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Cover: The Coralline Crag (Pliocene) bryozoan *Cribrilina* sp. showing a group of ten feeding zooids each with an ovicell and paired adventitious avicularia on either side of the orifice. This specimen was figured as *Lepralia punctata* Hassall in G. Busk's Palaeontographical Society monograph of *Crag Polyzoa* (1859, pl. 4, fig. 1). It is reillustrated here by means of a new technique, scanning electron microscopy of the uncoated specimen using back-scattered electrons. × 75.

THE DIPLOPORITA OF THE OSLO REGION, NORWAY

by J. FREDRIK BOCKELIE

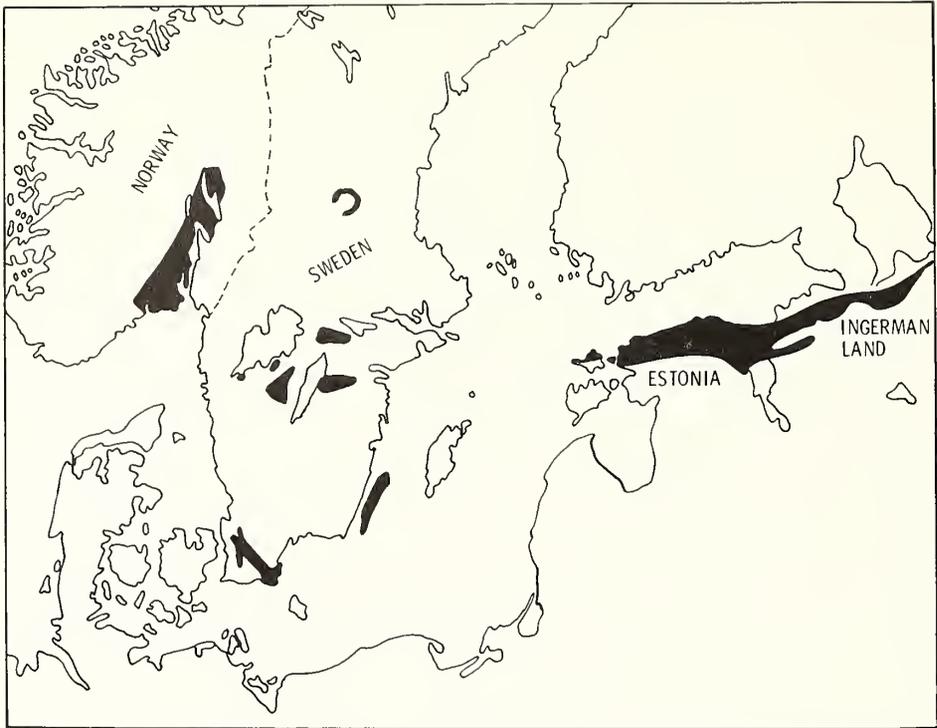
ABSTRACT. The Ordovician diploporite fauna from the Oslo Region is examined morphologically and taxonomically. The brachioles of *Protocrinites* are shown to be biserial. Pore-structures are described, including peripore connections and the structure of the skeletal mesh work. Internal morphological structures indicate a possible basal nerve ring and oral ring structures. Aspects of ontogeny and phylogeny dealt with include changes in plate number, an increased complexity of pore structures, and possibly an increased complexity of brachioles. A new family Parasphaeronitidae is described, comprising two new genera intermediate between Sphaeronitidae and Holocystitidae on the one hand and Aristocystitidae on the other. Fifteen taxa from three families are described, including three new genera (*Tetreucystis*, *Parasphaeronites*, and *Pachycystis*) and nine new species (*Protocrinites rugatus*, *Haplosphaeronis bratterrudensis*, *Eucystis langoyensis*, *Tetreucystis kalvoeyensis*, *T. elongata*, *T. tetrabrachiolata*, Sphaeronitidae sp. A, *Parasphaeronites socialis*, and *Pachycystis norvegica*). The stratigraphical and geographical distribution of genera and species within the Oslo Region is compared with the type of sediment in which they occur. Many genera have a relatively wide stratigraphical and geographical distribution but individual species are restricted. Morphological variation is relatively great and phylogenetic changes within the Norwegian diploporites are probably very complex.

THE term cystoid is a collective name for certain echinoderms found in marine strata of Ordovician, Silurian, and Devonian age. Cystoids possess a bladder-like body (theca) of plates with respiratory pores. In the oral area they generally bear a number of food-gathering appendages (brachioles). A stem may be present but many forms, particularly among the class Diploporita, were directly attached to any available substrate by the basal plates of the theca. The echinoderm nature of cystoids was pointed out as early as 1772 by the Swedish miner J. A. Gyllenhaal in his studies of *Sphaeronites pomum* and *Echinospaerites aurantium* (Regnéll 1945, p. 1). Later von Buch distinguished them as a separate group of echinoderms. Paul (1972) dropped the name Cystoidea and elevated the two previous orders Rhombifera and Diploporita to class rank. Several questions regarding the morphology and taxonomy of diploporites remain unanswered. The question whether or not they are referable to the subphylum Blastozoa (Sprinkle 1973, pp. 57, 186) is answered in the present study by the discovery of biserial brachioles in *Protocrinites*.

Norwegian cystoids are often so well preserved that fine details of morphology can be studied; ontogenies, phylogenetic trends, and relationships to lithologies can be demonstrated. Detailed geological mapping, combined with a compilation of stratigraphical and geographical distributions within the Oslo Region (text-fig. 1), enables the relationship between echinoderms and lithofacies to be studied. The only previous comparable studies in Europe were restricted to Estonian rhombiferans *Hemicosmites* (in relation to reefs, Männil 1966) and *Echinospaerites* (distribution, Orviku 1927). The large numbers of *Haplosphaeronis* from the Gagnum Shale and the Gagnum Limestone (lower Ashgill) of Hadeland have enabled both ontogeny and variation within the genus to be studied. This is important in understanding aspects of phylogeny (see Bockelie 1978a).

STRATIGRAPHICAL OUTLINE

Norwegian diploporite cystoids are restricted to the middle and upper Ordovician (text-figs. 2-4); their appearance is sometimes more or less synchronous with those elsewhere, such as in Britain, Sweden, and Estonia. A comprehensive stratigraphical outline for the Oslo Region has been given by Henningsmoen (1960). The Cambro-Silurian sequence has been divided into ten units termed Stages; the Cambrian comprising Stages 1-2d,



TEXT-FIG. 1. Ordovician outcrops in the Oslo Region of Norway, central Sweden, and the Baltic states (black).

the Ordovician 2e-5b, and the Silurian 6-10. It has long been suggested that Stage boundaries are diachronous in the Oslo Region. This diachronism applies in particular to the Silurian, but it has also been proved for the Ordovician (Brenchley and Newall 1975; Owen 1978, 1979; Bruton and Owen 1979). The stratigraphical nomenclature whereby lithological units are named after their contained dominant fossil is now under revision by the author and others, and will be replaced by a lithostratigraphic terminology based on geographic names. In most areas the new formations will coincide with the previous stage names. The former use of a combination of numbers and letters for the stages is not continued here but is occasionally referred to in parentheses to allow comparison with previous work; published formation names are used. For the northern part of the Oslo Region references are made to Skjeseth (1963). Where no published names are available, the fossil names originally applied to the lithostratigraphic units are retained (Brøgger 1887).

The Oslo Region is generally considered to be an intracratonic depression in a Precambrian basement (Størmer 1967) with carbonate and terrigenous sediments on the Balto-Scandian foreland; a Precambrian land mass is considered to have been the source of the terrigenous sediments. Recent dating of the Ordovician sediments of Oslo-Asker confirms a Precambrian age for the source rock (S. Jacobsen, pers. comm.). Carbonate sedimentation prevailed in the more stable parts of the Balto-Scandian basin, including the middle Ordovician of central Sweden. Sedimentation rates in the Oslo Region appear to have been variable and sporadic influxes of mud flows to its more central portions have preserved some faunas more or less in life position.

MATERIAL, METHODS, AND PRESERVATION

Previously, museum collections of Diploporita were very limited and consisted mainly of *Haplospiraenon kjaeri* from the lower Ashgill. Since 1966 more than one thousand cystoids have been collected from the Oslo Region, together with large numbers of other echinoderms. Some of these have been described by Bockelie (1973, 1979a, 1981) and Bockelie and Briskeby (1980). Large slabs were collected and usually decalcified using hydrochloric acid. The decalcified material was impregnated under one-third of atmospheric pressure. Casts were made from

Series	Graptolite zones	Estonian stages	S. Norway Fm.	DISTRIBUTION OF ECHINODERM CLASSES IN S. NORWAY									
Ashgill	D. anceps	Porkuni F _{II}	Langøyene sst. Fm.										
		Pirgu F _{Ic}	Husbergøya sh.										
	Isotelus beds												
	U. Tretaspis sh.												
	D. complanatus		Tretaspis lmst.										
Caradoc	P. linearis	Vormsi F _{Ib}	L. Tretaspis sh.										
		Nabala F _{Ia}	U. Chasmops lmst.										
	D. clingani	Rakvere E											
		Oandu D _{III}											
		Keila D _{II}	U. Chasmops sh.										
	D. multidentis	Johvi DI	L. Chasmops lmst.										
		Idavere C _{III}	L. Chasmops sh.										
	Llandeilo	N. gracilis	Kukruse C _{II}	Ampyx lmst.									
		G. teretiusculus	Uhaku C _{Ic}	T. bronni beds Ogygiocaris sh.									
Llanvirn	D. murchisoni	Lasnamägi C _{Ib}	U. Didymogr. sh.										
		Aseri C _{Ia}											
	D. bifidus	Kunda B _{III}	Endoceratid lmst. Asaphus sh.										
Arenig													

TEXT-FIG. 3. Stratigraphical distribution of Ordovician echinoderm classes in the Oslo Region. Stratigraphical data as for text-fig. 2.

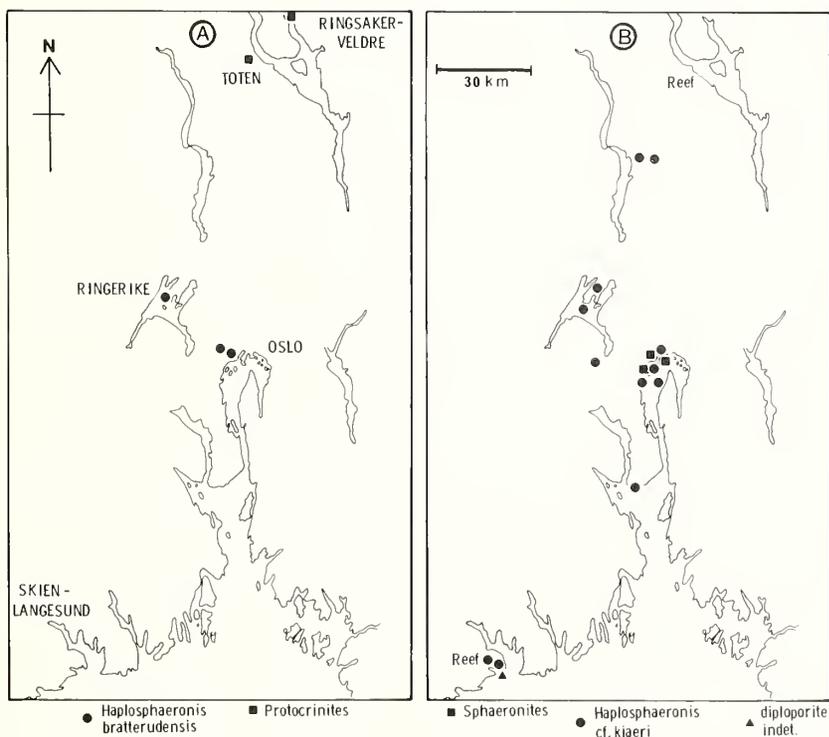
Series	Graptolite zones	Estonian stages	S. Norway Fm.	Distribution of Diploporita					no. of taxa
Ashgill	D. anceps	Porkuni F _{II}	Langøyene sst. Fm.						9
		Pirgu F _{Ic}	Husbergøya sh.						
	Isotelus beds								
	U. Tretaspis sh.								
	D. complanatus		Tretaspis lmst.						
P. linearis	Vormsi F _{Ib}	L. Tretaspis sh.							
Caradoc	D. clingani	Nabala F _{Ia}	U. Chasmops lmst.						
		Rakvere E							
		Oandu D _{III}	U. Chasmops sh.						
	D. multidentis	Keila D _{II}	U. Chasmops sh.						
		Johvi DI	L. Chasmops lmst.						
		Idavere C _{III}	L. Chasmops sh.						
Llandeilo	N. gracilis	Kukruse C _{II}	Ampyx lmst.						
	G. teretiusculus	Uhaku C _{Ic}	T. bronni beds Ogygiocaris sh.						
Llanvirn	D. murchisoni	Lasnamägi C _{Ib}	U. Didymogr. sh.						
		Aseri C _{Ia}							
	D. bifidus	Kunda B _{III}	Endoceratid lmst. Asaphus sh.						
Arenig									

TEXT-FIG. 4. Stratigraphical distribution of diploporite genera in the Oslo Region and number of taxa in the lower, middle, and upper Ordovician.

as observed by Chauvel (1941). Silicification started from both the inside and the outside of the theca. Most of the silicified Norwegian specimens have a rather ghost-like appearance due to incomplete silicification. There may have been two periods of silicification, the first close to the time of burial, and a later one usually of the coarse-grained type.

DISTRIBUTION AND COMPARISON WITH FAUNAS ELSEWHERE

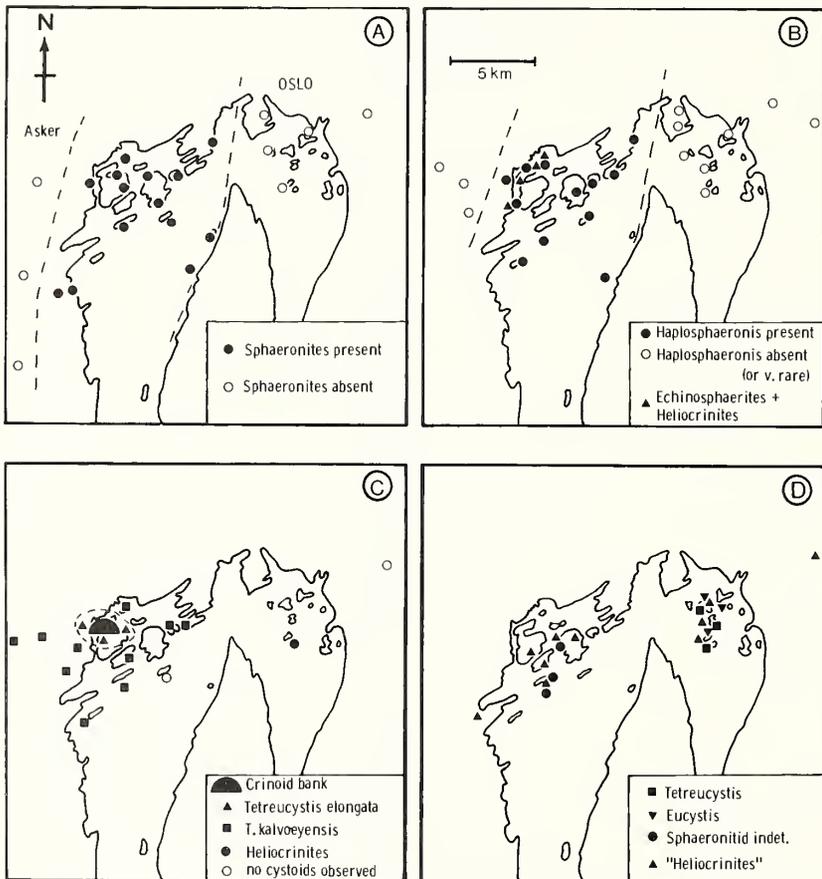
The echinoderm fauna of Norway is both extensive and diverse. Ten classes are known from the Ordovician of the Oslo Region (text-fig. 3), most of upper Ordovician age; echinoderms range from the Arenig to the Wenlock, but *Diploporita* are restricted to the Caradoc and Ashgill. Genera and species are restricted both stratigraphically (text-fig. 4) and geographically (text-figs. 5–7); most of the fifteen taxa present are found within a formation, and some in one locality only. The earliest known diploporite in the Oslo Region is *Haplosphaeronis bratterudensis* n. sp. (text-fig. 4), synchronous with *H. 'oblonga'* in the Dalby Limestone of Jämtland and Dalarna, Sweden. *Haplosphaeronis* is one of the most common diploporite genera in Sweden and Norway and ranges from the Caradoc to the middle-upper Ashgill. Its geographic and stratigraphic distributions depend on which of the original facies types are preserved. In the north Estonian confacies (Jaanusson 1976) *Haplosphaeronis* has never been found. However, in the Dalby Limestone of the central Baltoscandian confacies it has been recorded from several south Estonian borings (Männil 1966, figs. 13, 14), appearing at about the same stratigraphical level as in central Sweden (Dalarna). *Haplosphaeronis* occurs in the lower Ashgill of Britain (Paul 1973, p. 3) and Belgium (Regnéll 1951).



TEXT-FIG. 5. Geographical distribution of diploporites in the Oslo Region. A, in the *gracilis* Zone-multidens Zone. B, in the Lower Chasmops Limestone and equivalents (*Sphaeronites*) and in the *clingani* Zone.

In Estonia and Ingermanland three species of *Protocrinites* are known from the Arenig to the Caradoc. The genus is also found in the northern part of the Oslo Region at Brummundal (*Coelosphaeridium* beds of the Furuberg Formation; *peltifer* Zone). *Sphaeronites* is also restricted in Norway. *S. (Peritaphros) pauciscleritatus* is present in the Lower Chasmops Limestone of Asker and Bærum (text-figs. 5B, 6A). I suggest that this species was restricted to a narrow ecological niche. In Sweden, *Sphaeronites* ranges from the late Arenig or Llanvirn to middle or upper Ashgill, and several species are known. In Estonia one or possibly two species occur in the Uhaku and Keila (Rõõmusoks 1970; Hecker 1964). Outside the Baltoscandian area, *Sphaeronites* is only known with certainty from the lower or middle Ashgill of Britain (Paul 1973; Paul and Bockelie 1983).

Beyond the Oslo Region, *Tetreucystis* is known only from the Ashgill of Sweden and Britain. *Archaeogocystis* (text-figs. 2, 4) is restricted to the Ashgill of Norway and Britain, and to the Llanvirn of Bohemia. *Eucystis* is locally present in the upper Ashgill of Oslo (text-fig. 6D), is relatively common in the Ashgill of Sweden and Britain, and occurs in the Ashgill of Bohemia and Spain (Chauvel and Le Menn 1979). It also occurs in the Devonian of Bohemia and North Africa, but has not been located in the Silurian.



TEXT-FIG. 6. Geographical distribution of cystoid genera in the Oslo-Asker District, showing the limits of certain genera. A, *Sphaeronites* in the Lower Chasmops Limestone. B, *Haplosphaeronites*, *Echinospaerites*, and *Heliocrinites* in the Upper Chasmops Limestone. C, cystoids in the Lower Tretaspis Limestone. D, cystoids in the Husbergøya Shale Member.

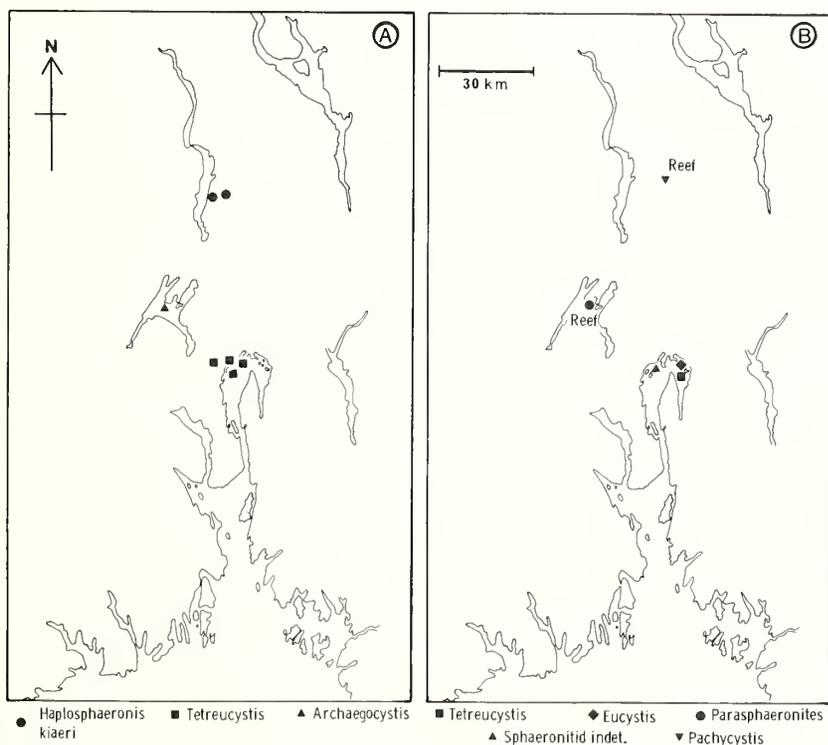
The diversity of the Diploporita increased from the lower to the upper Caradoc and from the lower to the upper Ashgill, coinciding with two major regressions in the Oslo Region. Consequently, I suggest that these cystoids were present in relatively shallow water, where several ecological niches were present (see later).

Diploporite cystoids first found their way into the Oslo Region in the late Kukruse Stage (text-fig. 2) and reached a first maximum diversity and expansion in the late Oandu-early Rakvere Stage. Another immigration took place in the Nabala Stage, reaching maximum expansion and diversity by the Porkuni Stage (text-fig. 2). Similar patterns can be demonstrated with other faunal elements (Bruton and Owen 1979). Diploporita were absent from the Oslo Region in the Arenig-lower Caradoc, whereas six taxa were present in the middle-upper Caradoc and nine taxa in the Ashgill. Patterns of geographical distribution of genera (text-figs. 5-7) are comparable with those of other fossil groups, both in the early Ordovician (Skjeseth 1952) and the middle Ordovician (Stormer 1953).

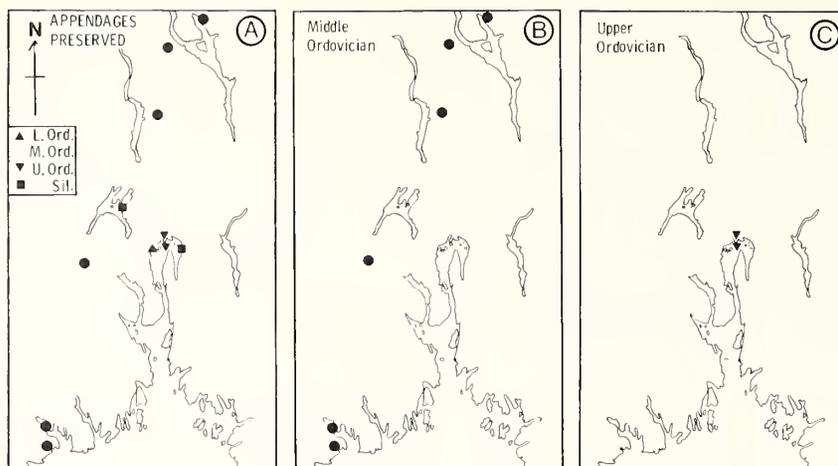
FAUNAL ASSOCIATIONS AND THEIR RELATIONSHIP TO SEDIMENT TYPE

The sediments within large areas of the Oslo Region are well exposed. Formations can be traced continuously for 15-20 km along strike; the distribution of species has been mapped (text-figs. 5-7). Detailed studies were made in Oslo-Asker, but only limited information exists for the rest of the Oslo Region because only parts of the area have been mapped in detail.

The preservation of echinoderms with brachioles and arms indicates that the animals were not transported far after death and before burial. The fauna was most probably periodically covered by rapid influxes of sediment. Echinoderms with appendages preserved are found in the westernmost areas in middle Ordovician sediments.



TEXT-FIG. 7. Geographical distribution of diploporites. A, in the *linearis* Zone. B, in the *anceps* Zone.



TEXT-FIG. 8. Areas where echinoderms have been found with appendages preserved (typically in areas of irregular sedimentation, and usually high sedimentation rate). A, Ordovician and Silurian. B, middle Ordovician only. C, upper Ordovician only.

and in the central Oslo–Asker part of the basin in upper Ordovician sediments (text-fig. 8). Diploporite genera and species, together with their faunal associations, are listed below; lithologies are also described and an interpretation of the environment is given.

Haplosphaeronis bratterudensis association. This is found in the Lower Chasmops Shale. The shale is interbedded with limestone beds, often planar and 5–10 cm thick. In Ringerike, where *Haplosphaeronis* is common, the shale is calcareous. The bioclastic content of the shale is slightly less than 20% in this area, decreasing to below 10% eastwards towards Oslo. Both the frequency of limestone beds and the carbonate content of the shale decrease in the same direction. The eastern limit of the faunal association is in Asker, about 20 km west of Oslo. Moving south-west from Ringerike the clay content of the sediment decreases and the rock becomes more bioclastic; these sediments are the result of a mixture between low and high sedimentation rates, and lack the *Haplosphaeronis* association. North-east of Ringerike the Lower Chasmops Shale grades into a shale with incursions of 20–50 cm thick sandstone beds which, from Hadeland northwards, also lacks *Haplosphaeronis*.

The fauna associated with *H. bratterudensis* is characterized by trepostome bryozoans (*Diplotrypa* sp.), trilobites (*Chasmops conicophthalma*, *Neosaphus ludibundus*, *Iliaenus* sp., *Atractopyge dentata*), various brachiopods (including *Christiania holtedahli*, *Eoplectodonta*(?) *percedens*, *Strophomena norvegica*), cephalopods (*Triptoceras*? *problematicum*), bivalves (*Cyrtodontula dubia*, *Ambonychia* aff. *amygdalina*, *Cunamyia multistriolata*, *Grammysia* sp.), gastropods (*Kokenspira estona*, *Helicotoma* sp.), ostracodes (*Ullerella holtedahli*), eocrinoids (*Bockia heintzi*), and crinoids (*Ristnacrinus* sp. and others). The fauna probably lived on a soft bottom, with moderate to low current velocities, below wave base in an offshore environment, and in the proximal part of the basin.

Protocrinites rugatus association. This is approximately contemporaneous with the *H. bratterudensis* association and occurs *in situ* at only one locality, in the Coelosphaeridium Beds, Furuberg Formation, in the Veldre–Ringsaker area (text-figs. 2, 4). The association has also been found in a loose block at Toten (text-fig. 5A). The cystoids occur in a silty shale interbedded with cyclic deposits of fine-grained quartz sandstones, 20–50 cm thick. The sandstones only occasionally contain fossils but the shales are usually very fossiliferous with a bioclastic content of 2–25%.

Other echinoderms associated with *Protocrinites* include several undescribed crinoids, eocrinoids (*Rhipidocystis norvegica*), rhombiferan cystoids (*Cystoblastus*? sp.), and more than two genera of Asterozoa. The remaining fauna comprises brachiopods (*Sowerbyella ringsakerensis*, *Mjoesina* cf. *mjoesensis*, *Kiaeroniena* cf. *juvenilis*, *Hedstroemia* aff. *robusta*, *Leptaena*(?) *indigena*, *Kjerulfina* sp., *Strophomena hirsuta*, *S. steinari*, *Eostrophacodonta williamsi*), trilobites (including *Chasmops conicophthalma*, *Iliaenus* cf. *glaber*, *Neosaphus ludibundus*?, *Calyptanlax* sp., and calymenids), algae (*Mastopora concava*, *Coelosphaeridium cyclocrinophilum*), and bryozoa (*Diplotrypa* sp.). The fauna lived on a soft bottom with terrigenous clay in an offshore environment.

A periodic influx of fine-grained sand killed the fauna from time to time. Such periodicity and high sedimentation rates prevailed in the northernmost part of the Oslo Region during the early Caradoc and may represent storm action and/or microtectonic activity (Bockelie 1978b).

Sphaeronites (Peritaphros) pauciscleritatus association. This is present in the Lower Chasmops Limestone (text-figs. 2, 4) and is restricted geographically and stratigraphically (text-figs. 5B, 6A). It is found approximately 6 m above the base of the formation in 75 cm of nodular limestones. Macroscopically there is little difference between that part of the formation with *Sphaeronites* and that without, but microscopically there is a difference in bioclastic content (about 8–10% bioclastics in rocks containing *Sphaeronites*). Beyond the eastern limit of *Sphaeronites*, there is a decrease in both the carbonate and bioclastic content of the rock. Beyond its western limit the carbonate content increases slightly, and bioclastic content exceeds 15% before decreasing again further west.

The small numbers of *Sphaeronites* at each locality (3–10 per m²) suggest *in situ* populations. Most of the associated fauna has not been described, but it includes bryozoans (mostly stick bryozoans and small spherical colonies), brachiopods (including *Platystrophia* sp., *Kiaeromena* sp., *Sowerbyella?* sp., and various orthids), trilobites (*Chasmops conicophthalma*, *Dionide* sp., and calymenids), and crinoid ossicles (*Encrinites snarocensis?* type). There is a clear dominance of filter-feeders.

The area where *Sphaeronites* is found was a submarine topographic high during most of the middle and upper Ordovician (Bockelie 1978b). The sediments may have been locally consolidated in small patches and acted as a relatively firm substrate for stem-bearing organisms, including the cystoids and crinoids. The environment was possibly one of low sedimentation rates, or even local erosion, because small phosphate nodules and remanié deposits occur locally.

Haplosphaeronis cf. *kiaeri* associations. These have a wide distribution in the Oslo Region. Future research may prove that more than one species is present. At present the associations are known from the Encrinites Limestone and its equivalents in the Skien-Langesund area (text-figs. 2, 5B), Ringerike, Hadeland, Oslo-Asker (text-fig. 6B), and elsewhere; these may all be contemporaneous (text-figs. 2, 4). *Haplosphaeronis* always occurs in sediments containing a mixture of calcareous shales and nodular limestones but its relationship to sediment type has only been fully studied in Oslo-Asker (text-fig. 6B). The pattern of distribution between Asker and Oslo is similar to that observed for *Sphaeronites* (text-fig. 6A). *Haplosphaeronis* is found both in bioclastic pockets in the limestones and in the interbedded shales. Specimens in the limestones are often sediment-filled and show signs of short transport. In the shales, however, they are filled with calcite and show no signs of transport. The distributional pattern of *Haplosphaeronis* coincides with a presumed slight elevation on the sea bottom which, during deposition of the top of the Upper Chasmops Limestone, was within a zone of reworking by currents. Breccias and stromatolite-like structures have been found.

Associated with *Haplosphaeronis* cf. *kiaeri* in Asker are trilobites (*Chasmops extensa*, *Platylichas laxatus*, *Stenopareia glaber*, *Lonchodomas* aff. *pennatus*, *Pseudosphacrexochus bulbosus*, *Calyptaulax* aff. *norvegicus*), several undescribed bryozoans (including *Diplotrypa* sp., stick-bryozoans, and thin almost dendritic types), brachiopods (including *Ptychoglyptus* aff. *munsteri*, *Hedstroemia* sp., a sowerbyellid and orthids), and ostracodes (*Platybolbina* sp.); a rugose coral *Coelostylis toernquisti* may occasionally be found (B. Neuman, pers. comm. Jan. 1980). Other echinoderms, including loose plates of *Cheirocrinus* s.l. and crinoid ossicles have been found in some localities.

The somewhat variable environments in which *H.* cf. *kiaeri* occurs represent a regressive stage of the sedimentary basin. It seems that most of the faunas were living below the zone of regular wave action in most areas. The environment was one of low sedimentation rates, occasionally non-deposition or even erosion. Some of the limestones were exposed at times, allowing the attachment of bryozoa and crinoids. Periodically the environment received influxes of carbonate-rich mud and bioclastic sand, probably after storm deposits or as mass flows. Such deposits are commonly found in Asker.

Haplosphaeronis kiaeri association. *H. kiaeri* has only been found in the calcareous Gagnum Shale and the overlying Gagnum Limestone (text-figs. 2, 7A) in the Ashgill of Hadeland. The best exposures are found at Tonnerud by Lake Randsfjord where detailed investigations (text-fig. 9B) indicate that *H. kiaeri* lived in both environments represented. The animals were rapidly covered by sediment after death which helped to preserve the details. The sedimentation rate was irregular, and periodically coarser clastics were brought into the otherwise quiet bottom conditions.

In the Gagnum Shale the associated fauna consists of bryozoans (mostly *Diplotrypa* sp.), numerous brachiopods (including *Mjoesina mjoesensis*, *Leptaena minuta*, *Platystrophia* sp., *Porambonites* sp.), other echinoderms (including a dendrocystid, cheirocrinids, edrioasteroids such as *Cyathotheca*, and crinoids such as

Ristnacrinus sp.), several trilobites (including *Tretaspis* of the *hadelandica* type and *Stygina minor*), and ostracodes (*Euprimites kahalensis*, *Bullaeferum* n. sp., *Balticella?* sp.). In the nodular Gagnum Limestone the associated fauna is more varied, with more than thirty recorded taxa of brachiopods (M. Bassett, pers. comm. Oct. 1979). It usually contains 2–5% bioclastic material, with bryozoans and rugose corals (*Coelostylis* n. sp.: B. Neuman, pers. comm. Jan. 1980) also making up an important part of the fauna. The limestone represents a more shallow water environment than the Gagnum Shale.

Archaegocystis occurs in the lower Ashgill, Sørbakken Limestone of Ringerike (text-figs. 2, 4, 7A); it derives from Frognoya and occurs in a nodular limestone somewhat similar to the Lower *Tretaspis* Limestone of Oslo-Asker. The interbedded shales in the Sørbakken Limestone are calcareous and often contain pyritized fossils. The limestone itself is a fine calcisiltite-calcimicrite which contains frequent *Chondrites* burrows and bears numerous *Planolites* traces. The associated fauna consists of trilobites (including *Tretaspis hadelandica*), a few orthid brachiopods, stick bryozoa (rare), and crinoid ossicles (not common). The sediments were deposited below wave base and are occasionally interbedded with coarse clastics which form thin bands at irregular intervals.

Tetreucystis elongata association. This is restricted to the nodular *Tretaspis* Limestone (text-figs. 6C, 7A) of Ashgill age on and around the island of Nesøya, west of Oslo. It surrounds a presumed topographic high on the sea floor, containing a crinoid bank (Bockelie 1978b), and may have lived in an unstable environment where bottom currents were relatively strong. It is unknown whether or not drifting of the populations occurred, but individuals are often found together in patches. Some specimens have been found growing on top of dead individuals, and it may be assumed that they lived close together. The only other fossil remains occurring commonly with *T. elongata* are trace fossils (*Chondrites*), and occasional trilobites (calymenids).

Tetreucystis kalvoeyensis association. This is contemporary with the *T. elongata* association and had a much wider geographical distribution (text-fig. 6C). Several populations of *T. kalvoeyensis* show little, if any, post-mortem transport. At Kalvøya in Bærum, west of Oslo, more than one hundred specimens were found together, associated with molt stages of trilobites (*Brachyaspis*), trace fossils (*Planolites* and *Chondrites*), and occasional cephalopods. The limestone has a low faunal diversity and seems to have formed in a shallow water environment. Quartz content is high (10–15%) and the average grain diameter is about 100 μm (three times larger than the average Ordovician grains from that same area). When traced further eastwards towards Oslo, cystoids become very rare. On the island of South Skjærholmen, in the Oslo fjord, a specimen of *Heliocrinites* was found (text-fig. 6C).

Tetreucystis tetrabrachiolata association. This is found in the uppermost part of the Husbergøya Shale (text-figs. 4, 6D). The Husbergøya Shale is silty with a quartz content of 20–35% (100 μm average grain size) and carbonate content of 25–50%. It can be traced for more than 15 km along strike, and there is a gradual change from Oslo towards Asker, both in coarseness of the sediments and the fossil content. *T. tetrabrachiolata* is found exclusively on the islands in Oslo (text-fig. 6D). Associated fauna consists of trilobites (*Dalmanitina mucronata*, *Tretaspis sortita*, *Stygina latifrons*), conularids, *Cornulites* worms, occasional brachiopods, and echinoderms (including *Eucystis langoeyensis*, '*Heliocrinites balticus*', and various crinoid ossicles). The sediments are heavily bioturbated, but show a relatively low faunal diversity; they seem to have formed well below wave base.

When traced westwards, the Husbergøya Shale on the islands in Asker contains an unidentified sphaerontid cystoid. Sphaerontidae sp. A. is found in sediments of relatively high bioclastic content and its associates suggest more shallow water than that in which *Tetreucystis tetrabrachiolata* and *Eucystis langoeyensis* occurred. The associated fauna in Asker consists of a trilobite (*Dalmanitina mucronata*), numerous brachiopods (more than ten taxa are being described by L. R. M. Cocks), bryozoans (stick and mat forms), and occasional rugose corals; associated echinoderms are '*Heliocrinites balticus*' (usually overgrown by bryozoa) and frequent crinoid ossicles of at least two types. *Cornulites* and worms have also been located. The sediments are heavily bioturbated.

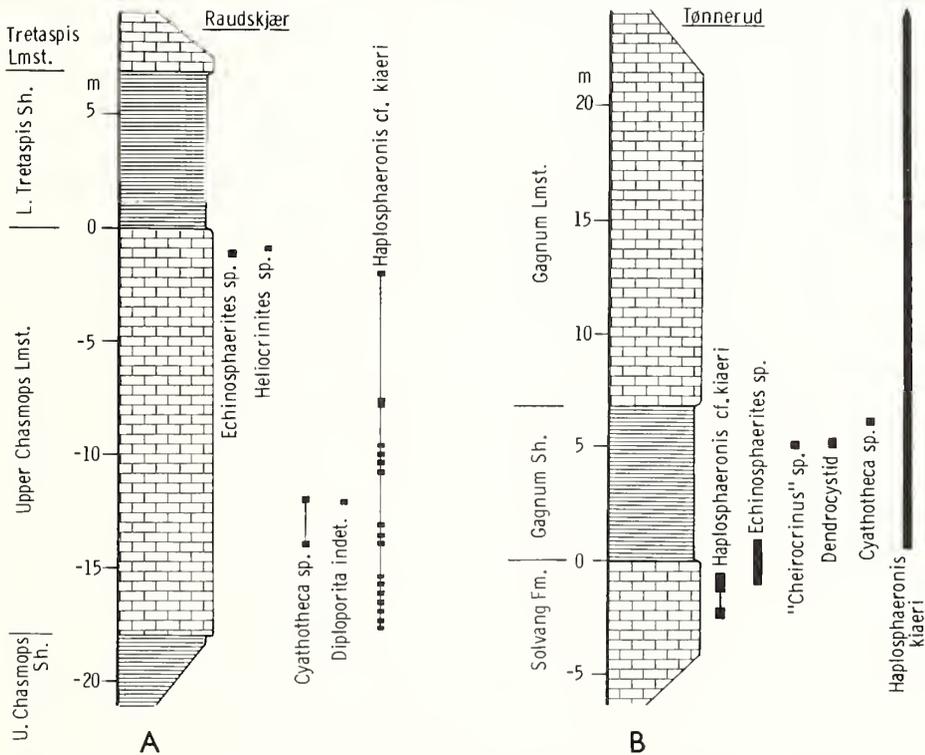
Two other diploporite genera from the Ashgill have a restricted distribution, *Pachycystis* n. gen. and *Parasphaerontes* n. gen. In the Kalvsjø Formation at Kalvsjø, Hadeland (text-figs. 2, 4, 7B), *Pachycystis* n. gen. occurs on the flanks of a carbonate mud mound. The terrigenous mud of the flanks is fine grained and has a calcium carbonate content of approximately 5–10% (including fossil debris). The sediments interfinger with the flank of the mound and are poor in corals, bryozoa, and trilobites, but rich in echinoderm fragments (including calyces of several crinoids, thecae of *Hemicosmites variabilis*, and numerous crinoid ossicles); brachiopods are not uncommon (and include *Sampo* sp., *Glyptorthis?* sp., *Leptaena* sp., *Dolerorthis* sp., a rhynchonellid, *Eospirigerina* and *Lingulella* sp.); trilobites include '*Calymene*' sp. and an illaenid. The preservation of the material and the type of sediment suggests quiet water, probably just below wave base or in a zone of weak currents.

Parasphaeronites n. gen. has only been located in channel fills within the upper Ashgill reef in an unnamed formation (text-figs. 2, 4, 7B) at Ringerike. *Parasphaeronites* occurs in large numbers (hundreds of specimens), closely packed, indicating that they were transported. Their thecae are filled with the same matrix as found in the channel fill, which may indicate a relatively short period of post-mortem transport. *Parasphaeronites* has not been found in the sediments surrounding the reef, and I therefore suggest that they lived either on the reef itself, or in close proximity to it. Their thick thecal walls also support this idea. The associated fauna in the channel fill consists of bryozoa (some of which grew on cystoids), rugose and tabulate corals, stromatoporoids, and algae, all indicative of a shallow water environment; associated echinoderms are *Hemicosmites sculptus* and numerous crinoid columnals and root structures.

CHANGES IN FAUNAL ASSOCIATIONS WITH FACIES, TIME, AND SPACE

The distribution of the echinoderms is closely related to environmental conditions, including the type of substrate, oxygen levels, nutrition, current velocities, and depth. It appears that the diploporites lived in a more restricted range of environments than the rhombiferans, and they may have occupied narrower ecological niches. In the Oslo Region almost all diploporites are restricted to relatively shallow water of four main environmental types: (1) areas with a soft bottom and slow sedimentation rates; (2) areas with a soft bottom but high sedimentation rates; (3) areas with a semiconsolidated bottom; and (4) reef or mud bank environments. The coarseness of the sediment also seems to have been important. Some faunas are restricted to terrigenous sediments, whereas others are found in carbonate sediments. Most stratigraphic sections contain diploporites only in limited intervals. In regressive sections changes in the faunal composition from deeper to more shallow water environments have been observed. Three such examples are described below.

Raudskjær, Asker. The section comprises the upper portion of the Upper Chasmops Shale, the Upper Chasmops Limestone, the Lower Tretaspis Shale, and the Tretaspis Limestone (text-figs. 2, 9A). The Upper Chasmops Shale



TEXT-FIG. 9. Comparison of faunas in the sections at A, Raudskjær, Asker and B, Tønnerud, Hadeland. The Lower Tretaspis Shale and the Gagnum Shale are correlated lithologically, but are considered to be slightly different in time. The differences in lithology and fauna are considered to be related to slight differences in water depth.

contains no diploporites, and is probably a deeper water shale. The size of the clastic grains and faunal diversity increases gradually through the Upper Chasmops Limestone. The upper part is a bioclastic limestone with wave-generated intraformational conglomerates. *Haplosphaeronis* cf. *kiaeri* is present through the Upper Chasmops Limestone, but disappears towards the top of the formation where it is replaced by *Heliocrinites* sp. and *Echinosphaerites* n. sp. of the *grandis* group (text-fig. 9A). The same pattern is found elsewhere in Asker and Bærum (text-fig. 6B), in Langesund and Hadeland, and in Dalarna, Sweden, towards the top of the Kullberg Limestone. No echinoderms with endothelial pore structures occur in this type of environment, possibly because such pore structures were susceptible to clogging by terrigenous sediment. The replacement of *Haplosphaeronis* cf. *kiaeri* by *Heliocrinites* and *Echinosphaerites* is probably related to depth; *Haplosphaeronis* cf. *kiaeri* lived in deeper water. Thus there is a marked upper and lower limit to the distribution of *Haplosphaeronis* at Raudskjær.

Tønnerud, Hadeland. This section comprises the Solvang Formation, the Gagnum Shale, and the Gagnum Limestone (text-figs. 2, 9B). The upper part of the Solvang Formation is a bioclastic limestone containing occasional *Echinosphaerites* of the *grandis* group and *Haplosphaeronis*. Further east, towards the Gagnum farm *Echinosphaerites* is found together with both *Heliocrinites* and *Haplosphaeronis* cf. *kiaeri*. The overlying Gagnum Shale is calcareous (20–60% carbonate) and echinoderms are common. *Echinosphaerites* occurs in the lower part of the section, and *Haplosphaeronis* *kiaeri* is very common from 1 m above the base. *H. kiaeri* is common through the Gagnum Shale and the overlying Gagnum Limestone. The sequence at Tønnerud can be correlated with that at Raudskjær (text-fig. 9; Bruton and Owen 1979). *Haplosphaeronis* is found at Tønnerud in the deepest water sediments. *Echinosphaerites*, and locally *Heliocrinites*, are found in shallow water sediments.

Husbergoya Shale Formation. No more than 2 m thick, this formation can be traced for about 20 km along strike from Oslo to Asker (text-fig. 2). In Oslo terrigenous material dominates, and the fauna includes *Tetreucystis tetrabrachiolata*, *Eucystis langoeysensis*, and '*Heliocrinites balticus*'. Westwards towards what is considered to have been shallower water, *Tetreucystis* and *Eucystis* disappear, but '*Heliocrinites balticus*' continues and an unidentified sphaeronitid cystoid is also present. This change is considered to be depth controlled. A 1° slope of the sea bottom would produce a difference in depth of approximately 25 m between the two major centres of these faunas.

Conclusion. These preliminary studies of echinoderm associations indicate that, although some faunal changes may be referable to differences in water depths, correlations which relate all the echinoderms to depth cannot yet be made. A generalized zonation of the diploporites in the Oslo Region is given in text-fig. 4.

COMPARISON BETWEEN FAUNAS AND COMMENTS ON 'PROVINCIALISM'

It has become popular to talk about faunal provinces of different fossil groups, the echinoderms included. The echinoderms were dispersed as larvae and their dispersal pattern was limited by three major factors: (1) how long the larvae remained free-living before settling; (2) water temperature; and (3) ocean currents. Kesling (1967, p. S136) suggested that the dispersal of cystoids was a slow process. The restricted patterns of distribution of many genera and species suggest that environmental conditions and ecological adaptations were amongst the most important controlling factors in diploporite biogeography. However, several cystoid families had strong geographical preferences at certain times, and this has led to a grouping of the faunas into faunal provinces. Few publications deal with these provinces in terms of plate tectonics (Paul 1976), but it seems that the Oslo Region was in the southern hemisphere during the Ordovician and migrated towards the equator in the upper Ordovician and Silurian.

Estonia, central Sweden, the Oslo Region, and parts of Britain were more or less in the same geographical province (Paul 1976). It has previously been suggested that Britain formed a faunal province separate from that of Norway, Sweden, Estonia, and Ingermanland. Regnéll (1945) described most Swedish diploporites, but three or four extra genera may be present. The Estonian faunas and those of Ingermanland have not been studied in detail since Jaekel (1899), and additional taxa are likely, as suggested by references made to *Haplosphaeronis* and *Sphaeronites* by Männil (1966) and Hecker (1964). The British Diploporita were monographed by Paul (1973); he described several genera not previously recorded from Britain and also pointed out similarities between British and Czechoslovakian mid-European faunas.

Norwegian diploporites are strikingly different from those of other areas, particularly Sweden. This difference is even more evident when rhombiferans are also taken into account. I believe that this reflects differences in environments. The Swedish and Estonian faunas are found mostly in carbonate platform sediments, whereas the Norwegian faunas and the Ashgill faunas of Britain occur in more clastic deposits. In the shallow water clastic environments of the Oslo Region, notably in its northern and south-western margins, the faunas resemble some of those found in similar environments in Estonia and Ingermanland, e.g. *Protocrinites*, *Bockia* (eocrinoid), and *Cystoblastus* (rhombiferan).

The diploporite faunas of Britain, the Oslo Region, central Sweden, Estonia, and Ingermanland are compared in text-fig. 10. The actual number of genera present in the different countries is influenced

DIPLOPORITE GENERA	Bohemia	Belgium	British isles	Norway	Sweden	Estonia Ingermanland
<i>Protocrinites</i>				M. Ord.		L. -M. Ord.
<i>Sphaeronites</i>			U. Ord.	M. Ord.	L. -U. Ord.	M. Ord.
<i>Haplosphaeronis</i>		U. Ord.	U. Ord.	M. -U. Ord.	M. -U. Ord.	M. Ord.
<i>Eucystis</i>	U. Ord. -M. Dev.		U. Ord.	U. Ord.	U. Ord.	
<i>Tetreucystis</i>			U. Ord.	U. Ord.	U. Ord.	
<i>Archaeocystis</i>	M. Ord.		U. Ord.	U. Ord.		
<i>Glyptosphaerites</i>					M. Ord.	M. Ord.
Total number of genera	5	1	7	8	5	11

TEXT-FIG. 10. Stratigraphical and geographical distribution of non-enigmatic diploporites from Bohemia, Belgium, Britain, Norway, Sweden, and the Baltic states (Estonia and Ingermanland). Totals of the known genera from the different areas give some information about the proportions of enigmatic to non-enigmatic forms.

both by collecting bias and by the extent to which the faunas have been described. Seven to ten genera may have been present in these areas during the Ordovician. It seems that individual species are very restricted even within a single area. This may be partly a preservational feature, reflecting the state of preservation of individual species and the type of environments preserved in different areas at different times, but it also indicates adaptation to particular environments; the appearance or disappearance of species, or even genera, mirror changes in environmental conditions.

There is no clear difference between the British and central and western Baltoscandian Diploporita. On the contrary a gradual shift of the faunas from east to west can be observed. Therefore, environment was the most important factor controlling their distribution.

APPEARANCE, EVOLUTION, AND EXTINCTION

Haplosphaeronis arose in Estonia (early Kukruse, C₁₁) and migrated into the Oslo Region during a transgression in the *multidens* Zone. Different sedimentary environments subsequently developed, to which the diploporites adapted themselves. A regression during the uppermost Caradoc caused a restriction of the diploporites to shallow water environments. By the Ashgill transgression several of the typical Caradoc cystoids had disappeared. These were replaced by new faunal elements which were adapted to shallow water environments. They reached greatest diversity by the maximum of the subsequent Ashgill regression. The base of the Silurian was marked by a transgression of great importance, but no diploporite cystoids seem to have survived into the Silurian in the Oslo Region. Even during several minor transgressions and regressions during the late lower and early upper Silurian no diploporite cystoids appeared. With very few exceptions this pattern is repeated in contemporary deposits elsewhere in the world. Consequently, studies of these changes observed in the Oslo Region may have a wider importance.

It is unknown why the Diploporita periodically disappeared and why there was a faunal shift between the middle and upper Ordovician. Several factors were involved. The Ordovician sediments

in the Oslo Region were deposited in a relatively flat epicontinental sea (Bjørlykke 1974). Most of the terrigenous components were either clay or wind blown quartz of silt fraction. In such environments selection pressure was probably not very great, and faunas were relatively homogeneous over large areas. During the Ashgill, sedimentation rates increased, there was more irregular sedimentation (Bockelie 1978*b*), and the terrigenous components probably increased by a factor of ten. Quartz grain size increased from an average of 35 μm in the middle Ordovician to more than 100 μm (Bjørlykke 1974) in the upper Ordovician. These changes and the development of shallow-water environments may have increased selection pressure and resulted in specialization. Failure to evolve the structures necessary to meet these environmental changes was probably the most important factor in diploporite extinction.

In the upper Ordovician most cystoids have exothecal pores, beneficial in environments with high sedimentation rates and in water with suspended sediment particles. Such areas are common in the uppermost Ordovician in the Oslo Region. Although mudbanks and 'reefs' became more common in the upper Ordovician, the climate was cooler than before; temperature gradients in the upper Ordovician sea would have had a significant effect (Sheehan 1979). Oxygen is more soluble in cold water than in warm water. Cystoids with exothecal pores (Diploporita and some Rhombifera) have many pores and thus a large respiratory surface. They may have thrived in shallow, warmer water with lower oxygen concentration. Most diploporites lacked a stem and were directly attached to objects on the sea floor or to the substrate itself. In times of increased sedimentation, they would easily have been buried.

During the Ordovician the Diploporita may have faced increased competition from other echinoderms, particularly crinoids and rhombiferans. The distribution of ossicles in the Oslo Region shows that the crinoids evolved rapidly and gradually invaded the shallow waters previously occupied by diploporites and rhombiferans. The rhombiferans themselves seem to have been in serious competition with the diploporites.

The cystoids were filter-feeders, so their distribution would depend on the size, composition, and quantity of suspended food. Changes in the plankton might therefore seriously affect cystoid distribution. The size of brachiolar facets in both diploporites and rhombiferans increased during the Ordovician (Bockelie 1979*a*), probably induced by change in food supply or increased competition. Larger brachiolar facets would have supported longer brachioles and thus allowed an increased food intake.

ANATOMY, TERMINOLOGY, AND FUNCTIONAL MORPHOLOGY

Diploporita are extinct echinoderms having a more or less globular *theca*, a calcareous skeletal body housing the soft tissue, and reproductive organs. The *theca* is composed of thecal plates, arranged randomly or in rings (*circlets*). Some or all of the plates may bear exothecal respiratory pore-structures. *Diplopores*, *humatipores*, and *haplopores* (text-fig. 12) are characteristic of the class.

Four major openings are present: (1) a *peristome*, at the centre of the food-gathering system, which may be covered by a few large or several small cover plates; (2) a *periproct* which in many genera is covered by an anal pyramid of triangular plates; (3) a small, circular *gonopore*; and (4) a slit or sieve-like *hydropore*, indicating the presence of a water vascular system. The hydropore and gonopore are usually situated close together between the peristome and the periproct (cf. *Celticystis*, Bockelie 1979*b*). The location of these orifices, and the number and positions of the plates in which they are present, are very important taxonomically.

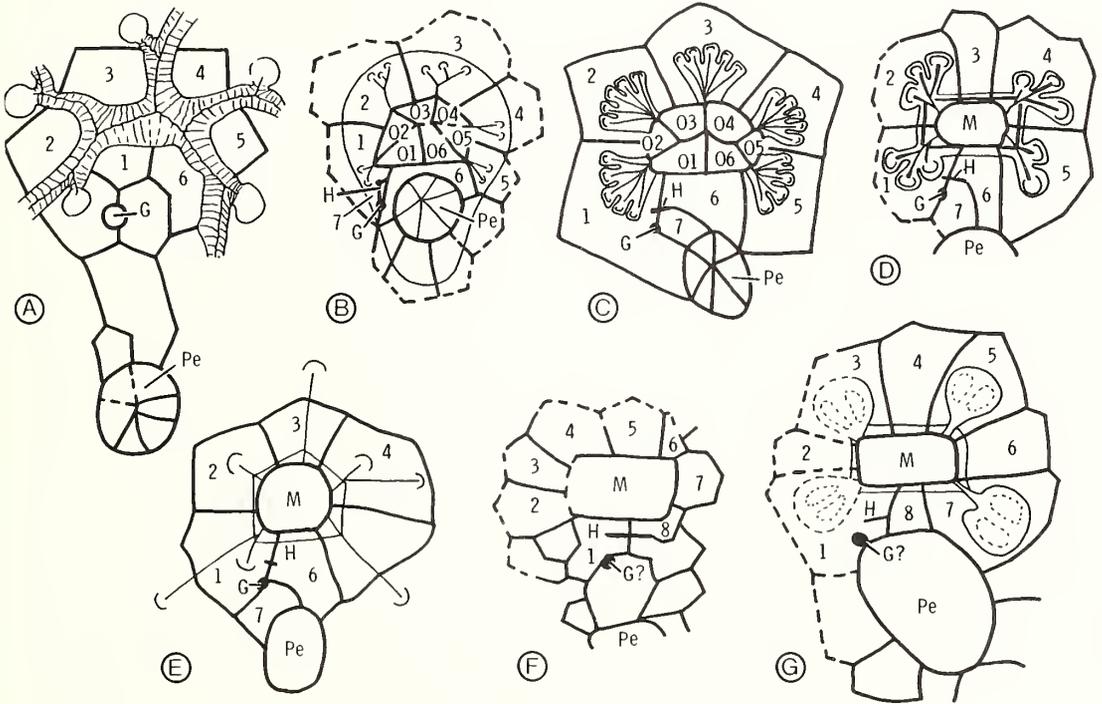
Two to five *ambulacra* extend from the peristome and were responsible for food gathering. Food was transported to the mouth along food grooves. Ambulacral appendages are very rarely preserved. Only four diploporites with well-preserved appendages are known: *Protocrinites*, *Calix*, and *Glaphrocystis* have biserial appendages (Chauvel 1966, 1977); those of *Asteroblastus* are uniserial (Eichwald 1862; see discussion by Jaekel 1899, p. 385). The *theca* was attached to the sea bottom by a column of small cylindrical or annular columnals, or by an extension of the basal plates forming a stem-like projection, or directly by its flat base. The *attachment area* can be small or of the same

diameter as the theca itself. Most diploporites were attached, but some may have been free and mobile or even floating.

