20; Text-figs 13–14

1979 Rhynchonellid, Stanley, pp. 14, 57, pl. 8, figs 5–6.
1979 Terebratulid, Stanley, pp. 14, 57, pl. 8, figs 8–9.

*Derivation of name*. For the late Paul Newby, of Esher, Surrey, England, family friend of M.R.S.

*Holotype*. UMIP 20410, Lower Member, Luning Formation, Dunlap Canyon, Pilot Mountains, Nevada.

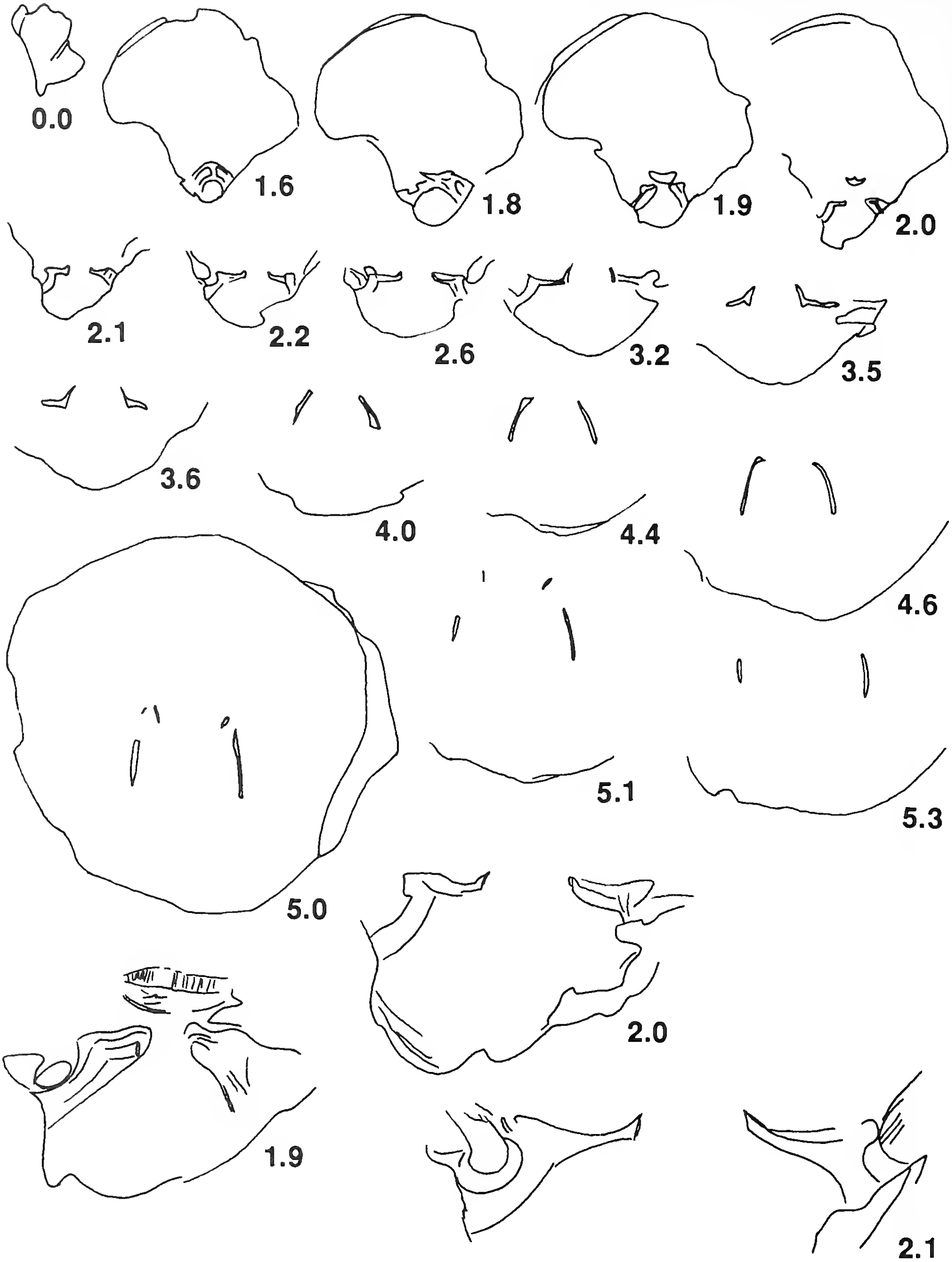
*Paratypes*. UMIP 20322, 20354, 20358, 20412, 20425, Lower Member, Luning Formation, Pilot Mountains, Nevada.

*Material*. Numerous specimens from the Luning Formation of Dunlap and Cinnabar Canyons. UMIP 6852, 20323–20327, 20332, 20333?, 20342, 20351, 20353, 20360, 20362–20363, 20367, 20372–20373, 20378, 20383, 20398, 20403, 20408, 20414, 20426?, MSM 6172, 6182–6183, 6189.

*Diagnosis*. *Plectoconcha* of medium size, rounded outline, costate margins, smooth stage posteriorly, rectimarginate to uniplicate anterior commissure. Flat cardinal process, ventrally concave hinge plates, high crural processes, moderately arched transverse band.

*Description*. *Plectoconcha newbyi* has a rounded outline and biconvex profile. Maximum length is greater than width which is greater than thickness (Text-fig. 13). The anterior commissure is rectimarginate to uniplicate and may develop an incipient biplication. The lateral commissure is gently deflected towards the pedicle valve. The anterior half of both valves is costate, but smooth posteriorly. Approximately ten costae are present at the commissure of each valve. The pedicle foramen is round, permesothyrid and labiate and the beak erect. Internal characters show a flat cardinal process (Text-fig. 14, section 2.5 mm) that has overgrown horizontal to gently ventrally concave hinge plates (section 2.6). Crural bases are small, attached to hinge plates, crural processes are high and develop rapidly from the end of the hinge plates (sections 4.2, 4.9, 5.4). Transverse band is moderately arched and rounded (section 7.6).

TEXT-FIG. 11. Transverse serial sections through a specimen of *Plectoconcha aequiplicata* (Gabb); UMIP 20448; limestone and secondary dolomite member, Luning Formation; West Union Canyon, Berlin-Ichthyosaur State Park, Nevada. Sections taken approximately perpendicular to brachial valve length. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Cardinal process (3.0, 3.2), gently concave to subhorizontal hinge plates (3.2–5.6), high-arched crural processes (7.1) and transverse band (9.5) present. Last section taken at 11·7 mm. Magnification of sections 0.0–10.7, ×4; sections 3.2 and 3.6 also shown at ×16. Dimensions of sectioned specimen: L = 29·6+; W = 25·2+; T = 20·4 mm.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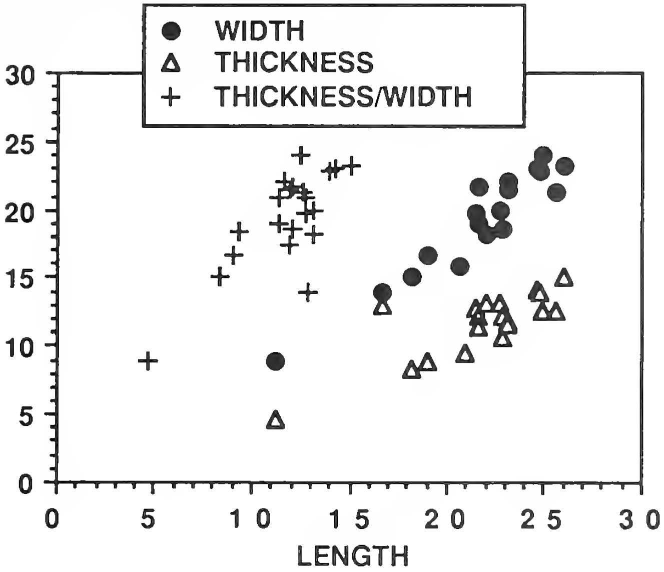


TEXT-FIG. 13. Plot of length versus width and thickness and of thickness versus width for *Plectoconcha newbyi* sp. nov.; Pilot Mountains, Nevada.

*Discussion.* Compared with *Plectoconcha aequiplicata*, *P. newbyi* sp. nov. is less strongly costate and has fewer costae, is smaller in overall length, width and thickness, and is not so markedly biconvex. The two species are probably very closely related.

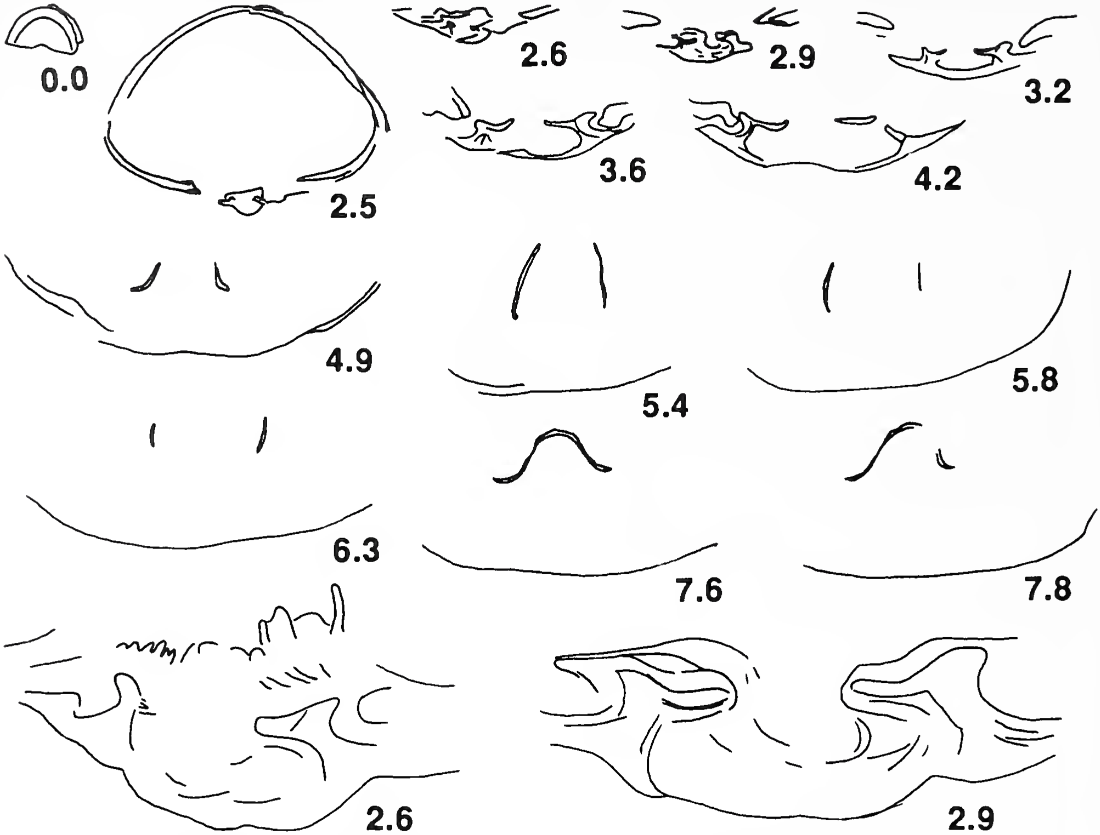
The transverse serial sections of *P. newbyi* sp. nov. (Text-fig. 14) show some differences from those taken of *P. aequiplicata* (Text-figs 11–12). The presence of small crural bases posteriorly in *P. newbyi* sp. nov. could be significant. However, it might reflect that the specimen of *P. newbyi* that has been sectioned is a juvenile.