Most Norwegian Diploporita belong to the family Sphaeronitidae, with one species from the Protocrinitidae; two new genera are erected and placed in a new family, the Parasphaeronitidae. The oro-anal areas of most cystoids are important both for discriminating genera and at family level (Bockelie 1972; Paul 1973). The terminology used in this study is essentially that of Kesling (1967) and Paul (1973). Additional morphological terms are described below.

Major thecal openings

The mouth. Located at the centre of the ambulacral system, the mouth is generally ovate. It is large in the Sphaeronitidae and Parasphaeronitidae n. fam., but relatively small in the Protocrinitidae. It is surrounded by a pentagonal or quadrilateral peristome which in life was covered by six palatals in the Sphaeronitidae, and possibly also in the Parasphaeronitidae. In the Protocrinitidae, ambulacral cover plates continued on to the peristome and covered the mouth (text-fig. 11). The peristome border ('oral laths' of Prokop 1964) of the Sphaeronitidae is present between the mouth and the peristome and on this the food grooves diverge before entering the mouth. In some Sphaeronitidae a complex dendritic pattern of grooves occurs, whereas in others the food grooves continue down into the mouth without branching or diverging (text-figs. 11, 29). The peristome frame is composed of six circum-oral plates in the Protocrinitidae and Sphaeronitidae, and eight plates in the Parasphaeronitidae. The terms *circum-orals* (CO plural COO) and *periorals* were adopted by Paul (1971). Provisionally I refer to the plates which surround the mouth in the Protocrinitidae as circum-orals, without necessarily implying a homology.



TEXT-FIG. 11. Plate configuration of oro-anal area of Norwegian diploporite genera. A, *Protocrinites*. B, *Sphaeronites* (*Peritaphros*). C, *Haplosphaeronis*. D, *Tetreucystis* n. gen. E, *Eucystis*. F, *Parasphaeronites* n. gen. G, *Pachycystis* n. gen. (A, Protocrinitidae. B-E, Sphaeronitidae. F, G, Parasphaeronitidae, n. fam.). M, mouth; G, gonopore; H, hydropore; Pe, periproct.

Food grooves radiate from the oral corners on to the circum-oral plates. In the Sphaeronitidae they may be located on these plates only or continue some distance down the thecal surface. The grooves may or may not branch. Each food groove ends in a small facet, generally less than 1 mm in diameter. The shape and size of individual facets varies at both generic and specific level and may have taxonomic value. In *Protocrinites* long biserial appendages are attached to the facets, and ambulacral cover plates are transformed into specialized brachiolar cover plates on the brachioles (text-fig. 13). The brachioles of *Protocrinites* may be characteristic of most diploporites (see below).

Paul (1973, p. 12) defined an ambulacral formula using the number of ambulacral facets per ambulacrum, starting with ambulacrum I. This number in the Sphaeronitidae has since been related to ontogeny (Bockelie 1978a), but the pattern of distribution over the theca may be typical at family level. In this pattern the number of facets would be the same in radii I and V, slightly less in radii II and III, with the smallest number of facets in radius IV (Bockelie 1978a, p. 36, fig. 5). In some species of *Tetreucystis* (Sphaeronitidae) only one facet per ambulacrum may be present even in adult stages. As reported by Paul (1973, p. 12) no cover plates have been found on the ambulacra of the Sphaeronitidae. In the Protocrinitidae cover plates of two 'generations' occur: large triangular plates along the edges of the ambulacral groove and smaller plates added between (text-fig. 13). Whether similar plates existed in the Sphaeronitidae is unknown. It is clear that food passed along the food grooves of Protocrinitidae and under their cover plates; by analogy, the Sphaeronitidae may have had the same system. Most of the palatals have ambulacral orifices large enough at the peristome for food to have entered beneath them (text-fig. 18). The oral cover plates may have been similar in the Sphaeronitidae and the Parasphaeronitidae.

The anus. Generally circular or oval in outline, it is often as large as or larger than the mouth. When oval, the long axis generally lies at an angle of 60–90° to the lower margin of the peristome. The anus of Sphaeronitidae is present in inter-radius V–I, in contact with circum-oral plates CO5, CO6, CO7, and occasionally CO1 (text-fig. 11). The distance from mouth to anus varies but is generally constant within a genus. In *Sphaeronites* the anus is set close to the mouth; in *Haplosphaeronis* the anus is closer to the mouth than in *Eucystis* and *Tetreucystis* n. gen. but not as close as in *Sphaeronites*; in *Protocrinites* it is separated from the mouth by at least two plate series (text-fig. 11A), while in *Archaegocystis* it is also well removed. The position of the periproct of Parasphaeronitidae may resemble that of the Sphaeronitidae (text-fig. 11), and is not unlike that of *Eucystis* or *Tetreucystis*.

The anus was covered by a pyramid of triangular plates (anals). These plates could open outwards in many genera (text-fig. 26c) because a ledge was present only in the lower half of the periproct (Bockelie 1972; Paul 1973, p. 13).

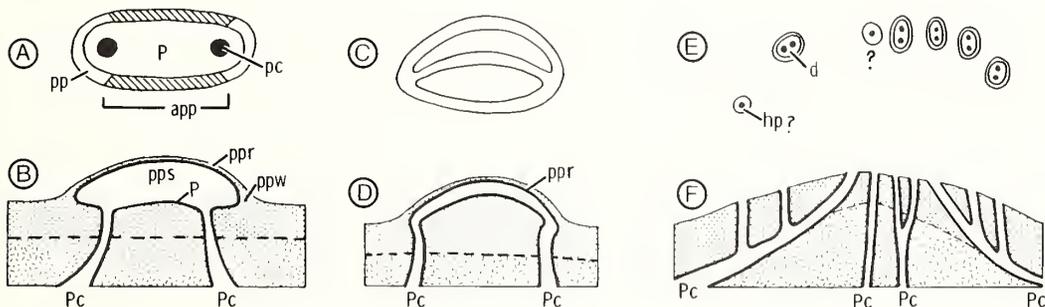
The gonopore. This lies between the peristome and the periproct and is usually slightly left of a line between them. It is a small circular pore generally about 0.5 mm in diameter. Small triangular plates forming a pyramid have been reported in Rhombifera, but have never been found in Norwegian material.

The hydropore. This is normally a narrow slit. In *Protocrinites* a circular opening occurs on top of a small tubercle but it is not known whether this is the hydropore or the gonopore. In the Sphaeronitidae and Parasphaeronitidae a slit is present on top of a ridge. Both the slit-shape and the presence of a ridge would have prevented suspended particles entering; this indicates an inlet rather than an outlet structure (see Paul 1971, pp. 27, 28). A hydropore implies the existence of a water vascular system. Sprinkle (1973) concluded that tube-feet were not present in the brachioles of Blastozoa. Consequently, the water vascular system may rather be related to the pore system (see later discussion). Breimer and Macurda (1972) disagreed with Sprinkle's interpretation and suggested the position of a ring canal in blastoids. Internal and external branches of the water vascular system may be present in both Rhombifera (Paul 1967, p. 234) and Diploporita.

Plates

Individual thecal plates vary in shape, pentagonal or hexagonal being the most common. They are mostly of one generation, i.e. plates formed at an early ontogenetic stage are the only ones involved in skeletal construction (primary plates). Some species and genera possess additional plates formed between others later during ontogeny and termed secondary, tertiary, etc., according to their time of formation. In the Norwegian Diploporita only primary plates occur in *Haplosphaeronis*, *Sphaeronites*, *Archaeocystis*, and *Eucystis*. Secondary or multigeneration plates occur in *Tetreucystis* n. gen., *Pachycystis* n. gen., *Parasphaeronites* n. gen., and in some indeterminable genera. Both Swedish and British species of *Sphaeronites* and *Eucystis* may have secondary or tertiary thecal plates. Thus, the plate pattern can be quite variable outside the oral area. *Haplosphaeronis* appears to be the only diploporite genus characterized by a constant plate number.

Plate structure. Well-preserved plates of *Parasphaeronites socialis* n. gen., n. sp. (Parasphaeronitidae n. fam.) show two layers of thecal mesh, an inner coarse mesh and an outer fine mesh (text-figs. 12, 33; Pl. 8, figs. 3, 6, 7). Similar observations were made by Paul (1971). However, the coarse layer does not show pillars and laminations as observed in *Archaeocystis*. The coarse layer has larger trabeculae than the fine layer; the long axes of the trabeculae seem to be orientated at random. In *P. socialis* branched haplopores occur at the boundary between these two layers (text-fig. 12; Pl. 8, figs. 6, 7). Pyrite filling the mesh of *Haplosphaeronis* plates and preservational features of other diploporites also suggest the presence of two layers. Sprinkle (1973) suggested that this pattern is characteristic of all blastozoan echinoderms.



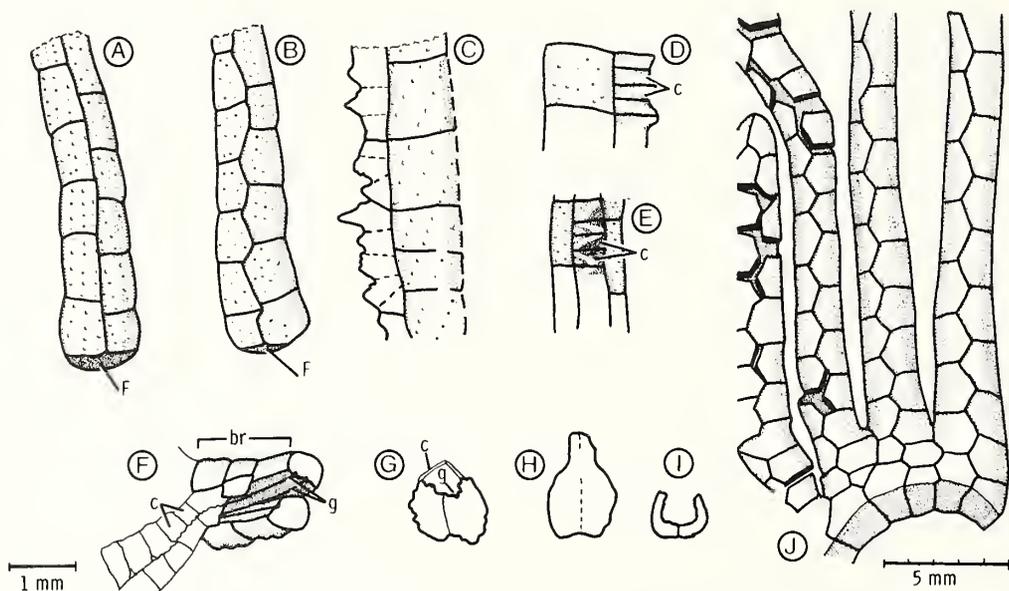
TEXT-FIG. 12. Pore structures in diploporites, showing measurements and terminology. A, C, E, in plan; B, D, F in cross-section. A, B, normal diplopores with or without a calcified periporal roof. C, D, humatipore (not present in Norwegian material). E, F, 'haplopores', simple and complex with unbranched and branched canals. (Originally haplopores were single canals opening in a peripore while diplopores were peripores with two canals. This present structure is much more complex. Notice that simple canals or simply branched canals go through the plate centre, whereas the complex canals lie at an angle to the side of the plate.) The plates are provided with an outer fine mesh of trabeculae (dotted) and an inner coarse mesh structure (irregularly hatched). app, aporal portion of peripore wall; hp, haplopore; P, peripore; Pc, pore canal; pp, poral portion of peripore wall; ppr, periporal roof; pps, periporal space; ppw, peripore wall.

Attachment. Thecae of most Norwegian diploporites were attached by a small or a broad attachment area to any suitable substrate, e.g. cephalopod shells, brachiopods, bryozoans, trilobites, and other cystoids. Some may have been attached to seaweed or soft-bodied animals like ascidians. The basal plates of some sphaeronitid cystoids, especially from Sweden but also from Norway, form a stem-like projection which was either cemented to a firm substrate or may have protruded down into the sediment. *Protocrinites* was the only diploporite in Norway with a stem. The stem was at least 10 mm long and rather complex, its columnals resembling those of shallow-water crinoids. No root structures have been observed.

Food-gathering appendages

Appendages are only very rarely found in diploporites, but facets suggest that they were of different types: some facets are large and indicate attachment for two or more muscular bundles (text-fig. 34A); others are small and hardly show muscle scars or ligament pits at all (e.g. *Haplosphaeronis*). The food-gathering appendages of blastozoans are termed brachioles (see Sprinkle 1973, pp. 12–20). Two major types of brachiole facets occur in the diploporites. Either there is only one facet present in each of the ambulacra even at an adult stage (Holocystitidae, Parasphaeronitidae) or more than one facet is present (most of the Sphaeronitidae, Protocrinitidae). At present only diploporites with the second type of facets have been found with brachioles in place.

Brachioles of Protocrinites. More than a dozen specimens of the Norwegian *Protocrinites rugatus* n. sp. have been found with brachioles in place (text-fig. 13; Pl. 1). The brachioles are biserial, unbranched, reach 15 mm in length, and thus exceed the total length of the theca. In cross-section they are slightly oval or irregular. The two plates that make up the major portion of the brachiole are of approximately equal size when seen in cross-section (text-fig. 13G, H). A set of cover plates is present over the food groove. Four cover plates seem to be attached to every brachiole element (text-fig. 13D, E). In this respect the brachiole resembles the eocrinoid *Gogia longidactylus* (see Sprinkle 1973, text-fig. 10). In *P. rugatus* no traces of nerve canals were found. However, the study was made from decalcified and cast material, and a nerve canal probably was present. In cross-section four minor furrows parallel to the food groove were observed. These grooves could have housed the radial extensions of the water vascular system and other vascular systems. Similar grooves have also



TEXT-FIG. 13. Brachioles of A–H, *Protocrinites rugatus* n. sp. from loose block, Toten, Oslo Region, and I, J, *Calix sedgwicki*. A, PMO 101.133, and B, PMO 101.130, showing dorsal sutures, both biserial but with slight differences in sutural areas. C–H, PMO 101.133, showing c, brachiole in side view with slightly irregular brachiolar cover plates; D, details of brachiolar cover plates (c) in side view; E, brachiolar cover plates from above showing their number and position; F, basal portion of brachiole (br) and brachiolar cover plates, and grooves within the brachiole (g); G, H, cross-sections of brachiole showing shape, brachiolar cover plates (c), and grooves along inside of brachiole (g). I, J, IRScNB 16001 showing I, cross-section of brachiole and J, brachioles showing complex basal portion and biserial appendages (from Chauvel 1977, pl. 1, figs. 5, 6). Scale on left for A–H; scale on right for I, J

been observed in other primitive echinoderms. They may have increased the cross-sectional area of a brachiole and were presumably covered with cilia. These additional furrows alongside the food grooves increased the efficiency and capacity of the brachioles for food transport, and possibly also for food collecting. If no podia were present in the brachioles, the alternative for trapping food particles would have been to possess as many cilia as possible. Similar furrows occur in *Echinospaerites* and *Calix*.

The shape of the brachioles of *P. rugatus* n. sp. suggests that they could stand out almost perpendicular to the theca; they are preserved in a retracted position, slightly bent towards the thecal surface (text-figs. 16, 17; Pl. 1, figs. 1, 6). Even though the animals were buried alive and killed by a rapid influx of sediment, some brachioles were shed. This shows that the contact between the brachioles and their facets cannot have been very strong. If this is typical for other cystoids, it explains the extreme rarity of preserved brachioles, particularly in the Diploporita.

Brachioles of other diploporites. Recent work by Chauvel (1977) has proved the existence of biserial appendages in two Aristocystitidae, *Glaphrocystis globulus* and *Calix sedgwicki*. The brachiole facets of these cystoids are grouped together around the peristome (text-fig. 13j), and partly interconnect to form a rigid brachiole complex before the individual brachioles separate. The brachioles of *C. sedgwicki* are more than 13 cm long, exceeding the length of the theca. Individual brachioles are almost circular in cross-section (text-fig. 13i), and were presumably covered by small plates in life (Chauvel 1977). At the base of and parallel to the food groove Chauvel discovered two minor grooves. A similar complex pattern of the basal portion of the brachioles has been found in a Swedish upper Ordovician aristocystitid (Bockelie, in prep.). On the basis of the observations above, the brachioles of the Aristocystitidae and the Protocrinittidae differ in their basal portions but not in their overall construction. *Asteroblastus* (Asteroblastidae) has uniserial brachioles (see Jaekel 1899, pl. 7, fig. 1) but their details are unknown. Recently a diploporite with *triserial* arms has been found (Parsley 1982).

Brachiole support. Two types of brachiole support seem to be present in cystoids. The Rhombifera and some Diploporita possess *flooring plates*. The ambulacra can be located directly on the thecal plates with brachiole facets (as in most diploporites), while in the majority of Rhombifera and some Diploporita ambulacral flooring plates are found cemented on to the thecal plates. Recently an intermediate situation has been observed in *Celticystis* (Bockelie 1979b) where ambulacral flooring plates occur only in the basal portion of the theca. In the remaining portion of the theca food grooves are developed on 'normal' thecal plates.

Pore structures

All respiratory pore structures of the Diploporita are exothecal, i.e. the body fluid extended from the inside to the outside of the theca and oxygen-carbon dioxide exchange took place through a membrane covering the exothecal pores. In many cystoids the external pores may have been covered by a calcite membrane (most of the Diploporita; see later). Two major types of external pore structures occur in the Diploporita: *humatipores* and *diplopores*. Humatipores are characterized by 'two internal circular pores leading to two or more tangential canals which lie beneath the flat external surface, or in a prominent external tubercle' (Paul 1971). They are confined to the Holocystitidae which are not found in Norway. Diplopores are composed of a simple thecal canal, the tangential portion of which was not normally calcified and probably formed a papula or a podium in life (Paul 1972, p. 5). The normal diplopore shows as two pores, usually paired within a shallow depression (peripore) on the external surface of the theca. In addition to these two major types, *haplopores* have been described by Bather (1900) and Chauvel (1941). A haplopore consists of a single perpendicular canal, apparently ending in a single pore on the thecal surface (see Kesling 1967, p. S89, fig. 33.7). Paul (1972, p. 9) only observed a true haplopore in a plate of *Eucystis* sp. Chauvel (1977) restudied *Calix*, in which haplopores have long been considered characteristic, and observed both normal diplopores and complexly branched or single 'haplopores' in the same individual. He stated that the latter could end in complex sieve-like pores with a peripore. Haplopores have always been considered

to lack a peripore, and Chauvel concluded that they may be regarded as a variety of diplopores rather than a pore structure on their own. It appears therefore that humatipores and diplopores are the only types of external pore-systems in the Diploporita.

Externally the pore-structures of the Diploporita are simple, but this is not the case with the canals leading from the pores through the plates to the thecal interior. Confusion over how the entire pore system was constructed has often been the result. The situation in most genera and species of the Sphaeronitidae is best known where canals lead to the peripores (text-fig. 14), forming part of a circulation system (Paul 1972, fig. 8B). In *Haplosphaeronis* connections of canals may or may not be present (text-fig. 20). *Parasphaeronites* n. gen. shows a complex pattern of canals (text-fig. 12E, F) in which single canals ending in a haplopore(?) go right through the plate close to the plate centre, whereas different types of branched canals occur towards the plate edges (see also Pl. 8, figs. 3, 6, 7). These latter complex canals occasionally end in haplopores, but more usually in diplopores (text-fig. 12E, F). Many or most of the canals of *Parasphaeronites* n. gen. end in diplopores on the thecal surface (Pl. 7, fig. 5), but the details of their connection within the theca are not clear. In *Calix*, the haplopores are located in particular portions of the theca, but their precise distribution is not known; nor is the distribution of these complex pores known in Norwegian material. Haplopores as originally defined may be trans-sutural and thus cross plate boundaries. This is most apparent in *Aristocystites? potens* (Chauvel 1941, p. 68).

Diplopores. These are the most common type of pore structures found in the Diploporita. They are characterized by a pair of canals which open to the exterior in a peripore. Both pores of the peripore are usually on the same plate, but exceptions occur (text-figs. 28, 29, 32). When present, the peripore wall can be divided into *poral* and *aporal* portions (pp, app; text-fig. 12). In *Haplosphaeronis* the aporal portions may develop spines and the poral portions may be almost reduced in some specimens of some species. All diplopores were covered in life by a thin membrane of organic material; some were also covered by a calcitic cupola, occasionally very thin, forming a *calcified roofed diplopore* (text-fig. 12B). Such calcified diplopores can occur in distinct areas (Pl. 5, figs. 2, 4). Inside the diplopore is a *periporal space* (text-fig. 12B). Various *Tetreucystis* n. gen. and *Eucystis* have no pores at thecal plate centres, which might be taken to indicate a lack of pores in extremely young specimens. Alternatively, pores formed at very early stages may later have been resorbed. However, in young individuals respiration could well have taken place directly through their small thin plates (Paul 1972; Bockelie 1979a).

Cystoids have different patterns of diplopore distribution and orientation. The most typical pattern is random, where the long axis of the peripore shows no preferred orientation (text-fig. 31), as in some *Tetreucystis* and *Eucystis* species. Other diploporites have a preferred peripore orientation. In *Tetreucystis kalvoeyensis* n. gen., n. sp. and *Sphaeronites (Peritaphros) pauciscleritatus*, the pore axes radiate from an often slightly elevated plate centre (Pl. 6, fig. 3; Paul and Bockelie 1983). In *Haplosphaeronis* the pore axes are orientated longitudinally in an ad-aboral direction along the radii and horizontally in the interambulacral areas of most species (text-fig. 21). This pattern is unique to *Haplosphaeronis*. *T. kalvoeyensis* has some of its longest pore axes orientated parallel to the oral frame (Pl. 6, fig. 1). These pores may have served a sensory function in addition to the normal respiratory function, becoming specialized and more closely connected with the oral nerve system. Paul (1971) observed numerous pores along the inside of the oral frame of holocystitids and concluded that they served a sensory function. Diplopores are distributed over most of the thecal surface, and are mostly of equal size. However, in a few genera (*Haplosphaeronis*, *Eucystis*, *Tetreucystis*) some diplopores at plate sutures are smaller or deformed.

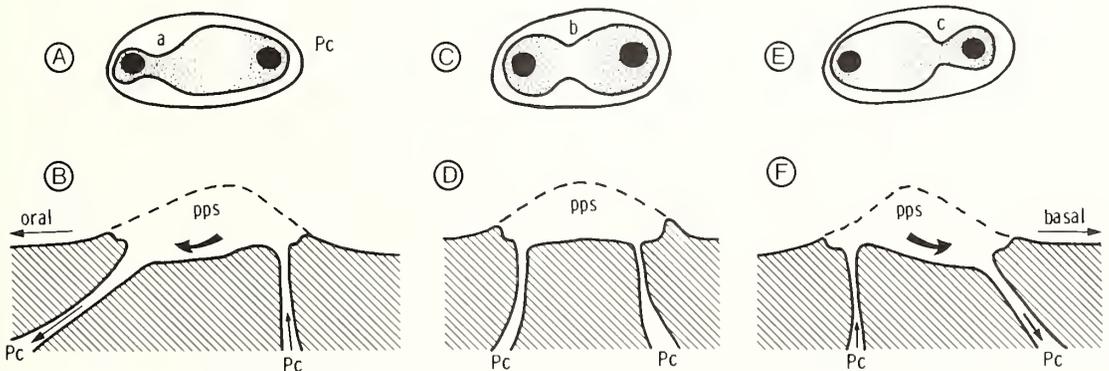
Diplopores may have formed in two ways, either at the plate sutures and gradually migrating towards the plate centre by additional growth (much like that of disjunct pore-rhombs) or alternatively, and most likely, by resorption of the plate. Many diplopores in *Haplosphaeronis* near the plate sutures are smaller than those closer to the plate centre (Pl. 3, figs. 3, 5). These may be in the position of formation, and thus resorption would have continued until maximum size of the diplopore was reached. Many individuals of *H. kiaeri* have pores at plate sutures, but apparently lack

pores closer to the plate centre (Pl. 5, figs. 2, 4). Instead, there are small knobs or 'ornament' randomly distributed on these plates which, when ground down, prove to be deformed diplopores with an originally calcified cupola.

The number and position of diplopores varies between individuals and some plates have more than others. The highest number is present in the circum-oral plates of the Sphaeronitidae. This upper portion of the theca is considered to have been in the zone of the highest water speeds passing over the theca, and it therefore possibly had the highest respiratory potential (Bockelie 1979b).

Covered diplopores. Diplopores are considered by many authors to have been covered in life by soft tissue. However, the presence of peripores covered by a calcitic cupola has been reported from many different genera and species of Diploporita. This has been explained as accidental preservation, or as being related to the sealing of parts of the respiratory system to prevent toxic gases from entering. Norwegian diploporites are often found with roofed diplopores in distinct areas, often towards the base or the oral area. Occasionally most of the theca is covered by roofed diplopores (Pl. 5, fig. 4). In addition to the roofed diplopores there are several pores that do not have a calcitic cupola, and probably never had one in the living state. This is particularly obvious in *H. kiaeri* (Pl. 5, fig. 3). The presence or absence of calcite-roofed diplopores is partly a preservational feature. Extremely well-preserved material often has the roof preserved, as in *H. kiaeri* (Pl. 5, figs. 2, 4) and *Protocrinutes rugatus* n. sp. (Pl. 1, figs. 1, 3, 5, 8). However, both these species were usually buried rapidly. In cases where burial was slower the roofed diplopores may have become abraded. Similar preservation on holocystitids confirms this. Even specimens of *Sphaeronites* (*S.*) *pomum* from Öland, Sweden, are occasionally found with extremely thin calcite roofs preserved.

The presence of calcite-roofed diplopores had several advantages. For the animal's internal flow system it would have helped keep a constant volume under the periporal roof. Previous suggestions that it would also have prevented toxic gases from entering the animals attached to the sea bottom may not be correct if the calcified diplopores were porous. (*P. rugatus* is provided with a stem and also has covered diplopores.) A third explanation implies protection from predation of soft tissue or papulae over the diplopores. There was no protection, such as spines, around most peripores (with the exception of *S. (S.) pomum* and some specimens of *H. kiaeri*). The formation of a calcite cupola would have reduced predation of soft tissue which might otherwise have been fatal to the animal. Covered diplopores are more common in the upper Ordovician and Silurian diploporites than in the lower and middle Ordovician forms.



TEXT-FIG. 14. Pore-structures of *Haplosphaeronis kiaeri*; A, C, E in plan, showing thickenings and spine development (a, b, c) on the peripore wall and B, D, F in cross-section showing angle of canals through the plates in different parts of the theca. B, near oral area, with oxygenated body fluid moving towards oral portion. D, midway down theca (note symmetrical arrangement of the two canals). F, near base with oxygenated body fluid moving towards basal portion. Arrows indicate direction of flow of body fluid inside canals. a, b, c, thickened parts of aporal portions of periporal rim; pps, periporal space; pc, canals (note they do not have the same thickness throughout the plate).

Diplopores are less efficient respiratory structures than endothelial dichopores and, consequently, more diplopores are needed to match the oxygen-carbon dioxide exchange rates achieved by cystoids with endothelial structures. A calcitic cupola would have reduced the efficiency of respiration only slightly, possibly as little as 10–15% (see Paul 1978).

Circulation in diplopores. In *Haplosphaeronis* the form of peripores differs according to their position on the theca (text-fig. 14). In the oral area, the adoral canal of any diplopore slopes towards the oral pole at an angle of 20–30° while the other canal is almost perpendicular to the surface. I suggest that oxygenated body fluid passed down under the oral area in this part of the theca (text-fig. 14B). Similar but reversed patterns have been found in the basal portion of the theca. Here oxygenated body fluid passed down into the basal portion of the theca (text-fig. 14E). Canals between these two extreme positions show variable angles, according to the location of the diplopore on the thecal surface. Peripore distribution over the theca of *Haplosphaeronis* suggests a flow direction of body fluids counteracting that of the external water current pattern around the theca (see Paul 1972). A similar pattern has also been suggested for *Hemicosmites* (Bockelie 1979a). The complex pattern of pore systems found in *Parasphaeronites* n. gen. cannot be evaluated at present in terms of thecal flow pattern. However, there appears to be a radiating pattern similar to that found in some species of *Tetreucystis* n. gen. and *Sphaeronites*.

Connections of canals inside the plates. In the aristocystitids branched haplopores have been known since the work of Barrande (1887). In the Sphaeronitidae Paul (1972, fig. 8A, B) illustrated the two possible models for peripore connections and argued strongly for the Y-shaped canals having fed separate peripores. He showed how unlikely it was that the Y-shaped canal fed the same peripore, because this would have created a mixing of oxygenated and deoxygenated currents. In some of the Norwegian species of *Haplosphaeronis* the canals are filled with tiny pyrite crystals and terrigenous mud. Careful dissolving of the thecal plates reveals canals going through the plate connected to canals of adjacent peripores, confirming Paul's fig. 8B (text-fig. 12).

Connections of canals of adjacent peripores occur frequently in *H. kiaeri* (text-fig. 20i) and have also been observed in *Eucystis globula* Paul (SM A74861) and *Parasphaeronites socialis* n. gen., n. sp. (text-fig. 12F; Pl. 8, figs. 3, 6, 7). These connections indicate the presence of an internal circulation system. Mapping the entire pattern of pore connections over the theca is exceedingly difficult and time-consuming and requires exceptional preservation. Some idea of the pattern can be obtained from *Haplosphaeronis* (text-fig. 20i). In this genus the diplopores are arranged parallel to the thecal axis over most of the animal, with the peripores radiating from each of the oral corners. Connections have only been observed between two adjacent diplopores at a time (text-fig. 20G). Pore canals merge in such a way that one gets the impression of a dichotomously branched pattern (text-fig. 20i).

Diplopores may have been produced by coelomic evaginations, which could have led to a random distribution of peripore connections. The radiating pattern observed in some *Tetreucystis* species may be related to such a system. On the other hand, peripore connections such as those found in *Haplosphaeronis* may indicate a more intricate and well linked flow system similar to the tube-feet connections of echinoids. These differences in pore systems have considerable taxonomic implications. The second explanation accounts for the presence of a hydropore, but the first does not. Which of the two alternatives is correct cannot be ascertained at present, but the fact that the diplopores appear interconnected suggests the presence of a complex connective hydrovascular system. The hydropore, which indicates the presence of a water vascular system, could thus be connected to the pore system, rather than to a system of tube-feet located in the brachioles. Sprinkle (1973, p. 21) suggested the absence of tube-feet in blastozoan brachioles. Paul (1967) suggested that both internal and external branches of a water vascular system might have occurred in the rhombiferans. This is also possible in the diploporites.

Internal morphology

Relatively little is known of the internal morphology of cystoids. Observations include mesenteria of *Echinospaerites* (Jaekel 1899; Regnéll 1945) and the intestine of *Caryocrinites* (Rhombifera)

described by Jaekel (1918). Sinclair (1948) and Regnéll (1951) also made internal observations. Termier and Termier (1959) suggested the presence of various oral ring canals. Internal features are known from the Oslo Region's echinoderms, particularly *Haplosphaeronis*.

Internal spine and basal pits. Many specimens of *Haplosphaeronis* have a hollow internal spine like that described by Paul (1973, p. 21, text-fig. 12) from *Sphaeronites* (*Peritaphros*) and *Haplosphaeronis*. This conical spine is well preserved in silicified specimens of *H. kiaeri* (text-fig. 22; Pl. 4, figs. 8, 9). It extends from the base for approximately one-third of the thecal height. It is a continuation of the inside of the basal plates but the plates themselves seem to have amalgamated at the base of the spine. However, one suture is present alongside the spine in some specimens. It may be open for some distance and is internally strengthened by calcite. A hole is present at the adoral end of the spine, indicating that it was hollow. An internal spine has been located in several genera of the Sphaeronitidae (*Haplosphaeronis*, *Sphaeronites* (*Peritaphros*), *Tetrecystis* but not as yet in *Eucystis* or *Sphaeronites* (*Sphaeronites*): Paul 1973, p. 41). An internal spine may be present in the Aristocystitidae (*Calix* and *Pachycalix*, Termier and Termier 1959), but it has not been recorded in other diploporites.

The functional significance of the internal spine is unknown. It shows similarities to the chambered organ of some crinoids, notably *Neocrinus decorus* as described by Reichensperger (1905) and *Eugeniocrinites caryophylatus* (see Ubaghs 1978, p. T192, fig. 162.1), and may have served a similar function. Regardless of its origin, the spine seems to have grown continuously during the animal's life, and must have served some function in both young and adult specimens.

Around the base of the spine and in contact with the inside of the basal portion of the basal plates lie seven cavities penetrating into the thecal plates of *Haplosphaeronis*, one at each of the plate sutures. In addition, a variable number of smaller cavities is found between the seven larger ones (text-fig. 22; Pl. 3, fig. 11). All cavities are present at approximately the same level and form conical depressions. Several dozen specimens with this type of structure preserved have been found. In some pyritized specimens (text-fig. 22D), a small depression surrounding the base of the spine is located between the grooves on the inside of the thecal wall and the internal spine. This depression may have housed an ectoneural nerve ring, and the grooves on the inside of the thecal wall may have been locations for side canals (text-fig. 22). The grooves on the inside of the thecal wall were not attachment areas for muscles or coeloms, since such attachment areas usually take the shape of bosses or evaginations rather than invaginations.

An ectoneural nerve ring is known in many fossil and recent crinoids, it being the main nerve system for innervation of arms and stem (Ubaghs 1978, p. T190), but there are great constructional differences between the arms of crinoids and the brachioles of cystoids (Ubaghs 1978, p. T133). Even so, an ectoneural nerve system was probably present around the base of *Haplosphaeronis*. Certain internal features in the basal portions of the thecae of the diploporite *Celticystis* (Bockelie 1979b) and in the rhombiferan *Hemicosmites* (Bockelie 1979a) may also represent traces of an ectoneural nerve ring. No traces of nerve canals leading from the base towards the oral area have been found.

Structures associated with the oral area. In sagittal view some specimens of *Haplosphaeronis kiaeri* have cavities within the plate just under the ambulacra (text-fig. 23B; Pl. 4, fig. 4). These may be parts of a circum-oral structure, but as yet too few specimens have been studied to confirm this. Steinkerns of decalcified specimens show an irregular underside of the theca just below the circum-oral area (Pl. 4, fig. 8) which may indicate that circum-oral structures were also present within the soft tissue below the skeleton. Silicified specimens of *H. kiaeri* show five lobes (0.4 mm thick) just under the ambulacral area (text-fig. 23A; Pl. 4, figs. 3, 5). Even though details of the lobes are not adequate, there is no doubt that at least one penta-lobate ring canal was present in the soft tissue of the circum-oral area. Similar structures have been suggested for other diploporites (Termier and Termier 1959; Bockelie 1979b). The reconstruction of *Pachycalix* (Aristocystiidae) is particularly interesting in this respect (Termier and Termier 1959; Kesling 1967, p. S245, fig. 143.2a) in which the presence of three ring canals was suggested. Whether or not the ring canal observed in *H. kiaeri* is associated with the water vascular system is not known.

Other internal structures. When decalcified, most specimens of *Haplosphaeronis* show traces of a 'gonoduct' and a 'stone canal' which are typical of other cystoids. These canals pass through the plate on the left side of the theca. The close proximity of gonopore and hydropore makes it difficult to decide which canal is the gonoduct and which the stone canal. However, in PMO 89996 (Pl. 4, fig. 2) the gonoduct and the stone canal are not connected, the former going straight down into the theca at the left side of the periproct. The hydropore, which at the thecal surface is a slit on the top of an elongated mound, becomes wider as it goes through the plate. When through the plate, the stone canal bends to the right and is located in a groove on the inside of the theca between the peristome and the periproct. The stone canal, which here has a circular cross-section, continues to the right and bends towards radius V where it is located just under the ambulacrum. At this position it becomes more flattened in cross-section and stops at the plate suture CO4:CO5. It is possible that the stone canal is connected to the penta-lobate ring canal just described. If this is the case, then it may indicate a well-developed ring canal of the water vascular system. Sprinkle (1973, pp. 21-27) discussed the possibility that tube-feet of the water vascular system were located in the brachioles but could find no support for such an assumption. I agree with Sprinkle, and prefer to relate the water vascular system to the blastozoan pore system. However, no fossil material exists to prove this assertion.

Occasionally thin films of pyrite can be seen attached to the thecal interior which follow a pattern not unlike that observed in *Echinospaerites* by Jaekel (1899). These may represent remains of a mesenterium, but the number of specimens involved is small.

MORPHOLOGICAL LINEAGES IN THE DIPLOPORITA

Evolutionary trends must fulfill two criteria: (1) they must involve closely related species (preferably within one family); (2) they must be time dependent. Even if these two criteria are fulfilled, one is often left with just the two end members, i.e. an early species and a late species. Two species of a genus might be quite different, not only because they occur at different stratigraphical levels, and thus may represent a phylogenetic lineage, but also perhaps equally important is the fact that they may occur in two different environments. Morphological lineages can be observed in some diploporite cystoids, but often they can only be inferred. In many cases the importance of morphological lineages in phylogenetic evolution cannot be evaluated. *Haplosphaeronis* illustrates some of the problems involved. Specimens occurring in shales are usually smaller than those in nodular limestones. The smaller specimens may be adults in the shale populations, whereas individuals of similar size occurring in nodular limestones may not have reached maturity. The number of brachiole facets of this genus increased during ontogeny (Bockelie 1978a), but to demonstrate this required large collections. One might have concluded that the number of brachiole facets changed with time, rather than ontogeny. Some morphological lineages, or what appear to be such, are discussed below.

Thecal plates. The number of thecal plates may increase or decrease with time in some genera. In *Sphaeronites* a reduction in plate number occurs from early to late Ordovician (Paul and Bockelie 1983). In other genera this has not been studied to the same extent. There is a general tendency towards reduction in the number of plates in many cystoids (see also Bockelie 1979b). A reduction takes place when the number of plates present in young individuals is retained to the adult stage. Enlargement of the theca then occurs by growth of individual plates only and not by the addition of secondary or tertiary generation plates. In this respect, *Haplosphaeronis* is an advanced genus because the number of thecal plates remains constant in young and adult specimens. *Celticystis* (Bockelie 1979b) and *Protocrinities* (text-fig. 16) add new thecal plates in particular 'growth zones'. Plate reduction with time is also marked in many primitive echinoderms. The change from a large number of irregularly arranged calyx plates to a much smaller number usually showing good pentamerous symmetry appears to have occurred independently in several groups of both Blastozoa and Crinozoa. In species with a large number of thecal plates, individuals seldom have the same arrangement of

calyx plates (see *Protocrinites*, text-figs. 16, 17). In species with a total plate number between fourteen and thirty-five the plates are arranged in symmetrical patterns, and most individuals of the same species have their plates arranged in the same manner.

Ambulacra. In the diploporite cystoids most genera and species have five ambulacra, but genera with two, three, and four exist. In the Sphaeronitidae genera with four ambulacra have radius III reduced (*Tetreucystis* n. gen., *Diplosphaeronis*). In other families genera and species with four ambulacra exist (*Trematocystis*, Holocystidae; *Parasphaeronites* n. gen. and *Pachycystis* n. gen., Parasphaeronitidae). These genera and species are parallel lineages in which radius III is reduced.

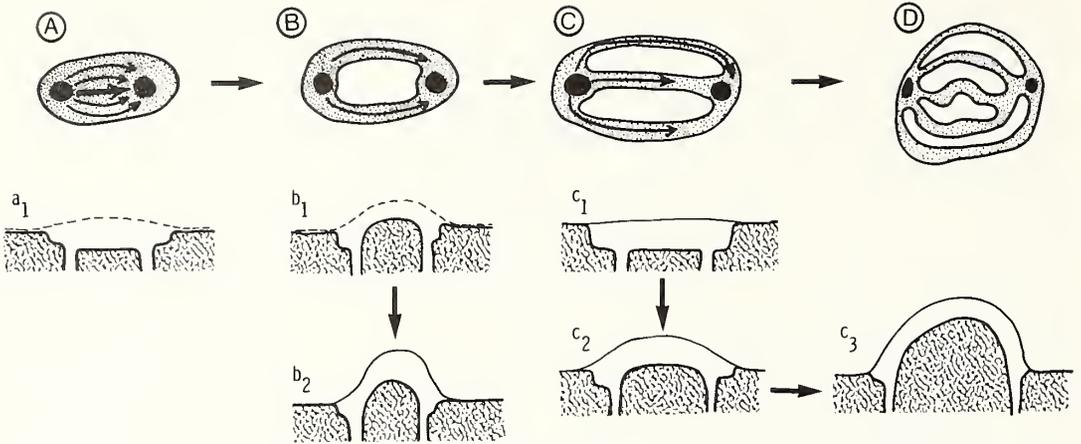
In *Eucystis* the number of brachiole facets and their position over the theca differs with time. Ordovician species may have from one to four facets close to the mouth. During the upper Ordovician and particularly in the Devonian the number of facets increased and the food grooves migrated down over the sides of the theca (Bockelie 1978a) resulting in an increased area for food collecting. An increase in the number of brachiole facets also occurred in *Tetreucystis* n. gen. and in *Haplosphaeronis*, but in complex ways. As mentioned previously, the highest number of brachiole facets in *Haplosphaeronis* is found in Britain, whereas contemporaneous species both in Norway and Sweden have fewer facets. In *Tetreucystis* n. gen., British species have few brachiole facets, Norwegian species have an intermediate number, and contemporary Swedish species have the highest number. What might appear to be a phylogenetic trend may in fact have been related to contemporary ecological conditions.

In *Haplosphaeronis* the brachiole facets may have different shapes (text-fig. 19). In an early species, *H. bratterudensis* n. sp., the first formed facets (Bockelie 1978a) usually have a rounded outline, whereas later ones are angular or almost square. During the late middle Ordovician and the upper Ordovician all facets became rounded in outline (text-fig. 19c, d). A general impression is that the facets also became larger during that same time span. Similar studies do not exist for other genera and species, and thus it is difficult to evaluate how common such a morphological trend may be. Early Ashgill species of *Tetreucystis* n. gen. generally have smaller brachiole facets than later Ashgill forms, and species with only one facet in each ambulacrum have larger facets than those with more. However, one facet in each ambulacrum is primitive while the presence of several facets is a derived character, as can be demonstrated in several genera and species (see also Bockelie 1978a). In *Protocrinites* young individuals have few facets, whereas older individuals have more (text-figs. 16, 17). In *Celticystis* new facets are added constantly (Bockelie 1979b).

Pore structures. The pore structures underwent changes throughout their history. A study of diplopores and their changes with time has been undertaken in *Sphaeronites* (Paul and Bockelie 1983) where there is an increase in the size of the pores and a corresponding decrease in their number. In *Haplosphaeronis* the width of the peripores decreased during the Ordovician (text-fig. 25). One of the most marked changes found in the pores of *Haplosphaeronis* is the elevation of the periporal floor from a position below the thecal surface in *H. bratterudensis* (early Caradoc) to a position level with or above the thecal surface in *H. kiaeri* (upper Ordovician). Together with this trend is an increase in the aporal portion of the peripore to form a spine-like peripore rim (Pl. 5, fig. 3).

The formation of a calcitic cupola can be observed in several genera and species throughout the Ordovician and appears to be a parallel development. No calcitic cupola is present in *H. bratterudensis* but it is very common in *H. kiaeri* and has also been found in British Ashgill species and some populations of the Swedish upper Ordovician *H. oblonga*. A calcitic cupola seems to accompany an elevation of the peripore from the thecal surface. Thus in most diploporites where the peripores are present on 'pustules', they have a calcitic cupola.

Haplopores have been considered the simplest type of pore structure but this may not be correct. The internal connections of pore structures are not well known so we do not know the course of canals through the plates in many diploporites. However, the external peripore in many of the early Ordovician species is sunk below the thecal surface and may have a weakly developed periporal rim and represent a simple stage (text-fig. 15A). During the middle Ordovician the periporal floor became elevated in *Haplosphaeronis* and *Sphaeronites* (*Peritaphros*) (text-fig. 15B). By a further elevation of



TEXT-FIG. 15. Morphological series of changes in pore structures. A, simple, open pores. B, formation of elevated periporal floor and slight diversion of body fluids into two separate currents. C, tri-partition of tangential canals. D, more complex pattern of tangential canal formation. a, b, c, cross-sections of pore structures within the general form patterns. a₁, simple peripores in *Glyptosphaerites* and early *Haplosphaerites* species. b₁, b₂, development of an elevated periporal floor, typical of *Sphaerites* (*Sphaerites*) and *S. (Peritaphros)* species (a broken line indicates non-calcified periporal roof; a continuous line indicates calcified periporal roof). c₁–c₃, stages of development in Holocystitidae and Aristocystitidae in which calcified cupola is commonly present (note elevation of the periporal floor to form knobs with large surface areas).

the periporal floor a calcitic cupola was formed over the peripore, probably to keep a constant volume within the pore space or to protect these vital structures from predation. Most diploporite pore structures did not evolve beyond this stage (text-fig. 15B). In some genera the periporal floor divided, thus separating the currents of body fluids into the two flow directions seen in *S. (Peritaphros)*, or into three or more such currents (text-fig. 15C, D). In extreme cases the cupola became strongly elevated (text-fig. 15C₃). The trend towards the formation of humatipores in the Holocystitidae and a pustule-like cupola may be regarded as stages in the evolution of a better protected respiratory system.

It seems that the changes with time found in the respiratory pore structures are most important for the class Diploporita. It is probably likely that morphological trends of the brachioles are equally important (see above), but without suitable material, this is speculation.

SYSTEMATIC PALAEOLOGY

Phylum ECHINODERMATA Bruguière, 1789

Subphylum BLASTOZOA Sprinkle, 1973

Class DIPLOPORITA Müller, 1854

Diagnosis. Thecal pores developed as units mostly confined to single plates, typically in the form of diplopores, but present in some as haplopores or humatipores. Lower Ordovician (Tremadoc)–middle Devonian.

Remarks. Brachioles of the Diploporita do not differ from those of most Rhombifera or most Eocrinoidea. Paul (1968a, p. 594; 1968b, pp. 726, 727) proposed that the name Cystoidea be dropped and that the Rhombifera and Diploporita be given class rank. This was accepted by Sprinkle (1973, p. 170) and is also accepted here. Sprinkle (1973) discussed whether or not the Diploporita should be

assigned to the Blastozoa. The discovery of biserial appendages in several genera of the Diploporita strengthens the assumption that this class belongs to the Blastozoa (see also discussion by Chauvel 1977, p. 317). The diagnosis given above differs to some extent from that of Ubaghs (1978, p. T362) who did not recognize the subphylum Blastozoa. However, this present study shows that the Diploporita have the type of plate growth which is characteristic of other Blastozoa.

The Diploporita appear to be a fairly homogeneous group of primitive echinoderms, all having exothecal pore systems. The Diploporita seem to form a natural group but this is not so with the Rhombifera. As suggested by Paul (1972) and discussed by Sprinkle (1973, p. 170), the Rhombifera consist of two distinct groups of cystoids, one with endothecal structures and one with exothecal pore structures. It is difficult to see how one could have given rise to the other.

Superfamily GLYPTOSPHAERITIDA Bernard, 1895

Diagnosis. Diploporite cystoids. Ambulacra radial, extending over theca, with alternating lateral branches (single or in groups) leading to brachiole facets; in many genera, ambulacra bordered by alternating 'adambulacrals' on which facets are located. Diplopores invariably present on ambulacra-bearing plates, in some forms also in the interambulacral areas. Most with column, a few moulting column as adults.

Family PROTOCRINITIDAE Bather, 1899

Diagnosis. Diplopores on ambulacral and interambulacral plates alike. Ambulacra extending radially from peristome, with short branches to brachiole facets more or less alternating. Ambulacral cover plates continue on to the oral area where they become oral cover plates. Thecal plates bearing rather regularly alternating ambulacral plates comprising so-called 'adambulacrals'. Brachioles biserial.

Remarks. Genera of the family Protocrinitidae differ considerably from those of the Glyptosphaeritidae. These two families are grouped together with the Dactylocystidae and the Gomphocystidae in the superfamily Glyptosphaeritida by Kesling (1967). *Glyptosphaerites*, the only representative of the Glyptosphaeritidae, has an oral cover resembling that of sphaeronitids but differs considerably from that of all other families. Thus the Glyptosphaeritidae may be more closely related to the Sphaeronitidae than to other families. The Protocrinitidae and the Dactylocystidae seem to form a natural unit, quite different from the other two families of the superfamily. A subdivision of the Glyptosphaeritida may prove necessary in the future.

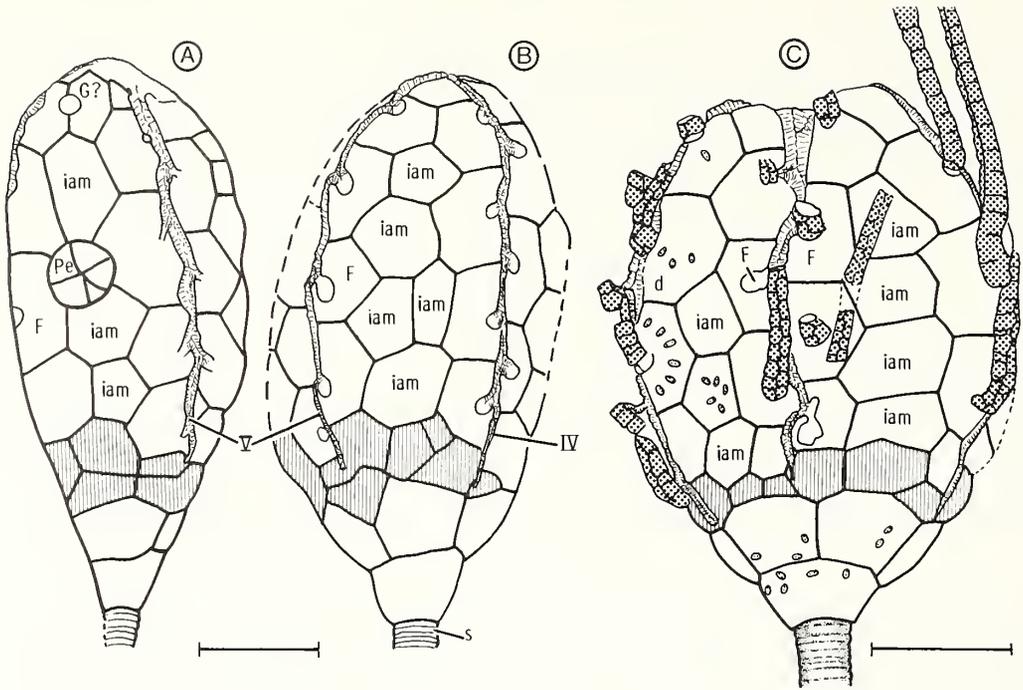
Genus *Protocrinites* Eichwald, 1840

Type species. *Protocrinites oviformis* Eichwald, 1840, p. 185, from Põõsaspea (Spitham), Estonia, Jõhvi Stage (DI), middle Ordovician.

Diagnosis. A genus of Protocrinitidae with triangular peristome surrounded by six circum-oral plates; five ambulacra, each containing dichotomously branched food grooves, terminating in a facet on each thecal plate, or continuing on to biserial appendages when present; ambulacra confined to specialized adambulacral with one facet on each adambulacral plate; adambulacral plates separated transversely by one or occasionally two interambulacral plate series.

Remarks. This diagnosis differs from that given by Kesling (1967) in several respects, partly because the number and distribution of circum-oral plates may be an important character of most cystoids. In the Sphaeronitidae, this is certainly the case. Jaekel (1899) regarded *Fungocystites* Barrande as a synonym of *Protocrinites* but later (1918) accepted the two as separate genera.

Description. The thecae are apple or egg-shaped. *P. rugatus* sp. nov. is small with thecal diameter 15 mm, whereas *P. oviformis* and some *P. fragum* are 50 mm. Five ambulacra, each containing dichotomously branched food grooves, extend from the mouth. The ambulacra do not reach down to the basal plates, but stop on the third



TEXT-FIG. 16. *Protocrinites rugatus* n. sp. Adult thecae. A, B, PMO 101.132, different views showing radii IV and V and position of gonopore (G?) and periproct (Pe) in relation to ambulacra and interambulacra (iam). Notice that ambulacral channels end in the growth zone (vertically ruled). C, PMO 101.138, showing biserial brachioles (dotted), brachiole facets (F) and some diplopores radially arranged on the ambulacral plates. s, proximal portion of the stem. Scale bar, 5 mm.

plate series up from the basals (text-fig. 16; Pl. 1, fig. 8). New ambulacral facets were added to the distal portions of the ambulacral furrows throughout life. The number of facets per ambulacrum increased from two in young specimens to nine in larger ones. The ambulacral furrows are covered by small cover plates arranged in an intricate pattern (text-fig. 17B; Pl. 1, fig. 3). A biserial appendage up to 15 mm long extended from each of the ambulacral facets. The appendages are as long as the theca itself (text-fig. 16; Pl. 1, figs. 1, 4).

The basals of *Protocrinites* vary in number. According to Volborth (1846) the number in *P. oviformis* can vary between three and six. In *P. rugatus* sp. nov. all the basals are fused into one unit. Diplopores are present all over the theca. In Norwegian species it appears that most or all the pores were covered in life, either by an organic membrane or, most likely, by a thin calcitic membrane. This membrane was easily abraded, leaving the pores open in specimens exposed for some time before final burial. The pores on adambulacral plates tend to be orientated with their long axes perpendicular to the ambulacrum, as observed by Jaekel (1899, pl. 5, fig. 6a).

The periproct is situated laterally on the theca, but its position may vary (Jaekel 1899). In general, two or three plates separate the periproct from the mouth (text-fig. 16A). The periproct is circular and covered by a pyramid of five or six triangular plates. Both a gonopore and a hydropore have been reported on *P. fragum* (Yakovlev 1940, fig. 1). In the Norwegian material a tubercle may be present either on the CO5:CO6 suture (PMO 101.138 and 101.136) or on the left sutural area of the upper interambulacral plate between radii V and I (PMO 101.132 and 101.130, text-figs. 16A, 17A). This tubercle may represent either the gonopore or the hydropore. Eichwald (1840) and Jaekel (1899, pl. 5, fig. 3) also observed a tubercle on CO6.

Attachment: some species had a stem, and one was certainly present in *P. yakovlevi* (Hecker 1964, pl. 5, fig. 5) and *P. rugatus* sp. nov. (Pl. 1, figs. 1, 2). In *P. yakovlevi* an attachment disc was present. Discs may also have been present in other species. In *P. fragum* no stem has been observed. Jaekel (1899, p. 430) suggested that this species lacked a stem in adult stages. *P. oviformis* is known to have had a stem when young, but it was lost in adults (Volborth 1846).

Growth: the growth pattern of *Protocrinites* was previously unknown. In the Norwegian material, however, one small specimen occurs together with larger ones. The plate configurations and food-gathering appendages give some indication of the growth pattern. In the smallest specimen (5 mm high, 5 mm in diameter) only two brachioles are present in each of the ambulacra, whereas in larger specimens seven to nine brachioles are present per ambulacrum depending upon the size of the theca. This indicates that new appendages were added through life. The length of the brachioles also seems to have been related to thecal size. However, few specimens have complete brachioles. The ratio of brachiole length to thecal size is greater in smaller specimens than in larger ones (text-figs. 16, 17c). This may indicate that the small specimens could obtain proportionally larger quantities of food for rapid growth.

New plates were added; the important growth zones seem to be in the third plate series from the base of the theca (text-fig. 16). The plates in this zone do not appear to be differentiated, whereas those immediately adorally do (text-fig. 16). Growth in this part of the theca did not interfere with food-gathering, nor with the stem and its attachment to the basals. The theca also grew by normal accretionary growth of individual thecal plates (Sprinkle 1973). The addition of new thecal elements in this growth band thus comprises: (1) addition of new thecal plates, including adambulacrals and interambulacrals; (2) continued extension of ambulacral furrows and ambulacral cover plates; (3) formation of new brachiole facets; and (4) possibly formation of new diplopores. Diplopores also appear to have been formed by resorption of skeletal material wherever a new pore was needed, and their formation may have been less important than the formation of other thecal elements in the growth zone.

Palaeoecology. The stem-bearing Norwegian species lived on a muddy bottom in an unstable sedimentary environment. *P. oviformis* is not uncommon in the Jõhvi stage in Estonia and Russia but little is known concerning its palaeoecology. According to Jaekel (1899, p. 430) *P. fragum* was heavy, stemless, and probably free-living on the sea bottom. Its size and shape suggested to him slow movement, if any. The somewhat flattened shape of the animal would have prevented it from sinking into the soft sediment on which it lived. *P. yakovlevi* was attached by a stem and a disc, but nothing is known about the environment in which it lived.

Regional distribution. Norway, Estonia, Leningrad district of Russia (Jaekel 1899; Hecker and Hecker 1957), Thüringen, Germany (Freyberg 1923), Burma, India (Bather 1906).

Stratigraphical range. Arenig–Caradoc.

Protocrinites rugatus n. sp.

Plate 1, figs. 1–8; text-figs. 13A–H, 16, 17

Diagnosis. A species of *Protocrinites* with a strongly rugose plate surface and stem present. Interambulacral rows may contain two interambulacral plates in interradius IV–V. Basals fused to form a solid basal cup for stem attachment.

Holotype. PMO 101.138 preserved as an external mould.

Horizon and locality. Coelosphaeridium Beds of Furuberg Formation (lower Caradoc), northern part of the Oslo Region. The type derives from a loose boulder, but equivalent sediments and associated fauna is restricted to the Toten–Brummundalen areas in the northernmost part of the Oslo Region.

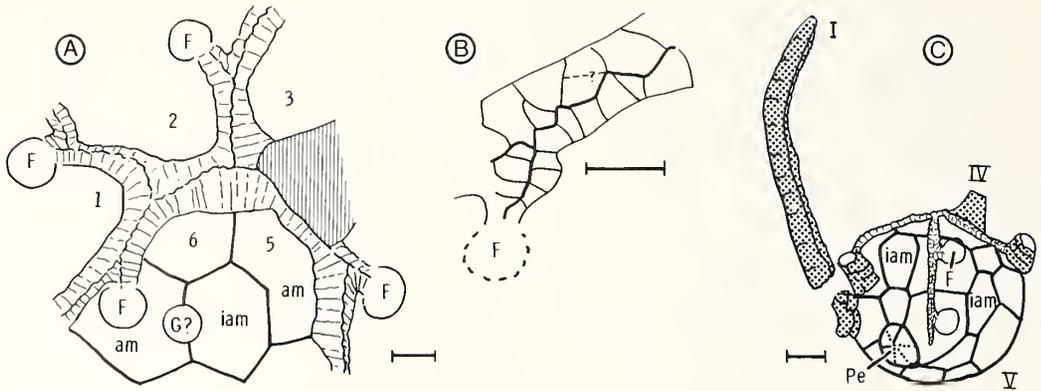
Material. In addition to the holotype, seventeen specimens (sixteen of which derive from the same boulder) are considered to belong to this species.

Description. Theca: egg-shaped, height/width ratio varies between 1.2 and 1.7.

Plates: about a hundred in adults. The plates are regular pentagonal or hexagonal. The main addition of new plates is considered to have taken place adoral to the basals (text-fig. 16; Pl. 1, fig. 8). The plate surface is usually strongly ornamented with nodes or spines, obliterating the diplopores. Plate thickness is approximately 1 mm. The sutures between contiguous plates are irregular and interlocking like those of *Celticystis* (Bockelie 1979b).

Diplopores: with or without a periporal rim; periporal floor below thecal surface. Diplopores seem to have been present on all thecal plates including the basals. The peripores are relatively small, seldom exceeding 0.40×0.25 mm.

Peristome: 1×2 mm in adults. In PMO 101.136, CO5 and CO6 may be partly fused, but in other specimens a clear suture is present. The mouth is covered by numerous ambulacral cover plates which are somewhat bigger



TEXT-FIG. 17. *Protocrinites rugatus* n. sp. A, PMO 101.130, oral area showing six circum-oral plates (1-6) and the relationship of ambulacral plates (am) to the inter-ambulacra (iam); ambulacral cover plates continue from brachioles towards and on to the mouth as oral cover plates. B, PMO 101.133, details of ambulacrum with cover plates of variable shape. C, PMO 101.458, juvenile specimen with complete brachiole in radius I (dotted); each ambulacrum has two brachioles; no gonopore developed. G?, gonopore; F, brachiole facets; vertically ruled area not exposed; scale bars 1 mm.

than cover plates in other parts of the theca (text-fig. 17A; Pl. 1, fig. 3). The ambulacral grooves are approximately 1 mm wide and covered by large triangular plates along their sides, with smaller often irregular plates intercalated. Towards the base the ambulacral grooves become thinner (0.25 mm). The food grooves continue on to unbranched biserial brachioles (text-fig. 17A; Pl. 1, figs. 1, 5-8), the largest of which measures 15 mm. Two cover plates seem to be attached to each brachiole element (text-fig. 13; Pl. 1, fig. 7). The structure of the brachioles thus may resemble that of the eocrinoid *Gogia longidactylus* (Sprinkle 1973, text-fig. 10).

Periproct: large, round, 2.5-3.5 mm in diameter and covered by an anal pyramid of five or six triangular plates (Pl. 1, fig. 6). The periproct lies about mid-height in interradius V-I separated from the mouth by three plate series (text-figs. 16, 17).

Gonopore/hydropore: a tubercle present on the CO5:CO6 suture, or at the suture between adambulacral and interambulacral plate just below CO6, may be a hydropore.

Attachment: a flexible stem was present in life, with complex nodals and internodals. The stem is similar to that of crinoids, and at least 8 mm long.

Palaeoecology. I believe that they all lived in fairly shallow clear water, on a muddy bottom with few properly sessile elements, in an area commonly covered by coarser sediments at irregular intervals.

Remarks. *P. rugatus* differs from other *Protocrinites* species in the amalgamation of its basals to form a solid socket.

EXPLANATION OF PLATE I

Figs. 1-8. *Protocrinites rugatus* n. sp. Coelosphaeridium Beds, Furuberg Formation, northern Oslo Region. 1, PMO 101.138, stereophotos of holotype, $\times 3$. 2, PMO 101.132, lateral view showing two ambulacra and stem, $\times 2$. 3, PMO 101.133, stereophotos of oral area showing plate configuration and ambulacral and oral cover plates, $\times 5$. 4, PMO 101.133, lateral view showing theca and incomplete brachioles, $\times 1$. 5, PMO 101.130, stereophotos of biserial brachioles and ambulacrum with cover plates preserved, $\times 7$. 6, PMO 101.130, stereophotos showing anal pyramid and brachioles, $\times 4$. 7, PMO 101.133, brachiole with brachiolar cover plates (two cover plates to each brachiole element), $\times 5$. 8, PMO 101.132, details of ambulacrum with cover plates. The ambulacrum stops in the third plate series from the base. This is the growth zone where new plates and extensions of the ambulacrum are added, $\times 5$.



BOCKELIE, *Protocrinites*

Superfamily SPHAERONITIDA Neumayr, 1889

Diagnosis. Stemless Diploporita with variable-shaped theca; almost all plates pierced by diplopores; peristome covered by a roof (palate) of six plates beneath which food grooves pass to the mouth; four or five ambulacra; food grooves narrow, generally short but extending over theca in some species; periproct covered by pyramid of triangular plates; circular gonopore and generally slit-like hydopore between peristome and periproct, and to the left.

Remarks. Paul's (1973, p. 18) definition of the superfamily is accepted here, but whether or not cover plates where present on the ambulacra is not known.

Family SPHAERONITIDAE Neumayr, 1889

Diagnosis. 'A family of Sphaeronitida with diplopores; peristome surrounded by six circum-oral plates with a small additional plate (CO7) between the peristome and the periproct but not in contact with the former; four or five ambulacra with one or more ambulacral facets each' (Paul 1973, pp. 18, 19).

Remarks. The pore structures of Diploporita seem to be more complex than previously considered—for instance, both haplopores and diplopores have been found in the aristocystitid *Calix sedgwicki*. Some diplopores of *Eucystis* also branch in an unusual way.

Genus *Sphaeronites* Hisinger, 1828

Synonymy. See Paul (1973, p. 19).

Type species. *Echinus pomum* Gyllenhaal 1772, by original designation, p. 242, pl. 8, figs. 1–3; from the Asaphus Limestone (Arenig), Kinnekulle, Västergötland, Sweden (Regnéll 1945, pp. 162, 163).

Diagnosis. A genus of Sphaeronitidae with globular to pyriform or fusiform theca composed of approximately forty to two hundred plates which are irregularly arranged except in the oral area; peristome and periproct very close together on smooth oral prominence; five ambulacra with one to three facets each; all thecal plates uniformly covered with diplopores (except in attachment area); attachment direct.

Remarks. The diagnosis agrees with that of Paul (1973, p. 19), except that the number of brachiole facets in an ambulacrum may reach three.

Subgenus *Sphaeronites* (*Peritaphros*) Paul, 1973*Sphaeronites* (*Peritaphros*) *pauciscleritatus* Paul and Bockelie, 1983

Plate 2, figs. 2–4; text-fig. 18A

Synonymy. See Paul and Bockelie (1983, p. 723).

Diagnosis: 'A species of *Peritaphros* with large globular theca reaching 40–50 mm in diameter in adult specimens; thecal plates limited (fifty to sixty); diplopores polygonal (0.4 × 0.4 to 0.4 × 0.6 mm in adult specimens), average pore density 7.40 per mm²' (Paul and Bockelie 1983, p. 724).

Types. Holotype, PMO 79687 (Pl. 2, figs. 2, 3); paratypes, PMO 6183, 90042, 90043, 90289, 90293, 90297, 90347, 90349, 90350, 90351 (Paul and Bockelie 1983, p. 724).

Horizon and locality. Middle part of Lower Chasmops Limestone (= Stage 4bβ), middle Caradoc, Oslo-Asker District of the Oslo Region, Norway.

Remarks. Morphology and palaeoecology is described by Paul and Bockelie (1983, p. 726).

Genus *Haplosphaeronis* Jaekel, 1926

Synonymy. *Sphaeronis* Angelin, 1878 (pars); *Sphaeronis* auctorum; *Pomocystis* Haeckel, 1896; *Pomosphaera* Haeckel, 1896.

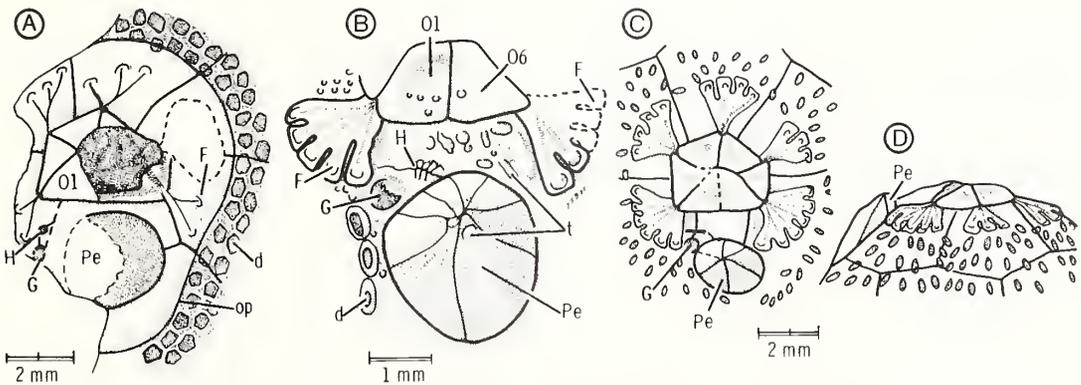
Type species. *Haplosphaeronis kiaeri* Jaekel, by monotypy, in Kiær, 1926, p. 20; from the Gagnum Shale Formation (= Sphaeronid Shale of Kiær 1926), lower Ashgill, Hadeland, Oslo Region, Norway.

Diagnosis. A genus of Sphaeronitidae with fourteen thecal plates arranged in two circlets of seven each; oval or dumb-bell shaped diplopores mostly arranged with their long axis in an ad-aboral direction; five ambulacra each with from one to ten food grooves in a fan-like arrangement at corners of peristome, confined to circum-oral plates.

Remarks. This diagnosis differs only slightly from that of Paul (1973, p. 27). Specimens containing only one groove per ambulacrum exist, especially in young specimens of at least two species. Bockelie (1978a) showed the number of food grooves per ambulacrum to increase with growth. The taxonomic value of the number of such grooves is dubious. However, stratigraphically younger species do have more grooves per ambulacrum than older species with the same thecal diameter. The type specimen of the genus is lost or mislaid; it has not been in the type collection for at least twenty-five years.

Description. The thecae of *Haplosphaeronis* are variable in shape, both between and within species. Mostly they are spherical to pyriform, but almost flat disc-shaped specimens occur. Many Norwegian specimens are shaped like an inverted pear or are mitre-shaped. British and Swedish species have a pentalobate outline in some populations. No stem is present. Most Norwegian specimens of both species are small, seldom exceeding 15 mm in diameter. In Sweden, however, individuals reaching 45 mm in height and 30 mm in diameter occur locally.

Plates: there are two circlets each with seven plates. The lower circlet has more or less equal-sized plates, while the upper circlet has five large plates bearing the ambulacra and two smaller plates (CO6 and CO7) inserted between the peristome and the periproct (text-fig. 11c). Jaekel's (1926, p. 19) original description of the genus appears to be correct, as discussed by Paul (1973, p. 28). Individual plates are thick (approximately 1 mm) and pierced by numerous diplopores. Little is known of the plate meshwork. However, silicified specimens often show the inner portion of the plates to be silicified more easily than the outer portion. Pyritization also occurs by filling the mesh of the inner portion of the plate more frequently than the outer part. By analogy with *Archaeocystis*, as described by Paul (1971, p. 11), and with *Parasphaeronites* n. gen., one may assume the



TEXT-FIG. 18. A, *Sphaeronites (Peritaphros) pauciscleritatus* Paul and Bockelie, PMO 79687 (see Pl. 2, figs. 2, 3); oro-anal area showing four oral cover plates (O1, etc.), hydropore (H), gonopore (G), and periproct (Pe) on the oral platform (op) which is devoid of diplopores (d). B, *Haplosphaeronis kiaeri* Jaekel, PMO 89972 from 5.5 to 6.0 m level, Gagnum Shale, Tønnerud, Hadeland; oro-anal area showing oral cover plates (O1, O6), major thecal openings, and characteristic tubercular ornament (t). C, D, *Haplosphaeronis bratterudensis* n. sp., PMO 89201 from Lower Chasmops Limestone, Bratterud, Ringerike, holotype; C, from above and D, in lateral view (note the radiate pattern of diplopores).

presence of an outer fine mesh and an inner coarse mesh. Weathered specimens of *H. cf. kiaeri* from 16 to 17 m below the top of the Upper Chasmops Limestone at Raudskjær, Asker, show the crystallographic orientation of palatals covering the mouth (text-fig. 20H). One weathered specimen (PMO 90965) shows fine lineations, representing cleavage, within the calcite plates. The direction seen on one plate always differs from those of the adjoining plates. The angle of dip cannot always be ascertained, but the direction of dip changes from one plate to the next, e.g. O1, O3, and O5 dip away from the mouth, whereas O2, O4, and O6 dip towards the mouth. A similar pattern has also been observed in other specimens, and may be typical for *Haplosphaeronis* species in general. All thecal plates have numerous rather specialized diplopores. Small knobs or tubercular ornament may be present between the diplopores. Occasionally these are either new pores in the process of formation, or pores that have been reduced.

Thecal openings: the peristome is large and covered by six palatals (Paul 1971), two of which may be almost fused (O1 and O6). The palatals are arranged in the usual manner for sphaeronitids (text-fig. 11C). The periproct is oval or pyriform with a covering pyramid of five to seven anals. The apex of the anal pyramid is frequently directed towards the oral region (text-fig. 18D). Laths are developed on the inside of the lower edge of the periproct, as also seen in *Tetreucystis* n. gen., and this suggests that three or four of the lower plates of the anal pyramid were able to open outwards, whereas the adorally located pyramid plates were not flexible (text-fig. 26B, C; Pl. 2, fig. 6). This arrangement would have permitted faecal matter to fall down over the theca into the zone of maximum current velocity around the theca and thus be transported away from the animal. The faecal matter was probably in the form of small pellets. Between the peristome and the periproct, and to the left, is a small usually circular gonopore and a slit-like hydropore (text-fig. 18B). The hydropore is always located on top of a slightly elevated ridge, reducing the possibility that sediment particles would have entered the slit. The gonopore may have been covered by a pyramid of small triangular plates, but this has never been observed. Such plates are only known in fistuliporite Rhombifera.

Diplopores of *Haplosphaeronis* are mostly elongated and typical of the genus. They are numerous and spread over the thecal surface, usually aligned in an ad-aboral direction. However, some of the pores near the plate edges (probably the last ones formed) are set perpendicular to this direction. In stratigraphically older species the perpendicular arrangement of diplopores is absent (Pl. 2, figs. 7, 8). In the circum-oral plates the diplopores are arranged in a fan-like manner (Pl. 3, fig. 3) with diplopores in rows. The number of rows gives some indication as to how many growth stages the cystoid has gone through (e.g. a specimen with five rows is probably older than a specimen with only three rows). As many as twelve rows have been observed in some specimens of *H. proiciens* Regnéll. The length and width of individual peripores in the different rows may vary. The diplopores at plate sutures are often smaller than other pores of the theca. It seems that new diplopores were added at plate sutures throughout the growth of the theca, and reached maximum size fairly rapidly.

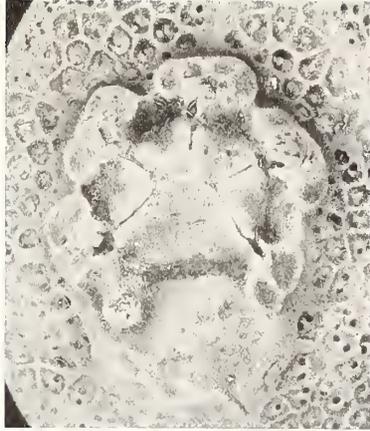
Ambulacral system: the peristome is always pentagonal and may have five raised ambulacral platforms at the corners. One to ten food grooves radiate in a fan-like pattern on each ambulacral platform and terminate in small (usually 0.5 mm in diameter) ambulacral facets at the outer edge (text-fig. 19). The brachioles were biserial, as indicated by the small ridge between the pair of muscle-scars on each facet. The ambulacral furrow leading to the first formed facet is always perpendicular to the adjoining oral edge, whereas later ones are not. Between adjacent ambulacral facets and their ambulacral structures, ridges are developed to separate them. These ridges are of different types and details of their structure may be of some taxonomic importance. Two main shapes of facet

EXPLANATION OF PLATE 2

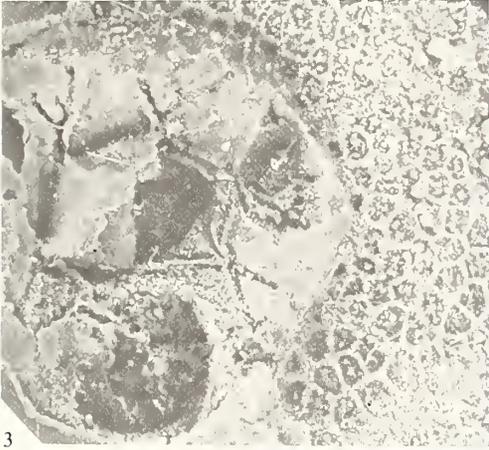
- Fig. 1. *Sphaeronites (Peritaphros) globuhus* (Angelin). Dalby Limestone, Böda Harbour, Öland, Sweden. RM Ec 4360, stereophoto of holotype showing oral-anal region, approximately $\times 10$.
 Figs. 2-4. *Sphaeronites (Peritaphros) pauciscleritatus* Paul and Bockelie. Lower Chasmops Limestone, Fyrsteilen, Oslo-Asker. 2, 3, PMO 79687, cast of holotype showing 2, diplopores and 3, oral view of oral area, $\times 6$. 4, PMO 90042, cast of oral area in oral view, Hareholmen at Ostoya, Bærum, $\times 6$.
 Figs. 5-8. *Haplosphaeronis bratterudensis* n. sp. Lower Chasmops Shale, Bratterud, Ringerike. 5, PMO 89201, cast of holotype, stereophoto of oro-anal area (specimen whitened with ammonium chloride sublimate), $\times 4$. 6, PMO 89202, stereophoto of cast showing anal region with shelf for attachment of anal plates in aboral side, $\times 7$. 7, PMO 89209, stereophoto of cast showing diplopores in circum-oral plates, $\times 6$. 8, PMO 89213, stereophoto of cast showing diplopores in basal plates, $\times 6$.



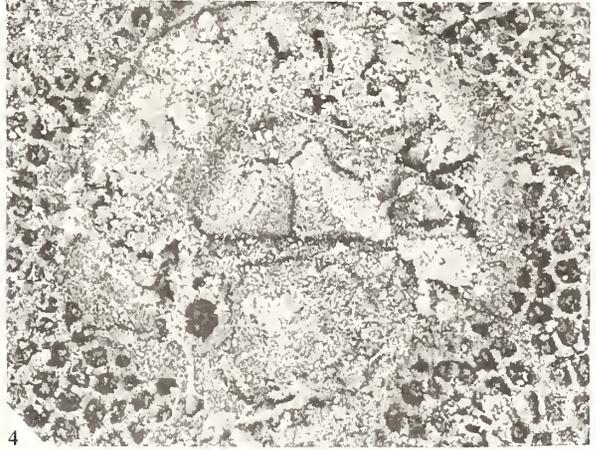
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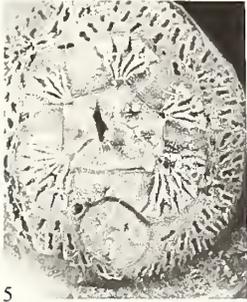
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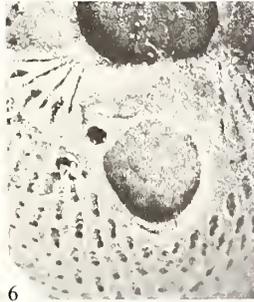
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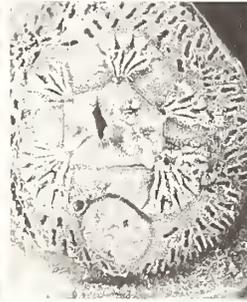
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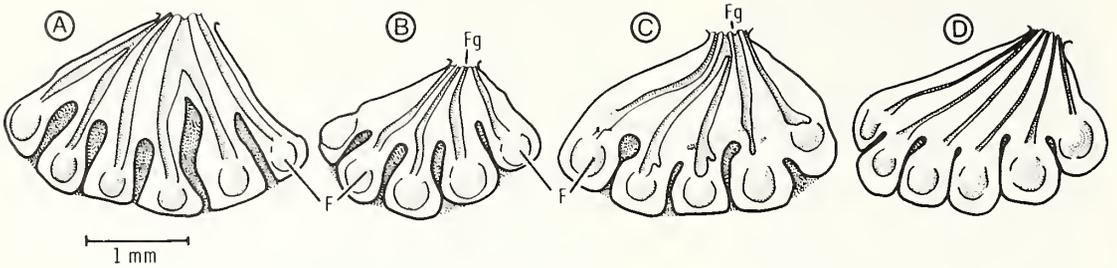


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8





TEXT-FIG. 19. Brachiole facets of *Haplosphaeronis* species. The stratigraphically oldest species to the left, the youngest to the right. A, *H. bratterudensis* n. sp., PMO 89201, holotype. B, *H. cf. kiaeri* Jaekel, PMO 102.757, from Solvang Formation, Gagnum Farm, Hadeland. C, *H. kiaeri* Jaekel, PMO 101.939, from Gagnum Limestone (27–28 m level), Tønnerud, Hadeland. D, *H. multifida* Paul, SM A 74796, original of Paul (1973, pl. 2, fig. 3). The oldest species has angular facets with deep incisions while later species have more rounded brachiole facets with small incisions, if any.

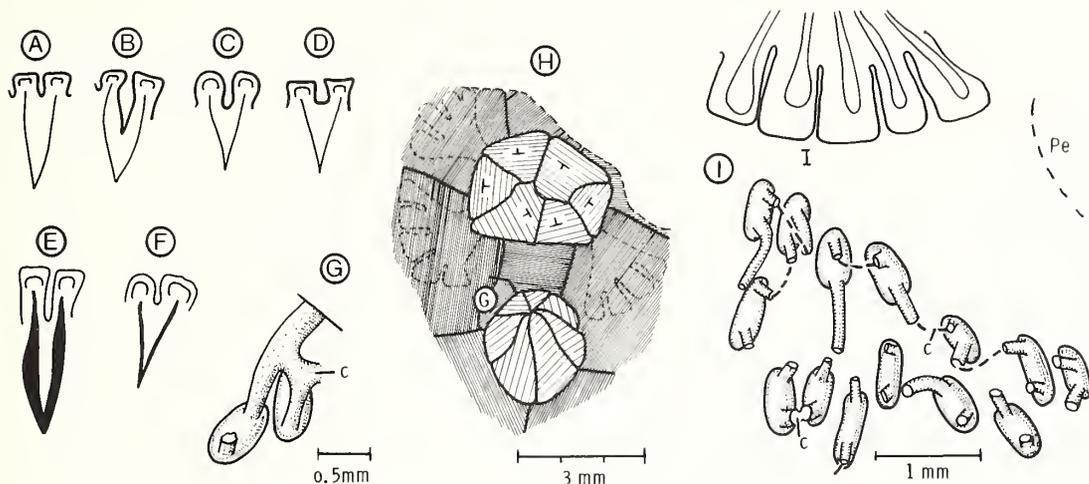
have been observed: ones with rounded edges and ones with square or angular edges (text-fig. 20c, d). The incisions between adjacent facets may be of two types: either deep and broad incisions, leaving fairly large spaces between individual facets, or small and narrow incisions, only just separating the outer edges of individual facets (text-fig. 20A, B). The deep incisions are found mostly amongst the earliest species and the smaller incisions amongst later ones. Both types can occur together in the same individual.

Nerve system: both a basal and an oral nerve ring occur in *Haplosphaeronis*. Paul (1973) also suggested the presence of an oral nerve ring, and nerve canals entering individual brachioles at their facets. Details of this are not known.

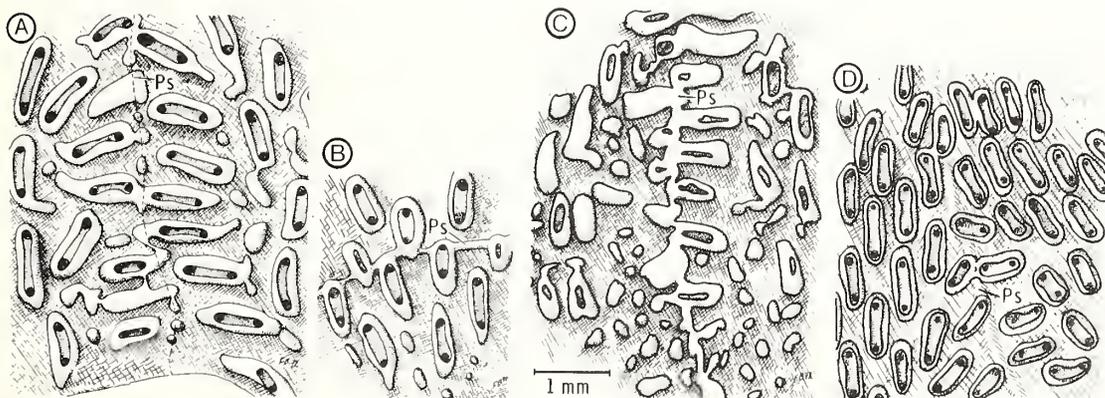
Attachment: all *Haplosphaeronis* species were attached directly by their base. The attachment area is usually concave and adjusted to the shape of objects to which thecae were attached. Specimens of *Haplosphaeronis* have been found attached to other *Haplosphaeronis* individuals, to stick bryozoa, brachiopods, cephalopods, trilobites, and crinoid ossicles. Many specimens show no imprints of the objects to which they were attached, and may thus either have been attached to soft-bodied animals, such as ascideans, or to algae.

Ontogeny and phylogeny. The shapes and sizes of individuals of *Haplosphaeronis* (and other cystoids) depend on the environmental conditions, such as substrate, nutrition, etc. Details of growth pattern can only be obtained through studies of large samples. Individuals from populations at different stratigraphical levels may vary considerably.

Ontogeny: in some populations it is possible to study parts of the ontogeny, but usually the youngest individuals (less than 5 mm) are extremely rare. The major thecal openings (mouth, anus, gonopore, and hydropore) increased in size isometrically during ontogeny. The number of thecal plates remained constant, and thecal size only increased by accretionary growth along the sides of individual plates. The attachment area increased with growth, but no relationship exists between the size of the attachment area and the size of the animal. The most striking ontogenetic change was in the addition of new ambulacral facets. Very young individuals all appear to have had one facet only in each of the five ambulacra (see Bockelie 1978a). New facets were added continuously during growth but, at a stage which might be interpreted as adult, a sudden rapid increase occurred. Whereas the number of brachioles in Norwegian adult *Haplosphaeronis* is relatively large, the total number of Swedish specimens of *H. oblonga* of the same diameter is lower. One explanation is that the brachioles of Swedish species were longer; alternatively, the uptake of food was greater in Swedish than in Norwegian populations. The addition of new diplopores during growth is not clearly understood, but possibly new pores were formed by resorption of the skeletal mesh. Pores were added throughout thecal growth. Pores close to the plate sutures are usually smaller than those towards the plate centre, which may indicate that they grew until a certain size was reached. It seems that the initial growth was more rapid than the later growth. The growth rates of thecae of *Haplosphaeronis* species may be different (text-fig. 24), resulting in different shapes.



TEXT-FIG. 20. Morphological features of *Haplosphaeronis*. A-F, types of brachiole facets and food grooves showing A, small incisions between facets; B, deep incisions between facets; C, rounded fringes of facets; D, angular fringes of facets; E, wide or expanded food grooves; and F, narrow food grooves. G, *H. cf. kiaeri* Jaekel, PMO 89933, from Upper Chasmops Shale, Solheim-Rud, Ringerike; connections of peripores within thecal wall showing two diplopores connected and possible connection to a third diplopore (c). H, *H. cf. kiaeri* Jaekel, PMO 90965, from Upper Chasmops Limestone, 16-17 m below Tretaspis Shale, Raudskjær, Asker; orientation of cleavage planes (?) and direction of dip in weathered specimen (note that direction of dip alternates regularly from one oral plate to the next). I, *H. cf. kiaeri* Jaekel, PMO 105.893, middle part of Upper Chasmops Limestone, Nesbrukrysset, Asker; inside, showing connections of pyritized diplopore canals (c).



TEXT-FIG. 21. Diplopores of *Haplosphaeronis*. A-C, *H. kiaeri* Jaekel from Gagnum Shale (5.5-6.0 m level), Tønnerud, Hadeland. D, *H. proiciens* Regnéll from near Fauquez, Belgium. *H. kiaeri* has irregular diplopores and these are often covered with a calcified periporal roof, whereas this is not so with *H. proiciens*. A, PMO 89924, basal plate. B, PMO 89970, showing boundary between circum-oral plate and basal plate. C, PMO 89920, basal plate with most diplopores covered. D, IRScNB 16c, basal plate showing sutural area. Ps, plate suture.

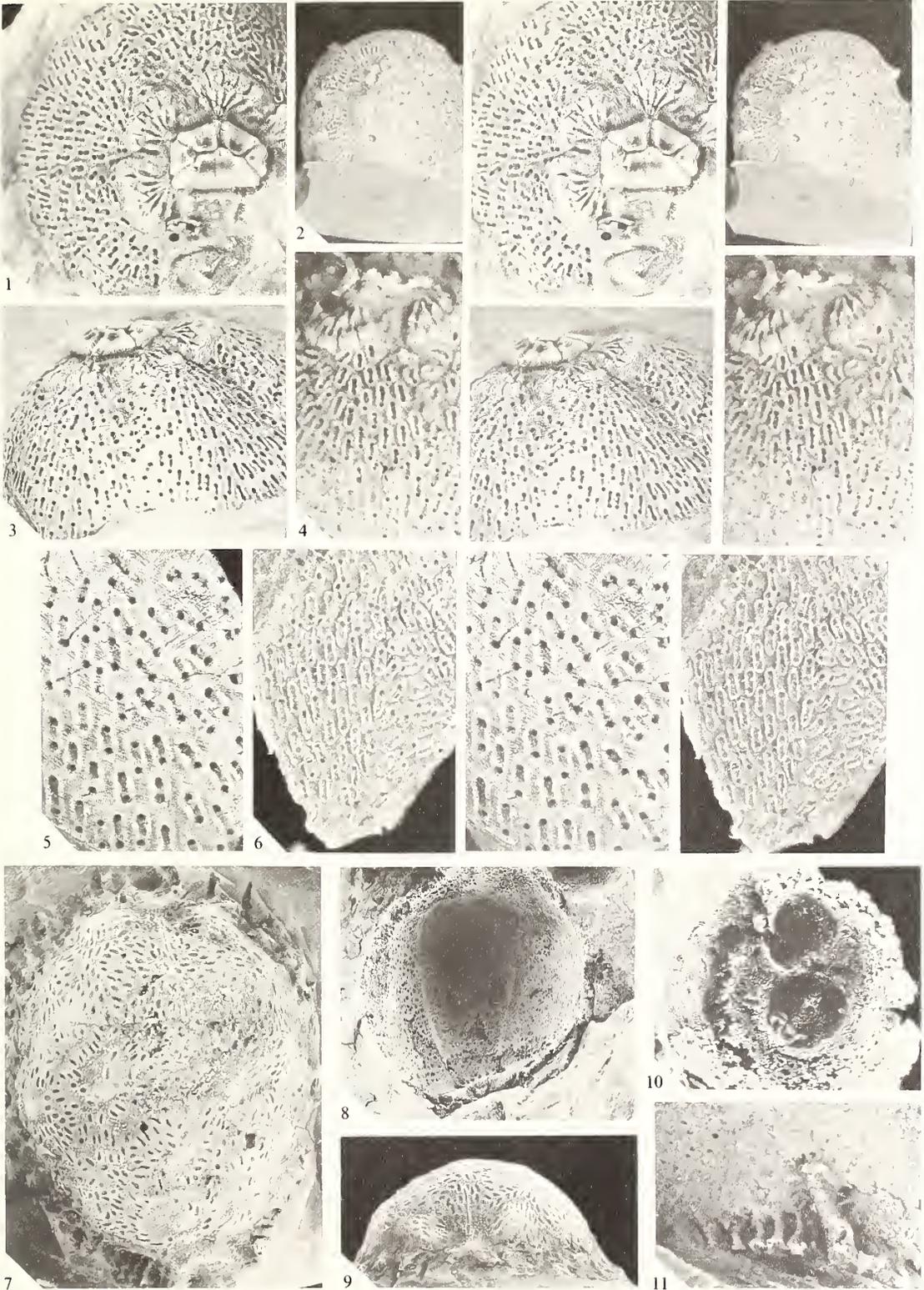
Phylogeny: Norwegian *Haplosphaeronis* ranged from the Caradoc to the lower part of the Ashgill and occurred in several different environments. Species morphology is to some extent a reflection of the environmental conditions under which they lived. When phyletic trends are sought, it should be kept in mind that we do not always see the same type of environment. The pattern of phyletic changes is often very complicated when several environments of the same age are preserved, as is the case with *Haplosphaeronis*.

The number of brachiole facets per ambulacrum is generally larger in Ashgill than in Caradoc populations of individuals with the same thecal diameter. In Norway this is certainly the case. In Sweden this cannot be conclusively stated. In Britain *Haplosphaeronis* occurs in the Ashgill only where the species has numerous brachioles. The shape of brachiole facets changes from the lower Caradoc *H. bratterudensis* to the Ashgill *H. kiaeri*. *H. bratterudensis* always has square facets separated by large spaces, often with deep incisions (text-fig. 19). In *H. kiaeri* the facets are rounded or tongue-shaped and not separated by spaces (text-fig. 19C, D). During the later Caradoc several morphs combined the two types of brachiole facets (text-fig. 19B), clearly showing the direction of evolution. The British *H. multifida* has facets of the same type as the Ashgill species in Norway.

The most striking evolution is seen in the pore structures, which may be good stratigraphical indicators (see above). The oldest species in Norway, *H. bratterudensis*, has faintly developed rims around the diplopores or no rims at all; the peripore floor is sunk well below the thecal surface; the peripore is ovate with a length to width ratio of 3.6. In the late middle Ordovician and the upper Ordovician the diplopore floor migrated outwards to a position above the thecal surface. In the latest populations of *H. kiaeri* from the Oslo Region the aporal portion of the peripore wall developed spines (Pl. 5, fig. 3). Such spines have also been found in the British Ashgill species, but not in the Belgian Ashgill species which is otherwise very similar. The shift of the peripore floor from a deep to an outer position, and the outgrowth of the peripore wall to form spines accompanied by a narrowing of the diplopores in relation to pore length (length to width ratio is 4.5), is clearly part of a continuous evolution (text-fig. 25). Thus the length to width ratio of the diplopores increased from 3.6 to 4.5 during the Ordovician principally by a reduction of pore width. There was also some reduction of pore length (text-fig. 25). This change is accompanied by an increase in number of diplopores in some (but not all) populations of *H. kiaeri*. Narrow diplopores have been seen in the British and Belgian species (Pl. 3, fig. 6). The changes in diplopore shape during the Ordovician may be related to

EXPLANATION OF PLATE 3

- Figs. 1-5. *Haplosphaeronis* cf. *kiaeri* Jaekel. 1, 3, 5, Upper Chasmops Limestone, Raudskjær (8 m below top), Asker; PMO 69421, stereophotos of 1, oral area (note slightly lobate shape of theca, and complex hydropore with slit and circular opening), $\times 4$; 3, circum-oral plates showing diplopores with thickenings and spines on peripore wall, $\times 4$; 5, circum-oral plates and lateral plates showing details of diplopores (note development of spines on peripore walls, irregular diplopores at the plate suture to the right, and the thickness of the walls), $\times 7$. 2, 4, Solvang Formation, Gagnum Farm, Hadeland; PMO 102.759, stereophotos of silicone rubber cast showing 2, oral region, $\times 4$; 4, circum-oral plates with spines on peripore wall, $\times 6$.
- Figs. 6, 11. *Haplosphaeronis proiciens* Regnéll. Ashgill, near Fauquez, Belgium. 6, IRScNB 16c, stereophotos of plates showing development of spines on peripore wall (silicone rubber cast; note the very thin walls in comparison with fig. 5, and diplopores in horizontal position at the plate suture), $\times 6$. 11, IRScNB 199-1, basal portion of theca showing depressions which possibly housed extensions of basal nerve ring (silicone rubber cast), $\times 5$.
- Figs. 7, 9. *Archaeocystis* cf. *granulata* Paul. Sørbakken Limestone, Frognoya, Ringerike. PMO 97106 in 7, lateral view (note radial arrangement of elongate diplopores and granulated surface) and 9, showing oral area (outermost portion of two brachiole facets and a plate suture), $\times 2.5$.
- Figs. 8, 10. *Haplosphaeronis kiaeri* Jaekel. Gagnum Limestone, Tønnerud, Hadeland. 8, PMO 79921 from 14 m level, inside of theca showing plate sutures and depressions along inside of base, possibly a location for basal nerve ring with thickenings, $\times 2$. 10, PMO 91008 from 27-28 m level, showing inside of oral (smallest depression) and anal (largest depression) areas, with a furrow which previously housed the gonoduct leading from the right side towards and between the mouth and anus before entering the body cavity, $\times 3$.



BOCKELIE, *Haplosphaeronis* and *Archaeogocystis*

increased efficiency of respiration. Evolutionary changes in respiratory structures have also been seen in other cystoids.

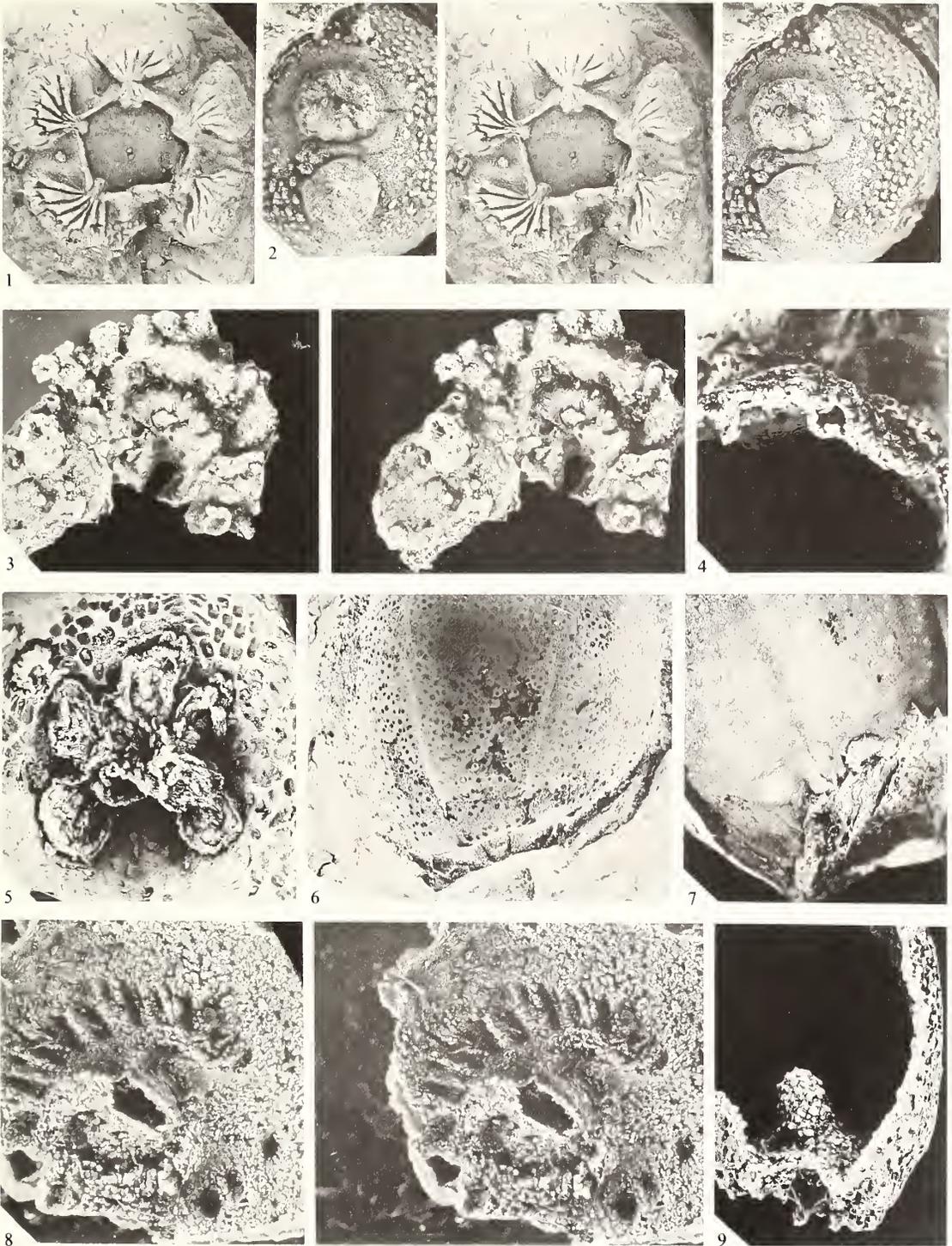
Upper Ordovician *Haplosphaeronis* species from Norway and Britain commonly have calcite-covered diplopores either in their basal portion, on their circum-oral plates, or occasionally all over the theca. Belgian and Swedish upper Ordovician species have not been found with covered pores; neither have they been found in the lower and middle Caradoc populations of *H. bratterudensis* and *H. kiaeri*. Whether covered pores are a response to local environmental conditions, some kind of disease, or a phyletic trend towards some kind of physical protection is not clear. Covered diplopores are relatively common amongst the *Diploporita*.

Palaeoecology. *Haplosphaeronis* seems to have occupied a wide range of ecological niches, and is found in rocks representing environments ranging from shallow, turbulent water to depths just below the wave base. They are distributed mostly in areas of regular sedimentation rates and dominate certain environments in the western part of the Oslo Region. In Sweden *Haplosphaeronis* species are common on the flanks of most carbonate mounds ('reefs') of middle and upper Ordovician age (Kullberg Limestone and Boda Limestone). British species were adapted to environments with more clastic sediments and are found in silts or shales with small amounts of carbonate (Paul 1973, p. 29). The shape of the attachment area is probably related to environmental position. The shallow water Swedish species were often attached to a firm substrate or large crinoid ossicles; the Norwegian species may have been attached mostly to small objects and needed to grow rapidly upwards to compensate for rapid sedimentation, giving *H. kiaeri* a characteristic mitre shape. The Swedish species in contrast, living in areas of low sedimentation rates, have a flat base.

Remarks. The holotype of the Swedish *H. oblonga* (RM Ec96) derives from the upper Ordovician Boda Limestone, and not from the middle Ordovician as previously stated by various authors. Regnéll (1945, p. 171) made all the species of *Haplosphaeronis* erected by Angelin synonyms of *H. oblonga*. *H. oblonga* thus comprises all Swedish *Haplosphaeronis* species and ranges from the lower Caradoc (Dalby Limestone) to the middle-upper Ashgill (parts of the Boda Limestone). It is rare to find species with such a long range. However, Angelin's species are all strongly corroded and his distinctions were mostly based upon differences in size. In view of the evolutionary changes found amongst Norwegian species, it seems justified to expect similar changes to have taken place in Swedish populations. Thecal shape shows great variation and may be more related to ecological factors than to anything else. The number of facets was ontogenetically controlled, at least in part (Bockelie 1978a). The shape and distribution of the diplopores currently seem to have most taxonomic value.

EXPLANATION OF PLATE 4

Figs. 1–9. *Haplosphaeronis kiaeri* Jaekel. Tønnerud, Hadeland. 1, PMO 101.939, stereophoto of oral area showing peristome with ambulacral platform entering mouth, $\times 5$. 2, PMO 89996, stereophoto of steinkern showing peristome, periproct, and traces of gonoduct (note lack of diplopores in oral and anal area; gonoduct goes down through the plate, is embedded horizontally in the plate between peristome and periproct, and bends towards radius IV before entering the thecal interior), $\times 5$. 3, PMO 101.954, stereophoto of silicified specimen in oral view (just below peristome looking down oesophagus) showing one oral lobe and parts of two more; upper part of gonoduct at left (cf. text-fig. 23A), $\times 6$. 4, PMO 90976, sagittal view of silicified specimen showing cavities within circum-oral plates below ambulacral facet (cf. text-fig. 23B), $\times 4$. 5, PMO 91007, inside view showing circum-oral lobes and parts of oesophagus(?), $\times 4$. 6, PMO 79921, basal portion of pyritized specimen showing large primary depressions at plate sutures around basal ring, and several minor depressions, $\times 3$. 7, PMO 79885, steinkern showing depressions (as lobes), $\times 4$. 8, PMO 101.953, stereophoto of silicified basal portion of theca possessing hollow internal spine, surrounded by outer wall and several local depressions (see also text-fig. 22A, D), $\times 6$. 9, PMO 91004, coarsely silicified specimen showing internal spine (cf. text-fig. 22B, C), $\times 4$. 1, 3–5, 8, 9, 27–28 m level and 7, 18–20 m below Solvang Formation in Gagnum Limestone; 2, 5.5–6.0 m level and 6, 14 m level in Gagnum Shale.



BOCKELIE, *Haplosphaeronis*

Sphaeronites shihtienensis Reed, of which no specimens were available for study, was referred with some hesitation to *Haplosphaeronis* by Regnéll (1945, pp. 170, 171). This species, however, differs from both *Sphaeronites* and *Haplosphaeronis* and in my opinion does not belong to the Sphaeronitidae, but to the Aristocystitidae.

Regional distribution and stratigraphical range. Oslo Region (middle–upper Ordovician), Sweden (middle–upper Ordovician; Regnéll 1945, p. 171), southern Estonia (middle Ordovician; Männil 1966, pp. 41, 43, 45), Ingermanland (middle Ordovician; Hecker 1964, pl. 4), Wales (upper Ordovician; Paul 1973, p. 3), Belgium (upper Ordovician; Regnéll 1951, p. 31), and Burma (Ordovician; Reed 1917, p. 12).

Haplosphaeronis kiaeri Jaekel, 1926

Plate 3, figs. 8, 10; Plate 4, figs. 1–9; Plate 5, figs. 1–4; text-figs. 18B, 19C, 21A–C, 22, 23

1926 *Haplosphaeronis kiaeri* Jaekel, p. 20, pl. 1, figs. 1–7.

1926 *Haplosphaeronis kiaeri* Jaekel; Kiaer, p. 8.

1945 *Haplosphaeronis kiaeri* Jaekel; Regnéll, pp. 171–174.

1945 *Haplosphaeronis kiaeri* Jaekel; Størmer, p. 381.

1953 *Haplosphaeronis kiaeri* Jaekel; Størmer, pp. 68, 87, 94.

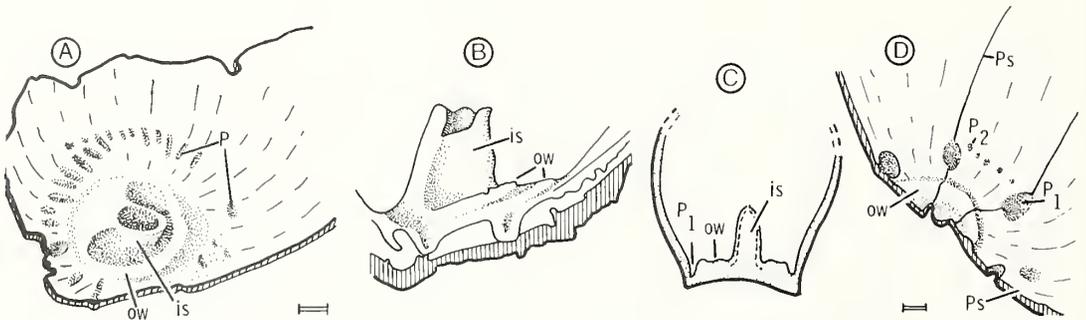
Diagnosis. A species of *Haplosphaeronis* with peripores elevated above the thecal surface or level with it, their periporal walls often developed as high ridges in the adoral portion. Diplopores often coalescent, usually irregular or oval, occasionally dumb-bell shaped, most numerous in circum-oral plates, but strongly reduced in size and number in the basals where they are covered by a calcified diplopore roof. Tubercles may be present over most of the thecal surface and are most numerous in the basal circum-oral areas.

Holotype. Unnumbered specimen in the PMO collections; pl. 1, figs. 1, 2 of Jaekel (1926). It has not been in the PMO collections for at least twenty-five years and is probably lost. Topotype material exists in the PMO collections.

Type horizon and locality. Gagnum Shale Formation (= Sphaeronid Shale), lower Ashgill; Tønnerudodden, Hadeland, Oslo Region, Norway.

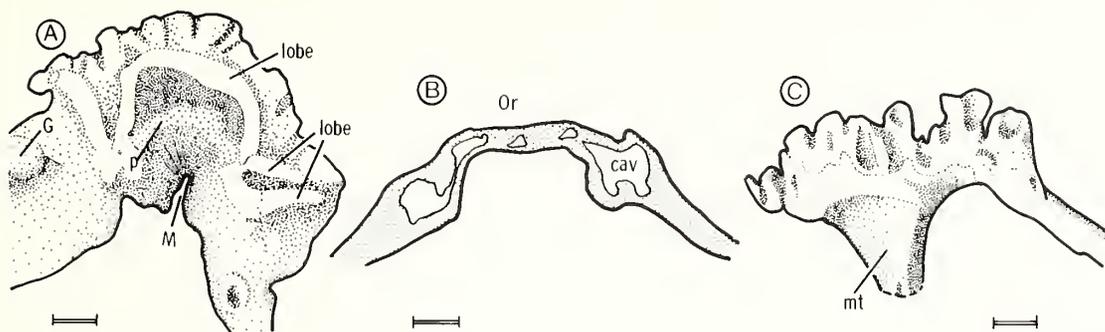
Material. Several hundred specimens.

Description. Theca: taller than broad, seldom exceeding 15 mm in height and 10 mm in diameter. The base is variable in shape and size.



TEXT-FIG. 22. Internal features of *Haplosphaeronis kiaeri* Jaekel. A, B, PMO 101.953, from Gagnum Limestone (27–28 m level), Tønnerud, Hadeland; silicified specimen showing internal spine (is), a basal wall structure (ow), and basal pits (P) in A, oblique view and B, lateral view. C, reconstruction in sagittal view showing hollow internal spine (is), wall structure (ow), and primary basal pits (P_1). D, PMO 79921, Gagnum Limestone (14 m level), Tønnerud, Hadeland; oblique view of basal portion of pyritized theca showing basal wall (ow), plate sutures (Ps), and primary (P_1) and secondary (P_2) pits (note that primary pits are located at the plate sutures).

Scale bar, 1 mm.



TEXT-FIG. 23. Internal features (oral region) of *Haplosphaeronis kiaeri* Jaekel from Gagnum Limestone (27–28 m level), Tønnerud, Hadeland; silicified specimens. A, PMO 101.954, oblique view from oral area showing lobate circum-oral ring structure with steep sides down to the platform (p), and the slope down into the mouth tract (G, gonopore); this silicified portion is just below the calcite skeleton of the oral area. B, PMO 90976, lateral view showing silicified theca with a circum-oral cavity within the skeleton, and the oral plates (or). C, PMO 101.954, lateral view of A showing irregular upper portion of the mouth tract (mt). Scale bar, 1 mm.

Plates: all except CO6 and CO7 are pierced by numerous diplopores. An ornament frequently occurs between the diplopores of the basal plates and is characteristic of some populations. This surface ornament is usually reminiscent of calcified diplopores.

Diplopores: small; many coalesce or have irregular extensions (text-fig. 21). The peripores are oval, averaging 0.49×0.11 mm (text-fig. 25). The periporal floor is usually elevated above the thecal surface. Various populations have the aporal portions of the periporal rims developed with thickenings of the wall (Pl. 5, fig. 3). No specimens have been found within the type stratum with more than twenty facets. The small size of the animals may indicate a stunted population. There are pronounced thickenings of the sides of the food grooves, as seen also in the British species *H. multifida* Paul. Facets usually have a rounded outline but more irregular shapes occur; they are 0.28–0.32 mm in diameter and have a slightly raised circular central process (text-fig. 19C).

Periproct: size related to animal size; 4.2×3.6 mm in PMO 89972. Plates of the anal pyramid occasionally bear small tubercles near the summit.

Gonopore: small circular pore, 1.3 mm in diameter in PMO 89972, almost in contact with the first facet in radius I.

Hydropore: a slit of variable length. In PMO 89972 it is zigzag shaped and very irregular.

Attachment: direct, by an aboral attachment area, usually one-third to one-half the ambital diameter.

Remarks. Jaekel (1926) distinguished two subspecies by size, *H. k. kiaeri* and *H. k. norvegica* (the latter not figured). *H. k. kiaeri* came from the Gagnum Shale Formation (= Sphaerionid Shale) and *H. k. norvegica* from the overlying Gagnum Limestone Formation (= Sphaerionid Limestone). The morphology of the pore system shows a rather complex relationship between *H. bratterudensis* n. sp. and *H. kiaeri*. It is difficult to decide at present whether or not a subspecific determination can be made, due to the observed continuous morphological series. Jaekel's concept of *H. k. norvegica* is not clear nor did he state from which part of the limestone his material was derived. Differences in size of *Haplosphaeronis* in these populations are due to various ecological features. They may reflect differences in sedimentation rates which killed off certain populations at different growth stages. Other populations could have been stunted by low rates of nutrition.

H. kiaeri differs from *H. bratterudensis* n. sp. in that the latter has wider peripores and a peripore floor sunk below the thecal surface. *H. kiaeri* differs from the Belgian *H. proiciens* by the latter's lack of ornament and irregularities in the peripore wall. *H. kiaeri* differs from *H. multifida* by the lack of elevation of the oral area (in this respect *H. multifida* resembles *H. proiciens*). *H. multifida* has larger diplopores than *H. kiaeri* (length 0.64 versus 0.49 mm; width 0.21 versus 0.11 mm). *H. kiaeri* differs from *H. oblonga* in general shape, the latter always having a broad flat base and relatively few brachioles in relation to thecal size. However, the Swedish species also lacks ornament on the basal

plates as well as the irregularities of the periproctal rims seen in *H. kiaeri*. *H. oblonga* is difficult to define; specimens from 10 to 12 m below the main bentonite band of the Dalby Limestone up to the Boda Limestone itself have all been referred to *H. oblonga*, giving that species a vertical range which includes most of the middle and all the upper Ordovician. This is most unlikely and several species may be involved. Differences in size of specimens occurring in off-reef and reef facies have also been observed in Dalecarlica, the reef forms being larger. *H. kiaeri* resembles the British *H. sparsipora* more than any other species, but the latter has very wide peripores (0.26 versus 0.11 mm). The peripore length of *H. sparsipora* is 0.54 mm and falls just within the range of variation in *H. kiaeri*.