The similarities in external morphology between *P. aequiplicata* and *P. newbyi* (the form of pedicle foramen, costation) and their internal morphology (the form of the cardinal process, hinge plates, crural processes and transverse band) suggest that *newbyi* should be referred to *Plectoconcha*. It is possible that *P. aequiplicata* and *P. newbyi* sp. nov. represent ecophenotypic variation within one species. The latter species has not been identified at Berlin-Ichthyosaur State Park, Shoshone Mountains.

*Occurrence.* Lower Member, Luning Formation, Pilot Mountains, Nevada.

### Superfamily DIELASMATACEA Schuchert, 1913
### Family DIELASMATIDAE Schuchert, 1913
### Subfamily DIELASMATINAE Schuchert, 1913
### Genus RHAETINA Waagen, 1882

TEXT-FIG. 12. Transverse serial sections through a juvenile specimen of *Plectoconcha aequiplicata* (Gabb); UMIP 20439; limestone and secondary dolomite member, Luning Formation; West Union Canyon, Berlin-Ichthyosaur State Park, Nevada. Sections taken perpendicular to maximum length. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Last section taken at 6.7. Cardinal process (1.9), gently concave to horizontal hinge plates (1.9–3.5) and high-arched crural processes (4.6) present. Magnification of sections 0.0–5.3, ×6·6; sections 1.9, 2.0 and 2.1 also shown at ×17. Dimensions of sectioned specimen: L = 18·0; W = 14·6; T = 11·4 mm.



TEXT-FIG. 14. Transverse serial sections through a specimen of *Plectoconcha newbyi* sp. nov.; UMIP 20412, paratype; Lower Member, Luning Formation; Dunlap Canyon, Nevada. Sections taken perpendicular to maximum length. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Cardinal process (2.5, 2.6), horizontal to gently ventrally concave hinge plates (2.6–4.2), high-arched crural processes (5.4) and transverse band (7.6, 7.8) present. Last section taken at 8·6 mm. Magnification of sections 0.0–7.8, ×4; sections 2.6 and 2.9 also shown at ×17. Dimensions of sectioned specimen: L = 23·1; W = 21·4; T = 11·9 mm.

*Type species*. *Terebratula gregaria* Suess, 1854, p. 14, pl. 2, figs 14–15, from 'Mandling-Wand bei Wallegg'.

*Discussion*. *Rhaetina* is a very well known and abundant brachiopod genus of the southern Alpine Carpathian and Caucasian Late Triassic (Pearson 1977). Ching *et al*. (1979) recorded the genus from the Triassic of China. Pearson (1977) stated that the genus ranges from the Middle Triassic to the Early Jurassic. In addition, Hoover (1979) recorded the genus from the Early Triassic of Idaho, USA.

### *Rhaetina gregaria* (Suess, 1854)

Plate 3, figs 7–22; Text-figs 15–16

| | |
|---|---|
| *1854 | *Terebratula gregaria* Suess, p. 14, pl. 2, figs 14–15. |
| v cf. 1864 | *Terebratula humboldtensis* Gabb, p. 34, pl. 6, figs 35, 35*a*–*b*. |
| v cf. 1877 | *Terebratula humboldtensis* Gabb; Hall and Whitfield, p. 282, pl. 6, figs 22–24. |

v cf. 1914 *Terebratula humboldtensis* Gabb; Smith, p. 147, pl. 64, figs 3–5.
1977 *Rhaetina gregaria* (Suess); Pearson, p. 35, pl. 4, figs 1–13 [with a detailed synonymy].
1988 *Rhaetina gregaria* (Suess); Siblik, p. 97.

*Type material.* Suess's originals are lost. Pearson (1977) chose a lectotype from specimens figured by Suess (1854, pl. 2, fig. 14.)

*Material.* Lower Member of the Luning Formation, Cinnabar and Dunlap Canyons, Pilot Mountains, Nevada. UMIP 20311, 20315, 20352, 20359, 20377, 20401, 20411, 20413, 20422, MSM 6182. A few small, rare specimens from Berlin-Ichthyosaur State Park, Shoshone Mountains, Nevada (Hogler Collection).

*Description.* Specimens from Nevada have the characteristic slightly elongate outline of *Rhaetina gregaria*, broadest near the anterior end. The beak is prominent and erect, with a small pedicle foramen and rounded beak-ridges. The valves are smooth for two-thirds of their length, then two strong rounded costae develop on the brachial valve deflecting the anterior commissure.

The internal structures of two specimens of *Rhaetina gregaria* have been investigated, one a large, possibly mature adult specimen (Plate 3, figs 15–18; Text-fig. 15), the other a smaller, juvenile specimen (Plate 3, figs 19–22; Text-fig. 16). The larger specimen has a prominent cardinal process (Text-fig. 15, section 3.4). Anterior to the cardinal process is a large boss-like process (sections 3.5, 3.9), probably an extension of the cardinal process but lacking the typical comb-like muscle attachment structure. Hinge plates are attached to the floor of the brachial valve (sections 3.3–6.0), a characteristic feature of *Rhaetina*. One of the crural processes is damaged (sections 6.6, 6.9). The smaller specimen (Text-fig. 16) also has a well-developed cardinal process (section 1.9) but there is no sign of a boss-like process. The hinge plates also join the floor of the brachial valve (e.g. section 3.3). The crural processes are concave, and converge ventrally (section 4.7). The transverse band was not seen in either set of sections although it may be partially preserved in the smaller specimen (Text-fig. 16, section 6.9).

A few rare specimens share the external characters of *Rhaetina gregaria* but in addition have costae on their lateral flanks (Plate 3, figs 23–25). There are about four lateral costae on each side and are slightly sharper than those in the median fold. Such lateral costate have not been recorded in species of *Rhaetina*. The presence of these lateral costae may prove to be sufficient justification for erecting a new species. However, more material is needed for study of the internal characters. At the present time these specimens are recorded as *R.* sp. cf. *R. gregaria* (Suess). If *Plectoconcha newbyi* sp. nov. developed a strongly biplicate anterior commissure it might resemble this form. It is externally similar to *Misolia noetlingii* (Bittner, 1899) (e.g. in Hudson and Jefferies 1961, pl. 1, figs 5–8) although the extent of the costae across the posterior of the valves is difficult to determine for the poorly preserved figured specimen from Nevada (Pl. 3, figs 23–25).

*Discussion.* Pearson (1977, pp. 35–36) gave an extensive synonymy list for *Rhaetina gregaria*. Although all of his references have not been examined, the species is interpreted as variable, as did Pearson. '*Terebratula*' *humboldtensis* Gabb was originally described from the East Range, Nevada. It is probably from the Dun Glen Formation (Silberling, personal communication) which has also been dated as Kerri Zone (late early Norian), as has the lower member of the Luning Formation in the Pilot Mountains. Examination of Gabb's original figured specimens of '*T.*' *humboldtensis* (USNM 12533*a*–*b*) suggests that it is a junior subjective synonym of *R. gregaria* (Suess). The elongate outline of Gabb's original figure (1864, pl. 6, figs 35, 35*a*–*b*) resembles a zeillerid. The anterior commissure is commonly rectimarginate among zeillerids, not broadly uniplicate as seen in Gabb's illustrated specimen (1864, pl. 6, fig. 35*a*). Subsequently, Hall and Whitfield (1877, pl. 6, figs 22–24) and Smith (1914, pl. 64, figs 3–5, from Hall and Whitfield) described and figured '*T.*' *humboldtensis* Gabb. The figures by Hall and Whitfield (1877) and Smith (1914) confirm that USNM 12533*a*–*b* are those illustrated. The figures are somewhat idealized, but the specimens are 'distorted' (damaged) as Gabb recorded (1864, p. 34). Whiteaves (1889, p. 129) recorded '*T.*' *humboldtensis* Gabb from Nicola Lake, British Columbia. It is possible that '*T.*' *liardensis* described by Whiteaves (1889) from British Columbia may be referable to *Rhaetina*. Similarly, terebratulids recorded by Lees (1934) from the Yukon, and referred to *Dielasma suttonense* (Clapp and Shimer) and *T*? *piriformis* Suess, may prove to be *Rhaetina*. The median septal structures recorded by Whiteaves and Lees in the brachial valves of these species may reflect where the hinge plates attach with the floor of the brachial valve. Lees (1934, p. 33) recorded dental lamellae as scarcely visible in his cf. *Dielasma julicum* (Bittner). Whiteaves and Lees' collections have not, however, been investigated during the present study.

*Occurrence.* Lower Member of the Luning Formation, Pilot Mountains, and the limestone and secondary dolomite member, Luning Formation, Berlin-Ichthyosaur State Park, Shoshone Mountains and also probably the Dun Glen Formation, East Range, Nevada. Pearson (1977) recorded this variable species from the Late Triassic–Early Jurassic of Central, Southern and Eastern Europe and the Middle East (see Siblik 1988, p. 88 for a detailed listing). Next to *Spondylospira lewesensis*, *Rhaetina gregaria* is the rarest element of the brachiopod fauna described herein from Nevada.

### Suborder TEREBRATELLIDINA Muir-Wood, 1955
### Superfamily ZEILLERIACEA Allan, 1940
### Family ZEILLERIIDAE Allan, 1940
### Genus ZEILLERIA Bayle, 1878

*Type species. Zeilleria quadrifida* Lamarck, 1819, p. 253, fig. 35, from the Lias of France. Delance (1974, p. 178) considered the specimen in the Lamarck Collection, Museum of Natural History, Geneva, Switzerland, as the type.

*Discussion.* Delance (1974) made a thorough revision of *Zeilleria* and the species that occur in western Europe. He considered *Cincta* Quenstedt a subgenus of *Zeilleria.*

### *Zeilleria* cf. *Z. elliptica* (Zugmayer, 1880)

Plate 3, figs 26–33; Text-figs 17–18

cf. 1880 *Waldheimia elliptica* Zugmayer, p. 17, pl. 2, figs 6–8, 10.
cf. 1963 *Zeilleria elliptica* (Zugmayer); Dagys, p. 192, pl. 28, figs 10–13.