Numerous populations of *Haplosphaeronis* occur in the middle Ordovician of the Oslo Region, mostly in the upper Caradoc of Oslo-Asker (Upper Chasmops Limestone), Skien-Langesund area (Encrinite Limestone), Ringerike (Solvang Formation), and Hadeland (Solvang Formation). These all differ from typical *H. kiaeri* in being transitional between the early Caradoc species *H. bratterudensis* and the Ashgill species *H. kiaeri* (Pl. 3, fig. 3). However, this transition is so complex that at present I prefer to place these upper Caradoc populations in *H. cf. kiaeri* since they show closer affinities to *H. kiaeri* than to *H. bratterudensis*. They usually have peripore rims, rounded brachiole facets, and peripores more like those of *H. kiaeri* than *H. bratterudensis* (text-figs. 19B, 25). See text-figs. 4, 9 for range and geographic distributions.

Haplosphaeronis bratterudensis n. sp.

Plate 2, figs. 5-8; text-figs. 18C, D, 19A

1953 *Haplosphaeronis* cf. *kiaeri* Jaekel; Størmer, p. 84.

Diagnosis. A species of *Haplosphaeronis* with submerged diplopores, equally numerous all over the theca but missing on CO6 and CO7. Diplopores wide, usually lacking periporal wall, peripore below thecal surface. No tubercles and no calcified diplopore roofs.

Holotype. PMO 89201, preserved as an external mould (text-fig. 18C, D; Pl. 2, fig. 5).

Type horizon and locality. Lower Chasmops Shale containing *Neosaphus ludibundus* (*multidens* Zone); shore at Bratterud, Ringerike, Oslo Region.

Material. In addition to the holotype some twenty specimens are referred to this species from Ringerike and Asker.

Description. Theca: spherical, with a flat or concave base. The sides are gently curved. In most specimens the height of the theca is about equal to its width.

Plates: the plate surface between the diplopores is relatively smooth.

Diplopores: relatively large, usually parallel-sided or slightly elliptical, averaging 0.65 × 0.18 mm (text-fig. 25), and submerged below the plate surface. The periporal wall is low or not developed. The peripore width (pw_1) is significantly larger than in *H. kiaeri* (text-fig. 25; Pl. 2, figs. 7, 8), whereas the length does not differ to the same extent. In the basal area about five pores per mm² are present, whereas the number is five or six in the circum-oral plates.

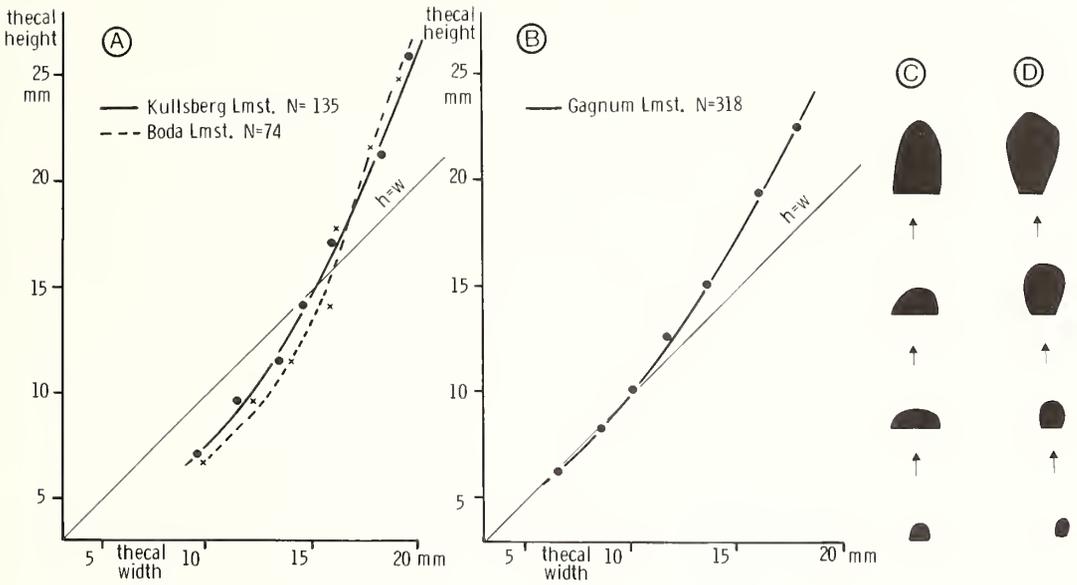
Peristome: the mouth is oval, the adanal side being almost straight in PMO 89202 (Pl. 2, fig. 6). The highest number of brachiole facets totals twenty-three. Most of the ambulacral furrows end in angular facets with deep incisions between them (text-fig. 19A). Commonly the first formed facets (see Bockelie 1978a, fig. 1) have rounded fringes, and later ones have more angular fringes (text-fig. 19A; Pl. 2, fig. 6). Individual facets are approximately 0.5 mm in diameter and are not as rounded as in *H. kiaeri*.

Periproct: adoro-lateral, oval to pyriform, and covered by an anal pyramid of five or six plates. The periproct lies about 1 mm below the oral margin. The anal pyramid is high, adorally inclined, and reaches almost to the level of the top of the palate (text-fig. 18D).

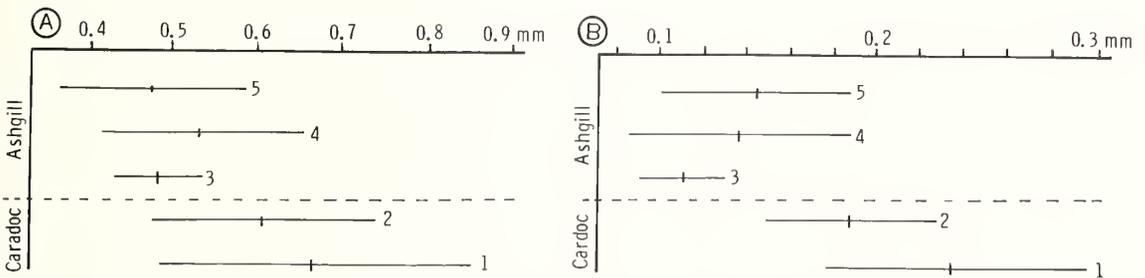
Gonopore: a relatively small circular pore, 1.5 mm in diameter, almost in contact with the first facet in radius I in the holotype.

Hydropore: a straight slit of variable length, adorally of the gonopore.

Attachment: direct, by an aboral attachment area, usually concave and about one-third to two-thirds the ambital diameter.



TEXT-FIG. 24. Thecal growth of *Haplosphaeronis oblonga* (Angelin) (A, C), and *H. kiaeri* Jaekel (B, D). All Swedish populations first produced a large basal surface ($h < w$), before attaining height. The points at which the growth gradients change may indicate the onset of maturity (see Bockelie 1978a). *H. kiaeri* has an equal growth rate both in height and width in young stages. Maturity in this particular population was reached at a thecal diameter of 10 mm after which the growth rate of thecal height increased ($h > w$). N, number of specimens in populations studied. Data arranged in size classes. C, D, ontogenetic changes in shape of the two species.



TEXT-FIG. 25. Peripore length (A) and width (B) of *Haplosphaeronis* species. A trend towards a decrease both in peripore length and width during the Ordovician is evident. 1, *H. bratterudensis* n. sp. (101 measurements); 2, *H. cf. kiaeri* Jaekel, Upper Chasmops Limestone (17–18 m level), Raudskjær, Asker (49 measurements); 3, *H. kiaeri* Jaekel, Gagnum Shale (5.5–6.0 m level), Tønnerud, Hadeland (120 measurements); 4, *H. kiaeri* Jaekel, Gagnum Limestone (21–22 m level), Tønnerud, Hadeland (88 measurements); 5, *H. kiaeri* Jaekel, Gagnum Limestone (27–28 m level), Tønnerud, Hadeland (80 measurements).

Remarks. *H. bratterudensis* differs from other *Haplosphaeronis* species (except some of the specimens referred to *H. oblonga* (Angelin) by Regnéll 1945) by the submerged position of the diplopores, and by the diplopores being almost as numerous in the basal portion as in the circum-oral plates. Some specimens from below the Kullberg Limestone of Sweden (figured by Paul 1972, pl. 6, fig. 1) are tentatively referred to *H. oblonga*. They are contemporary with the Norwegian *H. bratterudensis* and show similar structures. It is uncertain if these Swedish specimens should be referred to *H. bratterudensis*.

Genus *Eucystis* Angelin, 1878

Synonymy. *Proteocystites* Barrande, 1887; *Carpocystites* Oehlert, 1887; *Proteocystites* Bather, 1899; *Bulbocystis* Růžička, 1939.

Type species. *Eucystis raripunctata* Angelin, 1878, p. 31, from the Boda Limestone (Ashgill) of Osmundsberget, Dalarna, Sweden.

Diagnosis. A genus of Sphaeronitidae with pentagonal peristome; five ambulacra each with one or several food grooves terminating in ambulacral facets on circum-oral plates or somewhere on the thecal surface. Thecal plates arranged in three or more series and numbering twenty to fifty in total.

Remarks. As pointed out by Le Maître (1958, p. 304) and Prokop (1964, p. 30) a close relationship exists between *Eucystis* and *Bulbocystis*. *Bulbocystis* differs essentially in having a more regular arrangement of ambulacra (Kesling 1967, p. S242). I accept Le Maître's view and suggest a synonymy. Reed (1917, pl. 3, fig. 3, 3a) referred a specimen from Yunnan to *Eucystis* cf. *raripunctata*; the peristome is quadrilateral and each ambulacrum bears only one facet. To which genus Reed's species should be referred is uncertain. Paul (1973, p. 40) pointed out that several species of the rather variable *Eucystis* have stem-like projections formed by the basal plates, but no true stems are present. The Norwegian *Eucystis* species has a broad flat base.

Description. Theca: the shape and size of thecae of *Eucystis* species varies considerably. The largest species known is *E. barrandena* (Haeckel) which reaches 50 mm in height. Some species have a broad flat base, whereas others have stem-like projections of the basal plates; this may vary even within species.

Peristome: always pentagonal; those having a quadrilateral peristome which were formerly referred to *Eucystis* are now referred to a new genus, *Tetreucystis* n. gen.

Ambulacral system: five ambulacra are present, each with one or more facets at the end of short or long ambulacral furrows. New ambulacral furrows are added throughout life, in a manner typical of the family Sphaeronitidae (Bockelie 1978a); thus the total number of facets may not be a good taxonomic character. However, the distribution of ambulacral furrows in adults may at times be reliable at species level: one short furrow from each of the oral corners in *E. pentax* Paul, 1973; most facets present on the circum-oral plates in *E. angelini* Regnéll, 1945; and several facets below the circum-oral plates in *E. raripunctata* Angelin, 1878.

Periproct: the rounded, polygonal periproct is close to the mouth. It has ledges for insertion of plates; the aboral portion could open more than the adoral portion (text-fig. 26B, C). Neither oral nor anal plates have been found, and were probably very thin or more loosely joined to their relative openings.

Gonopore and hydropore: a circular gonopore and a slit-like hydropore are always present in positions typical for the Sphaeronitidae, the former across the suture CO7:CO1, and the latter across the suture CO6:CO1.

Plates: the plate arrangement varies in *Eucystis*: most species have only three plate series but *E. flava* has five or more. Only one generation of plates seems to be present. Details of the shapes of plate sutures within a species reveal considerable variation on one theme (text-fig. 26D-G). Such variations are more common in certain populations.

Diplopores: all plates are pierced by generalized diplopores with oval peripores but, as with other genera of the Sphaeronitidae, their width is less variable than their length and thus seems to be an important character for species discrimination. Covered diplopores have been found in individuals of some species.

Attachment: *Eucystis* was attached directly by an attachment area which differs in size from species to species. Some of the Swedish species have a small attachment area. No traces of an internal spine have been found.

Palaeoecology. *Eucystis* species from Norway occur in siltstones, presumably representing shallow water environments. They occurred, however, at greater depths than those containing rugose corals and seem to appear in environments of unstable sedimentation below wave base. The closely related

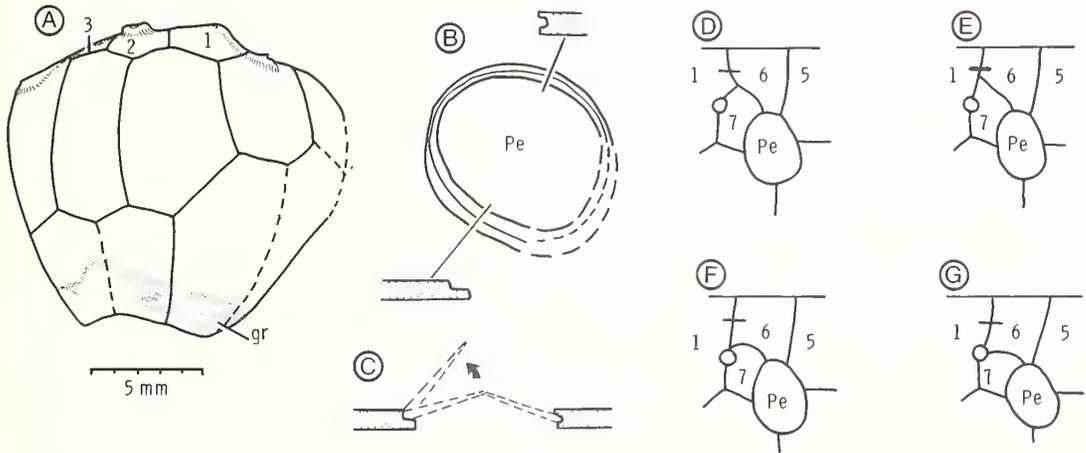
Tetrecystis n. gen. is rare in Britain (one species) and in Sweden (one species) but is not uncommon in Norway (three or four species). Ecological factors may have played some part in the distributional pattern of these genera. According to Paul (1973, p. 41) the number of ambulacral facets may exceed five in each of the British species where the total number is known. In the Swedish *E. angelini* the number of facets is fifteen to twenty, in *E. raripunctata* twelve to fifteen, and in the only Norwegian species five to seven. This may also reflect ecological conditions. The Swedish species may derive from more shallow water than both the Norwegian and British forms. Whereas a trend in the number of facets, as outlined above, can be observed in *Eucystis* species, the reverse trend occurs in *Haplosphaeronis* which lived in the same environments and which usually occur in the same beds as *Eucystis*. British *Haplosphaeronis* generally have more facets than Norwegian species, which in turn have more than Swedish species. As discussed elsewhere (Bockelie 1978a), ambulacral furrows and facets are added ontogenetically, probably to increase food-gathering capacity. It is possible that this increase also manifests itself phylogenetically; Devonian *Eucystis* species often have numerous and very long food grooves (Prokop 1964).

Regional distribution and stratigraphic range. Ashgill (upper Ordovician) of Sweden, Norway, Britain, Ireland, Bohemia, and ?Germany (*E. hercynica* Jaekel), Spain (Chauvel and Le Menn 1979); Devonian of Bohemia, France, Morocco, Algeria, and Central Sahara; so far totally unknown in the Silurian.

Eucystis langoeiensis n. sp.

Plate 5, figs. 5-8; text-figs. 26A, 27C, 32B

Diagnosis. A species of *Eucystis* with plates in three fairly regular circlets; in the lateral and basal plates the height exceeds the breadth ($x > y$); plates of the lateral series hexagonal. Circum-oral plates somewhat irregular in shape, but together forming a subcircular area. Diplopores not numerous; more common in the lateral than in the circum-oral plates; sparse or absent in the basal series. Five to seven ambulacral furrows and always one short furrow in radius II. Diplopores short (0.2 mm long) with faint periporal rim.



TEXT-FIG. 26. A, *Eucystis langoeiensis* n. sp., PMO 90947, holotype in lateral view showing plate configurations, some circum-oral plates (1, 2, 3), and irregular growth lines (gr) on basal plates, probably indicating that the specimen rested on the sea bottom during life. B, C, schematic view of periproctal opening (Pe) with a lower ledge, and an upper furrow for the insertion of periproctal cover plates; plates of the lower half were mobile whereas those of the upper half were not; this configuration is typical of *Haplosphaeronis* and *Eucystis*. D-G, *Eucystis angelini* Regn ll, from Sk lberget, Dalarna, Sweden; variations in the arrangement of circum-oral plates. CO6 always thins towards the periproct forming a pointed end; periproct surrounded by five plates. D, 56% of population; E, 11% of population; F, 22% of population; G, 11% of population.

Derivation of names. From Langøya, the type area.

Holotype. An almost complete specimen, PMO 90947 (Pl. 5, figs. 5, 8), from Langøya, Oslo, preserved as an external mould.

Horizon and localities. Top of Husbergøya Shale Formation (= uppermost part of Stage 5a), upper Ashgill, northern Langøya, south-western Rambergøy, western Gressholmen, and Husbergøya, Bunnefjorden, Oslo.

Material. Fourteen specimens in addition to the holotype.

Description. Theca: mostly globular with a height/width ratio close to one. Thecal diameter usually 12–15 mm. The base is broad, usually one-third to two-thirds the ambital diameter, and slightly concave.

Plates: three circlets of plates are present. The circum-oral plates are longer than wide. The CO6 : CO7 suture meets the CO1 : CO7 suture at the gonopore (seen in the holotype only). The hexagonal plates of the lateral and basal series are elongate. The lateral plate circlet contains nine plates, the basal circlet seven, and the circum-oral circlet always consists of seven plates. Fine 'growth' lines are present in the lowermost 2 mm of the basal plates of the holotype. These lines may indicate that the specimen lived with its base in the sediment (text-fig. 26A).

Diplopores: may be present on all plates, but are often sparse or absent in the basals. In CO1 to CO5, seven to ten diplopores were observed in each plate, but only two in CO6 and CO7. In the laterals there are usually two to three diplopores (five pores) per mm². On one plate (5 × 6 mm) twenty pores were counted. In the lateral series, diplopores are more numerous in the adoral than in the aboral part of the plates, and the long axes are more or less perpendicular to the plate margins, thus giving a radial arrangement. In PMO 92986 diplopores in the basal and lateral series are covered by a calcified diplopore roof. Peripore length: 0.42 ± 0.13 mm; peripore breadth: 0.21 ± 0.04 mm; length to breadth ratio: 0.09 ± 0.03 (mean ± 1 standard deviation, based upon forty-four measurements).

Peristome: measures 3.2 × 2.9 mm in the holotype; food grooves extend below the circum-oral plates. In radii II, III, and V one ambulacral side-branch occurs, whereas in radii I and IV there are two such branches. Two specimens, PMO 90877 and PMO 97139, each have five or six short ambulacral grooves and differ only slightly from other specimens of this species (Pl. 5, fig. 7).

Periproct: somewhat deformed in the holotype, but its original shape was probably subcircular, as can be seen from PMO 90872 where its diameter is about 3.6 mm.

Gonopore: at the upper left side of the anus with a diameter of approximately 1.5 mm.

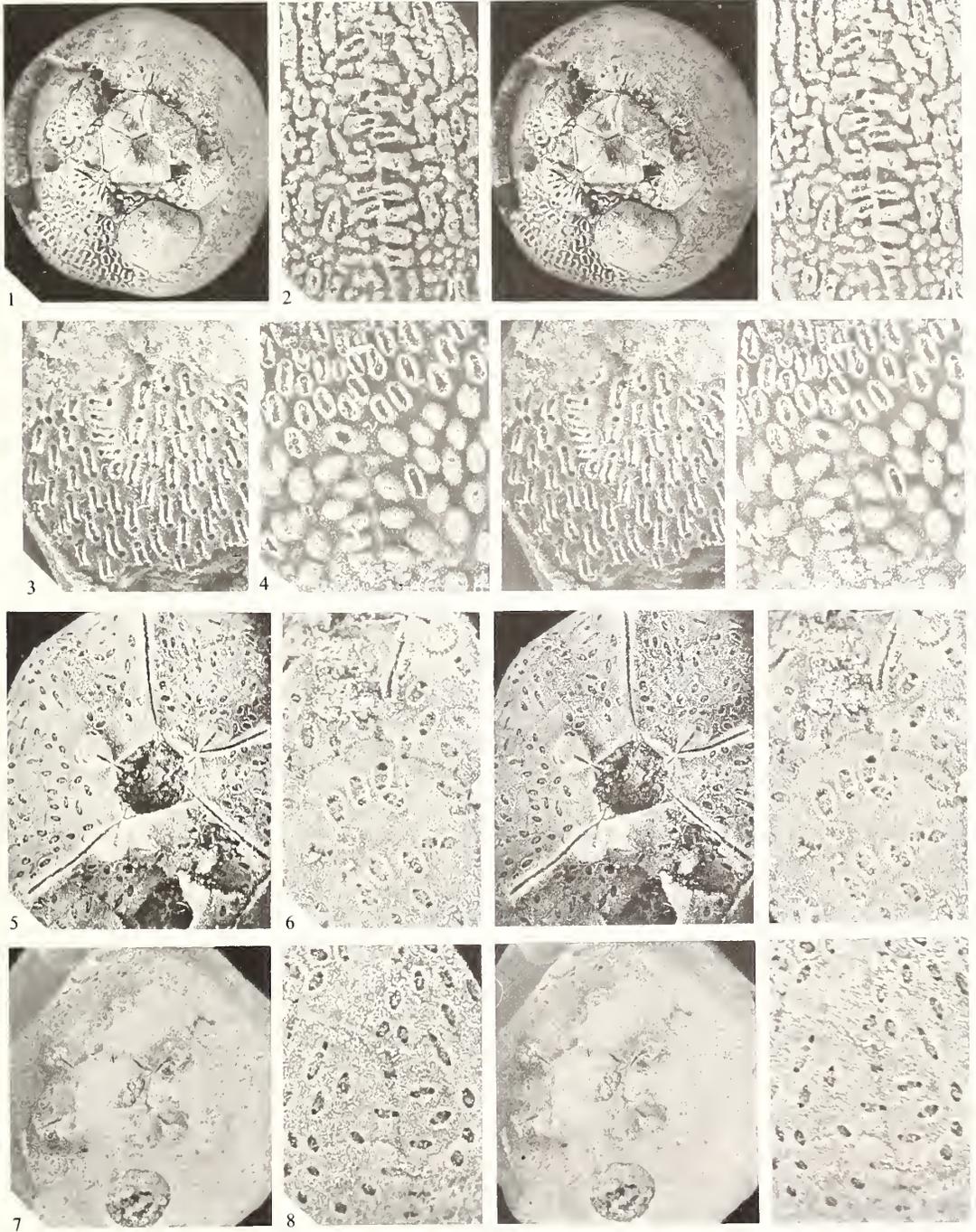
Hydropore: on a small ridge between the mouth and the anus, about 0.6 mm from the oral margin. The hydropore is bisected by the suture CO1 : CO6.

Remarks. *E. langøeyensis* differs from the British species in usually having more than one facet in each ambulacrum, and from the Swedish species in having fewer facets. It also differs from the other species by the shape of the circum-oral plates. It can be distinguished from the Devonian species of Bohemia by differences in facet distribution and surface ornament. Three species of *Eucystis* have been described from Sweden, i.e. *E. raripunctata*, *E. angelini*, and *E. acuminata*. A large number of specimens from the Riksmuseum, Stockholm, has been studied, resulting in some additional

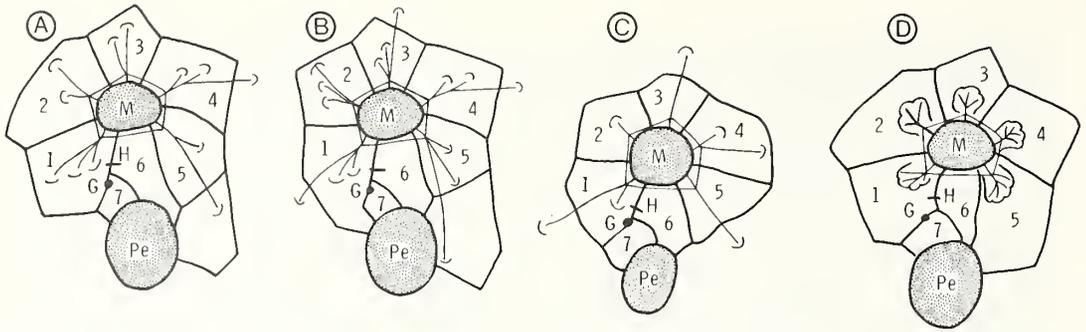
EXPLANATION OF PLATE 5

Figs. 1–4. *Haplosphaeronis kiaeri* Jaekel. Tonnerudodden, Hadeland. 1, PMO 79913, Gagnum Shale, × 4. 2, PMO 89920, cast showing details of pores on basal plate and suture (note that many pores are covered), Gagnum Shale, × 7. 3, PMO 90905, cast showing details of pores with development of spines on peripore wall in circum-oral plate, 21–27 m level, Gagnum Limestone, × 6. 4, PMO 90985, cast showing basal plate with covered pores in lower portion, open pores above and some pores partially covered, 31–32 m level, Gagnum Limestone, × 6.

Figs. 5–8. *Eucystis langøeyensis* n. sp. Upper part of Husbergøya Shale (Ashgill); 5, 6, 8, island off north-west Langøya, Oslo; 7, Gressholmen, Oslo. 5, PMO 90947, cast of holotype showing the continuation of food grooves into peristome border. (The number and position of ambulacral facets are characteristic of species), × 4. 6, PMO 90871, cast showing details of diplopores (note the large pores and peripore rims, and also the presence of some sutural pores), × 6. 7, PMO 97139, cast of young specimen with short ambulacra, × 3. 8, PMO 90947, cast of holotype showing details of diplopores at plate suture (note the faintly developed rim and some elongated peripores), × 6.



BOCKELIE, *Haplophaeris* and *Eucystis*



TEXT-FIG. 27. Plate configuration of *Eucystis* species. A, B, two varieties of *E. raripunctata* Angelin showing differences in CO1 near periproct and differences in number and extent of ambulacral furrows (A, RM Ec 2376; B, RM Ec 2370, holotype). C, *E. langoyensis* n. sp., PMO 90947, holotype showing the relatively small number of facets in this species. D, *E. angelini* Regnéll with all facets close to the mouth (compiled from RM Ec 2056 and RM Ec 1938).

information concerning the plates of *E. raripunctata* and *E. angelini*, including a new diagram for plate configuration of *E. raripunctata* (text-fig. 27A, B) to replace that of Regnéll (1945, fig. 22.4). The holotype of *E. raripunctata* is somewhat abnormal in that CO1 is in contact with the anus (text-fig. 27B), and the ambulacral grooves of radius V are extremely long, reaching more than half-way down the side of the periproct. In all specimens of *E. raripunctata* studied, CO5 is never in contact with the anus, whereas this is the case with *E. angelini* (text-fig. 27D).

Genus *Tetreucystis* n. gen.

Synonymy. *Eucystis* (*partim*) auctores.

Type species. *Tetreucystis kalvoeyensis* n. gen., n. sp. from the Tretaspis Limestone (= Stage 4c β), lower Ashgill, Kalvoya, Oslo Region, Norway.

Diagnosis. A genus of Sphaeronitidae with quadrilateral peristome. Four branching ambulacra, one from each corner of the mouth. Theca composed of a limited number of polygonal plates in three or more series and numbering twenty to fifty.

Remarks. There is a distinct difference in the shape of the peristome of *Eucystis* and *Tetreucystis* n. gen. which I consider justifies the erection of the new genus for species possessing a quadrangular mouth. *Tetreucystis* n. gen. has a quadrilateral peristome like *Diplosphaeronis* Paul, but differs from the latter by having the periproct widely separated from the peristome, with more than three plates between the two orifices. At present five species can be assigned to *Tetreucystis* n. gen.; these include *T. munita* (Forbes, 1848), *T. quadrangularis* (Regnéll, 1945), *T. elongata* n. sp., *T. kalvoeyensis* n. sp., and *T. monobrachiolata* n. sp.

Description. *Tetreucystis* agrees in most respects with *Eucystis*, except in the shape of the oral area and that the ambulacral furrows seldom reach below the circum-oral circle (*T. quadrangularis* being the exception). Most *Tetreucystis* species have only one ambulacral furrow in each radius, but *T. kalvoeyensis* n. sp. has a total of eleven or twelve facets and *T. quadrangularis* twelve to sixteen facets. The general shape of the theca, the plate distribution, and type of pores are similar to *Eucystis*, apart from the rather elongated pores of *T. munita* and *T. elongata* n. sp.

Palaeoecology. *Tetreucystis* occurs in environments similar to those of *Eucystis* and in lithologies such as carbonate mud mounds (*T. quadrangularis* in Dalarna, Sweden), siltstones (*T. monobrachiolata* n. sp. on the islands in the vicinity of Oslo, Norway), and in nodular limestones (*T. munita* in

the Rhiwlas Limestone at Bala, North Wales; *T. kalvoeyensis* n. sp. and *T. elongata* n. sp. in the Bærum-Asker districts, near Oslo, Norway). *T. kalvoeyensis* and *T. elongata* seem to be mutually exclusive, one occurring in deeper water than the other (text-fig. 6C).

Regional distribution and stratigraphic range. Ashgill of Norway, Sweden, and Britain.

Tetreucystis kalvoeyensis n. sp.

Plate 6, figs. 1-4, 7; text-figs. 29C-E, 31A

Diagnosis. A species of *Tetreucystis* with theca composed of plates in five or six series, each individual plate varying in shape and size, being pentagonal or hexagonal. Circum-oral plates higher than broad ($x > y$). Diplopores usually numerous in the lateral and circum-oral plates, decreasing in number towards the basal portion of the theca and occasionally present even in the basal plates. Ambulacra often with three side-branches each, all confined to circum-oral plates. Total number of brachiole facets in adult specimens ten to twelve.

Holotype. An almost complete specimen, PMO 80030, preserved as an external impression (text-fig. 29C, E; Pl. 6, figs. 1, 3).

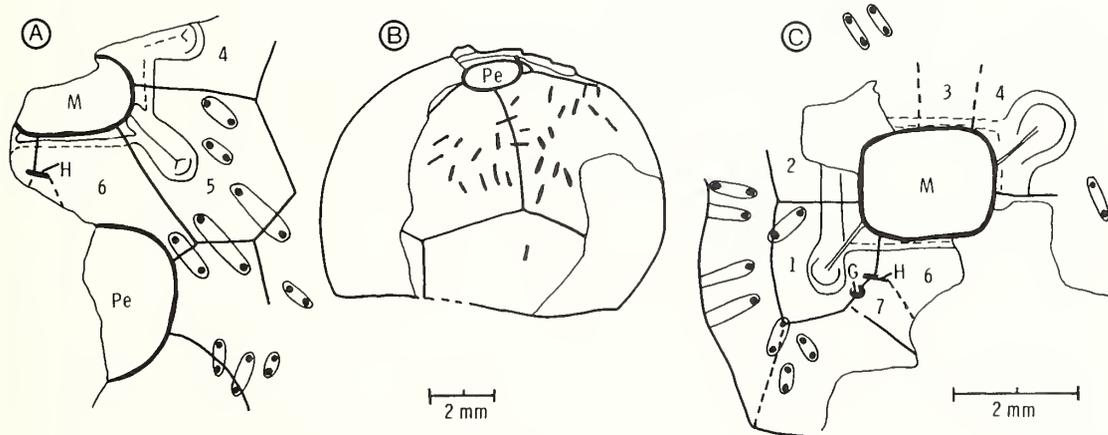
Type horizon. Tretaspis Limestone (= Stage 4c β), lower Ashgill.

Material. Over fifty more or less fragmentary specimens from Kalvøya (Bærum), Nesoya, Hvalstad, Raudskjær (Asker).

Description. Theca: variable in shape from spherical to inverted conical (text-fig. 29D, E). In the holotype, the height is 37 mm, the width 15 \times 13 mm.

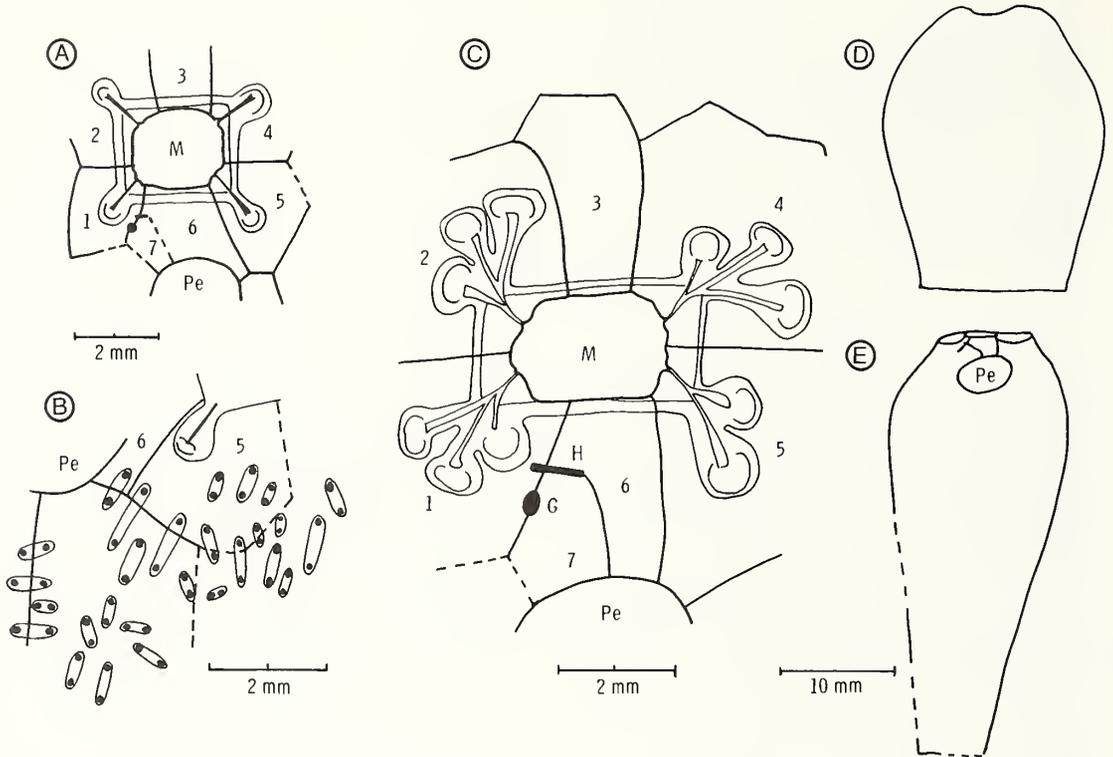
Plates: circum-oral plates are higher than broad; lateral plates vary in shape but are usually higher than broad. Eight or nine plates occur in the upper lateral series. In the oral region the sutures between CO7 and the adjoining lateral plates are not displayed. Thecal plates are about 0.6-0.8 mm thick. As in *T. elongata* n. sp., granular ornament occurs on the plates (also seen in well-preserved specimens of *Eucystis* and *Tetreucystis* from Sweden). The base of the theca is usually flat and may have served as an attachment area (text-fig. 29D, E).

Diplopores: occur in all thecal plates, the number decreasing towards the base, where the number of pores is two or three per mm², whereas in circum-oral and lateral plates it is five or six. A distinct radial arrangement of the diplopores is developed particularly in the two upper laterals. Peripore length: 0.54 \pm 0.09 mm; peripore width: 0.31 \pm 0.04 mm.



TEXT-FIG. 28. *Tetreucystis elongata* n. gen., n. sp. from Tretaspis Limestone, west side of Nesoya, Asker. A, PMO 91311, oro-anal area of holotype, showing right side of theca with circum-oral plates (4-6), mouth (M), hydropore (H), and periproct (Pe). B, lateral view of holotype showing some elongated diplopores. C, PMO 91312, oro-anal region. A, B, to same scale.

Peristome: slightly raised; the opening of the mouth is oval and the peristome border dips gently from the peristome down to the mouth. Grooves diverge from the ambulacral furrows before entering the mouth on the peristome border. The mouth is 4.2×2.5 mm. In the holotype three ambulacral side-branches occur in radii I, II, and IV, whereas only two occur in radius V. In PMO 90982 three side-branches occur in radii II and V but they cannot be counted in the other radii because of weathering. The side-branches never extend beyond the circum-oral plates. The anus is oval, 3.3×2.5 mm. Its long axis subtends an angle of 60° with the oral margin, and its adoral boundary lies 4.7 mm from that margin.



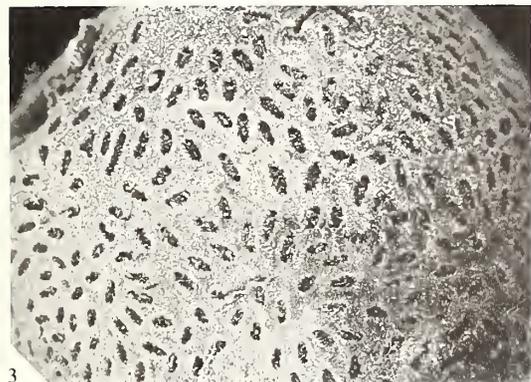
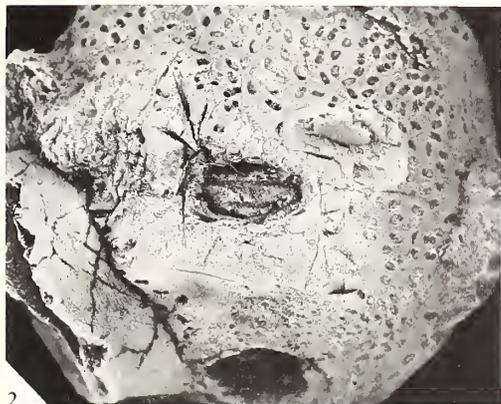
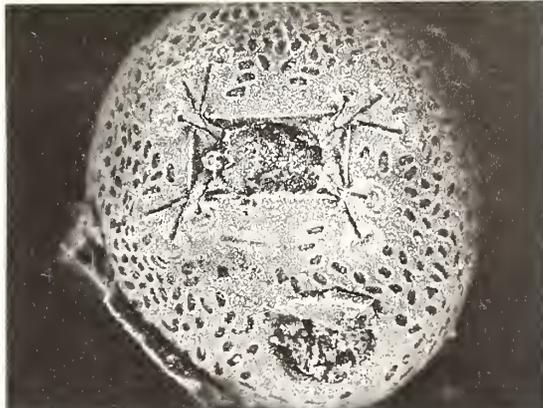
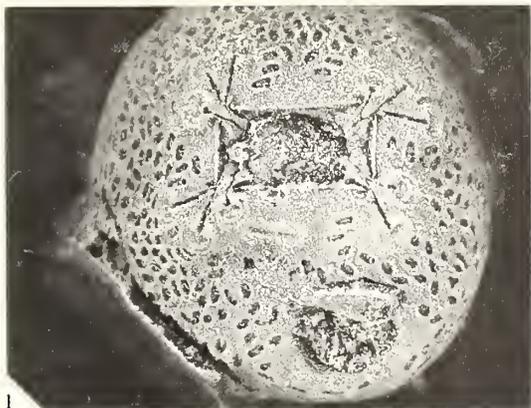
TEXT-FIG. 29. *Tetreucystis* n. gen. A, *T. elongata* n. sp., reconstruction of plate arrangement in the oro-anal area (cf. text-fig. 28). B, *T. elongata* n. sp., PMO 91311, holotype from Tretaspis Limestone, west side of Nesøya, Asker; diplopores (note their slight radial arrangement). C-E, *T. kalvoeyensis* n. sp. from Tretaspis Limestone, Kalvoya, Bærum. C, PMO 80030, holotype, reconstruction of plate configuration in the oro-anal area (note the somewhat elongated opening of the mouth, and food grooves leading on to a peristomal platform before entering the mouth); D, PMO 90981, lateral view showing shape of theca; E, PMO 80030, lateral view of holotype.

EXPLANATION OF PLATE 6

Figs. 1-4, 7. *Tetreucystis kalvoeyensis* n. gen., n. sp. Tretaspis Limestone (lower Ashgill), Kalvoya, Bærum. 1, PMO 80030, cast of holotype, stereophoto of oro-anal region, $\times 5$. 2, PMO 90982, stereophoto of oro-anal area, $\times 5$. 3, PMO 80030, cast of holotype showing details of diplopores in lateral circllet (note the radial arrangement of diplopores), $\times 7$. 4, PMO 90982, details of diplopores in circum-oral series, $\times 7$. 7, PMO 80022, outline of specimen with left side broken, $\times 3$.

Fig. 5. *Eucystis varipunctata* Angelin. Boda Limestone (Ashgill), Östbjörka, Dalarna, Sweden. RM Ec 2370, holotype showing peripores of upper lateral series with granulated plate surface, $\times 6$.

Fig. 6. *Tetreucystis elongata* n. gen., n. sp. Tretaspis Limestone (lower Ashgill), western side of Nesøya, Asker. PMO 91311, holotype in oral view. $\times 5$.



BOCKELIE, *Tetreucystis* and *Eucystis*

Gonopore: about 0.2 mm in diameter, occurs on the CO1 : CO6 suture and about 1 mm below the hydropore.
 Hydropore: 2 mm long and about 1 mm below the oral margin (text-fig. 29c).
 Attachment: direct by an aboral attachment area of variable size.

Remarks. *T. kalvoeyensis* differs from all other Norwegian *Tetreucystis* species in its larger number of brachiole facets. It differs from the contemporary Swedish *T. quadrangularis* in that the latter has more and longer food grooves, reaching down on to the lateral plates.

Tetreucystis elongata n. sp.

Plate 6, fig. 6; text-figs. 28, 29A, B, 31B

Diagnosis. A species of *Tetreucystis* with theca composed of plates in three regular circlets, the lateral plates having about equal height and breadth, whereas in the basal ones the height is less than the breadth. Diplopores elongate, about 1 mm long and 0.2 mm wide, more common in the lateral plates than in the circum-oral plates and sparse in the basal series. Brachiole facets small, 0.8 mm in diameter, close to mouth, never exceeding four.

Derivation of name. From the elongated shape of the diplopores.

Holotype. A somewhat imperfect specimen, PMO 91311 (text-figs. 28A, B, 29B, 31B; Pl. 6, fig. 6), showing only the right half of the theca (CO4–CO6) and in which neither the shape of most of the thecal plates nor the total plate number can be seen.

Type horizon. Tretaspis Limestone, lower Ashgill.

Material. Several more or less fragmentary specimens from Nesøya and Nesbru, Asker.

Description. Theca: hemispherical with flat base. The plate configuration of the theca is based upon only two specimens in addition to the holotype, PMO 91310 and 91312. Thecal height: 9–11 mm; greatest diameter: 11–12 mm. Maximum diameter of base equals the thecal diameter. Three plate circlets containing seven circum-orals, seven to eight laterals (eight in PMO 80083), and seven basals.

Plates: plate thickness is about 0.9 mm. Granulated surfaces are common, particularly in the circum-oral plates, as in Bohemian *Eucystis* (Prokop 1964). Laterals of equal length and breadth, the basals slightly shorter than wide.

Diplopores: occur in all three plate circlets, but are less common in the basals. In the latter, five pores were counted per mm²; in the circum-oral plates the number is only two or three. The diplopores are often arranged with their long axes perpendicular to plate margins. Diplopores long, but quite variable in length; some cross plate sutures (text-fig. 29B). Peripore length: 0.70 ± 0.17 mm; peripore width: 0.20 ± 0.04 mm. Ratio of peripore width to length: 0.14 ± 0.06 (mean ± 1 standard deviation, based upon fifty-four measurements).

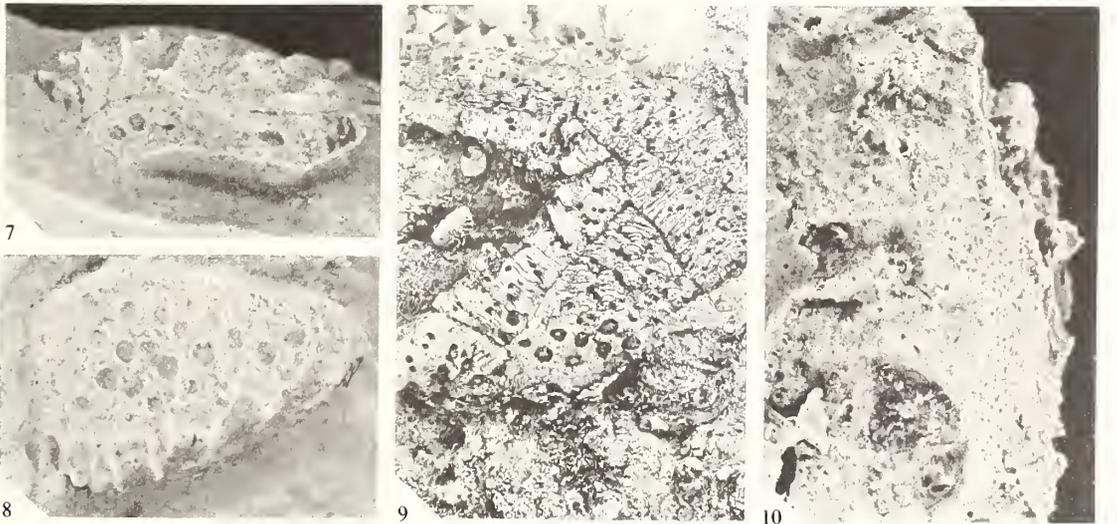
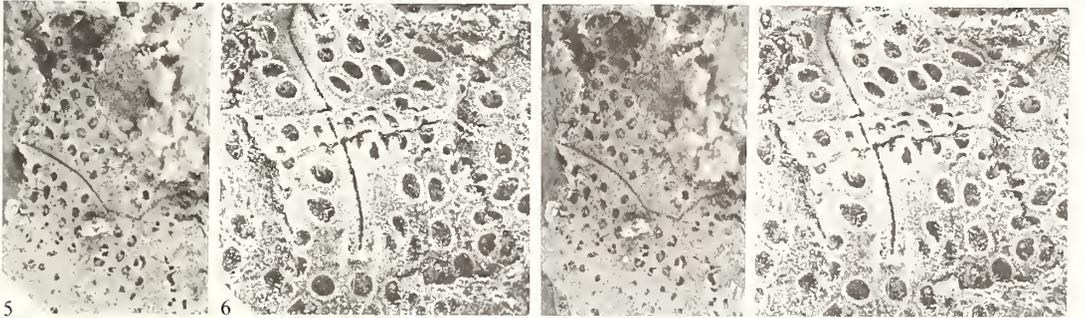
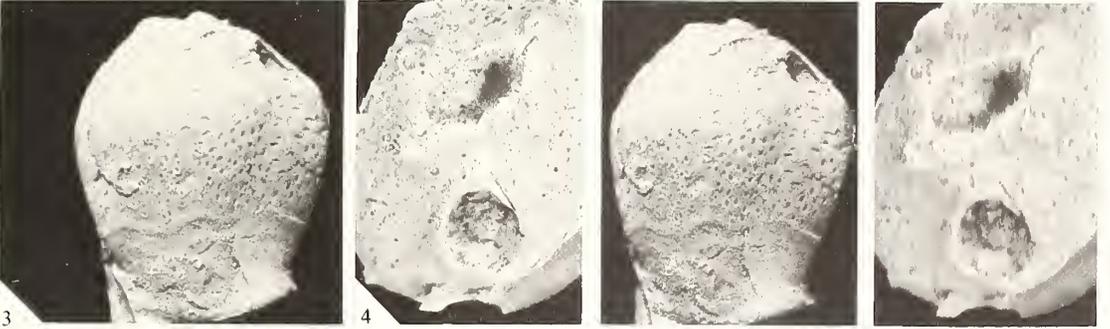
Peristome: measures 2.5 × 2.0 mm. The mouth is oval. Four ambulacra extend, one from each of the oral corners, to small brachiole facets about 1 mm from the oral corners.

EXPLANATION OF PLATE 7

Figs. 1–4. *Tetreucystis tetrabrachiolata* n. gen., n. sp. Husbergøya Shale (upper Ashgill); 1–3, Rambergøy, Oslo, and 4, north-west Langøya, Oslo. 1–3, PMO 92983, stereophotos of cast of holotype showing 1, oro-anal area, × 4; 2, diplopores in lower part of lateral plates, × 6; and 3, lateral view, × 2. 4, PMO 102.755, stereophoto of cast showing oro-anal area, × 4.

Figs. 5, 9, 10. *Pachycystis norvegica* n. gen., n. sp. Kalvsjø Formation (upper Ashgill), Kalvsjø Quarry, Lunner, Hadeland. 5, PMO 97103, stereophoto of cast of holotype showing diplopores on lateral series, × 4. 9, PMO 97141, part of theca with diplopores, × 6. 10, PMO 97103, cast of holotype showing quadrilateral peristome and large, circular anal area, × 5.

Figs. 6–8. *Sphaeronitid* indet. sp. A. Husbergøya Shale (upper Ashgill); 6, Skogerholmen, Asker, and 7, 8, Ostøya, Bærum. 6, PMO 90264, stereophoto of cast showing ambulacrum and diplopores, × 4. 7, PMO 97105, cast showing circum-oral plates with branching ambulacra seen from above, × 5. 8, PMO 97105, cast showing circum-oral plate seen in lateral view, showing diplopores, × 5.



Periproct: slightly ovate with its long axis perpendicular to the oral margin. It measures 2.5×1.8 – 2.0 mm with the adoral boundary 1.3 mm below the oral margin (in PMO 91311).

Gonopore: 0.25 mm diameter, set just below the hydropore and close to the brachiole facet in radius I.

Hydropore: occurring less than 0.5 mm from the oral margin. It is bisected by the CO1:CO6 suture (text-fig. 28c).

Remarks. *T. elongata* differs from most other *Tetreucystis* species in the characteristic shape of its diplopores. It resembles *T. munita* (see Paul 1973) but differs in that the diplopores of *T. munita* are shorter (0.54 mm) than in *T. elongata* (0.70 mm), the mouth frame of *T. munita* is elevated on the thecal surface, and the diameter of the brachiole facet in *T. munita* is almost twice that of *T. elongata*.

Tetreucystis tetrabrachiolata n. sp.

Plate 7, figs. 1–4; text-figs. 30, 31c

Diagnosis. A species of *Tetreucystis* with theca composed of plates in three circlets, lateral plates higher than wide. Diplopores rounded, common in the circum-oral plates. Brachiole facets 1.3 mm in diameter. The number of facets rarely exceeds four.

Derivation of name. The name alludes to the almost constant number of brachiole facets, one in each of the oral corners.

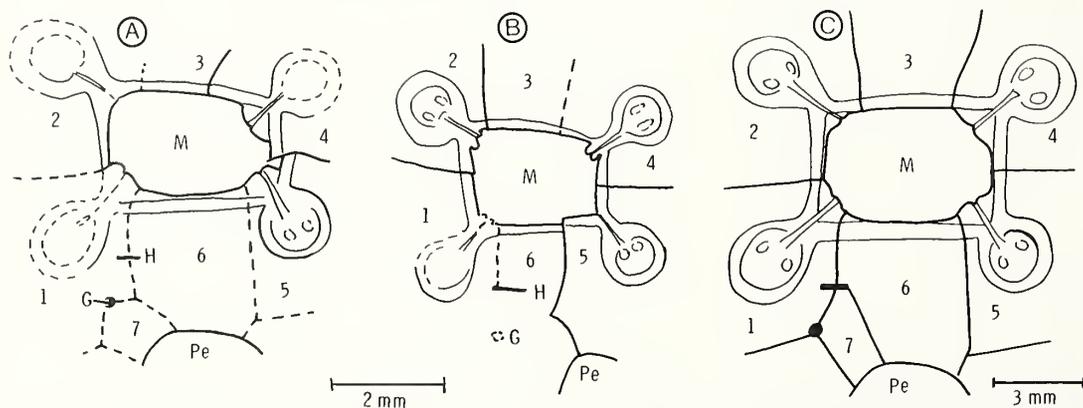
Holotype. A somewhat compressed specimen, PMO 92983, preserved as an external mould (Pl. 7, figs. 1–3). Only two-thirds of the theca is visible; some lateral and basal plates are not preserved.

Type horizon. Husbergøya Shale Formation, upper Ashgill, Rambergøy, Bunnefjorden, Oslo.

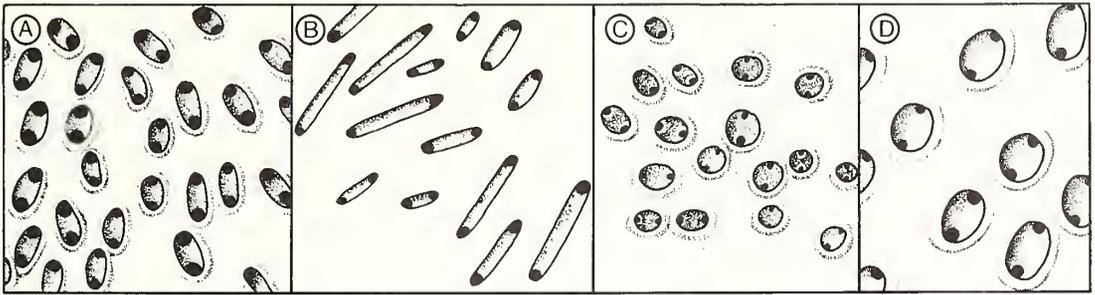
Material. In addition to the holotype, ten specimens from several of the islands in the Oslo district.

Description. Theca: globular with flat or slightly concave base. The plate configuration cannot be seen clearly in all specimens, partly due to cracks that confuse the issue. A composite reconstruction is made in text-fig. 30c. The theca consists of three series of plates, including seven circum-orals, eight laterals, and seven or possibly eight basals. Thecal height 13–20 mm; thecal diameter about two-thirds of thecal height. In most specimens the base is about one-third the thecal diameter but in some the base is slightly prolonged. In such cases the diameter of the base may be 5×7 mm (PMO 92991) or 5×8 mm (in the holotype).

Plates: approximately 1 mm thick. The plate surface is smooth. Both laterals and basals are higher than broad, whereas in the circum-orals the height and breadth is the same.



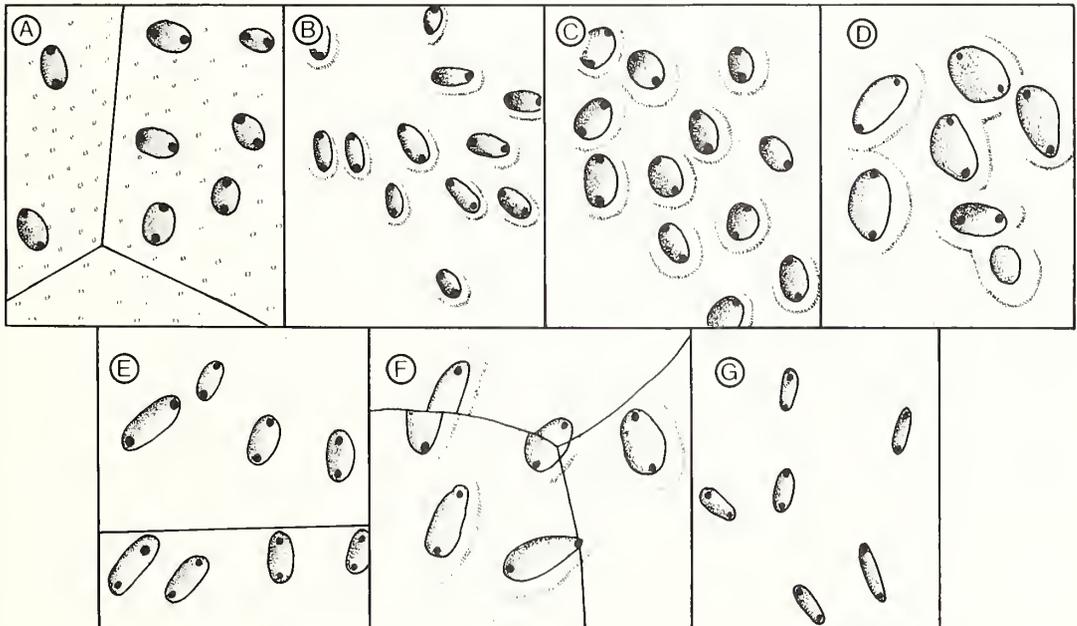
TEXT-FIG. 30. *Tetreucystis tetrabrachiolata* n. gen., n. sp. Plate distribution of oro-anal region. A, PMO 90890, Husbergøya Shale, south-west Rambergøy, Oslo. B, PMO 90873, Husbergøya Shale, north-west Langøya, Oslo. C, reconstruction. M, mouth; G, gonopore; H, hydropore; Pe, periproct.



TEXT-FIG. 31. Diplopores of *Tetreucystis* n. gen. A, *T. kalvoeyensis* n. sp., PMO 80030, holotype, Tretaspis Limestone, Kalvøya, Bærum. B, *T. elongata* n. sp., PMO 91311, holotype, Tretaspis Limestone, Nesøya, Asker. C, *T. tetrabrachiolata* n. sp., PMO 92983, holotype, Husbergøya Shale, Rambergøy, Oslo. D, *T. quadrangularis* (Regnéll), RM Ec 2119, Boda Limestone, Dalarna, Sweden (original of Regnéll 1945, pl. 14.2).

Diplopores: present all over theca, but most common in the circum-oral plates, where six to seven pores per mm^2 occur. In the lateral plates the number is four or five and in the basals only three or four. In some specimens the basals are devoid of diplopores. There is a tendency towards a radial arrangement of diplopores. Peripore length: 0.31 ± 0.10 mm; peripore width: 0.18 ± 0.02 mm. Ratio of peripore length to peripore width: 0.70 ± 0.02 (mean ± 1 standard deviation, based upon twenty-four measurements).

Peristome: 4.2×3.2 mm in the holotype, but the proportions may vary (in PMO 92984, 4.5×2.0 mm). In most specimens four ambulacra extend, one from each of the oral corners, just on to the circum-oral plates. In PMO 90896 two facets have been found in radius I.



TEXT-FIG. 32. Diplopores of *Eucystis* species. A, *E. varipunctata*, RM Ec 2370, holotype, Boda Limestone, Östbjörka, Dalarna, Sweden. B, *E. langøeyensis* n. sp., PMO 90947, holotype, Husbergøya Shale, north-west Langøya, Oslo. C, *E. angelini*, RM Ec 1974, Boda Limestone, Dalarna, Sweden. D, *E. globula*, SM A7800, holotype, Ashgill Shales (Paul 1973, text-fig. 27C). E, *E. acuminata*, RM Ec 2173, holotype, Boda Limestone, Gulleråsen?, Dalarna, Sweden. F, *E. hibernica*, BM(NH) E28758, Kildare Limestone (Paul 1973, text-fig. 27D). G, *E. pentax*, SM A74802, Ashgill Shales (Paul 1973, text-fig. 27F). All approximately $\times 10$.

Periproct: subcircular with a diameter of 3.1 mm in PMO 90890.

Gonopore: below the hydropore and nearer the brachiole facet of radius I than the anus.

Hydropore: on a slightly elevated ridge, 1.4 mm below the peristome border and bisected by the CO1 : CO6 suture.

Remarks. *T. tetrabrachiolata* n. sp. is the only species of the genus occurring in the Husbergøya Shale. The contemporary Swedish *T. quadrangularis* can readily be distinguished from the Norwegian species by the presence of many more brachiole facets, and longer food grooves, reaching down into the lateral plates. *T. tetrabrachiolata* is separable from *T. kalvoeyensis* by the latter's larger number of brachioles. *T. tetrabrachiolata* is distinguishable from *T. elongata* by the shape of the diplopores and the shape of the lateral plates. It differs from *T. munita* in the shape of the pores, those of the latter being elongate.

Genus *Archaeogocystis* Jaekel, 1899

Synonymy. *Pyrocystites* Barrande, 1887 (pars).

Type species. *Pyrocystites desideratus* Barrande, 1887, p. 170, by original designation of Jaekel, 1899, p. 395; Sárka Beds (Llanvirn), Osek, Bohemia.

Diagnosis. A genus of Sphaeronitidae with globular to spherical theca; plates more or less randomly arranged; ambulacra short, confined to peri-oral plates, branching fan-wise with three to seven facets each; diplopores oval to elongate with or without narrow unspecialized peripore rims and usually randomly orientated.

Archaeogocystis cf. *granulata* Paul, 1973

Plate 3, figs. 7, 9

Material. One specimen, PMO 97106.

Horizon and locality. Ashgill; Sørbakken Limestone, Frognoya, Ringerike, Oslo Region.

Description. One sagittally divided half theca. Two ambulacra are preserved but the mouth, anus, gonopore, and hydropore are missing. Thecal height 26 mm; thecal diameter 22 mm. Attached directly by aboral circular attachment area, 3.5 mm in diameter.

Plates: total number unknown, but approximately five plate circlets present. Plates of slightly variable size, the largest reaching approximately 6-7 mm. Most (possibly all) plates have diplopores arranged radially (Pl. 3, fig. 7). Plate surface covered with fine granular ornament and faint peripore rims.

Diplopores: with simple peripore rims, often strongly developed, but in several cases weak or almost missing. Oval to elongate, rarely extremely elongate as in *A. stellulifera* (Salter). Length 0.25-2.0 mm (average 0.65 mm); width 0.18-0.40 mm (average 0.32 mm); averages based on thirty-four measurements.

Peristome: not present. Outermost portions of food grooves are present, forming small knobs. Food grooves were probably short, reaching to the centre of the circum-oral plates only.

Periproct: unknown.

Gonopore and hydropore: unknown.

Attachment: direct, by circular aboral attachment area with a diameter of 3.5 mm.

Remarks. This specimen shows most similarities with *A. granulata*. The lack of information about the oral area makes the determination slightly uncertain. The mean values of diplopore lengths and widths are not very different from those of British material (0.79 mm and 0.31 mm respectively). The granular surface ornament of the Norwegian specimen is also very similar to that of the British form. The characteristic surface granulation clearly distinguishes *A. granulata* from *A. stellulifera* (Paul 1973, p. 39). Some differences exist both in the shape and in the ornament between the British and Norwegian forms. However, because no complete specimen has yet been found in Norway, a new species is not erected.

Sphaeronitidae sp. A

Plate 7, figs. 6-8; text-fig. 33f

Material. One partial theca, PMO 90264, and two circum-oral plates, PMO 97105 and PMO 97140.

Horizon and localities. Husbergoya Shale Formation, Skogerholmen, and Ostoya, Bærum, Oslo Region.

Description. About one-third of the theca is preserved; it may have been about 40 mm high \times 26 mm wide. Only part of the upper surface remains. The theca tapers slightly towards the base, with an oval attachment area originally about 20 \times 15 mm. Base concave. Two series of roughly hexagonal thecal plates are preserved, but as many as four or five may have been present. Thecal plates have a granular ornament. The shape of the peristome is unknown. Food grooves of possibly two radii are preserved, representing radii II and III, or III and IV. In one of these radii two branching ambulacra can be seen, one of which reaches below the circum-oral circlet. The two individual circum-oral plates contain five to six side-branches off one main food groove. This main groove is parallel to the nearest plate suture. The brachiole facets are unlike those of any other Norwegian cystoid, but show similarities *inter alia* to the facets of *Craterina*.

Diplopores: numerous in the upper portion of the theca of PMO 90264. The diplopores are subcircular in outline and provided with a thick peripore wall. Mean diplopore length 0.71 mm; mean width 0.50 mm; length to width ratio 1.46 (based on thirty-seven measurements). No traces of mouth, anus, gonopore, or hydropore.

Palaeoecology. Found in a shallow water siltstone sequence extending for about 10 \times 10 km, with abundant echinoderms, bryozoa, and brachiopods. The brachiole facets indicate the presence of delicate brachioles, and the animals thus may have lived in clear water with moderate sedimentation rates.

Remarks. No described cystoid is directly comparable to this species. However, it is clearly a sphaeronitid from the type of food grooves and diplopores. To some extent it resembles *Eucystis*, *Archaegocystis*, and *Craterina*, but most likely represents a new genus.

Family PARASPHAERONITIDAE n. fam.

Diagnosis. A family of Sphaeronitida with a relatively large quadrilateral peristome, surrounded by eight peri-oral plates. The margin of the peristome is pierced by a large number of small pits; diplopores are complex. Four ambulacra, each leading to one large brachiole facet; periproct large, not very far down on the theca.

Remarks. Parasphaeronitidae is erected for two genera, *Parasphaeronites* n. gen. and *Pachycystis* n. gen. It is separable from the Sphaeronitidae by the presence of eight peri-oral plates. The family resembles the Holocystitidae in the number and distribution of peri-orals, but differs in having diplopores. Parasphaeronitidae differ from the Aristocystitidae in the shape of the peristome, which in the latter family has two broad ambulacral tracts which meet at a small ovate mouth (see Paul 1973, p. 57).

The Parasphaeronitidae seem to represent a transition between the Sphaeronitidae and the Holocystitidae, at least as far as the oral area is concerned. The humatipores of the holocystitids are known only from their exterior appearance (at the outer portion of the thecal plates) and the connections of canals through their plates are not known. In *Parasphaeronites* the canals are extremely complicated and show patterns not unlike those of the Aristocystitidae. The Parasphaeronitidae thus may also show some similarities to the Aristocystitidae, as far as the internal portions of the pore-structures are concerned. The Parasphaeronitidae at present contains two genera only, and both occur in the upper Ordovician (Ashgill) Kalvsjø Formation (= Stage 5a) and an unnamed formation from Ringerike (= Stage 5b) (Hirnantian), of the Oslo Region, Norway.

Genus *Parasphaeronites* n. gen.

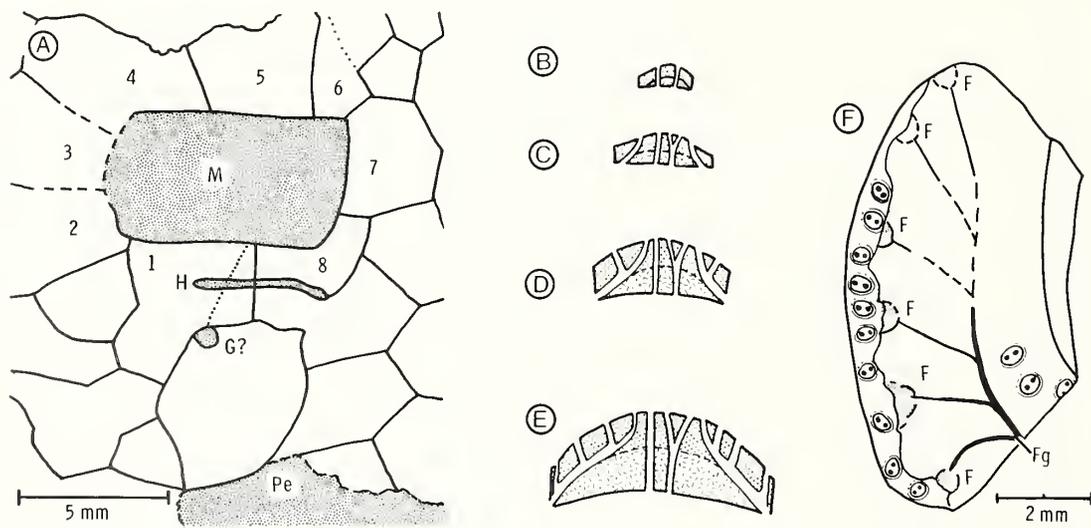
Synonymy. See *Parasphaeronites socialis* n. sp.

Type species. *Parasphaeronites socialis* n. gen., n. sp.

Diagnosis. A genus of Parasphaeronitidae with large globular theca composed of numerous irregular plates, with elevated plate centres forming irregular external surface; pores relatively close together with broad peripore rim, giving the appearance of *Sphaeronites*. One large ambulacral facet at each of the four oral corners. Periproct separated from the mouth by two plates.

Remarks. *Parasphaeronites* does not resemble any known cystoid. The presence of eight peri-orals and diplopores clearly distinguishes it from all others. The diplopores show similarities to both the Aristocystitidae and the Sphaeronitidae. *Parasphaeronites* is known from one species only, *P. socialis* n. sp. It differs from *Pachycystis* n. gen. in the arrangement of thecal plates around the peristome, the position of the periproct, the location of the gonopore, and in the more simple type of diplopores in the latter genus.

Description. The theca is globular, usually 40–50 mm in diameter, and consists of at least forty to fifty plates. The base is concave and irregular. The precise plate arrangement cannot be worked out easily, because the numerous specimens are usually crushed together and the thecae generally weather more rapidly than the matrix. The stereom of the thecal plates is often well preserved and shows an inner coarse mesh and an outer fine mesh structure. The pore structures are very well preserved, showing a rather complex pattern of canals through the plates. Three types of canals occur: (1) canals leading right through the plate from simple pores or a diplopore; (2) Y-shaped canals leading to two different diplopores; and (3) a main canal of low angle giving off several side-canals, each of which leads to a different diplopore (text-figs. 12F, 33B–E; Pl. 8, figs. 3, 6, 7). The periproct is situated some way down the theca and is separated from the mouth by one plate in addition to the peri-orals. The



TEXT-FIG. 33. A, *Parasphaeronites socialis* n. gen., n. sp. PMO 90974, holotype showing plate configuration of oro-anal area (drawing reversed in relation to specimen which is probably seen from inside); the quadrilateral mouth (M) is surrounded by eight peri-oral plates (1–8); hydropore (H), possibly gonopore (G?) and periproct (Pe) visible. B–E, *P. socialis* n. gen., n. sp., schematic representation of plate growth and additions of simple and complex canals; notice that the complex canals (branched) occur at the boundary between the fine mesh layer (dotted) and the coarse mesh layer (irregularly hatched); simplified. F, *Sphaeronites* indet. sp. A., PMO 97105, Husbergoya Shale, V. Ostoya, Bærum, circum-oral plate showing food groove (Fg) with six side-branches and facets (F), and diplopores on the side.

shape of the periproct is difficult to establish, but it seems to be as large as the peristome. The hydropore is a long slit-like opening crossing the sutures PO1 : PO6. The gonopore is located somewhat lower down on the theca and at the left side of the hydropore-periproct line. Attachment was direct, with a slightly concave base.

Palaeoecology. *Parasphaeronites* has been found in only one locality where it is extremely common, filling erosion channels in a reef.

Parasphaeronites socialis n. sp.

Plate 8, figs. 1, 3, 5-7; text-fig. 33A

1897 *Sphaeronites* sp.; Kier, p. 17.

1948b *Sphaeronites* sp.; Regnéll, p. 35.

Diagnosis. A species of *Parasphaeronites* with numerous thecal plates, not arranged in definite circlets; plates thick with elevated centres; diplopores present on most of the thecal plates, numerous, peripore with distinct rims, peripore length 0.5-0.6 mm.

Holotype. PMO 90974, a specimen showing the oro-anal area from the inside (text-fig. 33A; Pl. 8, fig. 1).

Material. In addition to the holotype, more than a hundred specimens.

Horizon and locality. Upper Ashgill; within channels in the reef of an unnamed formation, Ullerntangen, Ringerike, Oslo Region.

Description. As for the genus. The holotype shows the inside of the theca (Pl. 8, fig. 1); the plate diagram (text-fig. 33A) is reversed to show the external plate configuration.

Plates: one or possibly two generations in some parts of the theca. Four plate circlets at least in the holotype. Plates mostly elongated in oral-aboral direction. Most plates 6 × 4 mm. A circlet must have consisted of ten to fifteen plates; the basal circlet probably consisted of ten plates. Plate thickness 1-2 mm.

Respiratory pores: 0.54 × 0.33 mm with broad low periporal rim, or rimless peripores. Diplopores numerous all over the thecal surface including the basal plates, but absent near plate sutures. Some haplopores may be present. The canals within the plates are very complex (text-figs. 12F, 33B-E; Pl. 8, figs. 3, 6, 7).

Peristome: 8.1 × 4.4 mm, surrounding oval mouth. Small pits present on the peristome border resemble those of holocystitids (Paul 1971).

Periproct: the shape cannot be made out but it is about 7 mm from the lower border of the peristome frame.

Gonopore: circular, 0.48 mm in diameter.

Hydropore: present 1.2 mm below the peristome frame.

Remarks. *P. socialis* has pore structures resembling those of *Sphaeronites* on its external surface. The numerous pores all over the theca give it a high respiration potential, and in this respect it also resembles *Sphaeronites*. The complex pattern of pore canals within the thecal plates makes it one of the most difficult cystoids in Norway to study with respect to the peripore connections. However, it can be demonstrated that individual canals led to a peripore and that a complex circulatory system existed.

Pachycystis n. gen.

Type species. *Pachycystis norvegica* n. gen., n. sp., by monotypy.

Type horizon and locality. Kalvsjø Limestone, upper Ashgill; Kalvsjø, Hadeland, Oslo Region.

Diagnosis. A genus of Parasphaeronitidae with quadrangular peristome surrounded by eight peri-oral plates. Four ambulacra, each terminating in a large facet close to the mouth. A large periproct set closely to the peristome. Thecal plates numerous and irregular. Diplopores very common in the oral area, diminishing in number towards the base where they are absent. Directly attached by a slightly concave base.

Remarks. *Pachycystis* differs from *Parasphaeronites* by the periproct being close to the peristome border in the former, and separated by two plates in the latter. The gonopore of *Pachycystis* borders

PO1 and the peristome, whereas in *Parasphaeronites* the gonopore is located closer to the peristome. Thecal plates of *Pachycystis* are gently elevated, but strongly tumid in *Parasphaeronites*.

Description. The theca is sack-like with plates of different shape, often elongated, pentagonal, or hexagonal. No complete specimens exist, and thus the size cannot be clearly established. Total height of the theca seems to be in the range of 40–50 mm and diameter of 25–30 mm. PO1, PO3, PO5, and PO7 each contain one large brachiole facet, almost circular and 2.5–3.0 mm in diameter. Two muscle scars, both elongate, occur in each of the facets. The mouth may have been covered in life by a palate, but it has not been observed. A slit-like hydropore is present on PO1 and ends at the PO1:PO8 suture. A possible gonopore is located at the upper left side of the periproct, and is 0.6 mm in diameter. A large slightly ovate periproct, 7.5 × 5.5 mm, is set close to the lower margin of the mouth frame and is bordered by PO1, PO7, and PO8.

Diplopores are numerous in the upper half of the theca, usually 0.4 × 0.3 mm. They are densely packed in the circum-oral portion of the theca (four or five per mm²) but become reduced in number towards the base, where pores are absent. The long axis of the pores do not seem to show any preferred orientation. *Pachycystis* was attached directly by an attachment area which was slightly concave. Its diameter may be in the order of 20 × 20 mm from the general appearance of the theca, but has been found to be 5 × 3 mm in one specimen.

Palaeoecology. *Pachycystis* has been found only on the flanks of a mudbank at Kalvsjø, Hadeland, where it is preserved in a calcareous shale.

Pachycystis norvegica n. sp.

Plate 7, figs. 5, 9, 10; text-fig. 34A, B

Diagnosis. As for the genus.

Holotype. PMO 97103, an external mould of the oral area (text-fig. 34A; Pl. 7, figs. 5, 10).

Horizon and locality. Upper Ashgill; Kalvsjø Formation, mud bank, Kalvsjø, Hadeland, Oslo Region.

Material. Holotype, PMO 97141 and PMO 101.835, and two moulds, PMO 97102 and PMO 97104.

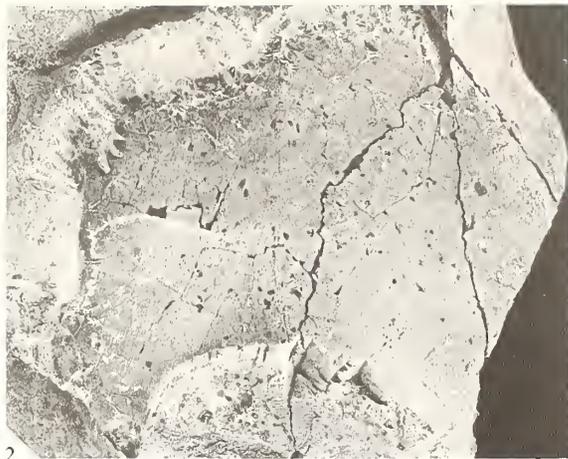
Description. As for the genus. In addition some measurements have been made on the sizes of diplopores. The peripores are slightly elongated with fairly large pores. Some of the peripores close to the plate sutures are smaller than those elsewhere, probably indicating that new pores are formed close to sutures. Peripore length 0.35–0.50 mm; width 0.25–0.40 mm (text-fig. 34B). Attachment was direct with a small elongate attachment area (5 × 3 mm in PMO 101.835).

EXPLANATION OF PLATE 8

Figs. 1, 3, 5–7. *Parasphaeronites socialis* n. gen., n. sp. Unnamed formation (Hirnantian), Ullerntangen, Ringerike. 1, PMO 90974, holotype, oro-anal area seen from inside (?) of theca (specimen strongly weathered). 3, PMO 105.707, etched specimen showing details of canals in sagittal view; the fine stereom layer (outer) is dissolved, the inner coarse mesh layer filled with asphalt (note how the canals parallel the surface of the coarse mesh layer), × 10. 5, PMO 55533, stereophoto of strongly convex plates with pores, × 5.5. 6, PMO 105.715, SEM stereophoto showing details of complex canals with main canals and side branches towards edge of plate (SEM 2362/61), × 20. 7, PMO 105.715, SEM stereophoto showing details of complex canals towards plate centre (note vertical position of canals as opposed to low angle canals at plate edge) (SEM 2356/57), × 20.

Fig. 2. *Incertae sedis* sp. A. Upper Chasmops Limestone (12.1 m below top), Raudskjær, Asker. PMO 103.320, basal portion of theca with minute diplopores, × 2.

Fig. 4. *Incertae sedis* sp. B. Encrinite Limestone (2 m above base, within lowermost portion of reef), Steinvika, Langesund. PMO 105.836, basal portion of a theca showing small diplopores, × 3.



BOCKELIE, *Parasphaeronites* and *Incertae sedis*

Incertae sedis sp. A

Plate 8, fig. 2

Material. One specimen, PMO 103.320.

Horizon and locality. Upper Caradoc; Upper Chasmops Limestone, 12.1 m below the top, Raudskjær, Asker, Oslo Region.

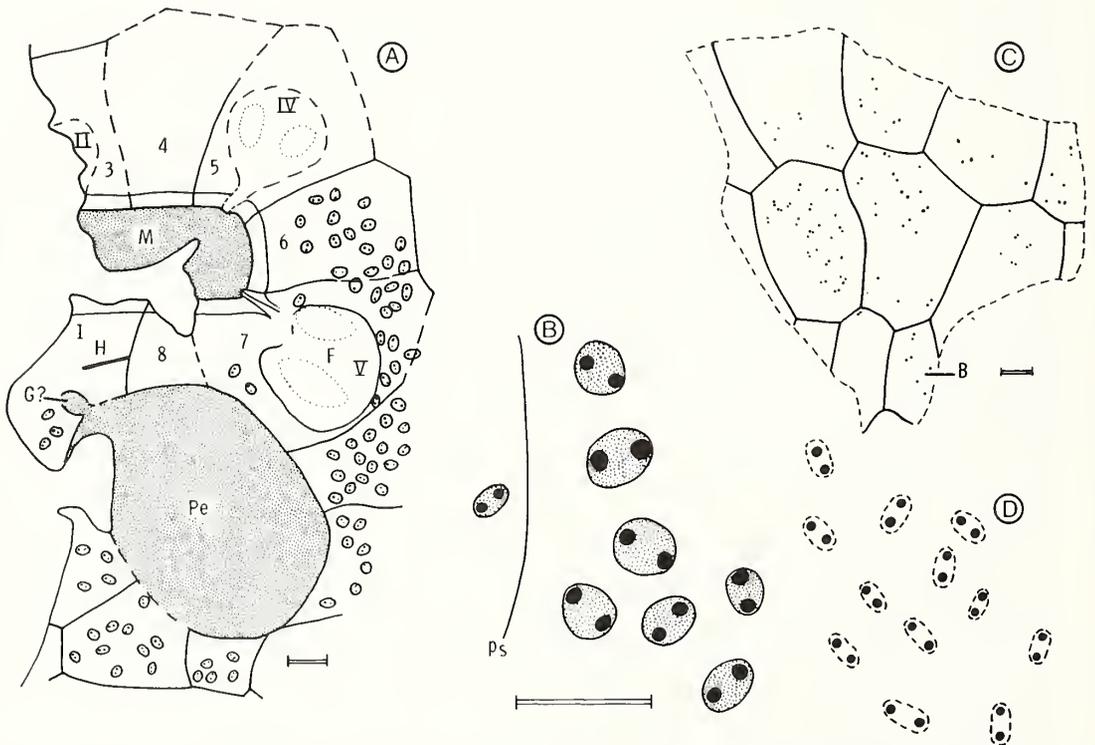
Description. Theca; presumably roughly spherical, about 30–35 mm in diameter, showing the basal portion. Five large lobate basal plates. Base concave, circular, 16 mm in diameter. Theca strongly weathered.

Plates: thick (1.8 mm) with few randomly arranged diplopores.

Diplopores: sparsely developed, small (0.26 × 0.16 mm) possibly with faint rims originally. All other features unknown.

Palaeoecology. The specimen was attached directly in life, probably to a brachiopod. When dead, the cystoid came loose from its attachment, fell over to the side, and was eventually covered by an epifauna of two different types of bryozoa and crinoid roots.

Remarks. This specimen is preserved in a nodular limestone with interbedded shales. The shape of the theca might suggest a sphaeronitid, but the minute and scattered diplopores make it difficult to suggest its affinities. The specimen might be a representative of a new genus, and is at least a new species. Due to lack of information about the oral area, however, I will avoid a new name.



TEXT-FIG. 34. A, B, *Pachycystis norvegica* n. gen., n. sp., PMO 97103, holotype, Kalvsjo Formation, Kalvsjo, Hadeland; A, plates of oro-anal area with peri-orals (1–8), one brachiole facet (F) in each of the four oral corners, a possible gonopore (G?) close to the large periproct (Pe), and a narrow hydropore (H) at the PO1:PO8 suture; B, diplopores. C, D, *Incertae sedis* sp. B., PMO 105.836, Encrinite Limestone, Steinvika, Langesund; C, plates of basal portion, including basals (B); D, diplopores with faintly developed or abraded peripore wall. Scale bar, 1 mm.

Incertae sedis sp. B

Plate 8, fig. 4; text-fig. 34C, D

Material. One specimen, PMO 105.836.

Horizon and locality. Upper Caradoc; within reef complex of Encrinite Limestone, 2 m above base, Steinvika, Langesund.

Description. Theca: only the basal portion showing three plate series is preserved. Maximum height and width both 1.2 mm.

Plates: thick (2.0 mm) with few, randomly arranged diplopores. All plates primary, elongated in ad-aboral direction; most plates hexagonal.

Diplopores: randomly distributed, 0.27 × 0.12 mm, usually strongly abraded; present on all thecal plates, including the basals. All other features unknown.

Palaeoecology. The specimen most probably lived in or very close to the reef environment and was attached directly by its base. Its presence in the crinoid-dominated community suggests that it might have been a low-level suspension feeder, unless it was attached to seaweed. The thick plates rather suggest that the animal was heavy and bottom dwelling.

Remarks. This specimen is preserved in a reef limestone together with crinoids, a few *Heliocrinites* sp., and occasional specimens of *Hemicosmites papaveris*. The weathered state of the specimen and the lack of the oral area makes determination even to family level impossible.

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Geological maps at a scale of 1 : 5000, a list of all fossil localities, drawn sections with occurrences of cystoids and other fossils, and the majority of the described material have been deposited in the Palaeontologisk Museum, Oslo.

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PERMINERALIZED OVULATE CONES OF *LEBACHIA* FROM LATE PALAEOZOIC LIMESTONES OF KANSAS

by G. MAPES and G. W. ROTHWELL

ABSTRACT. A diverse assemblage of permineralized conifer remains has been discovered in late Palaeozoic limestones from the mid-continent of North America, near Hamilton, Kansas. Ovulate cones described as *Lebachia lockardii* sp. nov., support the structural homologies among cordaites, primitive conifers, and modern conifers proposed by Florin, and reveal anatomical features that are remarkably similar to those of many extant conifers. Features not recognized from previously described cones of *Lebachia* are dorsiventral, bilaterally symmetrical fertile shoots, inverted orientation of the ovules, and the true bilateral symmetry of the ovules. In both morphological structure and cuticular features the specimens show more variability than has previously been documented for a single conifer species, and this calls to question the reliability of features previously employed for generic separation of *Lebachia* from *Ernestiodendron*. The specimens also provide the first histological evidence for ovule abscission in Palaeozoic gymnosperms, and allow for the interpretation of several aspects of ovule ontogeny and early conifer reproductive biology.

UPPER PALAEOZOIC conifers are a relatively common component of some northern Hemisphere compression floras. Remains assignable to several genera, including *Walchia*, *Lebachia*, *Ernestiodendron*, *Lecrosia*, and *Paleotaxites*, have been described from Westphalian B (Scott 1974) and more recent strata of Europe and North America. Much of our current understanding of the earliest conifers is derived from the detailed studies and interpretations of Florin (1938–1945, 1950, 1951). However, until recently our knowledge of these forms has been limited by an almost total absence of permineralized specimens. Notable exceptions are a single leafy twig from the Pennsylvanian of Kansas (Elias 1948), a Permian ovulate cone tip (*Moyliostrobus* Miller and Brown 1973), and various wood fragments described by Florin (1938–1945) and others.

Numerous compressed Pennsylvanian and basal Permian conifer remains have been described or reported from North America. Where preservation reveals pertinent morphology and epidermal detail, some of these have been recognized as species of *Lebachia* (Florin 1938–1945; Cridland *et al.* 1963; Cridland and Morris 1964; Mapes 1981). These include *L. americana*, *L. garnettensis*, *L. parvifolia*, *L. stricta*, *L. geoppertiana*, *L. schlotheimii*, and *L. stephanensis*. In addition, *Lecrosia gouldii*, *Paleotaxites praecursor*, and several species of *Walchia* have been reported (e.g. White 1912; White 1929; Darrah 1936; Elias 1936; Arnold 1941; Read and Mamay 1964; Darrah 1969; Leisman 1971; Tidwell and Ash 1980; Kues and Kietzke 1981). Though some poorly preserved cones have also been reported, the studies have dealt primarily with isolated leafy branches or sterile foliage shoots.

As the result of extensive collecting in sediments that contain plant fragments not known from contemporaneous coal-forming peats (*viz.* not from coal balls), permineralized conifer remains have recently been discovered in mid-continental deposits of Oklahoma and Kansas (Mapes 1981; Rothwell 1982*b*). Permineralized specimens from these deposits range in age from middle Pennsylvanian to late Pennsylvanian or perhaps early Permian. The most diverse flora thus far encountered is near Hamilton, Kansas (text-fig. 1), and contains a wide variety of conifer remains. Included are large numbers of plagiotropic branch systems bearing forked leaves on penultimate and more basal branch orders and either long-needled or short-needled simple leaves on the ultimate branches. Both compound cones bearing ovules and simple pollen cones with *Potomieisporites*

are present in the conifer assemblage (Mapes 1981). A large number of the specimens display morphological and cuticular features that allow for their assignment to *Lebachia* as circumscribed by Florin (1938–1945), and provide the first opportunity to describe internal anatomy and to interpret development and reproductive biology in one of the most widely reported of all Palaeozoic conifers. The material also allows us to evaluate, from anatomical evidence, the accuracy of the structural homologies proposed by Florin for cordaites and conifers. Moreover, we can for the first time examine the isolated parts of a single *Lebachia* based on both external and internal features, and ultimately reconstruct the entire plant.

In the present study we describe and interpret several aspects of cone organization, ovule structure, ovule development, and reproductive biology in a new species of *Lebachia*. Pollen cones and vegetative organs will be addressed in subsequent studies.

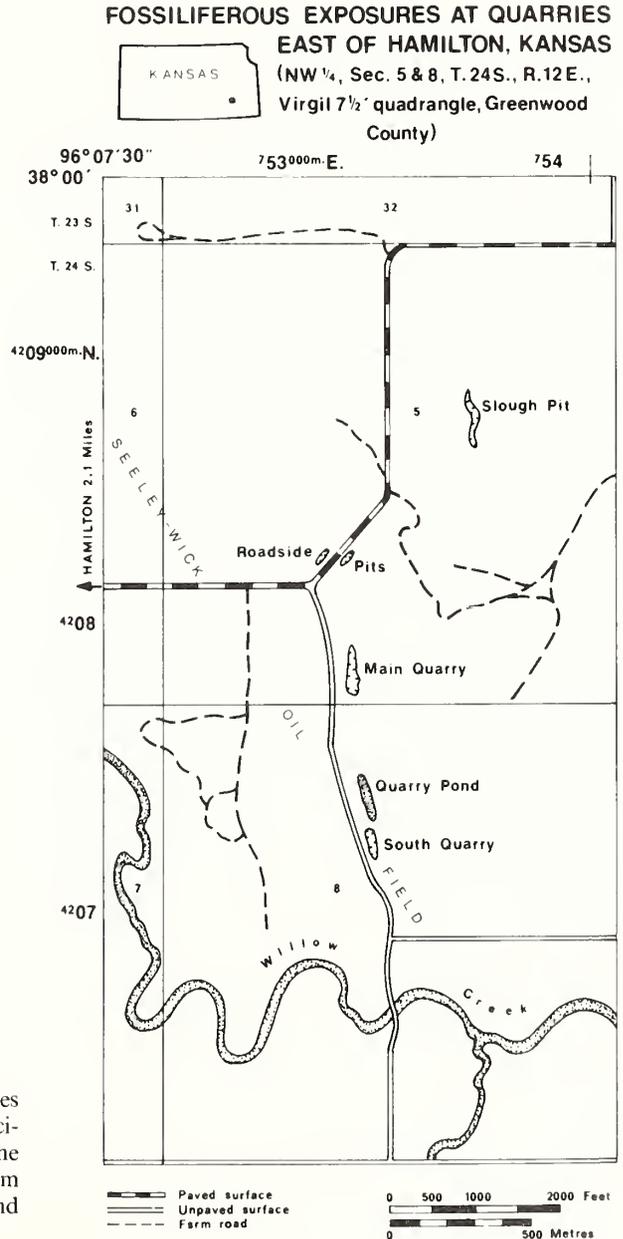
MATERIALS AND METHODS

Specimens of *Lebachia* are from an abandoned limestone quarry located east of Hamilton, Kansas (text-fig. 1). Conifer debris is common throughout the quarry (Leisman 1971), and ranges from finely disaggregated cuticles and wood fragments through compressed and/or permineralized cones and woody branching systems. The fossil flora at Hamilton is primarily gymnospermous, with conifers dominating in number and in diversity. Numerous animal remains also occur in this deposit, including insects (Hanson 1973), eurypterids (Anderson 1974), acanthodians (Zidek 1976), amphibians, foraminifera, and ostracods. Brachiopods and clams from the fossiliferous matrix have been identified as *Hystriculina wabashensis*, *Reticulatia heucoensis*, and possibly *Derbyia*, *Edmondia*, and *Myalina* spp. While these particular animal remains are sometimes poorly preserved, their occurrence in these sediments suggests strongly that the strata are of Pennsylvanian age (R. D. Hoare, Bowling Green State University, Ohio, pers. comm.).

The fossil-bearing unit at Hamilton quarry is a channel deposit, and consists of a basal conglomerate which grades into fine-grained laminated limestone. Although miscellaneous fossil remains are present in some of the clasts in the conglomerate, the permineralized plants and the majority of the animal fossils are in the limestone. While underlying and surrounding rocks have been recognized as the Hartford Limestone of the Topeka Limestone Formation, Shawnee Group, Virgilian (Andersen 1974; Zidek 1976), the age of the conifer-rich horizon *per se* has not been determined with certainty. In addition to the conifers, the Hamilton flora contains various cordaitan, fern, and seed fern remains. Certain highly dissected foliage was originally reported as the pre-ginkgophyte *Dichophyllum* (Andrews 1941), but has since been interpreted as *Callipteris flabellifera* (Remy *et al.* 1980). If this is correct, several alternatives are possible stratigraphically. The Hamilton beds could be equivalent to one of the Permian zones 11 to 14 (Remy 1975) of Read and Mamay (1964) or to the European Autunian (Remy and Havlena 1960, 1962; Remy *et al.* 1966), or *C. flabellifera* may have entered the flora earlier in the eastern and mid-continent U.S.A. than in the European section. While *Callipteris* spp. have been recognized as earliest Permian indicators, there are also reports of their occurrence world-wide in lower (older) strata (Barlow 1975; Gillespie *et al.* 1978). Assignment of these beds to either the upper Pennsylvanian or lower Permian awaits additional work with the more stratigraphically diagnostic forms of the biota.

Specimens were generally revealed by splitting the limestone matrix along the bedding plain. Morphological features were examined on the surfaces. The part and counterpart of some permineralized specimens were glued back together and serial sectioned in transverse or longitudinal plane. One part of other permineralized specimens was covered with liquid plastic then sectioned, while the counterpart was macerated in 2.5% HCl for cuticular preparations. Serial sections were prepared by the well-known cellulose acetate peel technique (Joy *et al.* 1956). Pertinent sections were mounted on standard microscope slides for transmitted light study and photography. Since the matrix was often nearly transparent while a peel was still attached, three-dimensional perspective could often be seen. Some of these surfaces were photographed with polarized reflected light (e.g. Pl. 16, figs. 1, 2). Photography was also with unpolarized reflected light, transmitted bright-field,

and Nomarski differential interference contrast (DIC) optics. Some macerated cuticle, tissue fragments, and prepollen grains were mounted on microscope slides for light optical study, while others were rinsed in distilled water, mounted on stubs with double-sided tape, and coated with gold for scanning electron microscopy. Specimens examined in this study are M26, M83, M144, M145, M147-152, and bear acquisition numbers 3834 to 4268 in the Paleobotanical Herbarium, Department of Botany, Ohio University, Athens, Ohio, U.S.A.



TEXT-FIG. 1. Fossiliferous exposures at quarries east of Hamilton, Kansas. *Lebachia lockardii* specimens have been recovered from all of the pits. The majority of the permineralized cones are from excavations directly west of the Main Quarry and the Quarry Pond.

SYSTEMATIC DESCRIPTION

Order CONIFERALES

Family LEBACHIAEAE

Genus LEBACHIA Florin 1938

Lebachia lockardii sp. nov.

Plates 9–16

Diagnosis. Ovulate cones, averaging 5.0 cm long \times 1.5 cm wide, borne as single terminal units on vegetative axes with helically arranged simple or bifid leaves. Cones comprised of primary axis with helically arranged bifid bracts and axillary fertile shoots. Fertile shoots bearing twenty-five to thirty sterile scales and one to two fertile scales (rarely three to five) positioned adjacent to primary axis. One terminal inverted ovule per fertile scale. Ovules bilaterally symmetrical and winged, with rounded or cordate base and attenuated micropyle. Nucellus free from integument distal to chalaza. Simple pollen chamber with nucellar beak; often containing *Potonieisporites* grains. Stomata with five to nine unipapillate subsidiary cells. Adaxial leaf structure with stomata in two parallel bands, each four to eight stomata wide with some shared subsidiary cells; single bands or isolated rows of stomata occurring on some leaves. Abaxial cuticles papillate and less stomatiferous. Unicellular hairs common at margins of leaves and bracts.

Holotype. Slides, peels, and remaining portions of specimen M26; repositied in the Palaeobotanical Herbarium, Ohio University, as numbers: 3834–3851; 3867–3912; 3968–4092; 4267, and represented herein as Plate 9, fig. 5; Plate 10, figs. 1–3, 5, 6; Plate 11, figs. 1, 3–6; Plate 12, fig. 4; Plate 13, figs. 1, 3, 5; Plate 14, figs. 1–8.

Paratypes. Specimens M147 and M148 repositied as above, as numbers 4093–4147; 4234–4251, and 3855–3865; 4160–4218; 4260–4262; 4268, respectively, and figured herein as (M147) Plate 9, figs. 1, 4, and (M148) Plate 11, figs. 2, 5, 7; Plate 12, figs. 5, 7, 8; Plate 13, figs. 1, 4, 6; Plate 15, figs. 1–3, 5–7; Plate 16, figs. 1–3.

Locality. Hamilton quarries; NW quarter, sec. 5 and 8, T.24S., R.12E., Virgil seven and a half foot quadrangle, Greenwood County, Kansas, U.S.A.

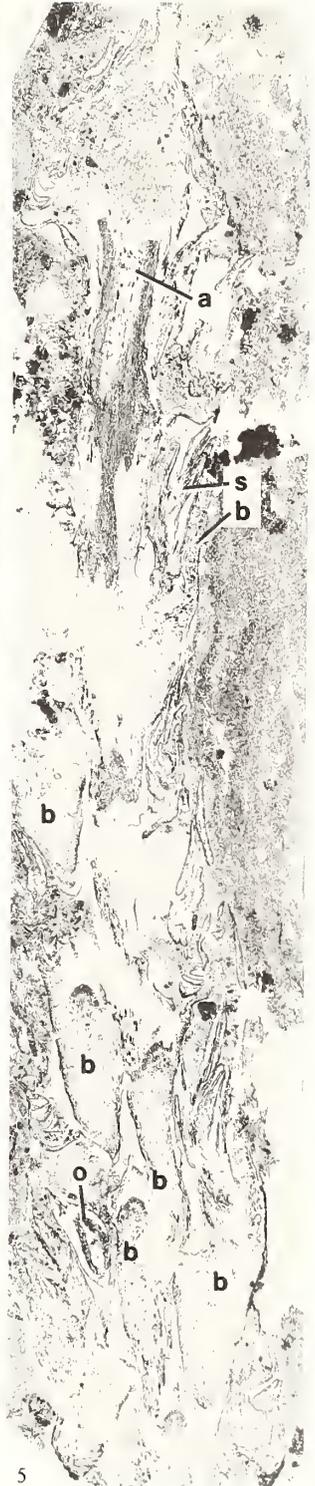
Etymology. This species is named for Walter Lockard, who recognized the potential of the unique Hamilton fossil assemblage over twenty years ago, and has diligently obtained and generously shared his extensive field collections for palaeontological studies.

Description. Fifteen whole and partial permineralized cones, and numerous compressed specimens were examined. These ovulate cones are cylindrical-ellipsoidal and quite compact (Pl. 9, figs. 1–4). Complete cones are generally 4.0 to 5.5 cm long with a maximum diameter of 1.5 cm in their mid-regions. While large branching systems with attached ovulate cones of *L. lockardii* have not been recovered, all known *Lebachia* cones are terminal, and some of the *L. lockardii* cones retain up to 4 cm of vegetative axis below the cone base (Pl. 9, fig. 1). Leaves on the subtending axes are either bifid or simple, and provide a clue to the original positions of the cones on the branch systems.

Because the ovulate cones represent compound shoots, by definition they occur on penultimate or antepenultimate branches (= ultimate and penultimate branches of Florin 1951). The primary cone axis represents the penultimate branch and the fertile, secondary shoot is homologous with the ultimate vegetative branch. Each primary cone axis bears many helically arranged fertile complexes, comprised of a bifid bract

EXPLANATION OF PLATE 9

Figs. 1–5. *Lebachia lockardii* sp. nov., ovulate conifer cones from Hamilton, Kansas. a, primary cone axis; b, bract; o, ovule; s, secondary shoot. 1, cone attached to vegetative shoot, M147, $\times 2$. 2, cone split longitudinally, note attachment of secondary shoots to cone axis, M150, $\times 2$. 3, abraded cone surface with prominent sterile scales of secondary shoots, M146, $\times 2.5$. 4, apex of cone in fig. 1, note sterile scales of flattened secondary shoots, M147, $\times 3$. 5, holotype, oblique longitudinal section, showing helical arrangement of bracts and the relative positions of bracts to axillary secondary shoots, M26 No. 1, $\times 5$.



and an axillary shoot with several sterile and fertile scales. Florin (1938, 1951) called the fertile shoots 'flowers' and characterized the fertile shoot axes of *Lebachia* ovulate cones as radially symmetrical. The often excellently preserved and undistorted fertile shoots (= secondary shoots) of *L. lockardii* are clearly bilaterally symmetrical; their flatness is biologic, not taphonomic. The stele of the secondary shoot (= cone scale trace of more recent conifers) is crescent-shaped in transverse section, not radial as are the secondary shoot steles of cordaitan strobili (Rothwell 1977; Daghljan and Taylor 1979). While unabraded external surfaces of *L. lockardii* cones often retain the bifid bracts, the axillary shoots with their numerous scales are more easily recognized (Pl. 9, figs. 1-4). In the apical region of the cone, the bracts have no secondary shoots in their axils (Pl. 10, fig. 4).

The primary cone axis has a eustele with the endarch xylem maturation that is characteristic of more recent conifers. Pith and cortical cells are typically 15 to 25 μm in diameter and always thin-walled (Pl. 10, figs. 2, 3, 5). Some of these cells are elongate, have dark contents, and are up to 70 μm in diameter; cells of this type may have had secretory or storage functions. Primary xylem tracheids are narrow, average 7.5 μm in diameter, and have angular-spiral and scalariform wall thickenings (Pl. 11, fig. 1). The secondary xylem is compact, basically pycnoxylic, and forms a cylinder averaging 1.3 mm in diameter (Pl. 10, figs. 1, 5, 6). In transverse sections, tracheids are ovoid-polygonal (Pl. 11, fig. 3). Throughout most of the wood the tracheids have uniseriate pitting (Pl. 11, fig. 6), but the tracheids adjacent to the primary xylem sometimes show uniseriate oval pits and/or biseriate opposite circular bordered pits (Pl. 11, figs. 4, 6). Rays are uniseriate to biseriate, one to five cells high, and composed of poorly preserved parenchyma with no evidence of ray tracheids (Pl. 11, figs. 1, 3).

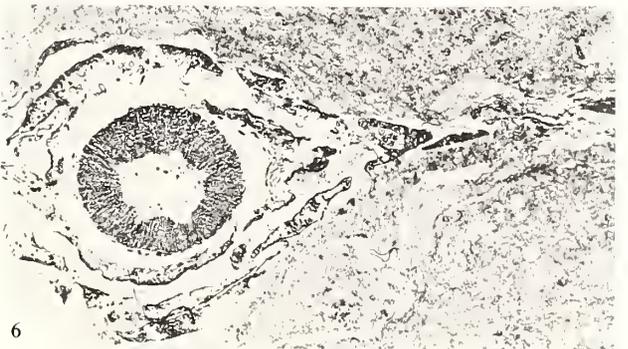
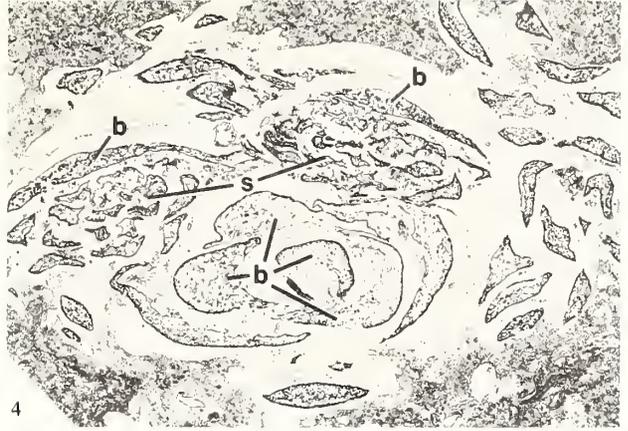
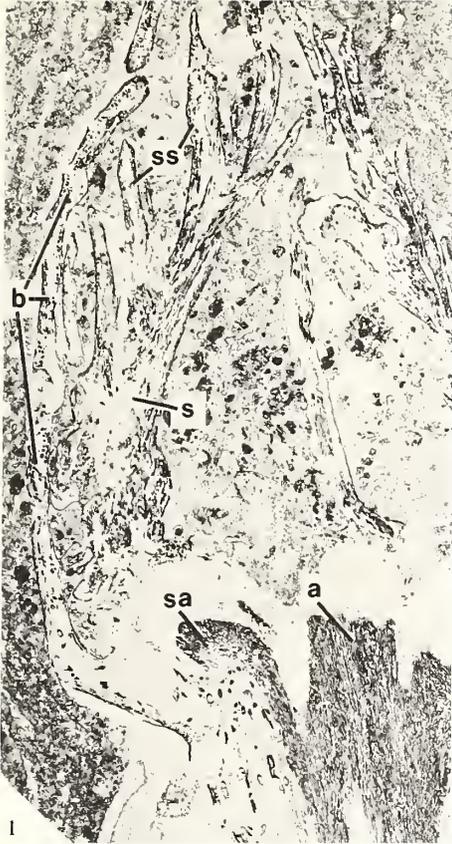
The bifid bracts have deeply heeled bases (Pl. 9, fig. 5; Pl. 10, fig. 3). Distal forking can be recognized in transverse sections near the bract apex (Pl. 14, fig. 1 at top). Similar forked leaves occur on penultimate and antepenultimate vegetative axes, and at the cone base/vegetative branch transition zone on lateral shoots bearing otherwise simple leaves (Florin 1951). Such bifid leaves and bracts are sometimes referred to *Gomphostrobus* Marion (1890) and are vascularized by a single trace which bifurcates below the bifid apex. The tracheids are usually poorly preserved, but scalariform wall thickenings have been observed. Ground tissue consists of isodiametric, loosely packed parenchyma cells (Pl. 10, fig. 3), many of which contain dark contents which may be secretory. An abaxial hypodermis occurs throughout the length of the bract, but diminishes in prominence distally. The hypodermis consists of two to four cell layers of elongate, closely packed cortical cells directly beneath the epidermis (Pl. 10, figs. 3, 5).

Lebachia leaf cuticle has been characterized by Florin (1938-1945) as thick, papillate, and amphistomatic, with each leaf commonly bearing two broad parallel bands of haplocheilic stomata. The stomata have two guard cells surrounded by four to eleven subsidiary cells with overarching papillae. Cuticles of *L. lockardii* have these features, and contribute additional information regarding variations of the cuticular features in a single species.

The stomatal bands of *L. lockardii* vary in width, length, and composition. There may be single bands or parallel bands, and stomata occur both on abaxial and adaxial leaf surfaces. Within individual ovulate cones of *L. lockardii*, there is a wide range of variation. Parallel bands, generally four to eight stomata wide, are present only on adaxial leaf surfaces. Single bands of comparable width are sometimes seen on sterile scales. Stomatal arrangement within a band is also variable. Generally, stomata are irregularly disposed, though longitudinally oriented, with some shared subsidiary cells (Pl. 12, fig. 1). In other areas there are more widely separated or even single rows of longitudinally oriented stomata (Pl. 12, figs. 3, 6) or isolated stomatal apparatuses. The least stomatiferous cuticles are those of the smallest sterile scales, the cone axes, and the abaxial surfaces of bracts. The ovulate cone cuticles of *L. lockardii* are certainly amphistomatic, but the majority of the stomata are adaxial. While comparable to the species of *Lebachia* characterized by Florin

EXPLANATION OF PLATE 10

Figs. 1-6. *Lebachia lockardii* sp. nov. a, primary cone axis; b, bract; o, ovule; s, secondary shoot; sa, secondary shoot axis, ss, sterile scales. 1, longitudinal section of cone near apex. Note arrangement of vascular tissues, bract, and axillary secondary shoot, M26 B side No. 5, $\times 14$. 2, tangential section of detached ovule and crescentic vascular trace of fertile secondary shoot, M26 No. 1, $\times 13$. 3, bract bases in tangential section. Note abaxial hypodermis, cortical cells with dark contents, and vascular trace at arrow, M26 A side No. 4, $\times 16$. 4, transverse section near cone apex, M83 Top No. 25, $\times 14$. 5, transverse section of cone, note two ovules of one secondary shoot, M26 B Top No. 58, $\times 12$. 6, transverse section of primary cone axis below fertile zone, M26 A Top No. 33, $\times 14$.



(1938–1945), each stoma of *L. lockardii* has five to nine subsidiary cells, each with a single papilla overarching the stomatal opening (Pl. 12, fig. 6). In bands of closely spaced stomata, subsidiary cells are sometimes shared by adjacent stomata, but papillae are usually single. More commonly, small epidermal cells intervene, separating the subsidiary cells of adjacent stomata (Pl. 12, fig. 6 at arrow). The guard cells are generally not preserved.

Epidermal cells within and between stomatal bands vary in shape and size, and in the presence or absence of papillae and hairs. Papillate epidermal cells are sometimes present on both abaxial and adaxial surfaces (Pl. 12, figs. 2, 7), but are most common on abaxial cuticles. In addition, they occur both in and between the bands of stomata. Although exceptions have been noted, there is usually only one papilla per epidermal cell. Papillae are most often on small, rather isodiametric cells, but they also occur on the tabular and the broadly polygonal epidermal cells (Pl. 12, figs. 2, 7). Uniseriate hairs are common on the margins (Pl. 12, figs. 1, 8) and can be seen on both surfaces of *L. lockardii* leaves. The longest hairs (up to 0.6 mm long) are often twisted and some may be multicellular.

A feature of considerable interest characterizes certain small epidermal cells. These cells are rounded rather than angular, and display a central circular area, av. 8–12 μm diameter, with raised rim and often dislodged cuticular surface (Pl. 12, figs. 4, 5). These areas resemble closely the waxy plugs or cuticular flaps which cover sunken stomata of certain species of fossil and modern *Araucaria* (Stockey and Taylor 1978a, b). However, these cells are not associated with the stomata of *L. lockardii*. Rather, they are often surrounded by larger epidermal cells and can be easily recognized in surface view or optical section by their coronas (Pl. 12, figs. 4, 5). We interpret the corona to represent the area between the rim of the circular area and the widest lateral extent of the walls of the small isodiametric cell, where the cell wall margin subtends that of the adjacent surrounding epidermal cells. The surface flap or plug of cuticle probably resulted from the collapse of a small hair or a broad low papilla. These cells resemble some of those Florin called hair bases (e.g. *L. americana*, text-abb. 20A, Florin 1938–1945).

In *L. lockardii* numerous irregularly arranged sterile scales and one or more fertile scales are typically present on each secondary shoot (Pl. 10, figs. 1, 5). This deviation from the helical arrangement of leaves on vegetative stems of *Lebachia* results from the combination of flatness of the secondary shoot axis (Pl. 10, fig. 5) and the smaller number of scales present on the side of the shoot that lies adjacent to the primary cone axis. Where the bracts are not preserved, fertile shoots often display a fan of nine to twelve sterile scales (Pl. 9, figs. 2–4). In some transverse sections, twenty to twenty-five scales can be seen at a single level, and serial sections indicate that more than thirty scales may be present on individual fertile shoots.

Within cones, the fertile secondary shoots are attached to the primary axis at intervals of approximately 5 mm, and average 2.0–2.5 mm long. In transverse sections below scale attachment, individual secondary shoot axes are 0.2–1.0 mm in diameter, expanding up to 3 mm wide in the zone of scale attachment (Pl. 10, fig. 5). On some bedding planes isolated shoots from disaggregated cones can be recognized among the coniferous debris. The isolated shoots are comparable to those within the ovulate cones, but never have mature ovules attached.