*Type material.* From the Rhaetian of Kitzberg, near Pernitz, Austria. A lectotype for the species has not been selected (Siblik 1988).

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EXPLANATION OF PLATE 3

Figs 1–4. *Zugmayerella uncinata.* UMIP 20320 (sectioned, Text-fig. 10A); Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All ×2.

Figs 5–6. ?*Zugmayerella* sp. UMIP 6952; Lower Member, Luning Formation, unnamed canyon, Nevada; pedicle and lateral views respectively. All ×1.

Figs 7–10. *Rhaetina gregaria.* UMIP 20315; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All ×1.

Figs 11–14. *Rhaetina gregaria.* UMIP 20311; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All ×1.

Figs 15–18. *Rhaetina gregaria.* UMIP 20359 (sectioned, Text-fig. 15); Lower Member, Luning Formation; Cinnabar Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All ×1.

Figs 19–22. *Rhaetina gregaria.* UMIP 20413; (sectioned Text-fig. 16), juvenile; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All ×1·5.

Figs 23–25. *Rhaetina* sp. cf. *R. gregaria.* UMIP 20317; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, lateral and anterior views respectively. All ×1.

Figs 26–29. *Zeilleria* cf. *Z. elliptica.* UMIP 20336; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All ×1·25.

Figs 30–33. *Zeilleria* cf. *Z. elliptica.* MSM 6186 (sectioned, Text-fig. 18); labelled 'Luning Ls.' (= Lower Member, Luning Formation; probably from Dunlap or Cinnabar Canyon, Nevada); brachial, pedicle, lateral and anterior views respectively. All ×1·5.

PLATE 3


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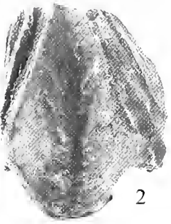
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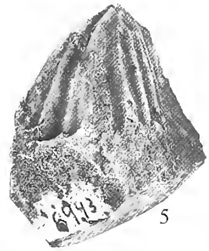

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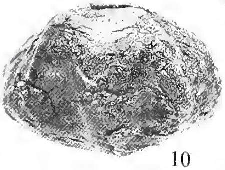
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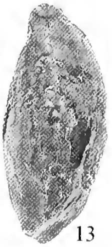
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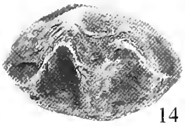
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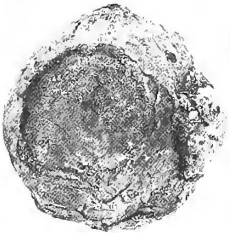
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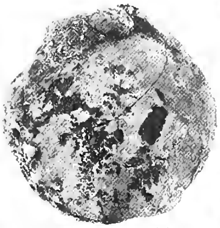
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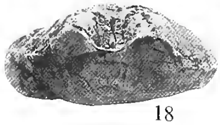
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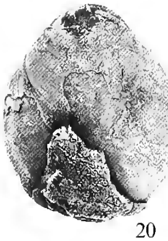
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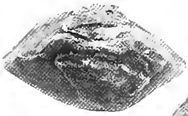
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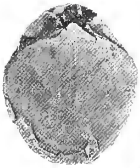
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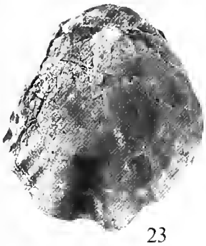
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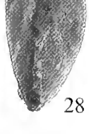
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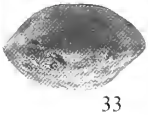
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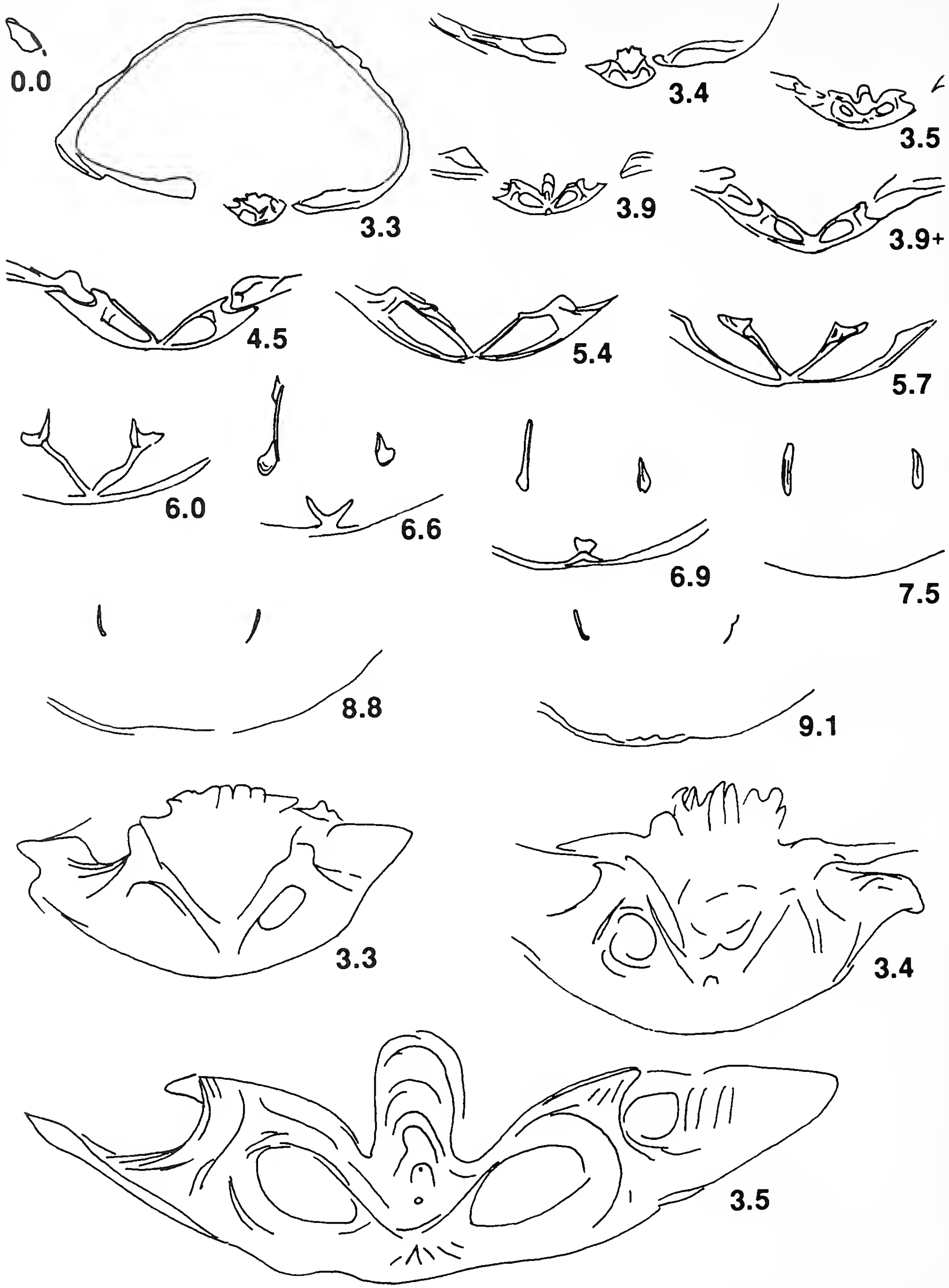
SANDY and STANLEY, *Zugmayerella*, ?*Zugmayerella*, *Rhaetina*, *Zeilleria*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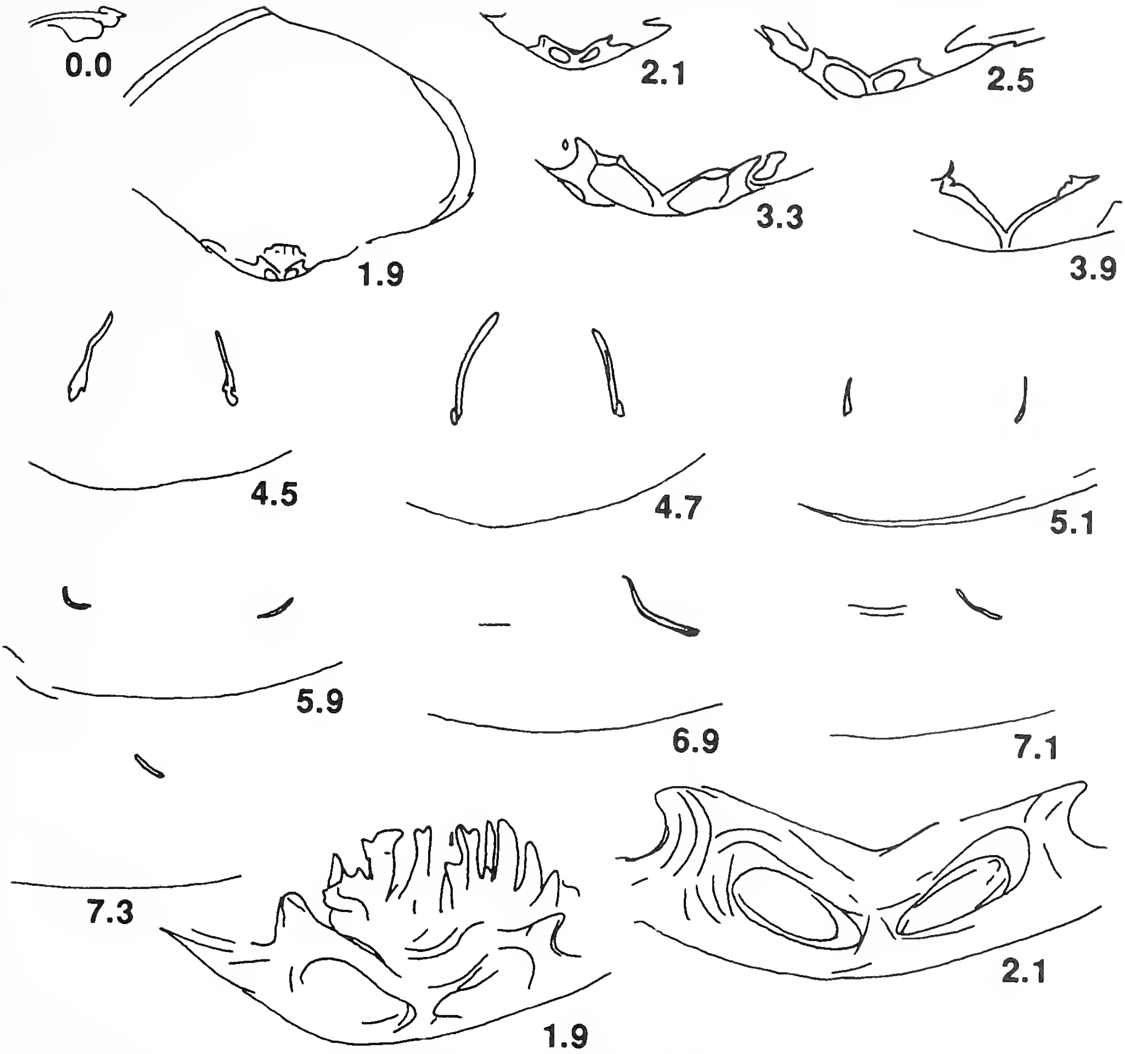

TEXT-FIG. 16. Transverse serial sections through a specimen of *Rhaetina gregaria* (Suess); UMIP 20413; Lower Member, Luning Formation; Dunlap Canyon, Nevada. Sections taken perpendicular to length of the brachial valve. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Cardinal process (1.9), dorsally inclined hinge plates (1.9–3.9), ventrally inclined crural processes (4.7) and transverse band? (6.9) present. Brachidium traced to 7·3 mm, last section taken at 7·7 mm. Magnification of sections 0.0–7.3; ×6·6, sections 1.9 and 2.1 also shown at ×40. Dimensions of sectioned specimen: L = 21·3; Lbv = 19·9; W = 17·5; T = 9·6 mm.

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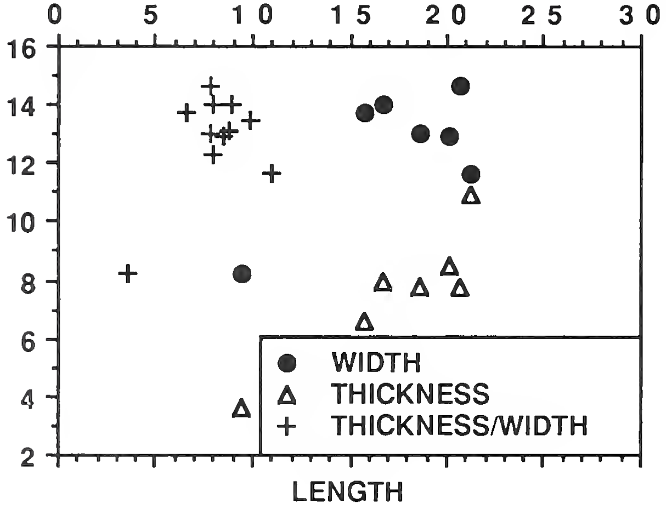
TEXT-FIG. 15. Transverse serial sections through a specimen of *Rhaetina gregaria* (Suess); UMIP 20359; Lower Member, Luning Formation; Cinnabar Canyon, Nevada. Sections taken approximately perpendicular to brachial valve length. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. For some of the sections before section 3.9+ the base plate on which the specimen was sectioned was slightly out of alignment with the grinding surface. Up until 3.9+, sections probably represent about 0·2–0·3 mm less removed than the actual value shown. Cardinal process (3.3, 3.4), boss-like process (3.5–3.9), dorsally inclined hinge plates (3.3–6.0), dorso-ventrally directed crural bases (6.0) and crural processes (6.6) present. Brachidium traced to 10·3 mm, last section taken at 10·9 mm. Magnification of sections 0.0–9·1, ×4; sections 3.3, 3.4 and 3.5 also shown at ×25. Dimensions of sectioned specimen: L = 27·2+; W = 27·3; T = 13·6+ mm.

*Material.* Lower Member, Luning Formation, Cinnabar and Dunlap Canyons and limestone and secondary dolomite member, Luning Formation, West Union Canyon, Berlin-Ichthyosaur State Park, Shoshone Mountains, Nevada. UMIP 6854, 6863, 20336, 20345, 20349, 20356, 20370, 20382, 20397, 20405, 20407, 20417, 20423. Specimens in the collection of the University of Reno are probably from the Pilot Mountains, MSM 6172, 6186, 6189.

*Diagnosis. Zeilleria* of elongate-oval to elliptical outline, may have an anteriorly truncated outline. Both valves are smooth, with some growth lines discernible. The anterior commissure is rectimarginate to incipiently uniplicate. Pedicle foramen small, beak ridges sharp. The presence of dental lamellae and a median septum can be determined in a number of specimens from external examination. Hinge plates horizontal.

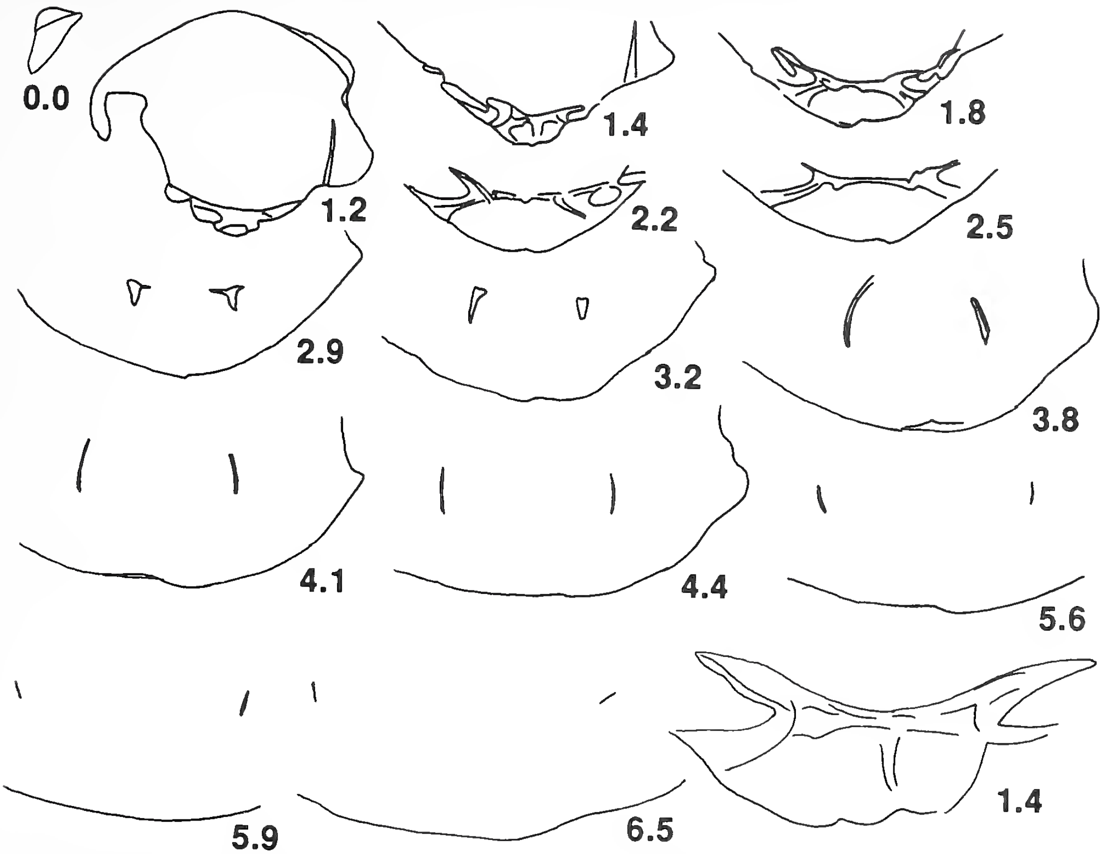
*Description.* Length is greater than width which is greater than thickness (Text-fig. 17). Transverse serial sections have been taken through one specimen (Text-fig. 18). Dental lamellae are present (sections 1.2, 1.4 mm). The median septum (section 1.4) is short, but a low median ridge continues anteriorly (section 3.8). The united hinge plates and inner socket ridges form a broad, ventrally concave septalium (sections 1.4, 2.2). Anteriorly the crura extend to crural processes (section 3.8). The descending branches of the loop are present until section 5.9. Beyond this it is difficult to trace the brachidium as the loop is believed to be broken.



TEXT-FIG. 17. Plot of length versus width and thickness and of thickness versus width for *Zeilleria* cf. *Z. elliptica* (Zugmayer), Pilot and Shoshone Mountains, Nevada.

*Discussion.* Zeilleriid brachiopods are difficult to characterize at the specific level. Like many of the taxa already considered, they may show considerable variation, particularly in their most obvious and readily observable characters – shell outline and profile. The zeillerids available for study from Nevada show a wide range of variation in outline and profile and there may well be more than one species present. There are a number of zeillerid species that have been recorded from the Triassic and Jurassic that are similar to the American specimens.

One specimen of *Zeilleria elliptica* figured by Dagys (1963, pl. 28, fig. 12) is very similar in outline to the specimens of *Z.* cf. *Z. elliptica* figured herein (Plate 3, figs 26–33). A few specimens (MSM 6186) are very similar to *Z. bukowski* (Bittner, 1892) figured by Dagys (1963, pl. 28, figs 14–18). Generally though, *Z.* cf. *Z. elliptica* from Nevada is smaller, has a more angular outline and less inflated profile than typical specimens of *Z. bukowski.* The American specimens are comparable to *Z. perforata* (Piette, 1856) which has been recorded from the Early Jurassic, but Delance (1974) recorded very similar forms from the Triassic. *Z.* cf. *Z. elliptica* tends to be more elliptical and



TEXT-FIG. 18. Transverse serial sections through a specimen of *Zeilleria* cf. *Z. elliptica* (Zugmayer); MSM 6186; labelled 'Luning Ls.' = Lower Member, Luning Formation; probably from Dunlap or Cinnabar Canyon, Nevada. Sections taken perpendicular to length and median septum of brachial valve (visible for 5·5 mm on exterior). Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Dental lamellae, median septum and broad septalium (1.2–1.4) and concave descending lamellae (3.2–5.9) present. Last section taken at 6·8 mm, brachidium damaged. Magnification of sections 0.0–6·5, ×4; section 1·4 also shown at ×25. Dimensions of sectioned specimen: L = 18·7+; Lbv = 17·7; W = 14·0; T = 8·9 mm.

laterally compressed than *Z. perforata*. Delance (1974, p. 391, fig. 21-1) recorded *Z. perforata* as ranging from the very bottom of the Jurassic in western Europe. In a phylogenetic diagram Delance regarded *Z. elliptica* as ancestral to *Z. perforata*. They are very similar in their morphology and presumably closely related. *Z. lingulata* Ching *et al.* (1979, p. 211, pl. 51, figs 4–9) is another zeillerid species that is similar in outline to *Z.* cf. *Z. elliptica*.