The sterile scales most distally attached to each secondary shoot are usually fused at their bases (Pl. 9, fig. 4; Pl. 13, figs. 4, 6), and can sometimes be macerated loose as dentate units of two to five scales. Most of the macerated sterile scales taper to an acutely pointed apex, but a small number of scales have an abruptly truncated tip with a central cleft and subapical protruberance (Pl. 13, fig. 5). The latter scales are remarkably similar to certain fertile scales of ovulate *Cordaianthus strobili*, where the ovules are either extremely immature

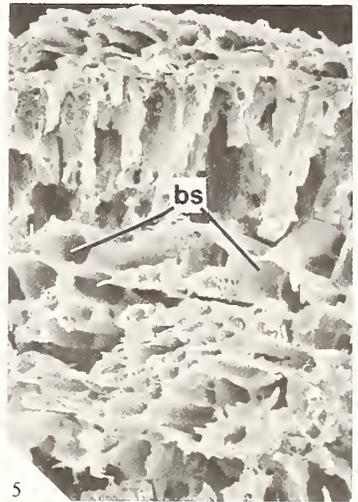
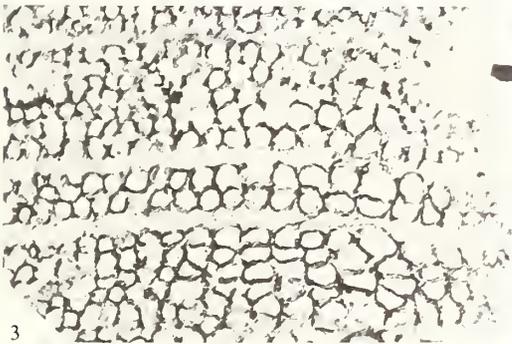
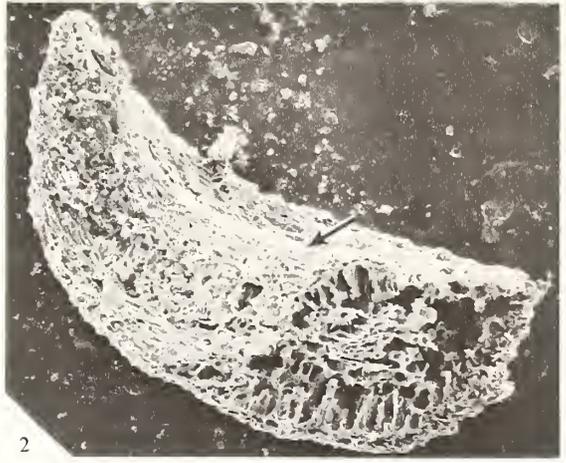
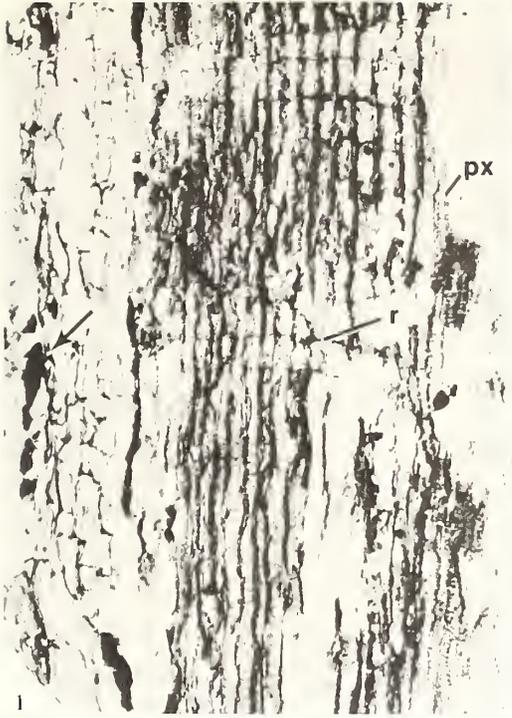
EXPLANATION OF PLATE 11

Lebachia lockardii sp. nov. Wood and leaf anatomy. bs, bundle sheath; px, primary xylem; r, ray.

Fig. 1. Radial section of wood of primary cone axis, arrow indicates secretory cells, M26 B side No. 1, $\times 130$. Figs. 2, 5, 7. Scanning electron micrographs of coalified sterile scales from ovulate cone maceration. 2, note adaxial ridge at arrow, and upcurved leaf tip, M148 Mac Leaf A, $\times 80$. 5, epidermis, palisade, and vascular trace with bundle sheath, M148 Mac Leaf A, $\times 250$. 7, spongy mesophyll tissue and vascular trace with bundle sheath, M148 Mac Leaf B, $\times 250$.

Fig. 3. Transverse section of wood from primary cone axis. Note poorly preserved rays, M26 B Top No. 33, $\times 185$.

Figs. 4, 6. Bordered pits (Nomarski DIC). 4, single tracheid with uniseriate to biseriate oval pits, M26 A side No. 1, $\times 820$. 6, tracheids with uniseriate circular pits, M26 A side No. 1, $\times 820$.



MAPES and ROTHWELL, *Lebachia* cones

or abortive (Florin 1951, fig. 21; Rothwell 1982*a*). Specimens of this type suggest that there was potentially a larger number of fertile scales on *Lebachia* fertile shoots than is reflected by the number of well-formed ovules.

Papillae are common on all surfaces and prominent hairs are sometimes preserved at the scale margins. Ground tissue of the scales is comprised of loosely packed spongy mesophyll (Pl. 11, fig. 7) comparable to the cortex of the bifid bracts, and a weakly developed palisade can sometimes be recognized (Pl. 11, figs. 2, 5).

The fertile scales, or sporophylls, are comparable to the sterile scales in both anatomical and morphological features. They are sometimes rounder in cross-section, averaging 0.3 to 0.8 mm (Pl. 13, fig. 4), and are from 0.5 to 2.0 mm long (Pl. 13, fig. 1). Fertile scales are always located adjacent to the primary axis, and are either abruptly truncated, with no epidermis at the apex, or terminate in a single ovule. Some fertile shoots bear one or two ovules, but many have none, possibly because the ovules had already dropped off, or because none had formed.

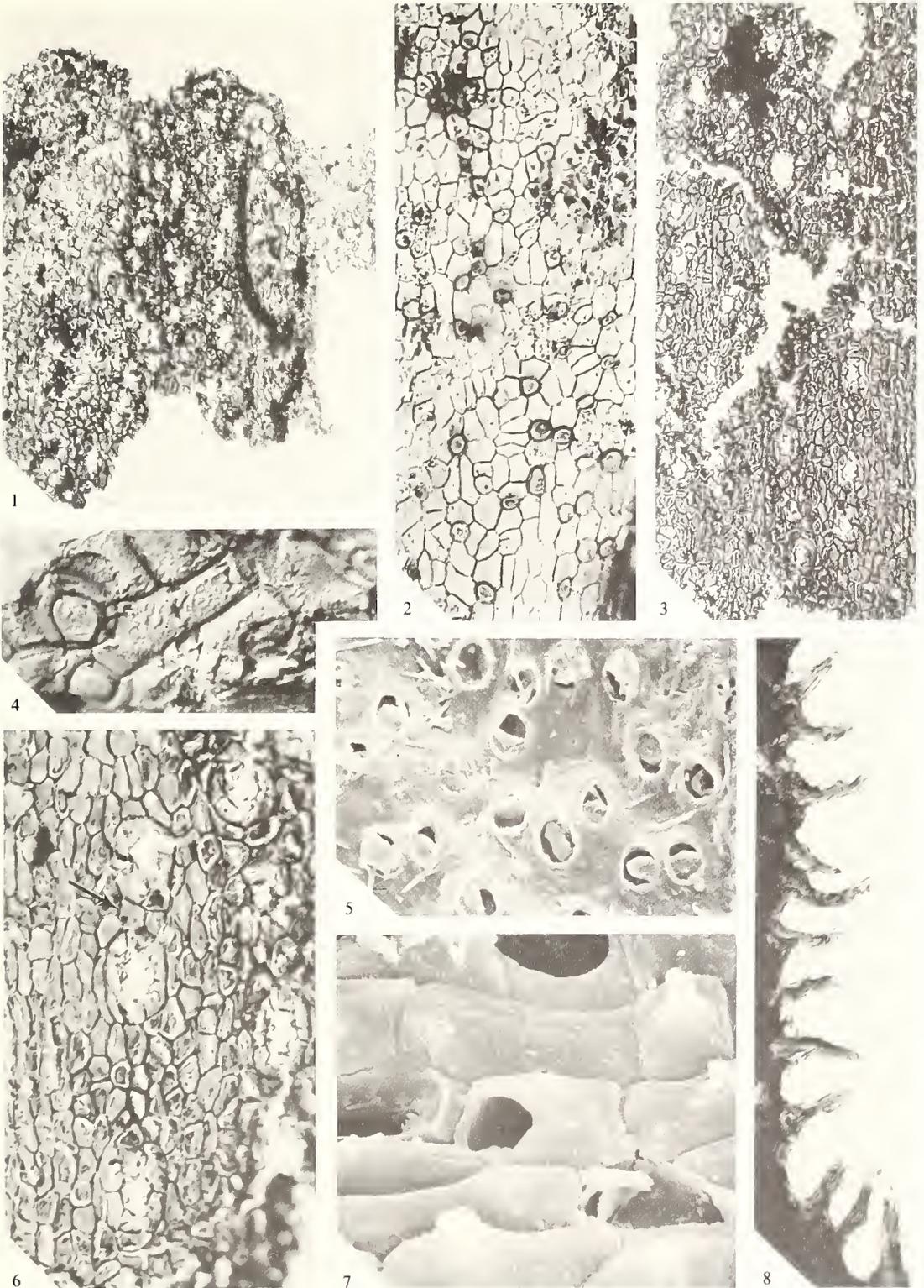
Of particular interest are ovulate scales with histological features like those of extant plants in which organs have been sectioned at various stages of abscission (e.g. Barnell 1939). Some specimens show good cellular continuity between the scale tip and the chalaza of the ovule (Pl. 13, fig. 2), but the width of the attachment is noticeably reduced by a prominent groove extending around the periphery of the constricted attachment area (Pl. 13, fig. 3). In other specimens the ground tissue at the level of the groove is poorly preserved with only the darker, apparently thicker-walled, cells at the centre of the zone connecting the ovule to the scale (Pl. 13, fig. 3). In still other instances, the cellular continuity between scale and ovule is completely disrupted (Pl. 13, fig. 4). Upon closer examination of the groove region, most of the cells of the ground tissue appear thin-walled, relatively isodiametric, and randomly disposed (Pl. 13, fig. 2). In specimens with partly or completely disassociated ovules (Pl. 13, figs. 2–4), cells in the groove region are like those in the separation layer of abscising organs, after the cell walls have undergone enzymatic gelatinization and dissolution. Two or three cell layers proximal to the separation layer of some fertile *Lebachia* scales there exists a small number of cells that are rectangular in section view and aligned both parallel to and at right angles to the line of abscission. Cells of this latter type conform closely to those of the protection layer often formed proximal to the separation layer in the abscission zones of extant plants (Esau 1965). Prominent cell walls containing lignin and/or suberin have not been observed in these *Lebachia* specimens.

Perhaps the most surprising feature of *L. lockardii* is the mode of ovule attachment. While the ovules are terminal on the scales of the secondary shoots, they are inverted, rather than erect as interpreted by Florin for all previously known species of *Lebachia* (Florin 1938–1945, 1951). The basipetal serial sequence of transverse sections illustrated in Plate 4 clearly demonstrates the relationship of two ovules with the secondary shoot upon which they were borne. Figure 1 is closest to the cone apex and shows the bases of both ovules. The left ovule is sectioned just below the level of attachment to its fertile scale, while the right ovule is sectioned above the level of attachment, and is represented only by its two basal lobes. Several sterile scale tips can be seen at this level and the distal portion of the bract subtending the secondary shoot is at the top of the figure. The central constriction marks the position where the bract apex forks distally. The helical arrangement of the cone parts is indicated by the broad bract base and the secondary shoot stele diverging from the primary cone axis at the lower left.

Progression basipetally shows the basal lobes of the right ovule join (Pl. 14, fig. 2) and the ovule becomes attached to its fertile scale. Note the cuticle in the area of the abscission zone is continuous (Pl. 14, fig. 3) except for a small mechanical break at far right. By the level represented at fig. 4, the right ovule has separated from its fertile scale and the seed cavities of both ovules are evident. The nucellar beaks of the left ovule and right ovule are seen in figs. 5 and 6 respectively, and the remaining sections proceed through the

EXPLANATION OF PLATE 12

Figs. 1–8. Cuticular features, *Lebachia lockardii* sp. nov. 1, bract cuticle, adaxial surface with band of stomata and prominent marginal hair, M149 Mac No. 6, $\times 100$. 2, abaxial cuticle with many coronate and/or papillate cells, M149 Mac No. 1, $\times 210$. 3, longitudinally oriented rows of stomata, M145 Mac No. 9, $\times 110$. 4, portion of cuticle viewed from inside. Note coronate, circular rimmed cells (Nomarski DIC), M26 A side No. 1, $\times 740$. 5, cuticle surface with apparent cuticular flaps or plugs, M148 SEM-13, $\times 600$. 6, stomata with overarching papillae. Arrow notes epidermal cells between adjacent stomata, M145 Mac No. 9, $\times 260$. 7, papillate epidermal cells, M148 SEM-9, $\times 1200$. 8, hairs at bract margin, M148 Mac No. 3, $\times 290$.



MAPES and ROTHWELL, *Lebachia* cones

narrowing, attenuated micropyles (Pl. 14, figs. 6–8). The longitudinal section in Plate 13, fig. 1, and text-fig. 2, also demonstrate the relative positions within a fertile complex. Although ovules are often found dislodged laterally within the cones of *L. lockardii*, when attached they are always in an inverted orientation with micropyle located between the primary cone axis and the base of the secondary shoot (Pl. 13, fig. 1).

Approximately seventeen ovules remain within the cones of *L. lockardii*. Several of these are poorly preserved, incomplete, and/or possibly abortive, but others are more complete. All of the ovules are clearly bilaterally symmetrical (Rothwell 1982b) and have an attenuated micropyle. In transverse sections the micropylar canal tapers gradually toward the apex of the ovule (Pl. 14, figs. 6–8) and may be reduced to as little as 0.1 mm in maximum diameter. However, none of the specimens is well preserved at the apex. The base of the ovules is either cordate (Pl. 14, fig. 1) or rounded (text-fig. 2). Individual ovules measured in transverse sections average 2.3 mm in the major plane and 0.6 mm in the minor plane.

The integument consists of several zones of thin-walled cells (Pl. 15, figs. 1–3) and is free from the nucellus except at the chalaza. Clearly defined sarcotesta, sclerotesta, and endotesta that characterize most mature gymnosperm ovules are not present. This may be due in part to incomplete tissue differentiation. The outer margin of the integument is delimited by a uniseriate epidermis covered by a conspicuous dark line that represents the cuticle (Pl. 15, figs. 1, 2). The epidermal cells are uniformly thin-walled and usually have empty lumina.

Individual epidermal cells are rectangular-polygonal and many are papillate. There are also conspicuous uniseriate epidermal hairs preserved on many ovules (Pl. 15, figs. 2, 6). Inside the epidermis there is a zone of variable thickness where many of the thin-walled cells contain prominent dark contents. Cells of this type are preserved only at the margins of the wings in the ovules figured on Plate 14 (Pl. 14, fig. 4), but are more uniformly preserved in other specimens (Pl. 15, figs. 1–3). Immediately to the inside of this zone is another zone of thin-walled cells which typically lack internal contents (Pl. 15, figs. 1–3). The inner margin of the integument is delimited by a conspicuous epidermis; the cells typically have dark contents (Pl. 15, figs. 1, 2). In some specimens the thin-walled cells are separated from the inner epidermis either by an empty space or by the inconspicuous remnants of extremely thin-walled cells (Pl. 15, fig. 2 at arrow). These remnants resemble the undifferentiated sclerotesta of immature Palaeozoic ovules assignable to cordaites (Stidd and Cosentino 1976) and pteridosperms (Rothwell 1971, 1980). In two specimens there are two patches each of poorly preserved, thick-walled cells at the level of the pollen chamber (Pl. 16, figs. 1, 2 at arrows). These are preserved in the minor plane and resemble the first differentiated areas of sclerotesta in previously described Carboniferous cardiocarpean ovules.

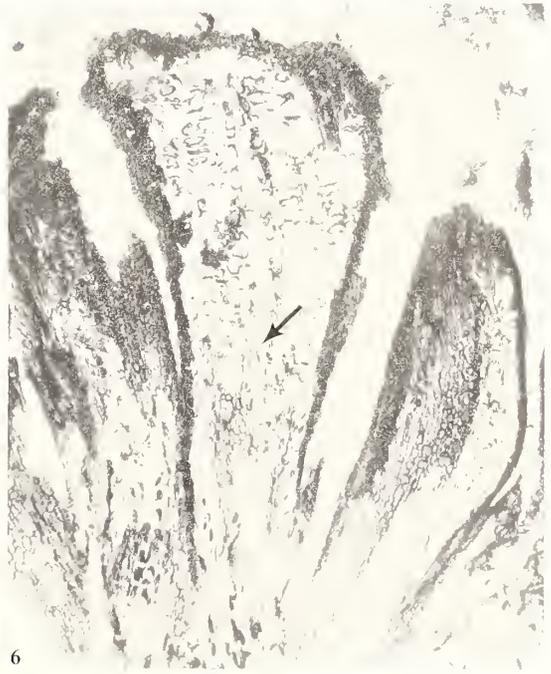
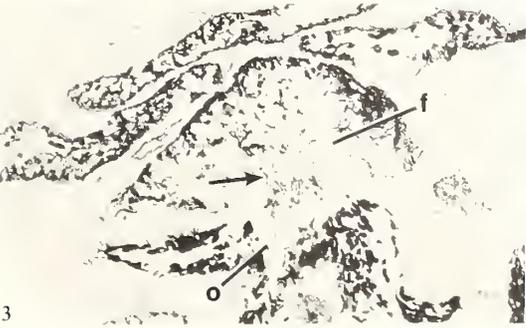
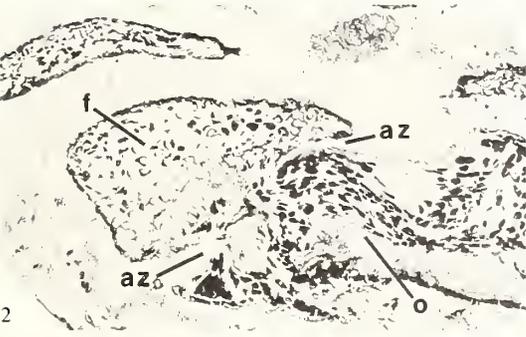
Vascular tissue has been difficult to identify within the ovules of *L. lockardii*, but in one specimen poorly preserved tracheids have been located (Pl. 15, fig. 7). These were observed near the base of the ovule in a position which is comparable to that occupied by the integumentary bundles of cardiocarpean ovules (e.g. *Mitrospermum vinculum* Grove and Rothwell 1980).

As is also characteristic of Palaeozoic cordaites ovules, the nucellus of *L. lockardii* is attached to the integument at the chalaza and free distally (Pl. 15, figs. 1, 2). It surrounds the megaspore membrane of the megagametophyte, and forms a prominent pollen chamber distally (Pl. 16, figs. 1, 2). In the midregion the nucellus is several cell layers thick (Pl. 15, fig. 2). Nucellar cells are usually small and thin-walled, and many contain dark substances (Pl. 15, figs. 1, 2, 4). A cuticle is present at the outer margin of the nucellus, and in surface view reveals the size, shape, and orientation of the nucellar epidermal cells (Pl. 15, figs. 4, 5).

The pollen chamber is round in transverse section (Pl. 15, figs. 1 at top, 4), and tapers distally to engage the base of the micropylar canal. The pollen chamber wall consists of one to two layers of cells that are like

EXPLANATION OF PLATE 13

Figs. 1–6. *Lebachia lockardii* sp. nov. a, primary cone axis; az, abscission zone; b, bract; f, fertile scale; o, ovule; s, secondary shoot; sl, separation layer. 1, longitudinal section of attached secondary shoot and subtending bract. Arrows indicate area where fertile scale adjoins ovule, M26 B side No. 9, $\times 25$. 2, fertile scale and ovule with groove at abscission zone, transverse section, M148 B Top No. 32, $\times 47$. 3, ovule incompletely abscised from fertile scale, note protection layer at arrow, M26 B Top No. 50, $\times 47$. 4, transverse section near tip of secondary shoot, showing ovule and scale from which it has abscised, M148 B Top No. 28, $\times 47$. 5, lobed tip of scale with small central protrusion, M26 Mac No. 7, $\times 75$. 6, sterile scales with mesophyll, central vascular trace (at arrow) and partial cuticle, M148 B Top No. 5, $\times 74$.



MAPES and ROTHWELL, *Lebachia* cones

those at more proximal levels of the nucellus (Pl. 15, fig. 4). Distally, the pollen chamber wall thins to one layer of distinct cells that form a conspicuous nucellar beak like those of many Palaeozoic trigonocarpalean and cardiocarpalean ovules (Pl. 14, figs. 5, 6; Pl. 15, fig. 1; Pl. 16, figs. 1, 2). Cells of the nucellar beak are large, with conspicuous walls and empty lumina (Pl. 15, fig. 1). In some sections the cells are rectangular, and often exhibit thickened radial walls (Pl. 15, fig. 1). There is no evidence of an organized pollen chamber floor region.

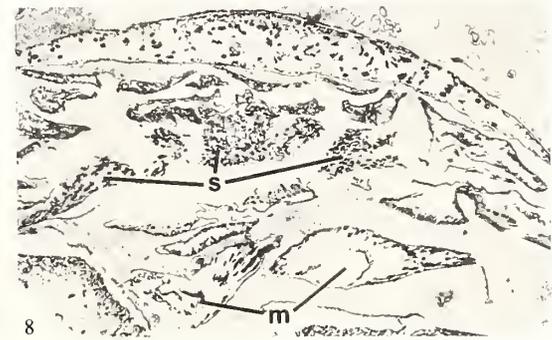
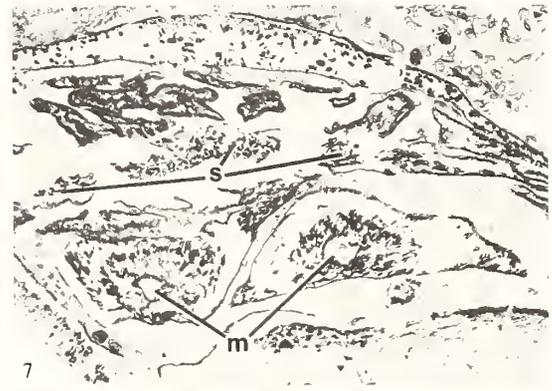
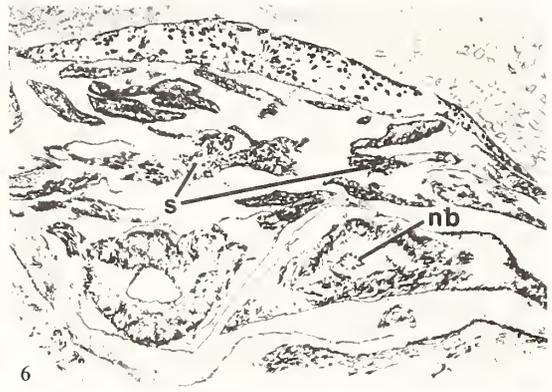
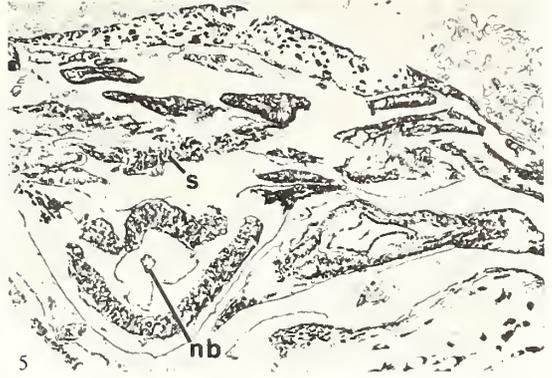
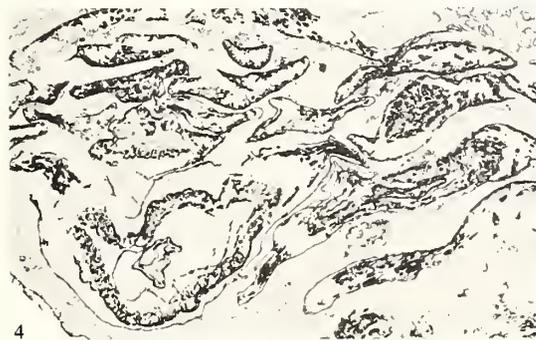
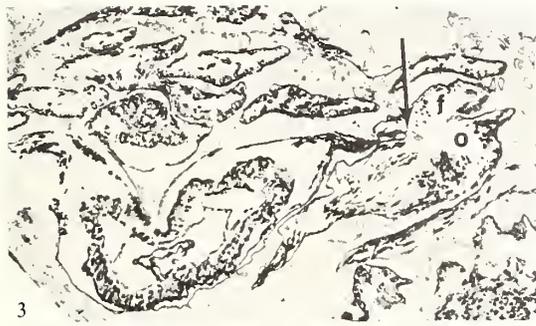
The megagametophyte in all available specimens is represented only by a megaspore membrane and the hollow it surrounds (Pl. 15, fig. 2). The megaspore membrane is golden-brown and, when viewed with light optics, is apparently homogeneous, not granular or pitted as are some (Pettit 1966; Zimmerman and Taylor 1970). Cellular megagametophyte tissue has not been observed.

Microgametophytes are preserved within the pollen chamber and micropyle of several ovules (Pl. 14, fig. 7 at right; Pl. 15, fig. 4; Pl. 16, figs. 1-3). The grains are all of one type and assignable to *Potonieisporites* Bhardwaj (1954). Apparently identical grains are abundant in the matrix within and immediately surrounding the ovulate cones, and also within the pollen sacs of associated *Lebachia* pollen cones (Mapes 1981). *Potonieisporites* is commonly reported from upper Palaeozoic strata world-wide (Wilson and Venkatachala 1964; Nygreen and Bourn 1967; Upshaw and Hedlund 1967; Gupta 1970; Neves and Belt 1971; Bharadwaj 1972; Balme 1980). It is also known *in situ* from compressed conifer pollen cones such as *L. piniformis* and *L. hypnoides*, *Ernestiodendron filiciforme*, and *Walchianthus crassus* and *W. cylindraceus* (Florin 1938-1945; Bharadwaj 1964).

Individual grains are monosaccate with a monolet suture proximally and usually two dark, crescent-shaped areas distally (Bharadwaj 1954; Pl. 16, fig. 4). The latter areas have been interpreted by previous authors as compression folds (Bharadwaj 1956), which may delimit the germinal area on the distal surface (Potonie and Lele 1961; Clarke 1965). Maximum saccus diameter observed was 118 μm , while the corpus diameter averages 50 μm . The girdling saccus is formed by separation of the sexine from the nexine in the equatorial region, and exhibits prominent internal reticulations (Pl. 16, figs. 3, 4). The intrareticulum is generally finer than that of most *Florinites* species. In section view the intrareticulum attaches the saccus to the corpus across the distal pole (Pl. 16, fig. 4). In our specimens the nexine is more dense optically at the point where the saccus separates from the corpus at the margins of the distal surface (Pl. 16, figs. 3, 4). This produces two dark, crescent-shaped areas like those interpreted as folds by previous authors. It is also clear from our specimens that there is no thin area distally, through which germination may have occurred (Pl. 16, fig. 4). On the proximal surface the corpus and saccus are more completely fused, and form a more optically dense exine (Pl. 16, fig. 4). Previous authors have interpreted the exine on the proximal surface of *Potonieisporites* as thicker than that of the distal surface. Scanning electron microscopy reveals that the proximal surface of the corpus is ornamented by irregular crowded rugae (Pl. 16, figs. 5, 6). In areas where the outer surface of the exine has been removed from the proximal surface of the grain (e.g. Pl. 16, fig. 6 at rectangle), the inner exine layer (= nexine) shows an ornamentation of dense, irregular granula (Pl. 16, fig. 5 at bottom). Therefore, in these specimens, intrareticulations are absent from the proximal surface of the grains. In addition, the monolet suture is clearly open in all specimens (Pl. 16, figs. 4, 6). This, together with the absence of a thin area on the distal surface, indicates that germination was proximal, and that these grains fall within the concept of prepollen (Renault 1896; Schopf 1938; 1948; Rothwell and Mickle 1982).

EXPLANATION OF PLATE 14

Figs. 1-8. *Lebachia lockardii* sp. nov. Holotype, basipetal series of transverse sections illustrating ovule attachment and orientation. All M26 B Top series, $\times 20$. a, primary cone axis; b, bract; f, fertile scale; m, micropyle; nb, nucellar beak; o, ovule. 1, section near levels of ovule attachment. Note broad base of ovule at left (just below level of attachment) and bilobed segments of ovule at right (at arrows; just above level of attachment to fertile scale). Primary cone axis and secondary shoot axis at lower left, with sterile scales and subtending bract at top, No. 76. 2, lobes of right ovule joined, No. 75. 3, right ovule base attached at fertile scale with cuticle continuous at arrow. Left ovule at level of seed cavity with nucellus and megaspore membrane, No. 72. 4, right ovule flattened at level of nucellus and megaspore membrane, No. 67. 5, sterile and fertile scales at tip of flattened secondary shoot. Left ovule with nucellar beak, No. 61. 6, left ovule showing micropyle; right ovule with nucellar beak, No. 56. 7, micropyles of both ovules narrowing. Note pollen grain in ovule at right, No. 53. 8, apex of both ovules near base of fertile shoot, No. 48.



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DISCUSSION

L. lockardii displays both the general morphology and the cuticular features that delimit the genus as circumscribed by Florin, and presents the first anatomical evidence upon which to characterize and interpret development and reproductive biology within the walchian conifers. The new species also provides an opportunity to clarify the nature of several features that have been interpreted as significant to the evolution of more modern conifers, and to explore the significance of variation among specimens of the Palaeozoic Lebachiaceae. As is typical of previously described *Lebachia* ovulate cones, *L. lockardii* consists of a primary axis that bears helically arranged bifid bracts with axillary fertile shoots. The fertile shoots each have a short axis that bears numerous scale-like leaves, one or two of which have terminal ovules. Fertile scales are consistently located adjacent to the primary axis.

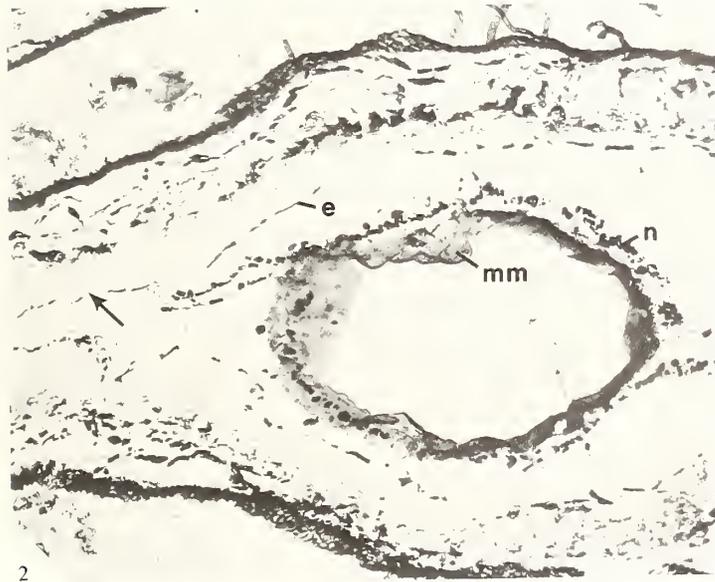
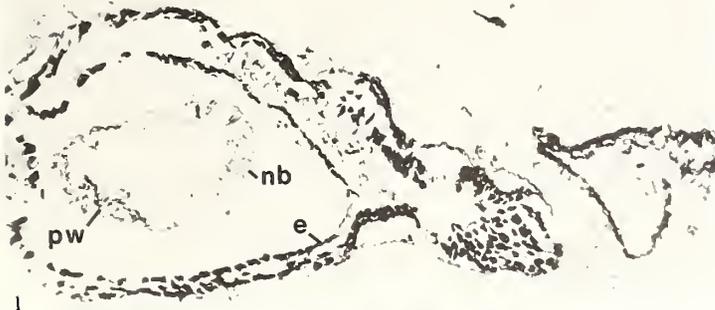
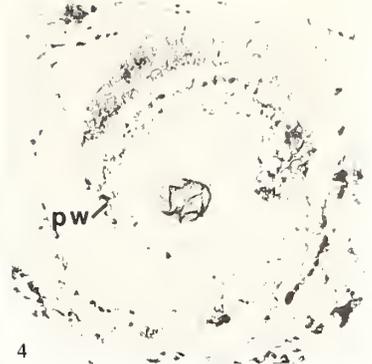
The different expression of features preserved by compression vs. permineralization precludes detailed specific comparison and assignment to a previously described species. However, split surfaces of slabs containing fertile *L. lockardii* reveal general morphologic features, and incomplete branches are attached below some cones. Numerous isolated vegetative branches are also present in the matrix and will undoubtedly yield additional information regarding branching patterns. As described by Florin and others, the *Lebachia* compression species most comparable to *L. lockardii* are *L. parvifolia*, *L. americana*, *L. hypnoides*, and *L. piniformis*. However, until information about the internal features of these species has been obtained, serious questions regarding their specific relationships to *L. lockardii* will remain. Features of *L. lockardii* that could not have readily been determined from compression remains alone include the inverted orientation of the ovules and the bilateral symmetry of the secondary shoots. Our permineralized, uncompressed cones clearly demonstrate the bilateral symmetry of the secondary shoots. Each secondary shoot has a crescentic stele and a smaller number of scales toward the primary cone axis. While these features are useful for separation of *L. lockardii* from other species of the genus, some of the apparent differences may also be due to our less complete understanding of compression specimens.

Prior to the discovery of *L. lockardii*, *Moyliostrobus* Miller and Brown (1973) was the only Palaeozoic conifer cone known in anatomical detail. *M. texanum* is a silicified voltzialean cone apex from the lower Permian of west Texas (Miller and Brown 1973). Each flattened fertile shoot bears thirty to fifty sterile scales and one apically cleft erect ovule attached at the shoot base. Each fertile shoot is subtended by a non-bifid bract. Cuticular features are not known, but the cone morphology allows both for assignment to the Lebachiaceae and for generic separation from *Lebachia* and *Ernestiodendron*. While *Moyliostrobus*, *Ernestiodendron*, and *L. lockardii* all have flattened fertile shoots in the axils of helically arranged bracts, the bracts of *Lebachia* and *Ernestiodendron* bifurcate at the tip. Mesozoic voltzialeans all display much more reduced and modified fertile shoots, and, like *Moyliostrobus*, commonly have simple, non-bifid bracts (Miller 1977, 1982).

Florin was the first to perceive the basic homology among fructifications of cordaites, early conifers, and modern conifers. Specifically, he recognized the equivalence of the fertile secondary

EXPLANATION OF PLATE 15

Figs. 1-7. *Lebachia lockardii* sp. nov., ovule histology. e, epidermis; mm, megaspore membrane; n, nucellus; nb, nucellar beak; pw, pollen chamber wall. 1, two ovules in transverse section. Nucellus of left ovule obliquely sectioned through pollen chamber wall and nucellar beak, M148 B Top No. 23, $\times 92$. 2, transverse section through seed cavity. Arrow indicates position of undifferentiated sclerotesta. Note epidermal hairs at top and prominent epidermal papillae at bottom, M148 B Top No. 12, $\times 73$. 3, two zoned 'sarcotesta', M148 A Bot No. 7, $\times 81$. 4, *Potoniopsisporites* grain in pollen chamber, M145 B Top No. 4, $\times 71$. 5, cuticle of nucellar epidermis, M148 B Top No. 13, $\times 105$. 6, hairs on ovule integument, M148 B Top No. 19, $\times 170$. 7, integumentary tracheids near ovule base, M148 B Top No. 7, $\times 670$.



shoots of *Lebachia*, *Ernestiodendron*, and *Cordaianthus* to the ovuliferous scales found in cones of more modern conifers (e.g. *Pinus*). In seeking to bring order to the heterogeneous morass of compressed plant fossil fragments attributed to *Walchia*, he examined branching patterns of vegetative shoots, cuticular features, and basic cone organization.

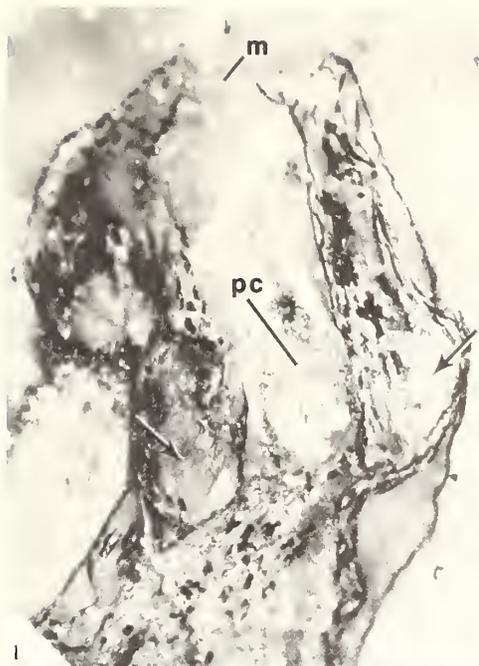
As characterized by Florin, *L. piniformis* and *E. filiciforme* are quite distinct. In particular he draws attention to ovule orientation, fertile shoot morphology, and patterns of stomatal arrangement. While as end members these taxa are distinct, examination of Florin's illustrations clearly demonstrates these features represent morphologic continua within the walchian complex. To some extent, Florin recognized this and identified in his studies (1938–1945) several species of cones as *Walchiostrobus* and *Walchianthus*, and several species of vegetative and fertile shoots as '*Walchia* (*Ernestiodendron*?)' or '*Walchia* (*Lebachia*?)'. For example, Florin illustrates a continuum of cuticular features in his photographs. Though not emphasized by Florin, many of the cuticles show narrow bands of densely packed stomata with shared subsidiary cells in some areas, and broad internally spacious bands with no shared subsidiary cells in other areas. In still other areas, the bands are so wide that there appear to be single isolated rows of stomata. Examples of stomatal pattern variation illustrated by Florin (1938–1945) for specific taxa are as follows: *L. piniformis*, Taf. 1–2, abb. 16, 17; Taf. 5–6, abb. 1; Taf. 15–16, abb. 7, 26, 27; Taf. 21–22, abb. 1, 2; *L. hypnoides*, Taf. 103–104, abb. 9; Taf. 107–108, abb. 16; *L. parvifolia*, Taf. 31–32, abb. 5; Taf. 37–38, abb. 13; *L. laxifolia*, Taf. 53–54, abb. 12, 14, 15; Taf. 55–56, abb. 12, 19; *L. intermedia*, Taf. 77–78, abb. 6–8; *L. angustifolia*, Taf. 39–40, abb. 11–13; *L. speciosa*, Taf. 65–66, abb. 9; *L. mucronata*, Taf. 75–76, abb. 5, 6; *E. filiciforme*, Taf. 111–112, abb. 15, 16; Taf. 113–114, abb. 9; Taf. 121–122, abb. 18; Taf. 127–128, abb. 13; *Walchianthus cylindraceus*, Taf. 155–156, abb. 15; *W. crassus*, Taf. 157–158, abb. 2; and *W. papillosus*, Taf. 157–158, abb. 8, 10.

This variation is of particular interest as the arrangement of the stomata in either bands or rows is the strongest point separating cuticles of *Lebachia* from those of *Ernestiodendron*. Comparison with *L. lockardii* reveals a comparable range of variation among the cuticles of its ovulate cones (Pl. 12, figs. 1, 3, 6), with typical lebachiate parallel bands and also isolated rows of stomata. The parallel bands of irregularly disposed stomata are commonly present on the adaxial surface of bracts and large scales, while the more widely separated longitudinally oriented single rows and/or isolated stomata usually occur on the very papillate abaxial or lower leaf surfaces.

Florin has described similar cuticles from vegetative leaves of *L. parvifolia*. On these, parallel bands of stomata are present on the adaxial surfaces, and the abaxial leaf surfaces often display 'more or less disaggregated bands of separate longitudinal rows of mostly lengthwise oriented stomata' (Florin 1940). *L. lockardii* and *L. parvifolia* each exhibit a considerable range of cuticular features including those usually used to separate *Lebachia* from *Ernestiodendron*. While Florin considered the single rows of stomata characterizing *Ernestiodendron* to be present on both surfaces of its leaves, their occurrence on the abaxial surfaces of *L. parvifolia* and *L. lockardii* calls

EXPLANATION OF PLATE 16

Figs. 1–6. *Lebachia lockardii* sp. nov. and *Potoniopsisporites*. m, micropyle; nb, nucellar beak; pc, pollen chamber; pw, pollen chamber wall. 1, oblique longitudinal section through apex of ovule showing pollen chamber, micropyle, and patches of undifferentiated sclerotesta (at arrows). Light area in pollen chamber is crystalline calcite surrounding grain shown in fig. 2 (polarized reflected light), M148 A Bot No. 7, $\times 89$. 2, oblique longitudinal section near section in fig. 1, note nucellar beak, *Potoniopsisporites* grain and patches of undifferentiated sclerotesta (at arrows) (polarized reflected light), M148 A Bot No. 9, $\times 89$. 3, grain in pollen chamber of fig. 2, arrow indicates monolete (Nomarski DIC), M148 A Bot No. 9, $\times 440$. 4, grain in section view. Note attachment of sexine to nexine by internal reticulum on distal surface (at arrow). Also note dense exine adjacent to open monolete on proximal surface, M26 B Top No. 55, $\times 680$. 5, proximal ornamentation. Tear reveals inner exine at bottom, M26 SEM-8, $\times 8000$. 6, grain with collapsed saccus. Proximal view with open monolete at top. Rectangle indicates area of fig. 5, M26 SEM-3, $\times 800$.



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to question the taxonomic importance of this feature. Other features that intergrade totally and therefore cannot be considered taxonomically diagnostic are cuticular papillae and epidermal hairs. The relative abundance of these probably more meaningfully reflects environmental stresses during growth.

An additional cuticular feature of *L. lockardii* can also be seen in Florin's illustrations and drawings of various *Lebachia* species (1938–1945). Small epidermal cells with a raised central circular area that is open or covered to some extent with cuticle, occur generally outside the stomatal bands (Pl. 12, figs. 2, 4, 5). Similar cells on many lebachian cuticles have been interpreted by Florin as hair bases (for examples, see Florin 1938–1945: Taf. 1–2, abb. 12, 13, 19; Taf. 31–32, abb. 10, 11, 19, 20; Taf. 49–50, abb. 13, 15, 16; Text-abb. 20A). Cells of this type somewhat resemble the podocarpalean 'Florin rings' described by Buchholz and Gray (1948) and Florin (1931, 1958) from living and fossil *Torreya*, where the surface cuticle of the subsidiary cells is fused into an optically distinct, differentially thickened, cuticular flange or ring that surrounds the stomatal opening. Certain fossil and modern *Araucaria* species display epidermal features that even more strongly resemble the distinct cuticular structures of *L. lockardii* and other *Lebachia* species. However, the araucarian epidermal features represent sunken stomata covered with waxy plugs or cuticular flaps (Stockey and Taylor 1978a, b), rather than single cells as in *L. lockardii*. Unlike those of *Araucaria* or *Torreya*, in no instance do the distinct circular rimmed areas on *L. lockardii* cuticles appear to be associated with either abortive or regular stomata. While abortive stomata were described by Florin for cuticles of *Lebachia* (1938–1945 text and illustrations such as Taf. 1–2, abb. 20; Taf. 3–4, abb. 7; Taf. 5–6, abb. 3; Taf. 17–18, abb. 13 for *L. piniformis*, and Taf. 39–40, abb. 18 for *L. angustifolia*), especially in the middle zones between bands of regular stomata, none has been observed on *L. lockardii*. On *L. lockardii* the circular rimmed areas apparently result from collapse of a very large papilla or a very short broad, unicellular hair.

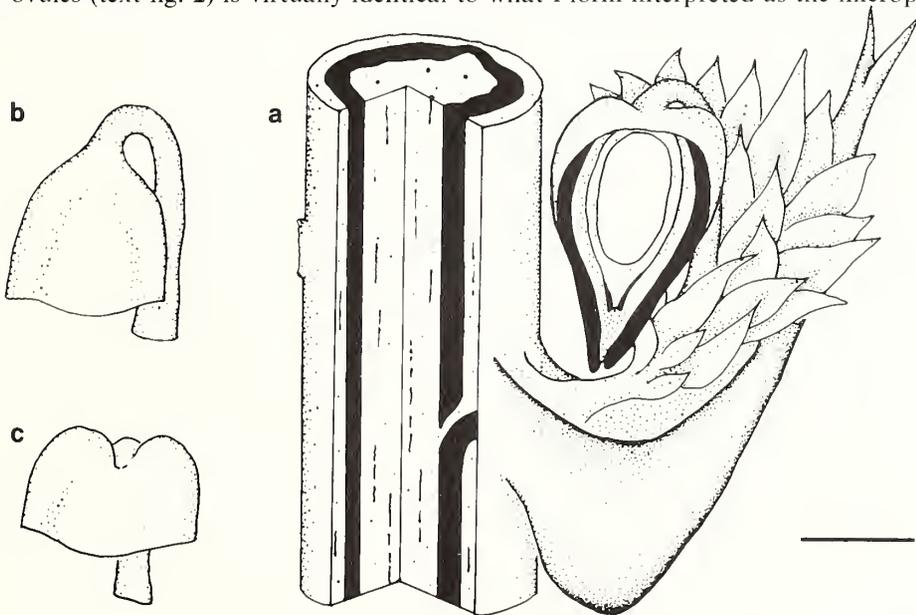
Ovulate cone morphology has been used as an important criterion for separating *Lebachia* from *Ernestiodendron*. The morphological features of *Lebachia* cones are considered by Florin to be more primitive than those of *Ernestiodendron* (Florin 1951). Though both are compound, *Ernestiodendron* cones are typically quite lax. Each fertile shoot axis is flattened with few to no sterile scales and three to seven megasporophylls, each bearing a single terminal ovule. *Ernestiodendron* ovules have been interpreted as either erect with the micropyle oriented outward, or inverted with the micropyle oriented downward and in toward the base of the fertile shoot (Florin 1951, fig. 34). Prior to the discovery of *L. lockardii*, all *Lebachia* ovules were interpreted as erect, with the micropyle oriented outward and away from the primary cone axis. Interpretive drawings of two detached fertile shoots of '*Walchiostrobus* (*Ernestiodendron*?)' sp. are figured by Florin (1951, fig. 34e, f). These are apparently drawn from specimens illustrated in his monograph (1938–1944; Taf. 163–164, abb. 3–4, Taf. 153–154, abb. 20–22), representing partially coalified impressions from the lower Permian at Thüringer Forest in Germany. The fertile shoots seem to be somewhat intermediate morphologically between those of *Lebachia* and *Ernestiodendron* as delimited by Florin, in that they each may have numerous fertile and numerous sterile scales. One shoot apparently bears four inverted ovules; the other bears four or five ovules that may be erect.

The ovulate cones of *L. lockardii* also display several morphological features which appear to be intermediate between *Lebachia* and *Ernestiodendron* as separated by Florin. There are numerous scales attached to the flattened fertile shoot axis, which often bears two megasporophylls (= fertile scales) with apparently functional terminal ovules. Some shoots also have one to three scales with poorly preserved or possibly abortive ovules (Pl. 13, figs. 2–4). In addition, attached ovules are clearly inverted, with their micropyles oriented toward the junction of the flattened fertile shoot and the primary cone axis, features generally considered restricted to *Ernestiodendron*. In general appearance, however, *L. lockardii* cones are plainly lebachiate. They are relatively compact, have numerous sterile scales per fertile shoot, and display broad stomatal bands on many leaves.

The erect ovule orientation ascribed to all previously known *Lebachia* species appears to be based primarily on cones of *L. piniformis* and *L. hypnoides*. Florin considered many of the ovules in these cones to be of *Samaropsis*-type. He also recognized two ovule types on species of

Cordaianthus, *Samaropsis* for the stratigraphically older forms (Westphalian) and *Cordaicarpus* for the more recent strobili (Stephanian). Compressed platyspermic ovules of both types are often found in sediments that yield cordaites and *Walchia*. The biological affinities of these ovules, however, are not always with only cordaites or conifers (Rothwell 1981). *Samaropsis* Goeppert (1864–1865) designates broadly winged, compressed ovules with a cleft apex forming two horns. *Cordaicarpus* or *Cordaicarpus* (Geinitz 1862) is employed for rounded, compressed ovules with a narrowed border and often a cordate base. Incomplete samaropsid impressions without the broad sarcotestal border are included in *Cordaicarpus* (Seward 1919). *Samaropsis*-like ovules have been observed on the cordaitan fructification *Cordaianthus pitcairnae* (Seward 1919), on the pteridosperm foliage *Pecopteris pluckeneti* (Schlotheim) Brongniart (Kidston 1886), and possibly on *Emplectopteris triangularis* (Andrews 1961).

As emphasized above, the ovules of *L. lockardii* are terminal and inverted, while those of *L. piniformis*, *L. hypnoides*, and other lebachias have all been interpreted as terminal and erect. It is clear that Florin considered the attached *Lebachia* ovules to be comparable to isolated ovules such as *Samaropsis delafondi* (Florin 1938–1945, Taf. 21–22, abb. 17; Taf. 161–162, abb. 20). In addition, he describes ovules in cones of *L. hypnoides* as most comparable to impressions illustrated by Goeppert (1864–1865) as '*Cardiocarpus orbicularis*'. In describing these ovule impressions (Florin 1938–1945, Taf. 109–110, abb. 23–25), Florin draws attention to the fissured coaly crack in the narrow flange beyond the seed cavity (toward the distal end of the cone), and mentions the lack of preservation at the other end of the ovule (which he considers to be the chalazal end of the ovule). Examination of the ovule-bearing fertile shoots macerated from cones of *L. piniformis* (Florin 1938–1945) also reveals the bilobed end of an ovule with a conspicuous groove and oval scar below the cleft. Although Florin interpreted this groove as the micropyle, its appearance is remarkably like the chalazal end of the isolated *Samaropsis* ovules that he also figured (Taf. 161–162, abb. 1–5, and especially abb. 20). Moreover, the distally directed, cordate chalaza of *L. lockardii* ovules (text-fig. 2) is virtually identical to what Florin interpreted as the micropylar end



TEXT-FIG. 2. *Lebachia lockardii* sp. nov. 1a, reconstruction of cone segment showing general features of axis, bract, and fertile shoot. Note orientation of ovule, which has been sectioned longitudinally in the major plane to reveal nucellus and megaspore membrane. Vascular tissue of axis and sectioned surface of integument represented in black. 1b and 1c, ovule bases showing range of variation in structure and attachment to fertile scales. Scale bar = 1 mm.

of his compressed *Lebachia* ovules. Similarities shared by the chalaza of Florin's *Samaropsis* and *L. lockardii* ovules, and what Florin interpreted as the apex of *L. hypnoides* ovules, include cordate shape, oval scar below the groove (attachment scar of *Samaropsis* sp. and *S. delafondi*, and *L. lockardii*), and gentle taper toward the other end of the ovule (cf. text-fig. 2; Florin 1938–1945, Taf. 161–162, abb. 20; Taf. 21–22, abb. 17; and Taf. 19–20). In all these features the ovules of *Lebachia* figured by Florin (1938–1945, 1951) are consistent with the interpretation that they may be recurved or inverted at the tips of their fertile scales.

Ovule ontogeny and reproductive biology

The attached ovules of *L. lockardii* display relatively narrow ranges of variation in size, integument structure, nucellus and pollen chamber histology, and gametophyte disposition that suggests they were all preserved at about the same developmental stage. Nevertheless, comparisons with similar features of ovules of extant conifers and other Palaeozoic gymnosperms provide an opportunity to interpret several features of development and reproductive biology (Rothwell 1971, 1980, 1982a). In general, development of the integument, nucellus (including pollen chamber), and gametophytes are co-ordinated with pollination, abscission, and fertilization in a sequence that is characteristic of the taxon under consideration (e.g. *Chamaecyparis nootkatensis*, Owens and Molder 1975; *Picea engelmannii*, Singh and Owens 1981; *Callistophyton*, Rothwell 1980). In *L. lockardii* the ovules show features of the integument that are like sarcotesta and endotesta of other immature gymnosperm ovules, but no lignified sclerotestal cells are present in most of our specimens. In only two *L. lockardii* ovules have possible remnants of thick-walled sclerotestal cells been identified; these are confined to two groups of cells in the minor plane of symmetry at the level of the pollen chamber. These areas appear as lighter patches to either side of the pollen chamber in the specimen figured on Plate 16 (figs. 1, 2). Their disposition is consistent with that of mature fibres at the onset of sclerotestal differentiation in other gymnosperm ovules (Rothwell 1971, 1980), where cells are lignified first in the minor plane at the level of the pollen chamber and differentiation generally proceeds basipetally (Quisumbing 1925). This interpretation is also supported by the presence of extremely thin-walled and delicate cells between the endotestal epidermis and the sarcotesta in some specimens (e.g. Pl. 15, fig. 2 at left). Cells of this type are identical to those that have been interpreted as immature sclerotesta in several other Palaeozoic gymnosperm ovules (Stidd and Cosentino 1976, fig. 14; Rothwell 1971, 1980).

Several features of the nucellus in *L. lockardii* also suggest that the ovules are immature. During differentiation the nucellus of gymnosperm ovules characteristically becomes progressively thinner, until in the mature ovules it is represented by only a thin, cuticular membrane (Singh 1961; Rothwell 1971). The several cell layers of nucellus preserved in the midregion and at the base of the pollen chamber in *L. lockardii* are characteristic of early ontogenetic stages of many gymnosperm ovules, where the integument is not fully matured. The absence of cellular megagametophytes in the *L. lockardii* ovules further suggests their immaturity. Unless the *L. lockardii* megagametophytes did not exhibit the free nuclear stages that typically characterize all but the most mature of other conifer ovules (Singh 1978), or the cellular megagametophytes of *L. lockardii* were not preserved, this feature is consistent with the general developmental interpretation of the other tissues.

The histological features of integument, nucellus, and megagametophyte, interpreted above as indicators of ovule immaturity, are similar to those in Pennsylvanian gymnosperms with conifer-like reproductive biology, and also to ovules of many extant gymnosperms shortly after the stage appropriate for pollination (e.g. Rothwell 1971; Owens *et al.* 1981). The occurrence of pollen grains in the pollen chamber of several *L. lockardii* ovules (Pl. 15, fig. 4; Pl. 16, figs. 1–3) is also consistent with this interpretation. Shortly after pollination in many gymnosperm ovules, continued development of the integument leads to closure of the micropyle (Dupler 1920; Quisumbing 1925; Singh 1961; Rothwell 1971, 1980). Unless this developmental feature did not occur in *L. lockardii*, the open micropyles of all available specimens (e.g. Pl. 14, figs. 7–8; Pl. 16, figs. 1–2) suggest that they were preserved soon after pollination. If true, then ovule disposition in the specimens under investigation also provides evidence for the mode of pollination.

As stressed in the description of *L. lockardii*, the ovules are inverted with the micropyle located between the primary axis and the base of the fertile shoot (Pl. 13, fig. 1). Also, the minimum diameter of the micropyle (approx. 100 μm) is only slightly larger than the longest measurable dimension of the prepollen grains actually present within the pollen chamber of several ovules (viz., 95 μm). This combination of features makes it unlikely that the grains found their way into the pollen chambers by wind currents alone. While the occurrence of a pollination drop mechanism has been conclusively documented in only one Palaeozoic gymnosperm (Rothwell 1977), the prevalence of such a mechanism is extant conifers (Singh 1978), together with the features of ovule orientation and prepollen/micropyle size ratio, provides at least indirect evidence that a similar mode of pollination characterized *L. lockardii*.

The discovery of *L. lockardii* and associated permineralized remains provides the first extensive anatomical evidence for the reproductive organs of the earliest conifers, and also allows for the description of many morphological features not discernible from compressed specimens. Features important to our understanding of early conifer structure are the bilateral symmetry of the secondary fertile shoots and the inverted nature of the ovules. True bilateral symmetry also sets *L. lockardii* ovules apart from the cardiocarpalean ovules of Upper Carboniferous cordaites and pteridosperms (Rothwell 1982), and reveals an additional specialization among the reproductive structures of pre-Permian gymnosperms. The *L. lockardii* specimens further allow for the first correlation of epidermal features with internal anatomy of primitive conifers. The abundance of cuticular material forms the basis for evaluating the range of variability that may be expected of a single lebachian species. It is now clear that in both morphology and cuticular features walchian species may be far more variable than previously suspected.

From the viewpoint of phylogeny and evolution of the earliest conifers, *L. lockardii* allows us to test and support, with a new type of evidence, Florin's hypothesis of the structural homologies among ovulate cones of cordaites, Palaeozoic conifers, and modern conifers. Perhaps of greatest interest to students of fossil plant biology are the insights gained into the growth, development, and reproduction of the earliest conifers. It is now clear that *L. lockardii* had ovules that were pollinated while immature and still attached to the parental sporophyte, perhaps via a pollination drop mechanism. Likewise, the specimens support earlier interpretations of the mode of propagule dissemination in primitive gymnosperms (e.g. Emberger 1944; Rothwell 1982a) by providing the first histological evidence for early ovule abscission among Palaeozoic seed plants.