The septalium is not strongly developed or markedly concave in the sectioned specimen of *Z.* cf. *Z. elliptica* (Text-fig. 18). In many of the papers referenced above in which serial sections are given for the species discussed, the septalium is often markedly concave and the median septum well-developed. Sections of *Z. bukowski* in Dagys (1963, fig. 93) do show a broad, gently concave septalium. The concavity of the septalium is partly a function of the angle of sectioning and the incurvature of the umbo of the brachial valve, and the median septum is a variable character, liable to resorption during growth. A number of the Nevada specimens do show the presence of a median septum in the brachial valve, suggestive of *Zeilleria*, rather than the genus *Gusarella* Prosorovskaya, 1962, which lacks one.

*Occurrence*. Lower Member, Luning Formation, Cinnabar and Dunlap Canyons and limestone and secondary dolomite member, Luning Formation, West Union Canyon, Berlin-Ichthyosaur State Park, Shoshone Mountains, Nevada.

*Acknowledgements*. This research was supported by the National Science Foundation (Grant EAR-8916664 to G.D.S.) including an N.S.F. Research Opportunity Award to M.R.S. who also acknowledges University of Dayton Research Council and Student Fellows Employment Programme awards. We thank the late Professor Derek V. Ager for providing comments on the manuscript. Ms Jennifer A. Hoglcr, University of California, Berkeley, kindly assisted with the collecting of brachiopods, donated specimens, and showed sections in the Luning Formation in Berlin-Ichthyosaur State Park where Brad Kosch, Park Supervisor, allowed access to sections. Dr Norman J. Silberling, United States Geological Survey, Denver, provided valuable information on Triassic stratigraphy and comments that improved the manuscript. Dr John S. Oldow, Rice University, Houston, Texas, allowed access to and the use of unpublished field notes. Mr Frederick Collier, Ms Jann Thompson and Mr Rex Doescher, Smithsonian Institution, assisted with collections, and loans to M.R.S. Rex Doescher also supplied information from his brachiopod bibliography and English translations from Russian papers made by Mrs Josephine Cooper. Dr Thomas P. Lugaski provided access to collections in the Geology Museum, Mackay School of Mines, University of Reno, Nevada. Dr Franz Stojaspal, Geologische Bundesanstalt, Vienna, and Dr David Pearson, Laurentian University, Sudbury kindly loaned topotype material to M.R.S. Cindy McIlveen, University of Montana, took the photographs; John Moreau, University of Dayton, made the prints and Kevin Anderson, University of Dayton, assisted M.R.S. with the preparation of the serial sections.

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# SUBDIVISION OF THE LOWER PALAEOZOIC ARTICULATE BRACHIOPOD FAMILY TRIPLESIIDAE

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ABSTRACT. Reconsideration of the form of the triplesiid pseudodeltidium, which has been used as a basis for subdivision into subfamilies, together with the distinct forms of the forked cardinal process, indicates that while these criteria do form useful bases for generic distinction, variation both of combinations of characters and of characters within some genera and species mitigate against any meaningful subdivision of this intriguing and genetically plastic brachiopod family. A recent proposal to establish families of Triplesiacea based on shell ornamentation is shown to be similarly flawed, and the view is taken that at present the genera are best assigned to the single undivided family Triplesiidae.

ALTHOUGH the varied external appearance of the triplesiid brachiopods initially led to species being placed in such disparate genera as *Atrypa*, *Orthis*, *Rhynchonella*, *Spirifer* and *Strophomena*, the combination of strong fold and sulcus, straight hinge-line and short interarea in *Atrypa extans* and other species led Hall (1859) to erect the genus *Triplesia*. This was before any internal structures were known; as knowledge of the valve interiors accumulated, the discovery of the characteristic cardinalia with its long, forked cardinal process (Pl. 1, figs 1, 8, 13) served to confirm the closely knit nature of the group. Schuchert (1913) formally recognized the group as a Subfamily (Tripleciinae) of the Strophomenidae. The marked differences between this subfamily and other strophomenids prompted Öpik (1932) to raise the group to familial level. The distinctive combination of morphological characters was further emphasized by the single family being accorded the status of superfamily by Cooper (1944) and order by Moore (1952), although the latter designation was reduced to a suborder by Muir-Wood (1955) and was accepted as such for the brachiopod *Treatise* (Wright 1965).

Ulrich and Cooper (1936, p. 331), applying the thesis that the family characters of brachiopods are found principally in the dorsal interior and in the region around the ventral beak, noted that the features of the cardinalia were the more persistent, 'presenting practically identical structures in each of the genera'. At the same time they recognized that the genera were distinguished by the characters of the exterior, i.e. ornamentation, plication and shell outline. These characters were in fact the only ones used for generic differentiation until Amsden (1968) established the genus *Placotriplesia*, which he distinguished from *Triplesia* by its pseudodeltidium, which is flat, or at least flush with the interarea, and lacks the median fold seen on that of *Triplesia*. This morphological character was then used to subdivide the family for the first time: into the Placotriplesiinae, containing only *Placotriplesia*, and the Triplesiinae, containing the other ten genera. The two species initially included in *Placotriplesia* were *Triplesia praecipta* and *T. juvensis* (both Ulrich and Cooper 1936), from the St Clair Limestone, in which the former is common and the latter known only from a single specimen. Two species tentatively assigned to the genus by Amsden, *T. waldronensis* (Miller and Dyer) and *T. rostellata* Ulrich and Cooper from the Waldron Shale, were subsequently confirmed by him as lacking the pseudodeltidial fold (Amsden 1971, p. 149).

The morphological term *monticulus* (Cooper and Grant 1974) has recently been applied to the median fold which characterizes the pseudodeltidium in most triplesiacean stocks (Wright and

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Jaanusson 1993). Examples of the two contrasting styles of pseudodeltidia are illustrated here for *Plectotreta* and *Ogmoplecia*, the former possessing a well-developed monticulus (Pl. 1, fig. 3), which is lacking in the latter (Pl. 1, fig. 2).

The institutional abbreviations for the repositories of the specimens figured in Plate 1 are: BMNH, The Natural History Museum, London; IGT, Institute for Geology, Tallinn; RMS, Riksmuseum, Stockholm; USNM, National Museum of Natural History, Smithsonian Institute, Washington D.C.

## MORPHOLOGICAL VARIATION IN TRIPLESIIDS

The monograph on Silurian brachiopods from Arkansas and Oklahoma, USA, by Amsden (1968) included a revision of the diverse triplesiid stocks of the St Clair Limestone that were described by Ulrich and Cooper (1936). In this monograph three subgenera of *Onychotreta* Ulrich and Cooper were proposed along with *Placotriplesia* and the subfamily Placotriplesiinae. Concern was expressed by Wright (1972) that *Onychotreta* represented a very plastic and commonly deformed stock of highly variable form for which, in view of the distribution of all six *Onychotreta* species at one locality (Wright 1972, table 1), there was doubt over the reality of the species let alone the subgenera. The point was made in that paper that there is a 'variation of variation' (Wright 1972, p. 8) with some stocks having much greater plasticity than others, a point which has been recently illustrated from living populations of *Terebratalia transversa* by Schumann (1991). The variation of the St Clair triplesiid stock at the cited locality produced a further generic problem over a single ventral valve with the elongate form of *Onychotreta* for which Ulrich and Cooper (1936, p. 335) erected a separate species, *Brachymimulus elongatus*, this generic assignment being on the basis of the 'strong, wide (ventral) fold'. Amsden (1968, p. 38) felt that this was possibly a morphological variant of *Onychotreta plicata*, although he accepted the species questionably as *Brachymimulus* (Amsden 1968; Amsden and Barrick 1988); I would regard the specimen as a variant of

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EXPLANATION OF PLATE 1

Figs 1, 8, 13. *Triplesia* sp. Haraldstangen, east coast, Hurum, Norway; Ordovician (Ashgill), Langåra Formation; silicified hinge regions showing keeled cardinal process, clearly separated brachiophores and sockets of dorsal valves, and their relationships to the teeth and dental plates of the ventral valves. 1, antero-lateral view of RMS Br136900. 8, 13, anterior views of RMS Br136901 and RMS Br136902. All ×8.

Fig. 2. *Ogmoplecia* sp. IGT Br4350; Korgessare Quarry, Island of Hiiumaa, Estonia; Ashgill, Vormsi Stage (F 1b); postero-dorsal view of conjoined valves showing ventral interarea with flush pseudodeltidium lacking a median fold (monticulus), ×3.

Figs 3–4, 7. *Plectotreta lindstroemi* Ulrich and Cooper, 1936. Gotland, Sweden; Silurian; locality and horizon unknown; 3, RMS Br99526, dorsal view of ventral valve, showing well-developed monticulus. ×4. 4, 7, RMS Br99525; ventral and antero-ventral views of dorsal valve showing features of the grooved cardinal process and brachiophores. All ×5.

Figs 5–6. *Streptis* cf. *monilifera* (M'Coy). USNM 454645; Osmundsberget, Dalarna, Sweden; Ashgill, Boda Limestone; anterior and dorsal views to show sinusoidal anterior commissure. Both ×5.

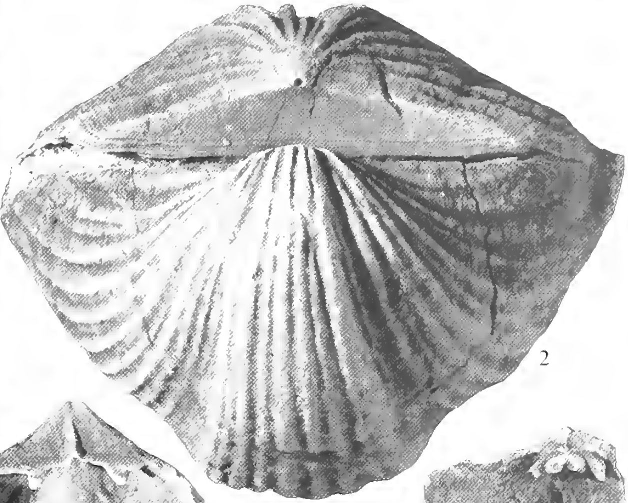
Fig. 9. *Ogmoplecia* sp. nov. RMS Br136899; Ireland; Ashgill (Cautleyan), Portrane Limestone; anterior view of silicified dorsal valve to show grooved cardinal process and brachiophores, ×4.

Figs 10, 12, 15. Triplesiid gen. et sp. nov. RMS Br13445; Kallholn Quarry, Dalarna, Sweden; Ashgill, Boda Limestone; dorsal, ventral and anterior views of conjoined valves. All ×2.

Figs 11, 14. *Streptis grayii* (Davidson). BMNH B.8072 (Davidson Colln); Gotland, Sweden; 'Wenlock', locality and horizon unknown; details of cardinalia in a disarticulated dorsal valve. 11, postero-ventral view showing cardinal process hood, forked cardinal process and brachiophores. 14, antero-ventral view showing grooved nature of cardinal process. Both ×5.

PLATE 1


1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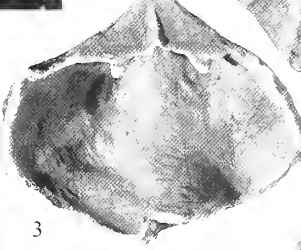
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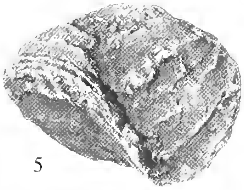
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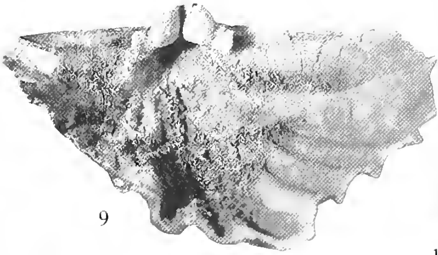
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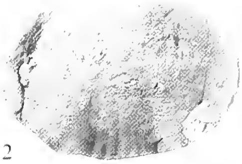
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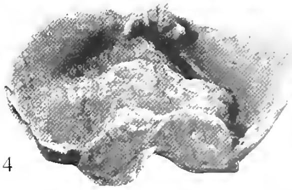
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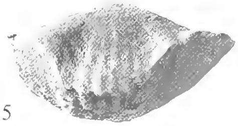
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WRIGHT, triplesiid brachiopods

*Onychotreta*. In other stocks, such fold reversion is standard and therefore appears to be a valid generic character. *Brachymimulus* is separated generically from *Triplesia* on the criterion of having a ventral and not a dorsal fold; the recently erected *Paraonychoplecia* Percival, 1991, is similarly differentiated from the older *Onychoplecia* by its ventral fold.

Regarding *Placotriplesia*, variation in the development of the median fold on the pseudodeltidium in various triplesiids further raised doubts as to whether a genus and subfamily should be defined on this single character (Wright 1971). Examples cited in that paper of the variation of the pseudodeltidial fold included: the sample from the Ashgill Portrane Limestone of *Oxoplecia* cf. *plicata* (Wiman) in which the median fold was only occasionally developed; a sample of *Oxoplecia* sp. from the Chair of Kildare Limestone (Ashgill, Ireland) again predominantly without the fold; and the species *Oxoplecia filosa* and *O. multicostellata* described by Cooper (1956) from rocks of Caradoc age in Oklahoma and Virginia, USA, respectively in which the fold of the young stages is lost in the adult. Amsden (1974), in his redescription of the Ashgill *Cliftonia tubulistriata* (Savage) from Missouri, USA, recorded that in this form also the pseudodeltidial fold may or may not die out towards the front of the pseudodeltidium. Amsden's assertion (1973, pp. 253, 273) that 'Wright's observation that the type species of *Placotriplesia* (*P. praecipta*) has a pseudodeltidial fold is incorrect' needs to be corrected. The text on this species (Wright 1971, pp. 342–343) is as follows: 'Ulrich and Cooper (1936, p. 333) state that the median fold is possessed by "well preserved specimens", the implication being that any absence of the structure is a reflection of preservation. But Amsden (1968, p. 41) maintains that its absence in the case of *T. praecipta* is not the result of preservation, a view which my own studies of this and other triplesiid species would support. With some reservations, Amsden's observation of the flat nature of the pseudodeltidium in this species then is essentially acceptable.'

## THE CARDINALIA–PSEUDODELTIDIAL COMBINATION

In the typical systematic description of the triplesiid species, the cardinal process is implied or described simply as being forked, or perhaps further modified as being long, short or recurved. Ulrich and Cooper (1936, p. 333) additionally comment on variation within a species as ranging from 'rather stout' to 'comparatively slender'. A basic morphological difference in the cardinalia only came to light in 1964 when the strikingly different cardinal processes of species of *Triplesia* and *Oxoplecia* from the Cautleyan Portrane Limestone of Ireland (Wright 1964, pl. 11, figs 9, 12) were respectively described as having the fork fused proximally into a single unit, or deeply cleft with each prong fused more with the adjacent brachiophore than with the other prong. The two types, here represented in Plate 1, figures 8 and 9, were subsequently designated as 'keeled' or 'grooved' (Wright 1971, p. 354) and in attempting to assess the taxonomic value of the structures of the postero-median part of the valves, the point was made that the typical Portrane *Oxoplecia* with a grooved cardinal process also possesses a smooth pseudodeltidium. Although this was not considered by Amsden, his sections of *Placotriplesia praecipta* (1968, text-figs 23B–C, 24D–E) show that its process is also of the grooved type. Moreover, the lack of a cardinal process hood is also common to these two forms.

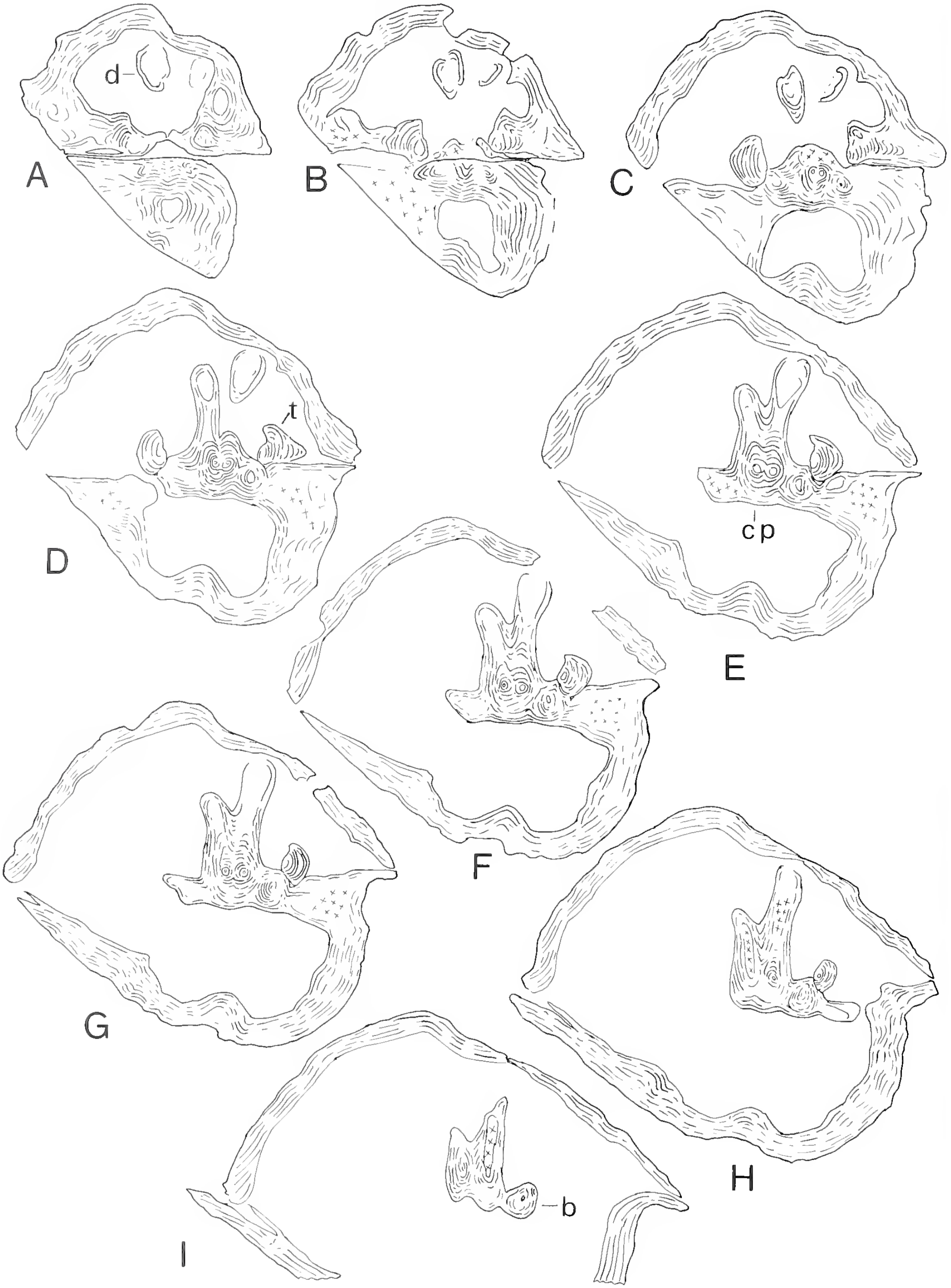
The basis for a subfamilial division on the combination of smooth pseudodeltidium and grooved cardinal process on the one hand and of fold-bearing pseudodeltidium and keeled cardinal process on the other seemed plausible. However, the presence of an *Oxoplecia* sp. from the Ashgill Kildare Limestone of Ireland, which in some specimens combined a grooved cardinal process with a pseudodeltidial fold effectively precluded a subfamilial division based on the linkage of the *Placotriplesia* characters (Wright 1971, p. 354); but the combination of characters does appear useful at a generic level. In contrast to my initial views (Wright 1971) I am now convinced of the soundness of Amsden's genus and its usefulness in biostratigraphy.

To accommodate species such as the forms noted above from Portrane and Kildare hitherto placed in *Oxoplecia* but which differ from that genus notably in the possession of a grooved cardinal process and a predominantly smooth pseudodeltidium, a new genus, *Ogmoplecia*, has been established (Wright and Jaanusson 1993). This is a widespread although rarely abundant form in the Ashgill of north-west Europe. The exact stratigraphical range and distribution have yet to be established; but any record of a coarse ribbed '*Oxoplecia*' must remain suspect until the diagnostic characters are ascertained.