While *L. lockardii* and the associated walchian organs allow us to begin formulating the first whole plant biology concept for a pre-Permian conifer, the new collection and preparation techniques employed in the study are of perhaps even greater potential significance. Through these methods we are now able to investigate a far greater range of features for plants that have previously been known only from compressed or mold-cast remains. In this regard we may now expect to begin characterizing in a biological sense the plant communities that inhabited the extrabasinal lowlands ('Upland Floras' of many previous workers; Pfefferkorn 1980), and thereby dramatically enhance our understanding of late Palaeozoic tropical vegetation.

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THE DINANTIAN *TAPHROGNATHUS* *TRANSATLANTICUS* CONODONT RANGE ZONE OF GREAT BRITAIN AND ATLANTIC CANADA

by PETER H. VON BITTER *and* RONALD L. AUSTIN

ABSTRACT. The *Taphrognathus transatlanticus* Range Zone is proposed to replace the earlier defined, and subsequently rejected, *Taphrognathus varians*-*Cavusgnathus*-*Apatognathus* Assemblage Zone. It is based on the occurrence and range of the conodont species *Taphrognathus transatlanticus* sp. nov. in strata of Viséan age on both sides of the Atlantic Ocean.

The *T. transatlanticus* conodont Range Zone is present in the upper part of the S₂ Zone of the Avon Gorge in Great Britain and the lower B Subzone of the Windsor and Codroy groups of Atlantic Canada. The B Subzone has previously been correlated with the S₂ (Sub)zone using megafaunal and microfossil criteria; the stratigraphically restricted occurrence of *T. transatlanticus* sp. nov. supports these correlations. The B Subzone has previously been correlated with the middle late Viséan using foraminifera and algal microflora but we suggest that it is middle Viséan in age. Our suggestion is supported by previous megafaunal correlations. The upper S₂ Zone and the lower B Subzone have both been correlated with the Holkerian Stage of the British Dinantian. The fauna of the *T. transatlanticus* conodont Range Zone has not yet been found at the boundary stratotype section of the Holkerian at Barker Scar, Cumbria.

THE *Taphrognathus varians*-*Cavusgnathus*-*Apatognathus* Assemblage Zone of Great Britain was defined by Rhodes *et al.* (1969, p. 43) who based it on the stratigraphic range of the conodont *Taphrognathus varians* Branson and Mehl in the upper part of the S₂ Subzone of the Avon Gorge (Samples S45 to S58), despite the fact that *T. varians* had (and has) not been found in the Avon Gorge. The conodonts assigned to *T. varians* by Rhodes *et al.* (1969, pl. 13, figs. 4, 5) came from Harden Burn, Roxburghshire, but the authors did note (p. 43) that 'specimens transitional between *Cavusgnathus* and *Taphrognathus* . . . have been found in this assemblage zone'. Von Bitter (1976, p. 231) reported the occurrence of *Taphrognathus* sp. in the Lower Windsor Group of Nova Scotia and observed them to be practically identical to the transitional specimens illustrated by Rhodes *et al.* (1969, pl. 13, figs. 1-3). The same species has been recovered from the Lower Windsor Group correlative, the Lower Codroy Group of south-western Newfoundland (von Bitter and Plint-Geberl 1979, 1982). On the basis of the rather well-defined and consistent stratigraphic distribution of the species over an extensive area, von Bitter and Plint-Geberl (1979, 1982) defined the *Taphrognathus* Zone and correlated it with the lower B Subzone of the Windsor Group, as designated by Bell (1929) on macrofaunal evidence.

Re-examination of the Avon Gorge collections of Rhodes *et al.* (1969), as well as examination of additional specimens from that locality recovered in 1981 by Mr. Julian Pearce working under the direction of the second author at the University of Southampton, verifies that *Taphrognathus* sp. of von Bitter (1976) and *Taphrognathus* n. sp. A of von Bitter and Plint-Geberl (1979, 1982), rather than *T. varians* Branson and Mehl, is present and moderately common in the Avon Gorge section. We name this new species *Taphrognathus transatlanticus* sp. nov.

Austin and Mitchell (1975, pl. 1, figs. 5, 6, 16, 18, 19, 30) reported *T. varians* from the upper division of the Lower Carboniferous Shale of County Tyrone, Northern Ireland, but this is a lower stratigraphic level than that from which *T. transatlanticus* sp. nov. has been recovered. We agree with Higgins and Varker (1982, p. 154) that the occurrences of *Taphrognathus* sp. and *Taphrognathus* n. sp. A (both = *T. transatlanticus* sp. nov. of this study) of von Bitter (1976), von Bitter and Plint-Geberl

(1979, 1982), and Plint-Geberl (1981), as well as the new occurrences in Great Britain and Atlantic Canada reported here, are all geologically younger than the *Taphrognathus* Zone of Ravenstonedale, Great Britain. The older faunas probably fall within the range of *T. varians* as recorded in North America by Sandberg (1979) and in England by Metcalfe (1981).

The absence of *T. varians* from the Avon Gorge strengthens our conviction that the specimens from that locality, as well as the taphrognathids from Atlantic Canada, do not represent juvenile individuals of a species of *Cavusgnathus* (as initially suggested by Rhodes and Austin 1970, p. 334, and subsequently reinterpreted by Austin 1973a, p. 527). The appearance of these unusual taphrognathids in a single narrow stratigraphic interval of lithologically diverse rocks which represent a wide range of environments on both sides of the Atlantic, suggests that the *Taphrognathus* Assemblage Zone of von Bitter and Plint-Geberl (1982) in Atlantic Canada and the *T. varians*-*Cavusgnathus*-*Apatognathus* Assemblage Zone in the Avon Gorge are the same zone and are time equivalent. This conclusion necessitates resurrection and redefinition of the zone originally recognized by Rhodes *et al.* (1969) but later suppressed by Austin (1973).

THE *TAPHROGNATHUS TRANSATLANTICUS* CONODONT RANGE ZONE

1969 *Taphrognathus varians*-*Cavusgnathus*-*Apatognathus* Assemblage Zone; Rhodes *et al.* p. 43.

1982 *Taphrognathus* Assemblage Zone; von Bitter and Plint-Geberl, p. 206.

non 1982 *Taphrognathus* Partial Range Zone; Higgins and Varker, p. 153.

Characteristic species. *T. transatlanticus* sp. nov.; in the Avon Gorge, Great Britain, associated with *Cavusgnathus windsorensis* Globensky and other species listed in Tables 1 and 2; in Newfoundland,

TABLE 1. Distribution of conodonts at locality 1, the *Taphrognathus transatlanticus* Zone of the Avon Gorge, Great Britain. Collections are those studied by Rhodes *et al.* (1969) and identifications other than those of the first two taxa are by R.L.A. Figured specimens deposited at the British Museum (Natural History). Unfigured specimens deposited at the Department of Geology, University of Southampton.

SAMPLE CODE AND WEIGHT OF SAMPLE PROCESSED (IN KILOGRAMS)					
<u>S 45</u>	<u>S 49</u>	<u>S 53</u>	<u>S 54</u>	<u>S 58.</u>	
8kg	7.5kg	7kg	3kg	7.5kg	
-	4xxx	6x	1	3	<i>Taphrognathus transatlanticus</i> sp. nov., Sp element
16	15xx	-	1	-	<i>Cavusgnathus windsorensis</i> Globensky, Sp element
4xxxx	57	-	-	-	<i>Cavusgnathus unicornis</i> Youngquist & Miller, Sp element
-	1	-	-	-	<i>Cavusgnathus charactus</i> Rexroad, Sp element
-	18	-	1xx	-	<i>Cavusgnathus</i> sp., dextral Sp element
3	-	1	-	-	<i>Spathognathodus campbelli</i> Rexroad, Sp element
-	-	1	-	-	<i>Spathognathodus scitululus</i> (Hinde), Sp element
6	20	-	-	-	<i>Hindeodus cristulus</i> (Rexroad), Sp element
1	-	-	1	-	<i>Hindeodus</i> sp., Sp element
-	1	1	-	-	<i>Apatognathus</i> sp.
-	1	-	-	-	Unidentified plectospathodiform element
-	1	-	-	-	Unidentified ligonodiniform element
2	10	-	-	-	Unidentified Hi element
1	9	-	-	-	Unidentified Ne element
1	3	1	-	-	Unidentified Oz element
2	3	2	-	-	Unidentified Tr element
1	3	-	-	-	Genus & species indeterminate

x One fragmentary specimen. xx One specimen doubtful. xxx Three of the specimens were figured by Rhodes *et al.* (1969, pl. 13, figs. 1-3) and deposited in the British Museum (Natural History). xxxx Two of these specimens appear to be transitional with *Taphrognathus transatlanticus* sp. nov.

American species, like *T. transatlanticus* sp. nov., is limited to a very narrow stratigraphic interval, falling in the upper Lower St. Louis Formation and the lower Upper St. Louis Formation (ibid., table 1). Although the zone defined by the occurrence of this species was not defined by Rexroad and Collinson (1963), it would not be unreasonable to expect it to correlate with the *T. transatlanticus* Range Zone. Rather than correlating the *T. varians*-*Cavusgnathus*-*Apatognathus* Zone tentatively with the Lower St. Louis Formation, as was done by Rhodes *et al.* (1969), we would tentatively correlate the redefined zone with the middle of the St. Louis Formation.

Higgins and Varker (1982) concluded that the association of *Cavusgnathus* spp. with *Taphrognathus* sp. reported by von Bitter (1976) from Nova Scotia probably indicated a younger age for these occurrences than for the *Taphrognathus* Zone of Ravenstonedale, Great Britain. The presence of *Cavusgnathus* spp. in only younger strata and the mutual exclusivity of species of *Cavusgnathus* and *Taphrognathus* at Ravenstonedale (Higgins and Varker 1982, text-figs. 6-8), the mutual occurrence of species of *Cavusgnathus* with *T. transatlanticus* sp. nov. in the Avon Gorge and in Atlantic Canada (Tables 1-4), and previous correlations made by Bell (1929) and Utting (1980) and discussed in the section that follows, cause us to agree with Higgins' and Varker's conclusions.

Conil *et al.* (1976a, table 11; 1976b, Enclosure 2) have indicated the presence of *Taphrognathus* in Zone V2a of Belgium. The species illustrated has not been examined but may be *T. transatlanticus* sp. nov.

Bell (1929, p. 71) used megafaunal criteria to correlate the B Subzone of the Lower Windsor Group of eastern Canada with the S₂ (Sub)zone of the Avon Gorge of Great Britain. Lewis (1935) could not correlate Lower Windsor Group strata with that of the Avon Gorge since he lacked corals from the Lower Windsor Group. He did, however, correlate the Upper Windsor Group with the upper *Dibunophyllum* (Sub)zone, the megafaunal zone overlying the S₂ Zone in the Avon Gorge. Finally,

TABLE 3. Distribution of conodonts at localities 2, 3, and 4 (see Appendix), the *Taphrognathus transatlanticus* Zone, area B of von Bitter and Plint-Geberl (1982), south-western Newfoundland, Canada. Identifications by von Bitter and Plint-Geberl (1982). All specimens deposited at the Royal Ontario Museum, Toronto.

Fish -1-1	Fish -1-2	Fish -1-3	Fish -1-4	Fish -1-6	Fish -1-7	Fish -1-8	Fish -1-9	Fish -1-10	Corrn -1-1	Corrn -1-2	Corrn -1-3	Corrn -1-4	Bara -1-1	Bara -1-2	
-	-	-	-	1	-	-	2	-	-	-	-	-	3	6	? <i>Bispathodus</i> spp.
16	-	-	-	-	-	-	-	-	-	-	-	-	6	-	<i>Spathognathodus</i> sp. nov. A
-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	<i>Spathognathodus campbelli</i>
1	1	-	-	1	3	1	-	-	-	-	-	-	-	-	<i>Cavusgnathus regularis</i> type, Sp element
-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	<i>Cavusgnathus regularis</i> type, Oz element
1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	<i>Cavusgnathus regularis</i> type, Ne element
5	2	5	1	-	1	13	4	1	5	2	-	7	11	2	<i>Taphrognathus transatlanticus</i> sp. nov., Sp element
1	-	-	-	-	-	-	-	-	-	-	1	-	3	-	<i>Taphrognathus transatlanticus</i> sp. nov., Oz element
-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	<i>Taphrognathus transatlanticus</i> sp. nov., Pl element
-	-	-	-	-	-	-	-	-	-	1	2	-	-	1	<i>Taphrognathus transatlanticus</i> sp. nov., Tr element
-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	Unidentified Oz element
-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	Unidentified Hi element
3	-	-	-	2	-	1	-	-	-	-	-	-	-	-	Unidentified Tr element
1	-	3	-	-	1	-	-	-	-	-	-	-	4	3	Unidentified Hi element
-	-	-	-	-	4	-	-	2	-	-	-	-	3	1	Genus and species unidentified
-	-	-	-	-	-	-	-	-	P	-	P	-	P	-	Vertebrate remains
2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	Weight of Sample processed (kg)
.93	1.22	.96	1.21	1.06	.95	1.62	1.75	1.27	1.91	1.98	1.96	1.95	2.00	1.23	Weight of Sample broken down (kg)

Utting (1980) correlated that part of his miospore zone I occurring in the B Subzone of the Lower Windsor Group with the S₂ macrofaunal zone of Great Britain. Our discovery of the stratigraphically restricted species *T. transatlanticus* sp. nov. in the S₂ Zone of the Avon Gorge and the lower B Subzone of Atlantic Canada strengthens the correlation made by Bell (1929) and Utting (1980).

Bell (1929) believed the B Subzone of the Lower Windsor Group to be of middle Viséan age, a point of view apparently shared by Giles (1981), but not by Mamet (1970) who placed its foraminifera and algal microflora in Foraminiferal Zone 15. Mamet (1970, fig. 4) correlated this zone with the European ammonoid zone Cu III_a of middle late Viséan age. Jansa *et al.* (1978) added support by stating that there is no evidence in Atlantic Canada for a middle Viséan marine microfauna.

TABLE 4. Distribution of conodonts at localities 5 and 6 (see Appendix), the *Taphrognathus transatlanticus* Zone, area A of von Bitter and Plint-Geberl (1982), south-western Newfoundland, Canada. Identifications by von Bitter and Plint-Geberl (1982). All specimens deposited at the Royal Ontario Museum, Toronto.

Cod								
1-1	1-2	1-3	1-4	1-5	1-19	1-20	1-21	
-	-	-	-	-	-	-	13	<i>Cavusgnathus windsorensis</i> , Sp element
-	-	-	-	-	-	-	3	<i>Cavusgnathus windsorensis</i> , Oz element
-	-	-	-	-	-	-	1	<i>Cavusgnathus windsorensis</i> , Ne element
-	-	-	-	-	-	-	4	<i>Cavusgnathus windsorensis</i> , Hi element
-	-	-	-	-	-	-	1	<i>Cavusgnathus windsorensis</i> , Pl element
3	-	-	-	-	-	-	-	? <i>Bispathodus</i> spp.
11	17	11	2	6	-	5	15	<i>Spathognathodus</i> sp. nov. A
10	-	-	-	26	-	-	5	<i>Spathognathodus campbelli</i>
-	1	12	2	1	-	2	-	<i>Cavusgnathus regularis</i> type, Sp element
-	3	-	1	-	-	-	-	<i>Cavusgnathus regularis</i> type, Oz element
-	1	-	2	-	-	-	-	<i>Cavusgnathus regularis</i> type, Ne element
50	1	15	2	18	3	10	1	<i>Taphrognathus transatlanticus</i> sp. nov., Sp element
2	-	-	-	-	-	7	-	<i>Taphrognathus transatlanticus</i> sp. nov., Oz element
-	-	3	-	-	-	9	-	<i>Taphrognathus transatlanticus</i> sp. nov., Hi element
-	-	-	-	-	-	-	-	<i>Taphrognathus transatlanticus</i> sp. nov., Pl element
1	-	-	-	-	-	3	-	<i>Taphrognathus transatlanticus</i> sp. nov., Tr element
2	-	2	-	6	-	-	-	Unidentified Oz element
10	15	33	4	3	1	37	9	Unidentified Hi element
6	8	2	4	-	-	-	-	Unidentified Pl element
3	4	4	2	-	-	-	-	Unidentified Tr element
2	7	1	-	2	-	-	-	Unidentified Ne element
2	5	2	-	2	-	-	38	Genus and species indeterminate
-	P	-	P	-	-	-	-	? Conodont pearls
2	2	2	2	2	2	2	2	Weight of sample processed (Kg)
1.61	1.91	1.87	1.75	1.76	1.39	1.39	1.48	Weight of sample broken down (Kg)

We suggest that the *T. transatlanticus* Zone (and the lower B Subzone, by extension) of Atlantic Canada is in fact middle Viséan in age. We have already stated that the *T. transatlanticus* Zone is present in the B Subzone of Atlantic Canada and in the S₂ Zone of the Avon Gorge. The B Subzone coincides approximately with Cycle 2 of the Windsor Group (Giles 1981) and this cycle in turn has been 'equated' (ibid., p. 1) with part or all of the Holkerian Stage of Great Britain. The S₂ Zone of the Avon Gorge was correlated with the Holkerian Stage by George *et al.* (1976, p. 11, table 1) who indicated (p. 73) that the base of Mamet's zone 13 is reasonably correlated with the base of the Holkerian. Mamet (1970, fig. 2) showed the base of foraminiferal zone 13 as middle middle Viséan.

We believe that the zone defined by the occurrence of *T. transatlanticus* sp. nov. marks a relatively brief interval of time that may be of considerable importance in correlation. The use of the Avon Gorge as a standard section is considered by some to be problematic in view of considerable non-sequences (Ramsbottom 1973, p. 595). The characteristic fauna of the *T. transatlanticus* Zone has not been reported from the recently defined stages of the British Dinantian. The zone by implication should be present within the Holkerian Stage (George *et al.* 1976) but has not been reported from above the base of the type Holkerian section nor from below the base of the type Asbian section (Ramsbottom 1981).

T. transatlanticus sp. nov., although a species that preferred shallow-water conditions, was apparently not as tolerant of variable salinities as was *C. windsorensis* Globensky. The former consistently defines a narrow faunal zone and occurs in a variety of marine sediments ranging from micritic brachiopod coquinas (Miller Limestone and Maxner Limestone at localities 9, 10, and 11, near Windsor, Nova Scotia) to black fissile shales (Fisher Limestone, locality 12, Miller's Creek, Nova Scotia).

SYSTEMATIC PALAEOLOGY

Order CONODONTOPHORIDA Eichenberg, 1930

Superfamily POLYGNATHACEA Bassler, 1925

Family CAVUSGNATHIDAE Austin and Rhodes *in* Clark *et al.*, 1981

Genus TAPHROGNATHUS Branson and Mehl, 1941

Type species. *T. varians* Branson and Mehl, 1941, by original designation.

Remarks. *Taphrognathus* was erected to include platform conodont elements possessing a 'median blade' that 'continued into the median trench as a short carina' (Branson and Mehl 1941). A number of later authors encountered specimens transitional in characteristics between species of *Taphrognathus* and those of the genus *Cavusgnathus*. Rexroad and Collinson (1963) and Rhodes *et al.* (1969) called these taxonomic intermediates *Taphrognathus*-*Cavusgnathus* transitions and Rexroad and Collinson (1963) interpreted them as evolutionary intermediates between the two genera. In recent years, the name *Taphrognathus* has been applied to conodonts for which a subcentral rather than a central blade can be demonstrated (Druce 1969, 1970), or to conodonts with a blade that is not only subcentral in position but clearly joined to the outer parapet (Baxter 1972; von Bitter 1976; von Bitter and Plint-Geberl 1982). *Cavusgnathus*, as redefined by Lane (1967, 1968), does not include species bearing platform elements that are symmetrically paired.

Neither generic category as presently defined is sufficiently broad to comfortably and unequivocally include the new species recognized and defined by us. *T. varians*, the type species of the genus, is known to be 'Highly variable in all aspects of its morphology' (Nicoll and Rexroad 1975, p. 27), and a small proportion of the specimens placed by these authors in *T. varians* were recognized to have the blade in a non-median position. Until the amount of variation exhibited by *T. varians* and other species of *Taphrognathus* is better documented, we hesitate to use another generic category for platform conodonts whose morphology is at variance with the type specimens of the genotype.

The element terminology which is used in the following descriptions is a slightly modified form of that proposed by Jeppsson (1971). The modification involves capitalization of the terms: Sp; Oz; Hi; Pl; and Tr elements. This is consistent with the terminology previously used by the senior author.

Taphrognathus transatlanticus sp. nov.

Plates 17 and 18

Sp element

- 1969 *Taphrognathus*-*Cavusgnathus* transitions; Rhodes *et al.*, p. 242, pl. 13, figs. 1-3.
 1973b Juvenile? *Cavusgnathus*-*Taphrognathus* transition; Austin, p. 108, fig. 1.1a.
 1973b Ontogenetic stages of *Cavusgnathus*; Austin, p. 108, figs. 1.2-1.4 only.
 1976 *Taphrognathus* sp. von Bitter, p. 231.
 1982 *Taphrognathus* n. sp. A; von Bitter and Plint-Geberl, p. 197, pl. 3, figs. 1-5, 7.

Oz element

- 1982 *Taphrognathus* n. sp. A; von Bitter and Plint-Geberl, p. 197, pl. 7, figs. 3, 4, 8, 14.

Hi element

- 1982 *Taphrognathus* n. sp. A; von Bitter and Plint-Geberl, p. 197, pl. 7, figs. 19, 23.

Pl element

- 1982 *Taphrognathus* n. sp. A; von Bitter and Plint-Geberl, p. 197, pl. 7, figs. 10, 11, 13.

Tr element

- 1982 *Taphrognathus* n. sp. A; von Bitter and Plint-Geberl, p. 197, pl. 3, figs. 6, 8.

Material. Holotype ROM 38474; paratypes ROM 38473, 38475; other figured specimens from Canada and those referred to in Tables 3 and 4 are also deposited in the Department of Invertebrate Palaeontology, Royal Ontario Museum, Toronto. Specimens from Great Britain referred to in Tables 1 and 2 are deposited in the British Museum (Natural History) (figured specimens) and the Geology Department, University of Southampton (unfigured specimens). Localities listed in Appendix.

Origin of name. With reference to the occurrence of the species, and the zone it defines, on both sides of the Atlantic Ocean.

Type horizon and locality. Fischells Limestone of Bell (1948). Sampled as Fish-1-1 to Fish-1-5 by von Bitter and Plint-Geberl (1982) (see Appendix). Locality 2, Fischells Brook, south-western Newfoundland, Canada (see Appendix). Section starting at and proceeding downstream from the base of the first major limestone (Fischells Limestone of Bell 1948), north-west of railroad trestle (Canadian National Topographic Series 1:50,000, Flat Bay Map Sheet 12B/7). The type locality corresponds to most, but not all, of locality 5 of von Bitter and Plint-Geberl (1982) and stops at the top of the third carbonate unit above the top of the Fischells Limestone. The uppermost part of the third carbonate unit was sampled as Fish-1-10 by von Bitter and Plint-Geberl (1982).

Diagnosis. A conodont species having an apparatus containing five element types, all of which, with the probable exception of the Tr element, were symmetrically paired. All the elements are small, including the diagnostic Sp or platform element. The Sp element is taphrognathiform and has unornamented sub-parallel parapets. The elements often show a strong but consistent tendency toward either recrystallization of, or overgrowth by, calcium phosphate. This phenomenon is best developed orally, suggesting some type of instability of white matter. Whether the overgrowth or recrystallization took place during or after the life of the species is unknown. All elements appear to have a greater tendency to recrystallization or overgrowths than those of other species, which makes the phenomenon useful in apparatus reconstruction.

Description. *Sp element* (Pl. 17, figs. 1-8, 10, 11; Pl. 18, figs. 1-10). A generally small element that occurs as both sinistral and dextral elements (Pl. 17, figs. 1, 2), with features that can generally only be demonstrated adequately by scanning electron microscopy. The blade is a continuation of the outer parapet and these two parts are separated from one another by an outer parapet notch. The inner parapet is of equal height to the outer parapet; the inner parapet is slightly shorter and terminates at the anterior trough opening (Pl. 17, figs. 5, 6). The parapets are unornamented although they may be covered with apatite crystals (Pl. 17, fig. 11; Pl. 18, figs. 1, 3-5, 7-10). The sub-parallel parapets are separated by a moderately deep trough which is closed posteriorly by the coming together of the parapets. The posterior end of the platform is pointed and in lateral view exhibits a vertical drop-off (Pl. 17, fig. 4).

The free blade bears up to seven laterally compressed denticles. The maximum number is generally five but, as with other platform conodonts, the blade denticle number is a function of size. The cusp is the largest and most posterior of these denticles and may be either considerably or only slightly larger than the more anterior denticles. The posterior edge of the cusp drops off vertically into the parapet notch mentioned previously. Aborally there is a large slightly asymmetrical basal cavity (Pl. 17, fig. 3). The basal cavity starts at the posterior tip, reaches its maximum width below the cusp, and then begins to be constricted under the blade. Throughout its length it bears a basal groove that reaches its maximum depth in a basal pit under the cusp. The lateral edges of the basal cavity are defined by prominent flaring aprons. These are apparently equally prominent on both the inner and outer sides of the element.

Oz element (Pl. 17, fig. 12; Pl. 18, fig. 14). A laterally compressed, unarched element characterized by abbreviated anterior and posterior bars, the latter being the weaker of the two. The anterior and posterior edges of the bars overhang the more aboral portion of the conodont in a characteristic sinuous fashion (Pl. 17, fig. 12). The short anterior and posterior bars each bear up to three denticles, anterior and posterior to the cusp respectively. The anterior and posterior bar denticles are of differing lengths, the middle of the three often being the longest. This variability in length is the cause of the irregular oral outline of the two bars when seen in lateral view.

Aborally the element bears a moderately large basal cavity that narrows and becomes constricted under the anterior bar. The basal pit under the cusp is the deepest part of the basal cavity and is directed anteriorly. The element is slightly flexed laterally and occurs as both dextral and sinistral elements. It is very similar to the *Oz* element of *C. windsorensis* Globensky (see von Bitter 1976; von Bitter and Plint-Geberl 1982). The latter species and *T. transatlanticus* sp. nov. rarely occur together in Atlantic Canada and this, as well as the criteria outlined in Table 5, serves to differentiate their *Oz* elements.

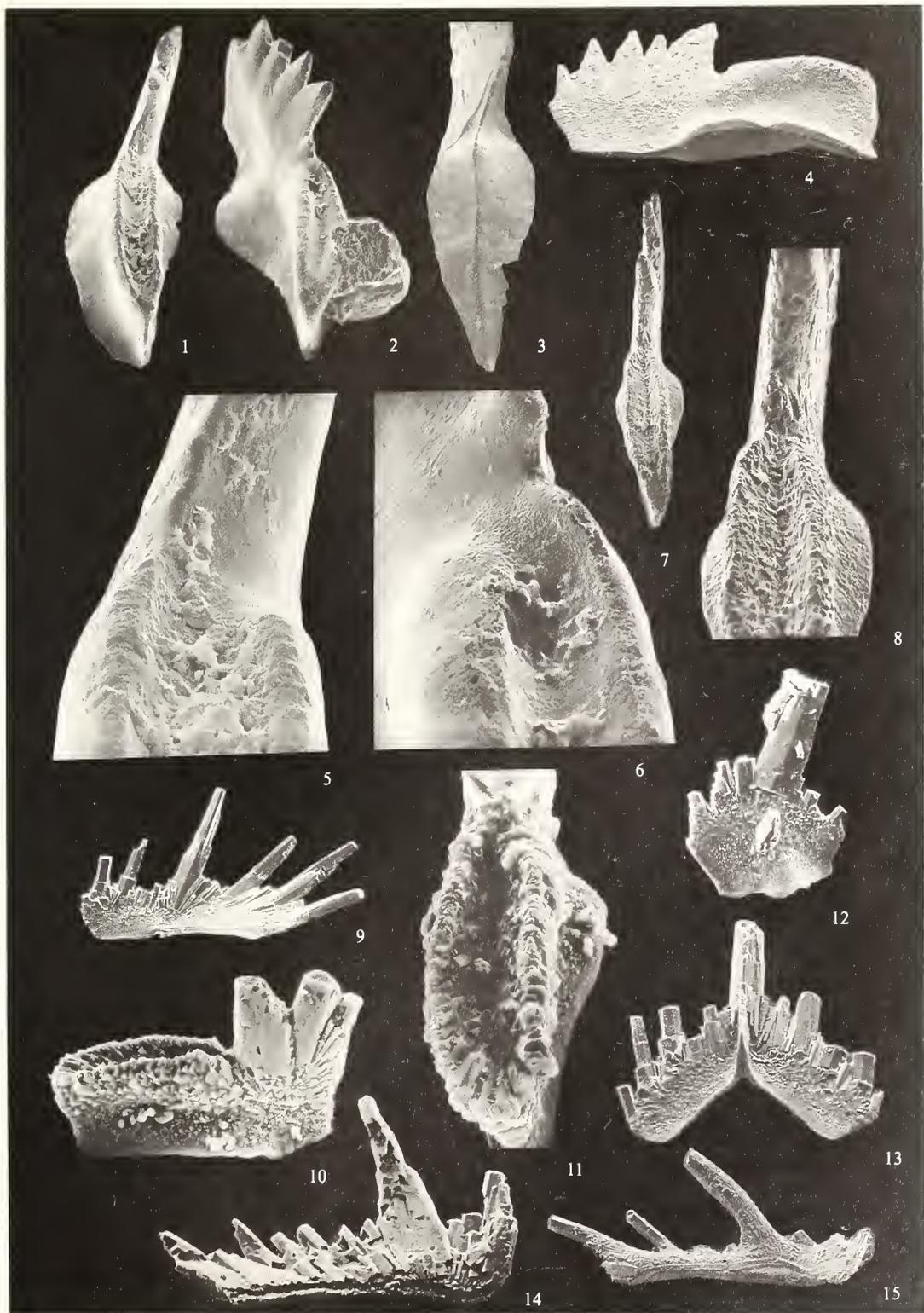
TABLE 5. Morphological characteristics of the *Oz* elements of *Taphrognathus transatlanticus* sp. nov. and *Cavusgnathus windsorensis* Globensky.

<i>Taphrognathus transatlanticus</i> sp. nov.	<i>Cavusgnathus windsorensis</i> Globensky
Oz element	Oz element
Relatively short anterior and posterior bars	Relatively long anterior and posterior bars
Irregular denticulation with middle of three bar denticles generally the largest	Regular denticulation with up to five denticles gradually and regularly increasing in size toward the cusp
Anterior bar strong; posterior bar weak	Anterior and posterior bars almost equally strong

EXPLANATION OF PLATE 17

Figs. 1-15. *Taphrognathus transatlanticus* sp. nov. Lower Codroy Group, Newfoundland (figs. 1-3, 5, 6, 9-15), and Windsor Group, Nova Scotia (figs. 4, 7, 8), Canada; *T. transatlanticus* Zone, Viséan, Lower Carboniferous. 1, holotype, ROM 38474, oral view of sinistral Sp or platform element, sample Fish-1-1, locality 2, $\times 235$. 2, paratype, ROM 38475, oral view of dextral Sp or platform element, sample Fish-1-1, locality 2, $\times 220$. 3, paratype, ROM 38473, aboral view of Sp or platform element, sample Fish-1-8, locality 2, $\times 160$. 4, ROM 38471, lateral view of Sp or platform element, sample Mi-1-1, locality 9, $\times 135$. 5, 6, ROM 38474 and 38475, detailed views of sinistral and dextral Sp or platform elements, $\times 1200$ and $\times 1120$ respectively. 7, ROM 38472, oral view of ?sinistral Sp or platform element, sample Mi-1-1, locality 9, $\times 150$. 8, ROM 38472, detailed oral view of ?sinistral Sp or platform element, $\times 390$. 9, ROM 38488, inside lateral view of dextral Pl element, sample Corm-1-3, locality 3, $\times 125$. 10, ROM 38485, lateral view of Sp or platform element, sample Corm-1-1, locality 3, $\times 225$. 11, ROM 38485, oral view of Sp or platform element, $\times 450$. 12, ROM 38477, lateral view of Oz element, sample Corm-1-3, locality 3, $\times 190$. 13, ROM 38490, posterior view of Tr element, sample Corm-1-3, locality 3, $\times 165$. 14, ROM 38489, inside lateral view of sinistral Hi element, sample Corm-1-2, locality 3, $\times 47$. 15, ROM 41846, inside lateral view of sinistral Hi element, sample Cod-1-3, locality 4, $\times 50$.

See Appendix for locality details.



VON BITTER and AUSTIN, *Taphrognathus*

Hi element (Pl. 17, figs. 14, 15; Pl. 18, figs. 11, 12). A relatively unarched, laterally bowed element dominated by a large cusp and a large anterior bar denticle. The anterior bar is variable in length depending on ontogenetic stage. Small specimens have only a very short bar whereas larger elements have a longer bar. Longer anterior bars bear three to four denticles while short anterior bars bear one or two denticles anterior to the cusp. The anteriormost denticle is generally the largest. The anterior bar is deflected inward very slightly and may also be directed either orally or aborally slightly. The posterior bar is generally three to four times the length of the anterior bar and bears a series of relatively stout posteriorly inclined denticles. The denticulation of the posterior bar is not noticeably 'hindeodellid' (i.e. consisting of alternating large and small denticles). Rather, the denticles increase in size posteriorly, culminating in the large inclined posteriormost denticle. Aborally a narrow aboral groove (Pl. 17, fig. 14; Pl. 18, fig. 11) that presumably opens into a basal cavity or basal pit under the cusp may be seen in some specimens. This groove may be completely closed and everted (Pl. 17, fig. 15), particularly in mature specimens, preserving only the smallest of basal pit openings.

The Hi element, like the Oz element of this species, can be differentiated from the homologous elements in the apparatus of *C. windsorensis* only with difficulty. The almost mutually exclusive occurrence of the two species in Atlantic Canada and the tabulated characteristics shown in Table 6 helps to distinguish them.

Pl element (Pl. 17, fig. 9; Pl. 18, fig. 13). A rarely preserved, laterally compressed, only very slightly arched element. It is recognized by its association with other elements of the apparatus; by its weakly to strongly inclined cusp approximately one-third to nearly one-half of the distance (measured from the anterior end) between the anterior and posterior ends; by its apparently hindeodellid denticulation; and by its characteristic posteriorly inclined, relatively large (compared with the Hi element) basal cavity. The anterior bar is not noticeably curved

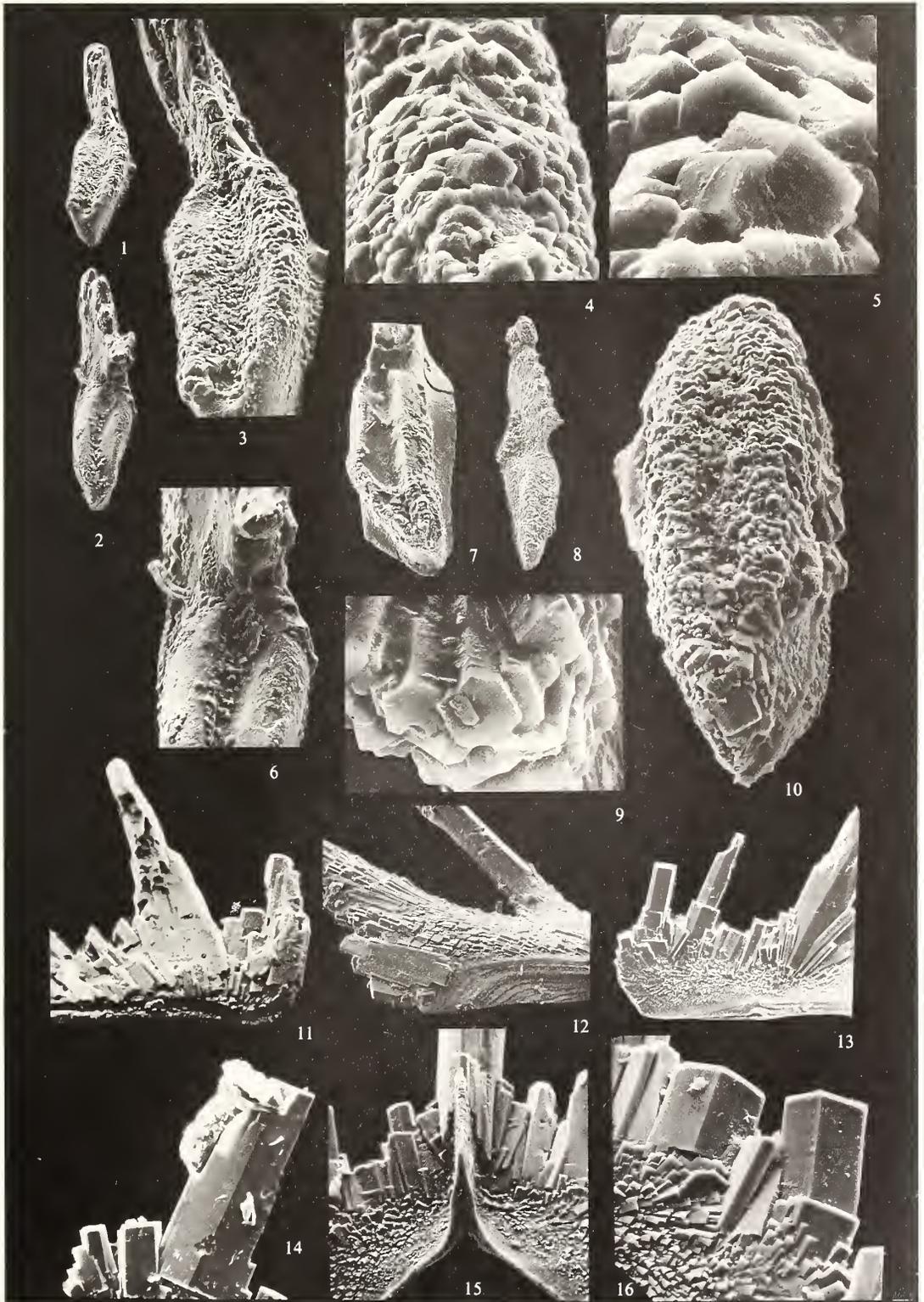
TABLE 6. Morphological characteristics of the Hi elements of *Taphrognathus transatlanticus* sp. nov. and *Cavusgnathus windsorensis* Globensky.

<i>Taphrognathus transatlanticus</i> sp. nov.	<i>Cavusgnathus windsorensis</i> Globensky
Hi element	Hi element
Slight inward anterior bar deflection	Greater inward anterior bar deflection
Large anterior bar denticle	Lacking large anterior bar denticle
Hindeodellid denticulation poorly developed	Well-developed hindeodellid denticulation

EXPLANATION OF PLATE 18

Figs. 1-16. *Taphrognathus transatlanticus* sp. nov. Avon Gorge, U.K. (figs. 1-8, 10) and Lower Codroy Group, south-western Newfoundland, Canada (figs. 9, 11-16) in part showing well and consistently developed recrystallization and/or overgrowth of calcium phosphate; *T. transatlanticus* Zone, Viséan, Lower Carboniferous. 1, BM X 755, oral view of dextral Sp or platform element, sample S53, locality 1, $\times 125$. 2, BM X 756, oral view of ?dextral Sp or platform element, sample S58, locality 1, $\times 120$. 3, BM X 755, detailed oral view of dextral Sp or platform element, $\times 320$. 4, 5, BM X 755, detailed views of outer parapet showing hexagonal calcium phosphate crystals, $\times 1270$ and $\times 3170$ respectively. 6, BM X 756, detailed oral view of ?dextral Sp or platform element, $\times 300$. 7, BM X 757, oral view of sinistral Sp or platform element, sample S54, locality 1, $\times 75$. 8, BM X 758, oral view of ?dextral Sp or platform element, sample S58, locality 1, $\times 95$. 9, ROM 38485, detailed oral view of posterior portion of platform showing well-developed recrystallization and/or overgrowth, $\times 1480$. 10, BM X 758, detailed oral view of ?dextral Sp or platform element showing recrystallization and/or overgrowth (note that blade shown in fig. 8 was broken off during preparation), $\times 360$. 11-16, detailed views of ramiform conodont elements showing calcium phosphate recrystallization and/or overgrowth developed on or toward the oral surface. 11, ROM 38489, anterior end of sinistral Hi element, sample Corm-1-2, $\times 340$. 12, ROM 41846, posterior end of sinistral Hi element, sample Cod-1-3, $\times 130$. 13, ROM 38488, anterior end of dextral Pl element, sample Cod-1-3, $\times 235$. 14, ROM 38487, cusp of Oz element, sample Corm-1-3, $\times 360$. 15, ROM 38490, detail of posterior projection of Tr element, sample Corm-1-3, $\times 320$. 16, ROM 38490, detail of lateral bar denticles, $\times 615$.

See Appendix for locality details.



laterally whereas the posterior bar is curved inward to a slight but noticeable degree. The anterior bar denticles are directed slightly toward the cusp. Those of the posterior bar are more inclined, become progressively larger posteriorly, and the terminating denticles may be as large as or larger than the cusp. The last feature aids in distinguishing the Pl from the Hi element. Aborally, the Pl element bears a narrow basal groove which opens into the characteristic asymmetrical posteriorly inclined basal pit under the cusp.

This element has been recovered so infrequently (Table 3) that it is difficult to differentiate it from the Pl element of *C. windsorensis*. The element may prove to have been vicarious. However, the fact that such samples as Corm-1-3 and Corm-1-4 (locality 3, south-western Newfoundland) are thought (von Bitter and Plint-Geberl 1982, p. 198) to have contained the component elements of only *T. transatlanticus* sp. nov., and that *C. windsorensis* almost never occurs with *T. transatlanticus* sp. nov. in Atlantic Canada, helps this differentiation. The Pl element of *C. windsorensis* is better known and appears to be more delicate than that of *T. transatlanticus* sp. nov., lacking the latter's large cusp and noticeably large splayed posterior denticles (ibid., pl. 7, fig. 12).

Tr element (Pl. 17, fig. 13; Pl. 18, figs. 15, 16). A bilaterally symmetrical butterfly shaped element possessing a short posterior keel or process. The lateral bars of mature specimens form an angle of approximately 120° with one another. That of juvenile smaller specimens becomes increasingly obtuse, reaching approximately 170° . The lateral bar denticles are recurved, discrete, and number three to four in mature elements. The denticle second from the end is the largest. The lateral bars curve inward, forming a small depression at their junction on the outer side of the conodont. The cusp is triangular in cross-section and is recurved and keeled on the inner side. An undenticulated keel is present at the base of the cusp on the posterior side and in its lower portion forms the upper limit of the sub-triangular basal cavity. The basal cavity varies in size with ontogeny, being larger in mature specimens (Pl. 17, fig. 13; Pl. 18, fig. 15). The basal cavity narrows laterally and becomes a narrow basal groove that disappears one-third to one-half the distance along the lateral bars.

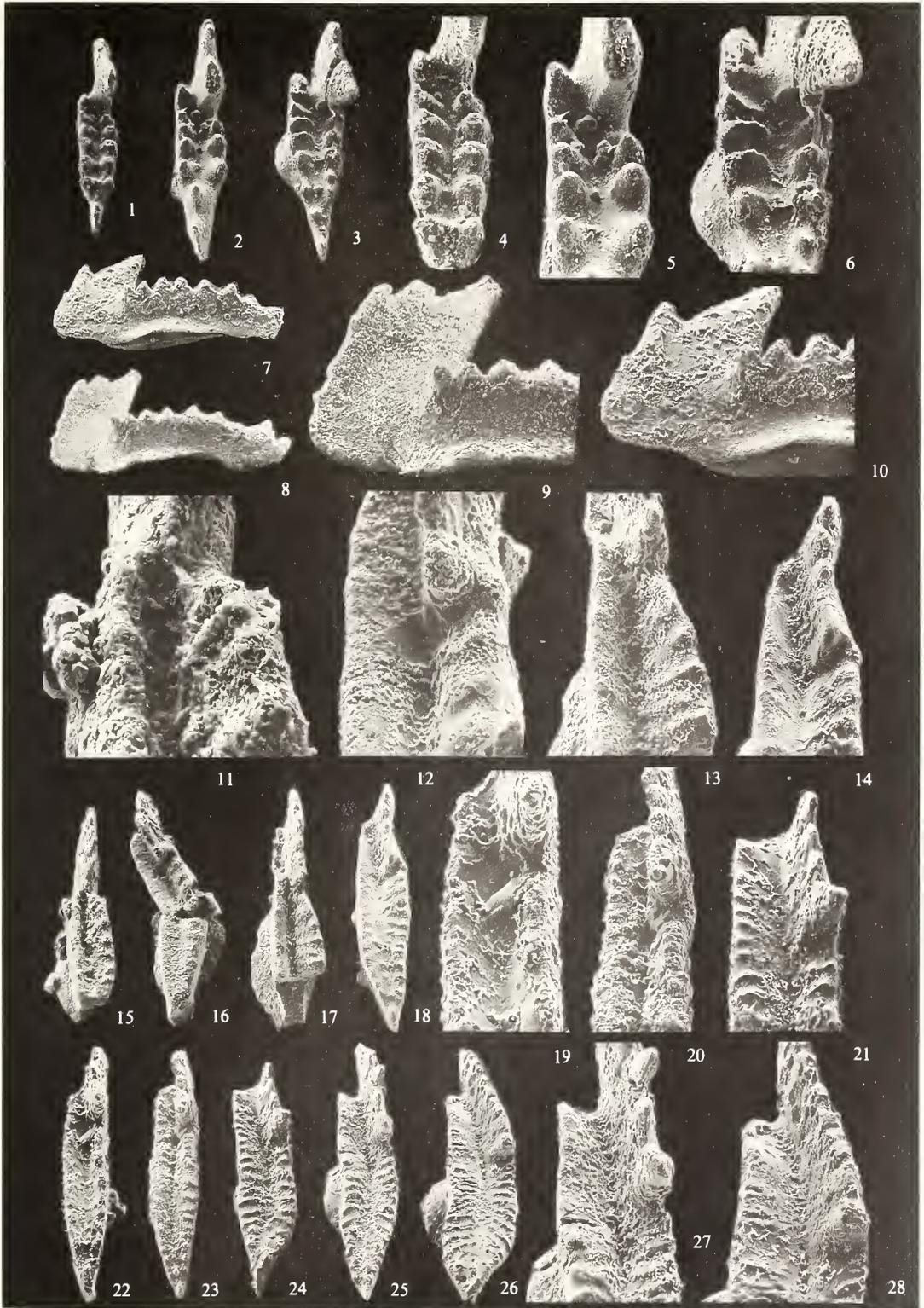
The element is similar to the Tr elements of *C. windsorensis* Globensky and *Hindeodus cristulus* Miller and Youngquist. It is therefore important to note which platform elements are present in any sample containing symmetrical butterfly shaped Tr elements. The characteristics tabulated in Table 7 may be used to differentiate the Tr elements of the three species.

Discussion. The distinctive Sp elements of *T. transatlanticus* sp. nov. occur as small sinistral and dextral elements (Pl. 17, figs. 1, 2, 5, 6; Pl. 18, figs. 1, 3, 7). Associated with these elements in the Avon Gorge (Tables 1 and 2) are platform elements that might initially be thought ontogenetic growth stages of *T. transatlanticus* sp. nov. The first ontogenetic series based on specimens from samples S45 and S49 contains cavusgnathiform elements herein identified as *C. unicornis* Youngquist and Miller, Sp element; these elements are weakly ridged on the outer parapet at all stages of their ontogeny (Pl. 19, figs. 11–18). The inner parapet, however, while still faintly noded in the largest specimen available, is not noded in smaller growth stages. The second ontogenetic series (Pl. 19, figs. 19–28)

EXPLANATION OF PLATE 19

Figs. 1–10. *Cavusgnathus windsorensis* Globensky, Sp elements. Locality 1, Avon Gorge, U.K.; *Taphrognathus transatlanticus* Zone, Viséan, Lower Carboniferous. 1–3, oral views, partial ontogenetic growth series showing nodosity typical of this species, sample S49; 1, BM X 759, $\times 75$; 2, BM X 760, $\times 72$; 3, BM X 761, $\times 70$. 4–6, detailed oral views; 4, BM X 759, $\times 150$; 5, BM X 760, $\times 145$; 6, BM X 761, $\times 140$. 7, 8, inside lateral views, sample S49; 7, BM X 762, $\times 65$; 8, BM X 763, $\times 68$. 9, 10, detailed inside lateral views; 9, BM X 762, $\times 135$; 10, BM X 763, $\times 130$.

Figs. 11–28. *Cavusgnathus unicornis* Youngquist and Miller, Sp elements. Locality 1, Avon Gorge, U.K.; *T. transatlanticus* Zone, Viséan, Lower Carboniferous. 11–14, detailed oral views of ontogenetic growth series showing initial weak ridges and nodes increasing in strength with size; 11, BM X 764, sample S45, $\times 340$; 12, BM X 765, sample S49, $\times 233$; 13, BM X 766, sample S45, $\times 150$; 14, BM X 767, sample S49, $\times 105$. 15–18, overall oral views; 15, BM X 764, $\times 68$; 16, BM X 765, $\times 60$; 17, BM X 766, $\times 60$; 18, BM X 767, $\times 53$. 19–21, 27, 28, detailed oral views of ontogenetic growth series showing initial nodosity developing into stronger ridges with increase in size, sample S49; 19, BM X 768, $\times 245$; 20, BM X 769, $\times 135$; 21, BM X 770, $\times 135$; 27, BM X 771, $\times 105$; 28, BM X 772, $\times 105$. 22–26, overall oral views; 22, BM X 768, $\times 100$; 23, BM X 769, $\times 68$; 24, BM X 770, $\times 68$; 25, BM X 771, $\times 53$; 26, BM X 772, $\times 53$.



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TABLE 7. Morphological characteristics of the Tr elements of *Taphrognathus transatlanticus* sp. nov., *Cavusgnathus windsorensis* Globensky, and *Hindeodus cristulus* Miller and Youngquist.

<i>Taphrognathus transatlanticus</i> sp. nov.	<i>Cavusgnathus windsorensis</i> Globensky	<i>Hindeodus cristulus</i> Miller and Youngquist
Tr element	Tr element	Tr element
Undenticled posterior keel present	Posterior keel may bear denticles and may grade into a posterior bar	Posterior keel or posterior bar absent
Cusp triangular in cross-section	Cusp sub-triangular in cross-section	Cusp elliptical to oval in cross-section
Element bilaterally symmetrical	Element bilaterally symmetrical	Element slightly asymmetrical
Discrete non-hindeodellid denticulation on anterior bars	Hindeodellid denticulation on anterior and posterior bars	

from sample S49 are cavusgnathiform elements, again identified as *C. unicornis* Youngquist and Miller, Sp element, whose traverse ridges, although decreasing in strength and length, are still present as nodes in even the smallest specimen recovered (Pl. 19, figs. 19, 22). The nodes in this smallest specimen are much more prominent on the outer bladed parapet. Smaller specimens almost without nodes, and thus intermediate with the largest Sp elements of *T. transatlanticus* sp. nov., have not been found. Note that the largest specimen of the first growth series (Pl. 19, figs. 14, 18) should be compared with the two largest cavusgnathiform conodonts of the second growth series (Pl. 19, figs. 25–28). As in the second growth series, the smallest specimens available (e.g. Pl. 19, figs. 11, 15) do not form convincing ontogenetic intermediates with the largest platform elements of *T. transatlanticus* sp. nov. However, the possibility that the illustrated specimen (Pl. 19, figs. 11, 15) is a sinistral specimen may be an indication of ontogenetic continuity between *T. transatlanticus* sp. nov. and *C. unicornis* (Pl. 19, figs. 11–18).

Cavusgnathiform conodonts identified as *C. regularis* type, Sp element, associated with *T. transatlanticus* sp. nov. have been reported from the Lower Codroy Group of south-western Newfoundland by von Bitter and Plint-Geberl (1982) (Tables 3 and 4). Similar associations have been noted in numerous samples from the Lower Windsor Group at localities in Nova Scotia and Quebec (see Appendix). Ontogenetic transitions between the *T. transatlanticus* sp. nov. Sp element and that of the *C. regularis* type have not been found at any of these localities, further demonstrating the taxonomic distinctiveness of *T. transatlanticus* sp. nov.

The other cavusgnathiform conodont species referred to earlier as being rare in the *T. transatlanticus* Zone of Atlantic Canada, but moderately common in that zone in the Avon Gorge, is *C. windsorensis* Globensky (Pl. 19, figs. 1–10). We believe this to be the first record of this species from Great Britain and to be distinct from *Windsorgnathus windsorensis* (Globensky) of Austin and Mitchell (1975) and Mitchell and Reynolds (1981).

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APPENDIX. LIST OF LOCALITIES

A. *Localities from which fauna of Taphrognathus transatlanticus Zone has been recovered and listed in Tables 1-4.* Description of lithologies and sample sites have been deposited with the British Library, Boston Spa, Yorkshire, U.K., as Supplementary Publication No. 14021 (14 pages). They may be purchased from the British Library, Lending Division, Boston Spa, Wetherby, Yorkshire LS23 7BQ. Prepaid coupons for such purposes are held by many technical and university libraries throughout the world.

1. Avon Gorge, Bristol, U.K. Riverside exposure of the uppermost part of *Seminula* Zone and concretionary bed on Leigh Wood side of River Avon at ST 562737 (O.S. Sheet ST 57, 1:25,000). Traverse 9 of Rhodes *et al.* (1969, p. 22, figs. 5, 65, 66); see also Kellaway (1971, fig. 4).

2. Fischells Brook, south-western Newfoundland, Canada (Flat Bay Map Sheet 12B/7, 1:50,000). Section starting at base of first major limestone, the Fischells Limestone of Bell (1948), north-west of railroad trestle and proceeding north-west toward mouth of stream. In part locality 5 of von Bitter and Plint-Geberl (1982).

3. Ship Cove, south-western Newfoundland, Canada (St. Fintan's Map Sheet 12B/2, 1:50,000). Section E of Bell (1948, p. 21). Cormorant Limestone of Bell (1948, p. 22) sampled from apparent top downward; upper contact not exposed.

4. Barachois Brook, south-western Newfoundland, Canada (St. Fintan's Map Sheet 12B/2, 1:50,000). Section is approximately 91 m south of Trans-Canada Highway bridge on west side of brook. Section J of Bell (1948, p. 30); locality 8 of von Bitter and Plint-Geberl (1982). Barachois Limestone of Bell (1948) sampled from the apparent base upward; contact with underlying beds not exposed.

5. Codroy, south-western Newfoundland, Canada (Codroy Map Sheet 11O/14W, 1:50,000). Section D of Bell (1948, p. 18); Lower Codroy Section of Baird and Cote (1964, p. 517); locality 11 of von Bitter and Plint-Geberl (1982). Thickness of strata over and underlying carbonate units taken from Baird and Cote (1964, p. 517).

6. Woody Cove, south-western Newfoundland, Canada (Codroy Map Sheet 11O/14W, 1:50,000). Section immediately south of outlet of Woody Head Brook. In part section D of Bell (1948, p. 17) and the upper part of section described by Baird and Cote (1964, p. 517). In part locality 2 of von Bitter and Plint-Geberl (1982); refer to their fig. 2 for position of samples.

B. *Other localities in Atlantic Canada from which fauna of Taphrognathus transatlanticus Zone has been recovered.* Deposition information same as in Appendix A.

7. Johnstown, Richmond County, Cape Breton Island, Nova Scotia, Canada (Grand Narrows Map Sheet 11F/15, 1:50,000). 7A, at beach on Bras d'Or Lake. 7B, a brook section on the south-east side of the road approximately 1.2 km south-west of the cemetery and church at Johnstown.

8. Port Hood Island, Inverness County, Cape Breton Island, Nova Scotia, Canada (Port Hood Map Sheet 11K/4, 1:50,000). Units B₀ and B₁ of von Bitter (1976) sampled. Section studied by Stacy (1953), Schenk (1969), and von Bitter (1976).

9. Windsor, Hants County, Nova Scotia, Canada (Windsor Map Sheet 21A/16 East Half, 1:50,000). Section 2 of Bell (1929, p. 47). Miller Limestone of Bell (1929, p. 47) sampled.

10. Avondale (Newport Landing), Hants County, Nova Scotia, Canada (Wolfville Map Sheet 21H/East Half, 1:50,000). Shore section on Avon River discussed by Bell (1929, p. 47) and studied and mapped by Waring (1967). 10A, the Miller Limestone, exposed a short distance north-east of the wharf at Avondale. 10B, the Belmont Limestone of Moore (*in* Geldsetzer *et al.* 1980), of which 1 m ± is exposed at Avondale.