In his 1971 paper, Amsden made the interesting stratigraphical point that the known *Placotriplesia* in North America are confined to the Wenlock, with *Triplesia* not ranging up beyond the Llandovery. In his consideration of material from outside North America, Amsden, basing his comments on Davidson's figure (1883, pl. 8, fig. 23), observed that the single specimen of the species *T. wenlockiensis* from the Wenlock Limestone has a pseudodeltidial ridge (Amsden 1971, p. 149); but re-examination of the specimen by Bassett (1972, p. 73) showed that the pseudodeltidium is in fact flat like *Placotriplesia*, and bears no trace of any median structure. Amsden also suggested that other smooth-shelled European species such as Barrande's species *Minulus moera* and *M. contrarius* from Bohemia could also be representatives of *Placotriplesia*. These Wenlock species have recently been re-examined by Havlíček (Havlíček and Štorch 1990, p. 58) and the flat pseudodeltidium confirmed. No smooth triplesiids have been described from the Wenlock of Gotland, but I have examined the IGT collections for triplesiids and these include a small amount of fragmentary material obtained by Dr Madis Rubel from marls of Wenlock age in south-west Estonia and which were provisionally ascribed to *Triplesia*. The sample, IKLA: 276.0–1 from the Paramaja horizon of the Jaani Stage (J1), consists of fragments of about ten valves including three well-preserved cardinalia, but no ventral valve interareas that show a complete pseudodeltidium. The three cardinalia, of which the largest is 3·1 mm wide as measured between the distal ends of the brachiophores, all possess a grooved cardinal process with a flat dorsal surface without any trace of a cardinal process hood. Thus, notwithstanding the lack of data regarding the pseudodeltidial fold, I regard these features in themselves as being sufficiently diagnostic so that, coupled with the smooth external surfaces, these Wenlock specimens from Estonia may therefore confidently be attributed to *Placotriplesia*. Thus all the European evidence presently available supports the evidence from North America that *Placotriplesia* seems to replace *Triplesia* in the Wenlock.

## VARIATION IN *STREPTIS*

The development of the cardinal process type is of particular interest in the small triplesiid *Streptis*, which invariably has a monticulus on the pseudodeltidium. *Streptis* occurs most abundantly in the form of conjoined valves so that separated valves revealing the features of the interior are of relatively rare occurrence at most horizons. In the BMNH collections, amongst the large numbers of the Wenlock species *Streptis grayii* (Davidson) from Shropshire and Staffordshire, is a dorsal valve of this species in the Davidson Collection (B.8072) from Gotland in which the cardinal process possesses a hood but which is also grooved (Pl. 1, figs, 11, 14). A single dorsal valve from the Wenlock Shale at Dudley in the USNM (86311) also displays a grooved cardinal process. In his redescription of this species, Bassett (1972, p. 77) noted the grooved nature of the cardinal process and its very small hood; the latter is visible on the accompanying illustrations (pl. 17, figs 4–5), although the dorsal surface of the proximal part of the cardinal process is not visible. Transversely sectioned specimens of conjoined *S. grayii* valves (Text-fig. 1) do not, however, show the typical proximal indentation on the dorsal side as illustrated for the grooved process of *Placotriplesia praecipta* (e.g. Amsden 1971, fig. 8B), *P. waldronensis* (e.g. Amsden 1973, fig. 15F) and *Oxoplecia* sp. (Wright 1971, fig. 2e–f; and as *Ogmoplecia* in Text-fig. 2A–B herein). Instead, the dorsal side of the process is essentially flat in this region, with the groove developing later on the anterior surface as the process curves posteriorly to become directed into the ventral umbonal cavity. This was the same in all three specimens sectioned to examine the cardinal process. Thus the grooved process of *S. grayii* differs from the other grooved processes noted above. The flat proximal part is also in contrast with that of the keeled process, illustrated here for *Triplesia extans* (Text-fig. 2C–D), which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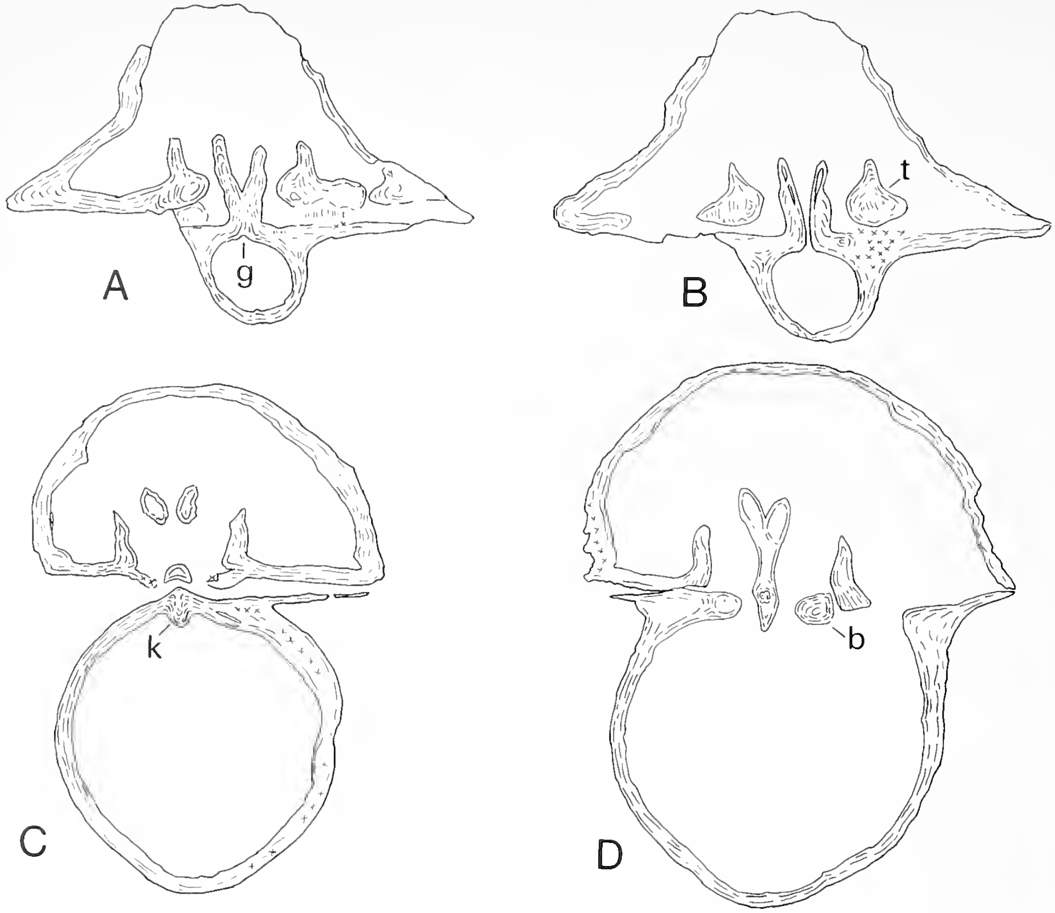
has a posterior ridge proximally that continues onto the anterior surface, with the fork only developing distally on the ventral facing surface.

But while the Wenlock *S. grayii* has a modified grooved process, a section taken of the Norwegian Early Llandovery form *S. altosinuata* Holtedahl and figured by Wright (1960, fig. 11F) shows this earlier species to be a keeled form. Similarly, the figure of Hints (1986, pl. 1, fig. 13) shows that the Late Ashgill Porkuni Stage *S. undifera* (Schmidt) from Estonia also possesses a keeled process. Since that paper was written, additional silicified material has been extracted from etchings for conodonts from Porkuni Quarry and is now in the collections of the IGT. The cardinalia of these exquisitely preserved specimens consist of very delicate, pointed, laterally directed brachiophores, well separated from a keeled cardinal process that possesses a well-developed hood. In the ventral valve, a pedicle tube with ventral margins advancing across the valve floor has been noted, such a tube having previously been recorded in *S. altosinuata* (Wright 1960) and *S. grayii* (Bassett 1972). The teeth are supported by receding dental plates, divergent to the valve floor, while the pseudodeltidium has a well-developed monticulus with an anterior invagination reflecting the presence of a curved, saddle-like plate internally.

The evidence of these forms of *Streptis* suggests either that the apparently consistent keeled process of these earlier species had evolved towards a grooved process by Wenlock times; or that the process is the more fundamental character, and that the Wenlock form developed independently from a lineage with a grooved process and converged towards the earlier *Streptis*. The latter interpretation is here regarded as demanding too much of evolutionary convergence in requiring the separate development of a species that, apart from the cardinal process, shares all its generic characters with other members of the genus. These characters are a small size, up to about 10 mm long; an ornamentation consisting of concentric lamellae that are extended into frills and crossed by radial ribs, the differing densities of which form the basis of the species; and a dorsal fold and ventral sulcus which are commonly lost in an asymmetrical twisting of the shell (hence the generic name), the end result of which is the development of a sinusoidal anterior commissure (Pl. 1, figs 5–6). The asymmetry characterizes all species, but to a varying degree. Thus although *S. altosinuata* is a species in which symmetrical forms predominate, about one in five shells in a sample of fifty-four showed some degree of asymmetry, with only one showing a sinusoidal anterior commissure (Wright 1960, p. 267). The Wenlockian *S. grayii* has an asymmetrical shell apparently invariably developed (Bassett 1972, p. 77), along with a sinusoidal anterior commissure. The St Clair Limestone Wenlock species, *S. glomerata* Ulrich and Cooper, 1936, is similarly twisted, apart from two ventral and one dorsal valves in Ulrich and Cooper's sample; Amsden (1968, p. 39) questioned the assignment of the dorsal valve to *S. glomerata*, but the specimen is probably best interpreted as a variant of that species in view of the indisputable variability of the asymmetry in other forms.

As regards intraspecific variation in *Streptis grayii*, although Bassett (1972, p. 74) recorded a pseudodeltidial fold as being present in every specimen examined, he made the point that its development was variable, between being hardly perceptible to being strong and prominent. Further, the presence of *S. grayii* of a pseudodeltidial fold in combination with a grooved cardinal process furnishes another example of the variable association of potential subfamilial characters that mitigates against any clear-cut subfamilial groupings. The distribution of these characters for some of the triplesiid taxa is illustrated in Table 1. While this covers many well-known and widespread forms, the list is far from comprehensive. In the first place many descriptions do not detail the precise form, particularly of the internal structures; and in the second, the necessary well-preserved ventral interareas and valve interiors are simply not available for description. For example, *Oxoplecia shallockiensis* (Davidson) from the early Ashgill of Girvan is a species long known, but from only a single dorsal valve exterior (Harper 1989, p. 100). Notwithstanding these gaps in the

TEXT-FIG. 1. Sequence of transverse sections to show the development of the cardinal process in a specimen of *Streptis grayii* (Davidson), taken at 0·1 mm intervals, A at 0·3 mm from the ventral umbo; ventral valve uppermost, × 12. Abbreviations: b = brachiophore; cp = cardinal process; d = distal ends of cardinal process; t = tooth.



TEXT-FIG. 2. Transverse sections comparing the grooved cardinal process of *Ogmoplecia* sp. (A at 1·3 mm and B at 1·5 mm from the ventral umbo) with the keeled cardinal process of *Triplesia extans* (Emmons) (C at 1·8 mm and D at 2·25 mm from the ventral umbo). Ventral valve uppermost. All × 8. Abbreviations: b = brachiophore; g = groove; k = keel; t = tooth.

information available, Table 1 does nevertheless show that the variation in these potentially supra-generic characters is such as to preclude any meaningful taxonomic grouping of the triplesiid stocks.

## PSEUDODELTIDIUM AS A MEANS OF SUBDIVISION

From the earlier discussion it is clear that while the characteristic of the presence or absence of a pseudodeltidial fold may be of systematic value at generic level, its use by Amsden (1968) to subdivide the family into two subfamilies is unacceptable, as the structure is too variable to allow any such clear-cut division. Additional examples are to be found in *Amphiplecia* and *Grammoplecia* (both Wright and Jaanusson 1993). Both show variation in the degree of development of the monticulus, which in the former is absent to weak and in the latter commonly developed posteriorly but fading with growth: this may be associated with the change in attitude of the interarea. The feature of a keeled or grooved cardinal process, while again quite distinct and useful as a valid generic character in some stocks, also shows itself to be of variable form in others; the basically keeled processes of *Oxoplecia multicostellata* Cooper and *Cliftonia tubulistriata* (Savage) fall into

TABLE 1. Distribution of potential supra-generic characters in some triplesiid taxa.

| Taxon and age | Monticulus | Pedicle tube | Cardinal process | Hood |
|---|---|---|---|---|
| *Triplesia* spp. (M. Ordovician–Llandovery) | Present | Absent, passage | Keeled | Present |
| *Placotriplesia* spp. (Wenlock) | Absent | Absent | Grooved | Absent |
| *Streptis undifera* (Ashgill) and *S. altosinuata* (Llandovery) | Present | Short | Keeled | Present |
| *S. grayii* (Wenlock) | Present, but variably developed | Short | Grooved | Present |
| *Ogmoplecia* spp. (Ashgill) | Absent, but may develop in some shells | Absent, passage | Grooved | Absent |
| *Cliftonia tubulistriata* (Ashgill) | Present, may be lost anteriorly | Present | Keeled variably | Absent |
| *Oxoplecia multicostellata* (Caradoc) | Present, but lost anteriorly | Passage | Keeled variably | Absent |
| *Bicuspina* spp. (Llandeilo–Caradoc) | Present | Present, long | Keeled low | Present |
| *Plecotreta lindstroemi* (Wenlock–Ludlow) | Passage | Present | Grooved | Present |

this latter category. Likewise, while the associations of these features, keeled process with pseudodeltidial fold and grooved process with smooth pseudodeltidium, are typical, other combinations do occur. Thus neither a single nor a set of characters has been found that can be used to produce a useful subdivision of the family into subfamilies. Not only is there variation in these particular characters, but a high degree of fluidity is present in various aspects of shell morphology among the genera, e.g. asymmetry in *Streptis*; radial ornament in *Onychotreta*. Indeed a commonly plastic shell form seems to be a hallmark of the family; and it is worth a reminder that while the secondary shell substance is apparently always lamellar and predominantly impunctate, the occasional stock does possess well developed pseudopuncta (Wright 1970).

## ORNAMENT AS A MEANS OF SUBDIVISION

Two main points were made by Havlíček (*in* Havlíček and Štorch 1990, p. 56) in his discussion of the Triplesiacea. First, regarding the taxonomic value of the pseudodeltidial fold, his quite independent view concurs with my own expressed above, i.e. that the structure is of value for the generic separation of *Placotriplesia* but is 'of little use when classifying triplesiids into higher systematic units' (Havlíček and Štorch 1990, p. 57). This last remark is based on the loss of fold occurring 'at least in three terminal links' of lineages. He further noted that the loss of the fold may be assumed to be a general trend in the evolution of upper Wenlock members of the suborder. *Streptis*, and also *Plectotreta*, would appear to be stocks that did not succumb to this trend; while *Ogmoplecia* showed the loss of the monticulus very much earlier.

Secondly, Havlíček (*in* Havlíček and Štorch 1990) made the radical proposal that the superfamily Triplesiacea may be subdivided into three families based on the shape of the shell and the ornamentation. The proposed families are the Triplesiidae s.s., containing the genera with smooth shells; the Oxopleciidae, containing the costate, costellate or imbricate genera; and the Onychotretidae, to contain those of claw-like outline with an extremely elongate ventral beak, i.e. the unusual and very variable *Onychotreta*. This proposal needs some consideration for, as indicated previously, the features around the ventral umbo and the dorsal cardinalia are the characters normally regarded as being of taxonomic significance at family level, with a role at higher levels for shell punctation and fabric. Ornamentation and variation in shape and other details are traditionally viewed then as having lower taxonomic significance. With regard to ornamentation, for example, that of *Eichwaldia* and *Dictyonella* could hardly be more dissimilar, with the fine concentric growth lines of the former contrasting with the 'very peculiar' net-like ornament of the latter (discussed in Wright 1981); but the two are so alike in all other respects that it is inconceivable that they should be placed in separate families or even subfamilies.

However, while accepting that the traditional view is not immutable, a problem with the new proposal is the inherent variation within the Triplesiacea that upsets the neat pigeon-holing of the two main smooth/ornamented groups. The following examples illustrate the point.

1. Williams's (1974) genus *Caeroplecia* is a costate form, distinguished from *Oxoplecia* by having a concentric ornament of rounded fila instead of lamellose growth lines, and also by its delayed rib development. Apart from the type species, Williams (1974, p. 123) included *Oxoplecia mutabilis* Williams, 1955, the original description of which emphasized the late development of the ribs. Williams pointed out that 'immature specimens (less than 14 mm wide) bear only marginal costae and much of the surface is without radial ornamentation' (Whittington and Williams 1955, p. 412). Here then are forms, along with, for example, several of the *Oxoplecia* species illustrated by Cooper (1956), in which either smooth forms develop ribs with age or else a ribbed form has undergone a neotenous suppression of the ribbing. Either way it casts doubt on the prudence of separating the rough from the smooth!

2. While *Onychoplecia* is defined by Cooper (1956, p. 529) as having a surface marked by concentric growth lines only, the earliest species, from the Llanvirn Table Head Group of Newfoundland, does show fine radial ribs in what Cooper described as exfoliated specimens (Cooper 1956, p. 532), although these are present on the *holotype* which is described as a perfect specimen, and the undulations visible on the lateral commissure (Cooper 1956, pl. 100, fig. 4) further suggest that this is a genuine feature of the external surface. Another sample, from the Hirnantian of northern England and which is identified as *Onychoplecia* sp. nov. by Temple (1968, p. 33), includes some specimens which develop marginal ribs. Temple considered these to be variant individuals of the essentially smooth-shelled species. Thus *Onychoplecia* could also be viewed as straddling two of the proposed families.

3. The genus *Grammoplecia*, described from the Ashgill Boda Limestone of central Sweden but including a number of other forms of upper Ordovician age (Wright and Jaanusson 1993), differs generically from *Triplesia* only in its capillate ornament, with the external form of the two type species having a particularly strong resemblance to each other. The fine ornament would however exclude the new genus from Havlíček's (Havlíček and Štorch 1990) smooth shelled Triplesiidae, a separation which would appear as anomalous as placing the well-known smooth Silurian pentameride *Stricklandia lens* in a separate family from the ribbed *Costricklandia lirata*.

4. Three other forms of the diverse triplesiid assemblage in the Ashgill Boda Limestone that were not known to Havlíček when he proposed his subdivision further demonstrate the impracticability of separating the smooth genera from those with variously developed concentric and radial ornamentations. *Amphiplecia* Wright and Jaanusson, 1993, is, like *Caeroplecia*, a ribbed form in which the ribs do not develop until after a smooth phase which encompasses the first 4–5 mm of growth, again producing a potential problem when classifying young shells in the proposed new families. A further problem is highlighted by a single adult specimen, which has been located in the RMS collections, from Kallholn Quarry, Sweden and which is identical with *Amphiplecia* (complete with the strikingly distinct shape where one-half of the shell is twisted with respect to the other along the mid-line of the shell) except that it is essentially devoid of radial ornament (Wright and Jaanusson 1993, fig. 4P–Q, T). This smooth individual is treated as being simply an aberrant member

of the *Amphiplecia* population, yet it would need to be placed in a separate family from its fellows according to the proposed new familial classification. A third problematic form in this assemblage is one which is smooth for the first 10 mm of growth, anterior to which ribs develop on the fold and in the sulcus, typically with 4 or 5 on the fold and one less in the sulcus, but which may be completely absent laterally (Pl. 1, figs 10, 12, 15). This form, which has a smooth pseudodeltidium lacking a monticulus, is known so far from only a dozen specimens of very variable preservation with information on the interiors lacking. Accordingly, although its distinct assemblage of characters indicate a new genus, it is at present considered best left under open nomenclature. But as regards Havlíček's familial classification, this is another form the placement of which would be uncertain.

5. A further example which presents a case similar to the smooth *Amphiplecia* specimen is an apparently smooth shell described by Poulsen (1943, p. 22) as *Streptis laevis*, a species distinguished from others of the genus primarily by the absence of radial ornamentation.

6. The extreme variation in *Onychotreta* includes the species *O. plicata* Ulrich and Cooper for which Amsden erected the subgenus *Lissotreta*. These shells are characterized (Amsden 1968, p. 37) by 'an exterior which is, excluding the pedicle valve sulcus and brachial valve fold, nearly smooth'. While this is here interpreted as one morphological expression of a highly plastic stock, a pigeon hole classificatory key based on ornament would technically place the form with the grouping containing the other smooth triplesiids, the surface of which is only modified by fold and sulcus. The proposed classification of Havlíček avoids this particular problem by giving *Onychotreta* a family of its own based in this case on its peculiar outline. *Onychotreta* is only known to occur in beds of Wenlock age, in Arkansas (Ulrich and Cooper, 1936), Oklahoma (Amsden 1968) and Bohemia (Havlíček and Štorch 1990). Re-examination of the single dorsal valve ascribed to this genus from the Ashgill of Ireland by Mitchell (1977, p. 66) shows that it is not an *Onychotreta* as it does not have the triplesiid cardinalia, although externally it does show similarities to the triplesiids now placed in *Amphiplecia*.

In summary, the known anomalies suggest that a separate family based on a smooth shell surface is far from satisfactory and would overlap with the family based on ornamented stocks, while the aberrant *Onychotreta*, stratigraphically appearing only in the final flourish of the superfamily, does not, in my opinion, merit separate familial status on present evidence. Likewise, the subdivision of the family based on the presence or absence of a monticulus cannot be sustained; in this connection it is of interest to note that the development of this structure has not been regarded as a suprageneric character in either the Stropheodontidae (Williams 1953) or the Derbyiacea (Cooper and Grant 1974). Accordingly, the view is taken here that the constituent genera are best assigned to the single undivided family Triplesiidae.

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