11. Windsor, Hants County, Nova Scotia, Canada (Windsor Map Sheet 21A/16 East Half, 1:50,000). Section 2 of Bell (1929, p. 47). Maxner Limestone of Bell (1929, p. 47) sampled.

12. Miller's Creek, Hants County, Nova Scotia, Canada; gypsum quarry operated by Fundy Gypsum Co. (Windsor Map Sheet 21A/16 East Half, 1:50,000). Stop 8 of Geldsetzer *et al.* (1980). The Belmont and Fisher limestones were sampled from their apparent bases upward in the south wall of the quarry.

13. Île Alright, Magdalen Islands, Quebec, Canada; east shore of island, north of Cap Alright and Ansé Firman (Île du Cap-aux-Meules Map Sheet 11N/5, 1:50,000). Locality D of Plint-Geberl (1981).

14. Île du Cap-aux-Meules, Magdalen Islands, Quebec, Canada; west part of island, 2 km east of Point Herisée, 2 km south-east of Cap-au-Trou (Île du Cap-aux-Meules Map Sheet 11N/5, 1:50,000). Locality E of Plint-Geberl (1981).

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PATTERNS OF STROMATOPOROID GROWTH IN LEVEL-BOTTOM ENVIRONMENTS

by STEPHEN KERSHAW

ABSTRACT. Stromatoporoids in argillaceous level-bottom limestones of the Upper Visby Beds in the Silurian of Gotland, Sweden, show a variety of features of growth form, within a spectrum of coenosteal shapes from laminar through low to high domical. Many coenostea show interdigitations of sediment in their margins, attributable to intermittent sedimentation, while others show abrupt changes in growth direction, which are the results of movement, often leading to overturning. Stromatoporoids frequently survived these agents and continued to grow, often resulting in different morphotypes from those which would have been produced in the absence of sedimentation and movement; serious problems of shape identification and shape classification exist as a consequence. Variations in the effects of sedimentation and movement are recognizable in the specimens studied and the stromatoporoids therefore record a variety of events occurring at the sea bed during their lives. The four most abundant stromatoporoid species in the Upper Visby Beds show variations in morphology. *Densastroma pexisum* Yavorsky is commonest and in general has a taller shape than *Clathrodictyon simplex* Nestor, *Pseudolabechia hesslandi* Mori, and *Stromatopora impexa* Nestor. The reasons for such variations are unclear but may be related to a number of factors such as sedimentation, current activity, substrate consistency, or availability of food and oxygen.

STROMATOPORIDS exist as a wide range of growth forms and the difficulties involved in dividing this range into recognizable groups of shapes are reflected in the small amount of literature containing useful information on stromatoporoid morphotypes (e.g. Broadhurst 1966; Abbott 1973; Kapp 1974; Cornet 1975; Kobluk 1975; Kershaw and Riding 1978, 1980). The majority of stromatoporoids have a common plan of accretionary growth by successive layers (laminae) leading to the familiar range of laminar, domical, and bulbous forms which can be expressed as a geometrical array (Kershaw and Riding 1978). Dendroid stromatoporoids form a distinct group and are not considered here.

Laminar, domical, and bulbous forms are most easily recognizable when the stromatoporoids grew on a flat substrate and were not subjected to sedimentation or dislocation so that their shapes are preserved as being clearly laminar, domical, or bulbous. However, stromatoporoids are relatively shallow-water benthic organisms and as such were exposed to dynamic factors of the environment, such as sedimentation and turbulence. Problems arise in classifying the shape of a particular individual which preserves the effects of these factors. A domical coenosteam which was overturned but continued to grow from undamaged surfaces developed an overall shape which is no longer domical, but was nevertheless created by a domical style of growth. This is also true for coenostea which have suffered frequent sedimentation, leaving them with ragged margins and an exaggerated vertical dimension. The problem is further compounded by inherent irregularity of many growth forms, particularly in Devonian carbonate complexes (e.g. Fischbuch 1968; Noble 1970; Cornet 1975) where a number of different types of mamelons and irregular protrusions can complicate the shape of a coenosteam. Various combinations of these factors can lead to an individual which is not immediately recognizable as belonging to a particular group of shapes in the Kershaw and Riding (1978) scheme. The problems involved in analysing the biological processes which determined the shapes are thus greatly increased.

These problems are of course a reflection of the growth and development of coenostea but a further consideration has a powerful influence on morphological groupings of stromatoporoids: the plane of section. Stromatoporoids, especially reef-building forms, are usually seen in vertical section in cliff

faces and drill cores and the practice of shape classification is mostly carried out on two-dimensional sections. Thus we are trying to classify three-dimensional shapes from two-dimensional views. Serial sectioning would allow the three-dimensional form of a stromatoporoid to be characterized but this is not practicable in most situations and we are, therefore, simply stuck with the problem. Plane of section is not a severe difficulty in stromatoporoid-bearing rocks where coenostea are preserved upright and lack the effects of changing growth direction (see Kershaw and Riding 1980), but forms which have been overturned and contain several episodes of growth in different directions present serious problems of classification based on a single plane of section.

In a typical assemblage of stromatoporoids there is a mixture of growth forms: (a) those which grew as regular laminar, domical, or bulbous forms and have not been disturbed during their lives; (b) those which began growth in such a way but subsequently were affected by dynamic environmental factors which produced effects attributable to movement and sedimentation; and (c) forms with inherent growth irregularities which may or may not include the effects of b. An example of such an assemblage is found in the Upper Visby Beds on Gotland, Sweden. This contains very few forms of category c. The assemblage usefully illustrates the problems outlined above and the means by which some of them can be filtered out so that the factors controlling the basic morphologies may be more clearly identified. The relationships between genotype and morphotype of the stromatoporoids can then be more easily examined. Cornet (1975) and Kershaw (1981) have already demonstrated that an

EXPLANATION OF PLATE 20

Stromatoporoids from the Upper Visby Beds showing effects of sedimentation and movement described in the text. All figures are vertical sections. Some material is deposited in the British Museum (Natural History) (prefix BM(NH): the remainder (prefix SGU) with the Swedish Geological Survey.

Fig. 1. Smooth enveloping domical coenosteum of *Denastroma pexisum*. Note that (a) the specimen is composed initially of two coenostea which merged as they grew, and (b) no sedimentation events are recorded in the specimen. Korpklint 1, $\times 0.6$. SGU Type 1439.

Fig. 2. Upper coenosteum: smooth non-enveloping low domical form of *D. pexisum* showing *Trypanites* borings in the upper surface. Lower coenosteum (below line): low domical ragged form of *Stromatopora impexa* showing small sedimentation events interrupting growth at regular intervals. A small heliolitid colony (centre) grew on the upper surface before the *D. pexisum* covered it. Ireviken 3, $\times 1$. BM(NH) H 5442.

Fig. 3. Domical coenosteum of *D. pexisum* (on coral debris) showing damage at the right-hand flank, the damaged area being encrusted by a laminar coenosteum of *Clathrodictyon simplex*. The latter extends underneath the *D. pexisum* suggesting that at one time the right edge was uppermost. Ireviken 3, $\times 1.25$. SGU Type 1440.

Fig. 4. Part of a coenosteum of *D. pexisum* (lower) encrusted by a bryozoan (thin white layer), in turn encrusted by a low domical smooth, non-enveloping form of *C. simplex*. Häftingsklint 1, $\times 1.25$. SGU Type 1441.

Fig. 5. Domical coenosteum of *D. pexisum* showing how movement has generated a bulbous outline. The right-hand coenosteum grew first and was then turned so that its left-hand edge was uppermost (with some damage to the fragile marginal areas on the left) and continued growth to produce a new coenosteum on the left of the photograph. Ireviken 3, $\times 0.8$. SGU Type 1442.

Fig. 6. Complex intergrowth of laminar and domical forms of *C. simplex* and alveolitid tabulates with intermittent sedimentation. The complex developed on a stable base of a halysitid colony (below line). Ireviken 3, $\times 1$. SGU Type 1443.

Fig. 7. Complex specimen showing development of ragged coenostea followed by overturning and regrowth. Specimen contains mostly *D. pexisum* but small coenostea of *C. simplex* and *S. impexa* are involved. Ireviken 3, $\times 0.6$. SGU Type 1444.

Fig. 8. Composite specimen of *D. pexisum*, *C. simplex*, and alveolitid tabulates to produce a structure with at least nine growth phases. It is clear that the specimen was overturned many times. Ireviken 3, $\times 0.6$. SGU Type 1445.



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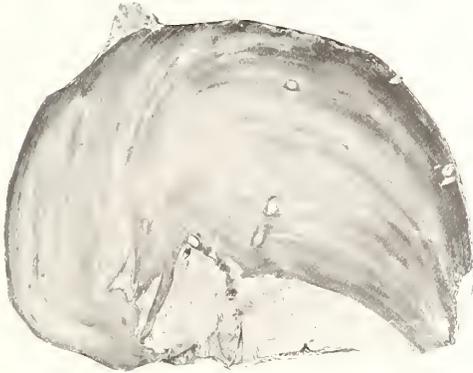
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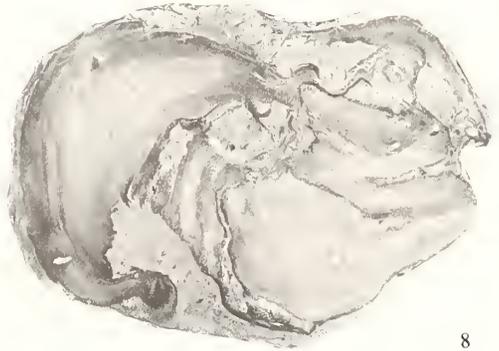
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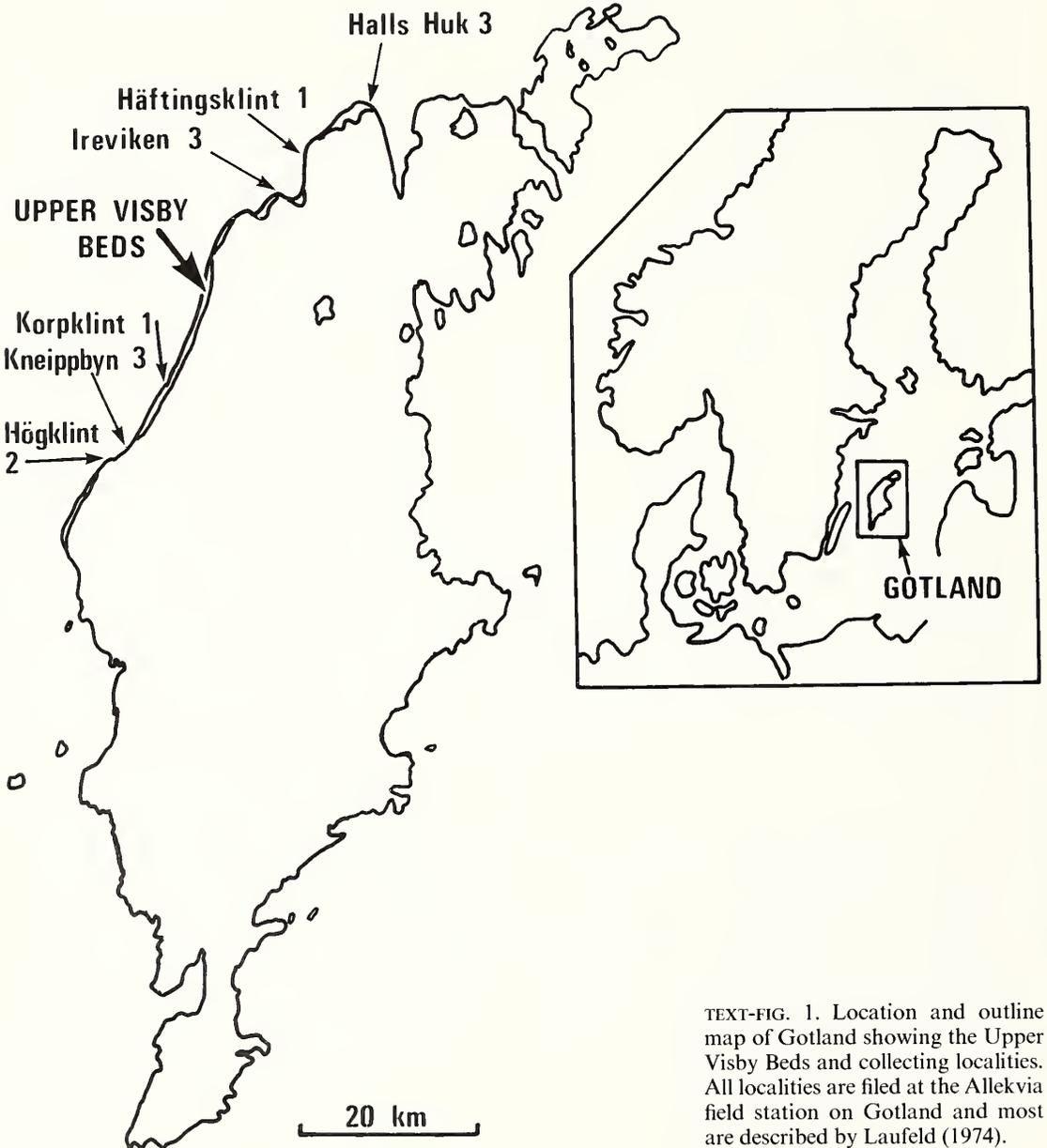
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understanding of stromatoporoids as organisms needs a conjunctive shape-species study: the Upper Visby Beds contain a small suite of species and the range of shapes of each is considered here.

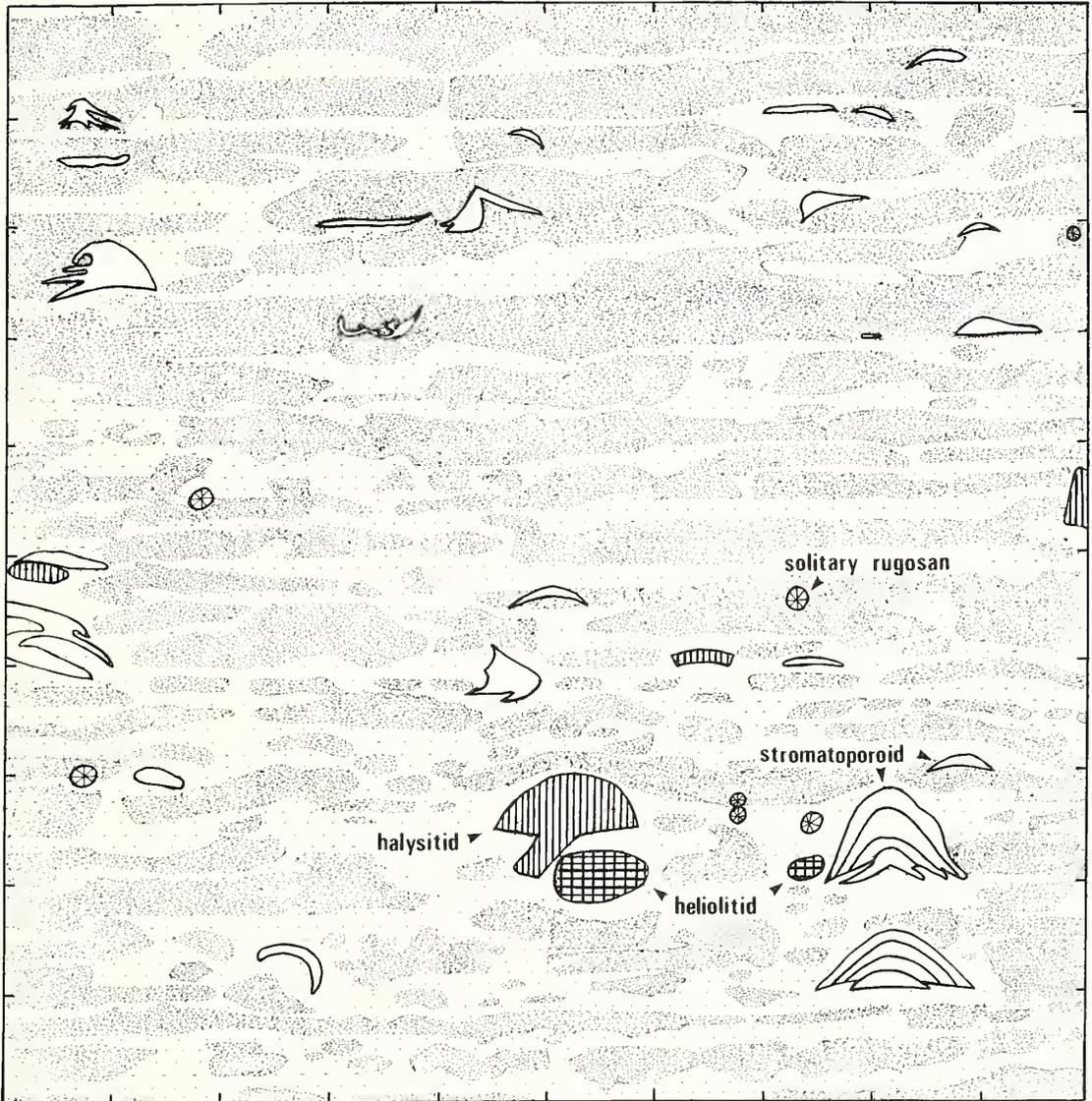
Importantly, stromatoporoids from the Upper Visby Beds can be easily extracted from the friable sediment; thus unlike rock sections where complete specimens are not normally obtainable, the three-dimensional structure of the Upper Visby specimens can be studied. Because of the availability of entire specimens, an adequate description of the history of growth or any coenosteum from these beds can be obtained by examination of a single (usually vertical) section through it, together with observations of its surface features.



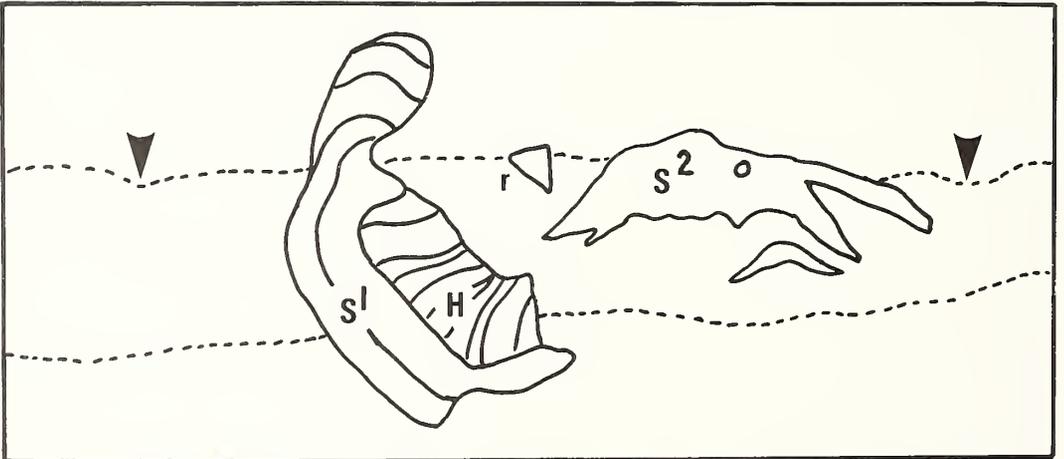
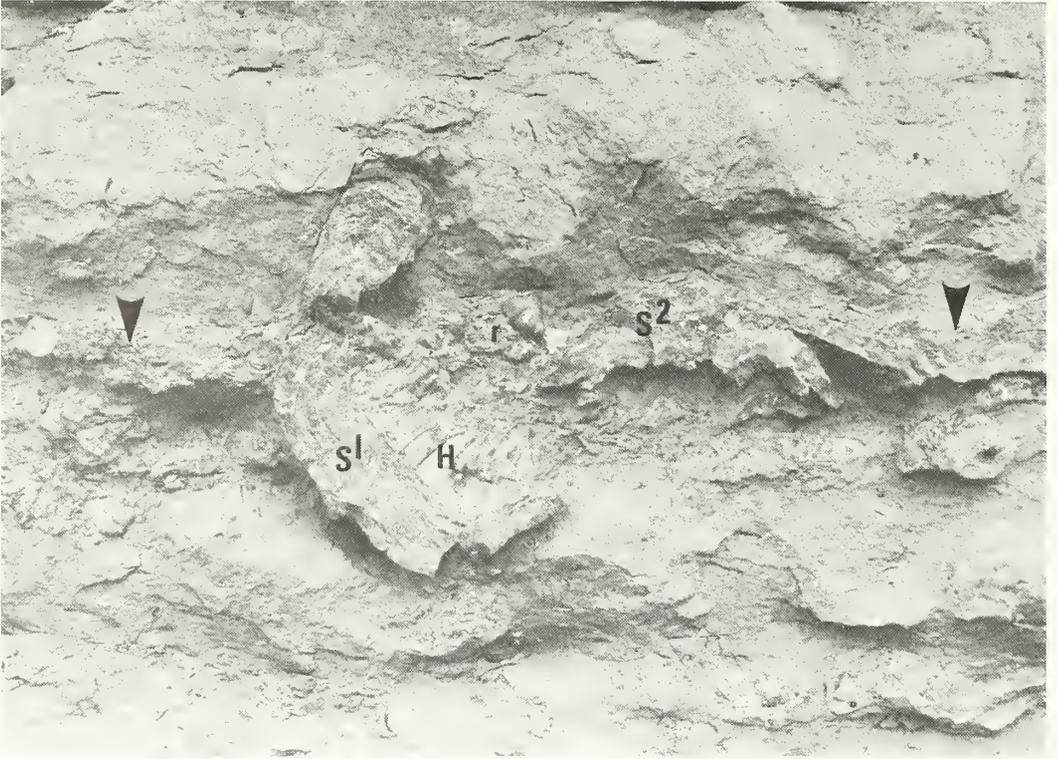
TEXT-FIG. 1. Location and outline map of Gotland showing the Upper Visby Beds and collecting localities. All localities are filed at the Allekvia field station on Gotland and most are described by Laufeld (1974).

THE UPPER VISBY BEDS

The Upper Visby Beds of Hede (1960) are dated as earliest Wenlock (see Jaanusson *et al.* 1979) and occur as a series of outcrops of maximum thickness 15 m, along the north-west coast of Gotland approximately following the strike of the beds (text-fig. 1). Dips are very low but there are local low amplitude folds due largely to the deformation of these incompetent beds by the weight of the overlying Högklint reefs (Eriksson and Laufeld 1978). Fossil contents are very variable and this is reflected by the occurrence of the stromatoporoids. The Upper Visby Beds are composed largely of alternating bands of mudstones and wackestones, much of the sediment being poorly consolidated.



TEXT-FIG. 2. Detailed map of 1 sq. m of vertical section of the Upper Visby Beds at Halls Huk 3 showing positions and attitudes of stromatoporoids and corals. Note the low faunal density. Heavy stipple: incomplete argillaceous limestone bands; light stipple: shale.



TEXT-FIG. 3A and B. Band of coarse debris (centre, arrowed) in fine-grained strata. Stromatoporoid (S1) overgrew a halysitid (H); the composite was overturned and S1 shows continued upward growth. Stromatoporoid S2 is preserved upright. r is a rugosan. Halls Huk 3, $\times 0.5$.

They form part of a shallowing-up sequence which begins with the underlying Lower Visby Beds (mostly unfossiliferous muds with little calcareous content), passes through the Upper Visby Beds, and ends with the Högklint and Tofta Beds (a complex mosaic of facies comprising reefs, inter-reef muds, and crinoidal grainstones as the main components). The Upper Visby Beds show a gradual upward increase in calcareous content and faunal diversity, but as a whole represent a relatively deep, generally quiet environment with a low diversity fauna. Accordingly the beds lack evidence of cross-bedding, scouring, or channelling by currents but indications of periodic disturbance (Jaanusson *et al.* 1979), particularly towards the upper parts, are present as packstone bands of skeletal debris which include not only shell material, but also stromatoporoid and coral coenostea (text-fig. 3) showing some damage. In addition, there are numerous examples of isolated coenostea of corals and stromatoporoids preserved out of growth attitude within the mudstones and wackestones themselves; these cannot be recognized as being restricted to particular horizons because coenostea are too sparsely distributed and because the Upper Visby Beds have a somewhat nodular appearance where time lines are not easily delimited (see text-fig. 2). The consolidated limestone bands are frequently heavily bioturbated, burrows being readily recognizable but having indistinct walls. Burrows are up to 5 mm in diameter. Sharp-edged excavations in the sediment are rare.

Small reefs in the Upper Visby Beds are dominated primarily by stromatoporoids and to a lesser extent by tabulates. There are proportionately more tabulates than in the shallower water Högklint reefs. The stromatoporoids used in this study have been collected only from the level-bottom sediments of these beds and the reefs have not been studied. Collecting localities in the Upper Visby Beds are shown in text-fig. 1.

STROMATOPOROID MORPHOTYPES AND SPECIES

Stromatoporoids from the Upper Visby Beds are somewhat variable in growth form, ranging from laminar to domical although most are domical. The distinction between laminar and domical is arbitrarily based on whether the ratio of vertical height/basal diameter (V/B) is respectively less or greater than 0.1. Low, high, and extended domical forms are additionally recognized; the (arbitrary) ranges of these are shown in text-fig. 4A.

A small number of laminar and domical forms are approximately circular in plan view and are flat-based. These show no evidence of the effects of sedimentation or movement and appear to have grown undisturbed on a plane substrate to produce smooth enveloping forms of Kershaw and Riding (1978), symmetrical in median vertical section. Others are identical except that the basal surface is concave (Pl. 20), the concavity being due to growth on debris of skeletal organisms or hummocks of sediment as discussed by Kershaw (1980). The majority of specimens, however, as seen in Plate 20, contain some interdigitation of sediment at their margins (ragged margins). Usually this only slightly affects the overall shape to produce a series of small frills at the lower edges of what can be regarded as smooth forms since raggedness is hardly apparent on surface inspection. In many specimens, however, the raggedness is a major feature of the shape (Pl. 20). Stromatoporoids may also show displacement while alive (having continued to grow after displacement). These tended to develop rounded coenostea in which the distinction between upper and lower surfaces is difficult to make. Their constituent growth forms can therefore be seen only when sectioned. Also, even in specimens which are apparently single coenostea, sections show that many contain several stromatoporoid and coral coenostea of different species overgrowing each other.

Measurements on vertical rock faces (Kershaw 1979) show that stromatoporoids are low in abundance, ranging from none to twenty-eight (average nine) individuals per square metre representing 0–5% of the rock volume (average 1%, one-tenth of the value for the overlying shallower-water Högklint reefs). Very few stromatoporoids show signs of penecontemporaneous damage, reinforcing the impression that environmental energy was generally low, but some overturned specimens reflect intermittent disturbance. These stromatoporoids are small, basal diameters ranging from 20 to 250 mm with vertical heights from 2 to 70 mm although they can be

considerably larger (Mori 1970). Attitudes of coenostea reflect their stable convex-up shape in that 80% of the forms measured are preserved upright.

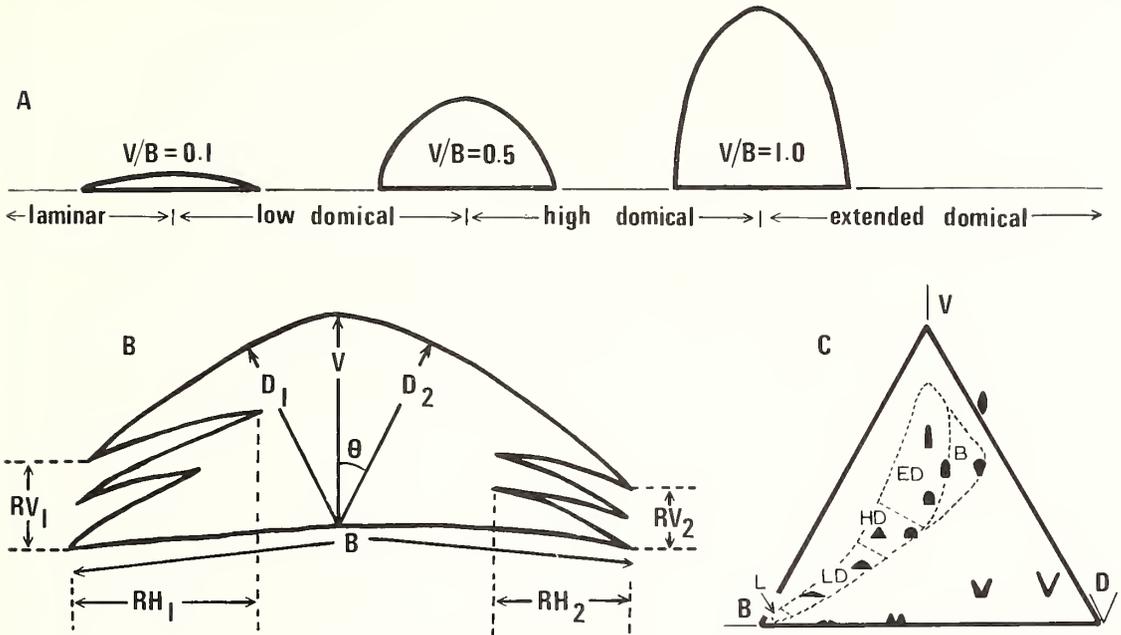
Other macrofossils are also low in abundance, particularly tabulate and heliolitid corals (often similar in gross morphology to stromatoporoids but can be more variable in growth form) which collectively occupy no more than a further 1% of rock volume. Low stromatoporoid abundance is also reflected in the low diversity stromatoporoid assemblage.

Nine stromatoporoid species have been reported from these beds (Mori 1969; Nestor 1979) but few of them occur commonly and only five were found in the sample used for this study. *Densastroma pexisum* Yavorsky is the most abundant, while *Pseudolabechia hesslandi* Mori, *Stromatopora impexa* Nestor, *Clathrodictyon simplex* Nestor, and *Clathrodictyon linnarssoni* Nicholson are much less common. All specimens of *C. linnarssoni* are incomplete and were not used in this analysis. Identifications are based on Mori's (1969) taxonomic work.

A range from laminar to high domical growth forms was found for all four species and suggests genotypic variability in all the stromatoporoids. *D. pexisum* formed 58% of the sample and so the environment must have been more suitable for its growth than for the other species. There is a temptation to suggest that *D. pexisum* is the dominant species, but since coenostea are generally isolated on bedding planes and the overall fossil content of these rocks is low (text-fig. 2), the idea of dominance for *D. pexisum* is inappropriate. Furthermore, there is no evidence of competition between stromatoporoids for space on topographic highs such as those created by the presence of dead stromatoporoids or other organisms.

Specimens were collected from all the localities in the Upper Visby outcrops shown in text-fig. 1, but only four of these were collected intensively. All specimens from these localities have been plotted on to the parameterization scheme of Kershaw and Riding (1978)—see text-fig. 5. The reader is referred to that paper for details of the triangular array; briefly, laminar forms plot in the bottom left-hand corner of the triangle and are increasingly domical towards the centre and top. Ragged specimens only are plotted in text-fig. 6. Text-fig. 4B illustrates the parameters used to plot data on to text-figs. 5 and 6. An amendment of the scheme allows an estimation of the amount of raggedness present in a specimen by measuring vertical raggedness (RV) and horizontal raggedness (RH) and then expressing them as ratios of V and B respectively (i.e. RH/B and RV/V). See Kershaw and Riding (1980) for details. Table 1A contains a summary of data on raggedness for the Upper Visby stromatoporoids. Text-fig. 4C shows the range of shapes generated by the array. Plate 20 shows examples of specimens containing several growth episodes; these could not be plotted as entire specimens because basal, vertical, and diagonal dimensions would be meaningless. Therefore it was necessary to treat each growth stage as an individual coenosteam with its own B, V, and D parameters and plot each separately in text-figs. 5 and 6. For example, Plate 20, fig. 5 contains two coenostea; Plate 20, fig. 7 contains three. In text-fig. 7 the distribution of basal diameters of all four species is illustrated; this is taken as a measure of coenosteal size. Although volume would be a more accurate estimate, it is not practicable to measure because two or more coenostea of the same or different species may form an inseparable composite and because of the variability of amount of sediment adhering to coenostea.

Chi-square analysis of the morphologies of the Upper Visby stromatoporoids reveals that *D. pexisum* is taller (higher V/B) than *C. simplex* and *P. hesslandi* at the 5% significance level and taller than *S. impexa* at the 7% level; this is regarded as sufficient for a significant difference to be accepted. *S. impexa*, *P. hesslandi*, and *C. simplex* display flatter distributions of shape, which are not significantly different from each other. The analysis involved only the non-ragged specimens, because ragged coenostea are exaggerated with respect to the vertical height which would give a false impression of the inherent shape of the coenosteam. Similar analysis of basal diameters demonstrates that *C. simplex* coenostea have significantly smaller diameters than those of the other species at the 0.1% significance level. The latter three species do not show a significant difference in basal diameters amongst themselves.



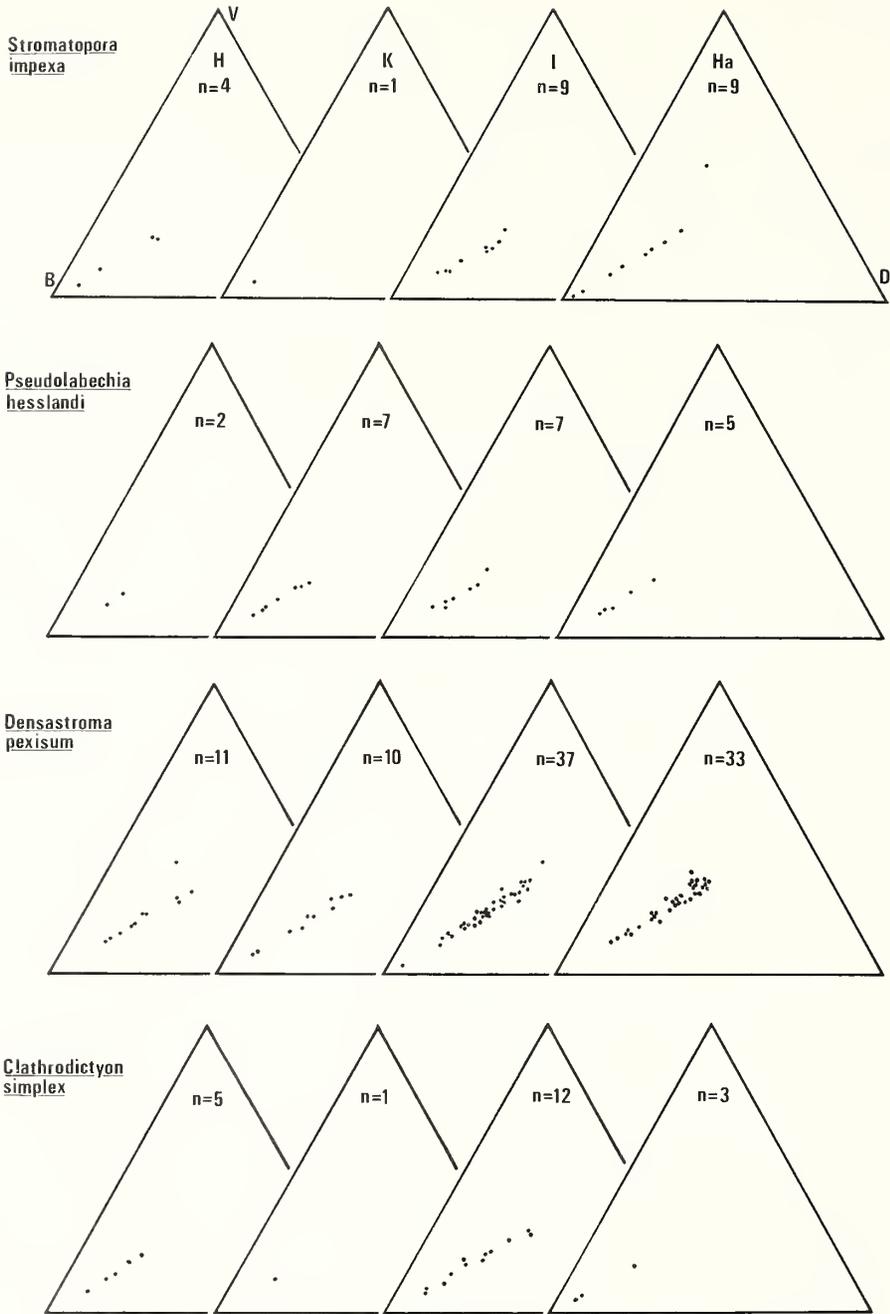
TEXT-FIG. 4. Shapes and parameters of stromatoporoid coenostea. A, terminology of stromatoporoid shapes used in this paper. V/B is the vertical/basal ratio. B, parameters measured for use in text-figs. 5, 6, 7 and Table 1A. V = vertical height, B = basal diameter, D (average of D_1 and D_2) = diagonal length at an angle (θ) of 25° from V . RV (average of RV_1 and RV_2) = vertical raggedness. RH (sum of RH_1 and RH_2) = horizontal raggedness. C, parameterization display of Kershaw and Riding (1978) showing examples of shapes generated by the scheme, the area occupied by stromatoporoids, and the approximate divisions of form. L, LD, HD, ED, and B are respectively: laminar, low, high, extended domical, and bulbous.

PATTERNS OF GROWTH

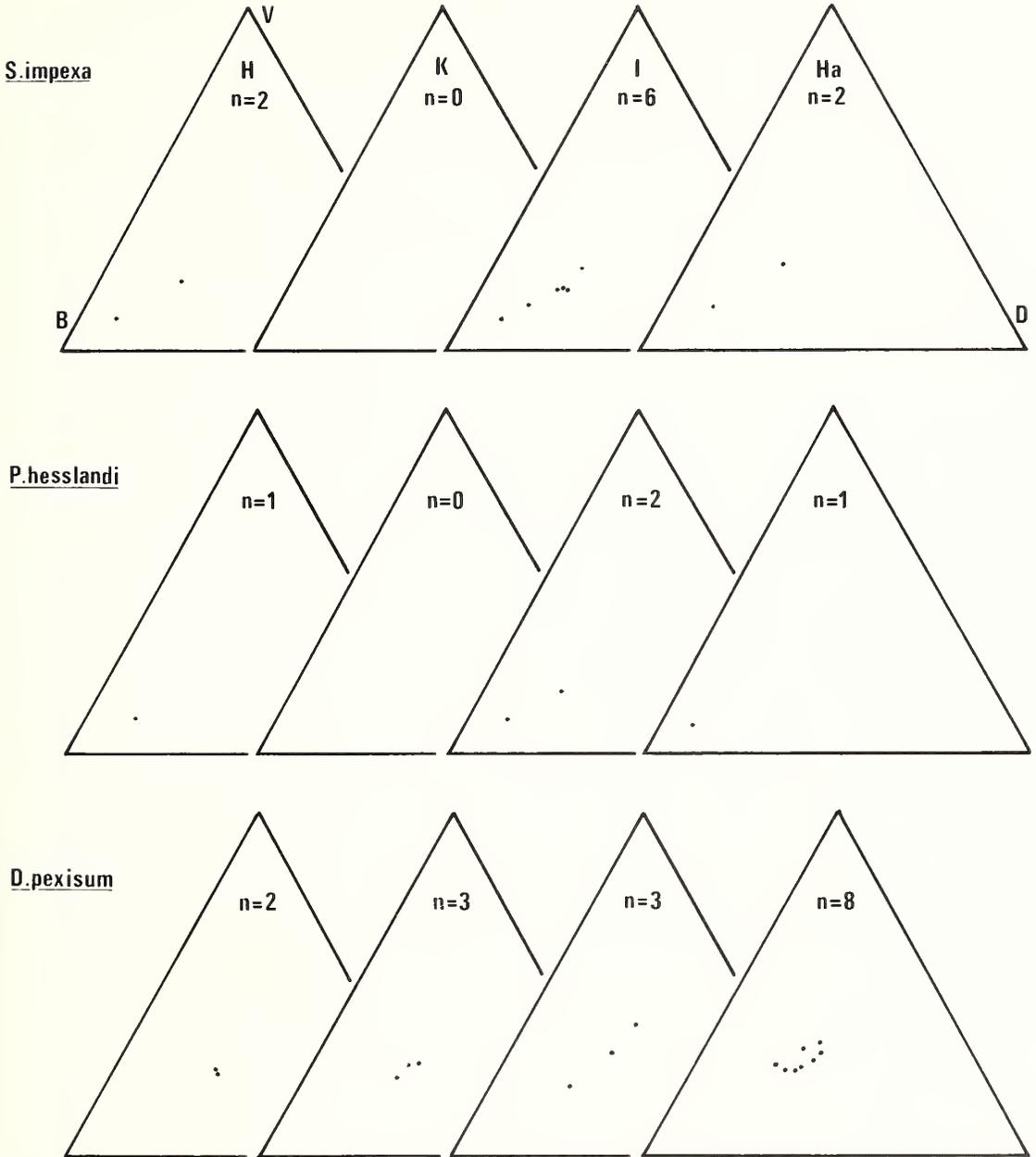
Stromatoporoids from the Upper Visby Beds, whether or not they have been affected by sedimentation or movement, do show a common style of growth in layers to produce laminar or domical coenostea; sedimentation and movement have merely disrupted that. Thus those specimens unaffected by these processes could be regarded as being the basic shapes of stromatoporoids from these beds. The basic shape is thus not a single form but a range of shapes from laminar through to high domical, each with smooth enveloping laminae (Kershaw and Riding 1978). Illustrations in Plate 20 show that sedimentation and movement had variable effects on the basic shapes of the Upper Visby stromatoporoids and although both processes may have operated on the same specimens, their effects can be considered separately.

Sedimentation

Several morphological features attributed to sediment choking are seen in the Upper Visby stromatoporoids. In smooth enveloping forms sedimentation has apparently not encroached upon coenostea during growth. However, while a lack of sediment interdigitations indicates that little or no sedimentation occurred up to the last-formed lamina (Pl. 20, fig. 1), cessation of growth at that point could be due to rapid sedimentation completely covering the growing surface. Such forms are uncommon; more usually in other individuals of the same species sediment is deposited on the marginal areas and although this is typically quite low in amount it can cover a large part of the coenosteal surface at any stage of growth (Pl. 20 figs. 2, 3, 6). Sediment forms discrete lenses and



TEXT-FIG. 5. Composite diagram showing morphology for each stromatoporoid species from the four main collecting localities, plotted on to the triangular display of Kershaw and Riding (1978). H, K, I, and Ha are, respectively, Högklint 2, Kneippbyn 3, Ireviken 3, and Häftingsklint 1.



TEXT-FIG. 6. Composite diagram showing triangular displays of morphotypes of ragged specimens only of each stromatoporoid species from the four main collecting sites. Note that text-fig. 5 includes these and the smooth forms. There are no ragged forms of *Clathrodictyon simplex* in the sample.

wedges which are indicative of intermittent deposition. The opposite view, that deposition was constant and growth episodic, is less likely because of the highly variable nature of sediment interdigitations in the stromatoporoids. Some have no such interdigitations (Pl. 20, fig. 1); others have a few large ones (see Kershaw and Riding 1978, fig. 2), while others have several small wedges in their margins (Pl. 20, fig. 2). Furthermore, any coenosteum may show a variety of thicknesses of sediment interdigitations and growth rates are unlikely to have varied to this degree in this fairly stable environment. However, stromatoporoid growth rates were almost certainly not constant since sediment deposition would presumably have caused a temporary reduction in growth rate. Stromatoporoid growth rate is poorly researched; the only really useful indicators are latilaminae—broad bands in coenosteum thought by some to be akin to seasonal growth banding. However, great uncertainty surrounds the significance of latilaminae (Mori 1970) and they are not clearly defined in the Upper Visby stromatoporoids, except in *P. hesslandi*.

Movement

As with sedimentation events, a spectrum of movement effects is preserved in these specimens. Coenosteum which have been moved would be expected to show damage at their edges, as in Plate 20, figs. 3 and 5. Domical coenosteum, especially high domical forms, which have been overturned, have a high chance of being righted again quickly (Brenchley and Newall 1970; Abbott 1974) and in these cases it would not be possible to determine whether they had been overturned at all. Overturning is most clearly seen either where specimens are preserved in a non-upright position or where the direction of growth has changed. Note that the stromatoporoids are assumed to have grown upwards, approximately normal to the sediment surface in the Upper Visby Beds, which is the case in the majority of stromatoporoid assemblages. Specimens such as that shown in Plate 20, fig. 5 have been moved only once, others two or three times (Pl. 20, fig. 7), while others have a complex history of movement, often with sediment between the growth stages (Pl. 20, fig. 8). This sediment may have been deposited between growth stages, or, because it is rich in non-carbonate mud, adhered to stromatoporoid surfaces which touched the sea bed during movement. Stromatoporoid composites are common. Of 149 specimens, eighty-eight are single coenosteum while fifty-one contain stromatoporoids which grew on, or were overgrown by, a number of organisms.

While some coenosteum grew on (presumably dead) rugosans, gastropods, and orthocone nautiloids, others grew on heliolitids and tabulate corals, and the corals are also found overgrowing stromatoporoids. Table 1B shows the relationship between each species and its substrate and demonstrates that *P. hesslandi*, *S. impexa*, and *D. pexisum* are more common on mud, while *C. simplex* is more frequently found encrusting other organisms. A chi-square analysis shows that *C. simplex* is significantly more common on skeletal debris at the 1% level than the other three species. The latter show no difference amongst themselves. *P. hesslandi* and *S. impexa* show a similar distribution and together with *D. pexisum* had a greater tendency to grow on the muddy substrate.

Many of the stromatoporoid composites are monospecific and developed on continued growth from undamaged surfaces of overturned specimens. Others, with or without corals, appear to have built up as a consequence of the dead skeleton of one providing a stable surface for the next, slightly higher than the surrounding sea bed, from which sediment could be shed. As explained by Kershaw (1980), previous skeletons were almost certainly dead before overgrowth by later coenosteum. Damage of coenosteum in composites which have been overturned is minimal and consists of delicate marginal edges of coenosteum having snapped off leaving sharply broken edges, frequently overgrown in later growth phases (Pl. 20, figs. 3, 5).

Internal lamination patterns

In addition to the variations of gross morphology and basal diameter, there are, in all species collected, differences in the arrangements of laminae within coenosteum, which have a bearing on this discussion. Both laminar and domical forms can have enveloping laminae, giving the coenosteum generally smooth outlines (text-fig. 8A, C; Pl. 20, fig. 1); most laminar forms are of this type. All but a few domical forms of all four species, while retaining a smooth outline, exhibit non-enveloping

laminae in the upper parts. Thus the lower parts started growth as laminar forms and became domical later on due to concentration of laminae in the central portion (text-fig. 8B; Pl. 1, figs. 2, 4, 5). Thus the overall pattern of development of laminae led to the same sort of smooth outline as individuals with fully enveloping laminae.

DISCUSSION

Sedimentation and movement effects preserved in the Upper Visby stromatoporoids may have been caused by a variety of processes and are considered in turn.

Sedimentation

Sediment settling from suspension may have produced the interdigitations seen in the stromatoporoids indicating intermittent sediment input. The Upper Visby Beds consist of alternating bands of mudstones and somewhat nodular limestones (text-figs. 2, 3) which may reflect regular, intermittent sedimentation events. Alternatively, sediment in stromatoporoid margins could have been deposited by transient currents. As mentioned earlier, there is no evidence of strong currents flowing across these beds but the presence of occasional debris bands suggest intermittent energy pulses, such as storm waves, stirring up the bottom currents, and redistributing sediment and benthic skeletal material. Such an interpretation is consistent with the view that the Upper Visby Beds represent a relatively deep water facies which would be only slightly affected by storm waves. Sediment in some interdigitations of the stromatoporoids contain coarse shell debris; others have fine-grained material only. Sediment may therefore have collected around stromatoporoid margins by both processes and in each case sediment settling on the higher parts of coenostea could have been easily shed on to the flanks. Thus laminar forms were more susceptible to choking by sedimentation than domical shapes, while the margins of all morphotypes in the Upper Visby Beds were prone to being smothered because of their subhorizontal aspect. That these delicate flanking areas of stromatoporoids grew in the first place indicates a low, if not zero, sedimentation rate most of the time. This is corroborated by three other lines of evidence: (a) the presence of (often abundant) encrusters on the undersides of upright stromatoporoids which appear to have grown in small cavities beneath coenostea; (b) the abundance of *Trypanites* domichnial borings in stromatoporoid upper surfaces (Kershaw 1980); and (c) considerable bioturbation of the sediment.

Movement

The agents causing overturning are unclear. Very small coenostea (e.g. where $B = 2$ or 3 cm) were conceivably overturned during bioturbation activity but since the bioturbation structures are rather small, larger coenostea would have needed more force to displace them. Orthocone nautiloids are present in the Upper Visby sediments and while alive may have predated on and dislodged stromatoporoids and corals from growth position, although there is a lack of the type of damage to coenosteal surfaces consistent with bite marks. The broken marginal edges of many larger coenostea suggest sudden movement of stromatoporoids consistent with displacement by storm activity as described above. Eddy currents produced by storm turbulence would have moved and overturned all coenostea below a certain size although the precise factors controlling movement of objects are complex and relate very much to local conditions as has been shown by models in flume experiments (Brenchley and Newall 1970; Abbott 1974; Kershaw 1979). These workers have shown that a combination of the following is involved: substrate composition and surface morphology, current velocity, and object size and shape. The responses of model stromatoporoids to a water current in a flume show that approximately equidimensional domical forms (where $V = B$) are the most stable of all, whereas laminar shapes tend to be flipped over by currents and tall domical forms which have a high centre of gravity are quite susceptible to overturning. Also, larger models are heavier and have higher competent velocities. These features would be expected to apply to the Upper Visby stromatoporoids. There is no evidence of attachment in the specimens studied and the assumption is that they grew on the unconsolidated sediment. Reef stromatoporoids, however, can be cemented to

TABLE 1. A, species totals and raggedness information for stromatoporoids from the Upper Visby Beds. R/S (ratio of numbers of ragged/smooth specimens), RV/V (ratio of vertical raggedness/vertical height), and RH/B (ratio of horizontal raggedness/basal diameter) are indices of raggedness. See text and Kershaw and Riding (1980) for explanation. B, relationship between the four stromatoporoid species and their substrates. The table was constructed by recording the substrate on which each coenosteum was found. 'other' includes the four species plus tabulate, heliolitid and rugose corals, gastropods, and orthocone nautiloids.

A

Species	Total	No. ragged	Mean R/S	Mean RH/B	Mean RV/V
<i>S. impexa</i>	23	10	0.43	0.63	0.51
<i>P. hesslandi</i>	21	4	0.19	0.59	0.36
<i>D. pexisum</i>	91	16	0.17	0.28	0.41
<i>C. simplex</i>	21	0	0.00	—	—

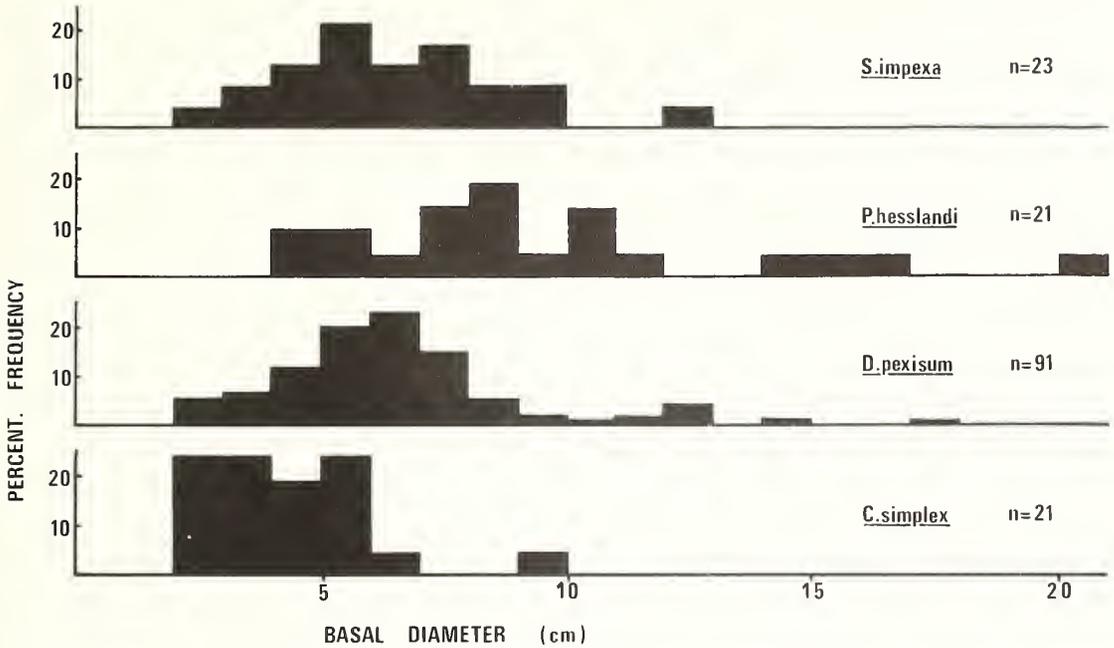
B

Substrate	Stromatoporoid species				
	<i>S. impexa</i>	<i>P. hesslandi</i>	<i>D. pexisum</i>	<i>C. simplex</i>	Total
Sediment	19	17	62	7	105
Other	4	4	34	17	59
Total	23	21	96	24	164

their substrate and may be in such close proximity to their neighbours that movement could be blocked in any case.

Competent velocity is also controlled by sediment type. On sand, low current velocities scour sediment from around objects and they can become buried as a result; at higher velocities a sandy substrate can facilitate coenosteal movement by creating a moving carpet of sand, reducing friction between stromatoporoid bases and the sediment. The Upper Visby Beds, however, are composed largely of mudstones and wackestones which provided a more coherent substrate than sand. Nevertheless, because bioturbation structures are not sharply defined, the sediment would not have been firm when bioturbated and probably, therefore, when colonized by stromatoporoids. Burial of objects by scouring of mud requires higher velocities than on sand because of the relatively lower mobility of muddy sediments. As a result, competent velocities are less on mud and once movement has started it is more easily perpetuated since the sediment is less yielding on impact. However, movement also depends upon substrate morphology. At water velocities just exceeding the competent velocity of a particular object, movement consists of a sliding motion across the sediment and may stop if an obstacle is encountered. At higher velocities an object may overturn when obstacles are reached and at even higher velocities overturning may occur regardless of presence of obstacles since the water is forced under the base of an object during its movement across the uneven substrate. The competent velocity of an object is increased if it is partially buried in the sediment because it has to be exhumed before movement can occur, and this necessarily involves some erosion of the substrate. Current surges, as would be expected during storms, can, however, produce eddies powerful enough to dislodge large objects which are unmovable by steady flow (Kershaw 1979).

The range of shapes and sizes of stromatoporoids in the Upper Visby Beds together with the unevenness of substrate must have given rise to a large variety of circumstances in the manner described above with respect to movement and overturning by turbulence. Also partial burial and variations of substrate composition played a part in determining the competent velocity for a given individual. Although it would be satisfying to have a series of values for competent velocities of the Upper Visby stromatoporoids, all these factors combine such that estimates for these particular



TEXT-FIG. 7. Size-frequency histograms of basal dimensions of each species.

coenostea are not very accurate; however, most coenostea would have been moved by velocities in the range 30–60 cm/s, based on experimental work with model stromatoporoids (Kershaw 1979).

Genotypic control on growth forms

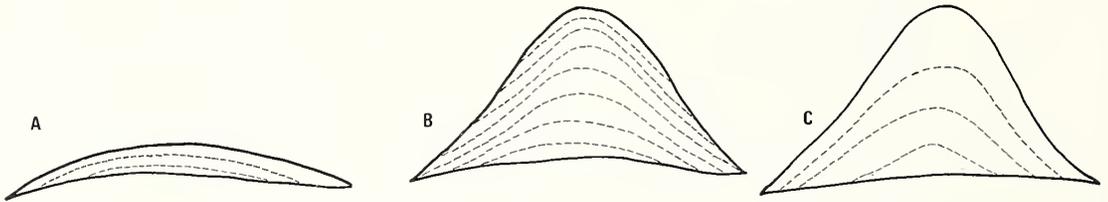
Recognition of the effects of sedimentation and movement and the consequent dismantling of composite specimens show up the true variations of coenosteal shape in the Upper Visby Beds (text-figs. 5, 6) and these in turn betray other processes at work. Each species shows a range of morphologies from laminar to high domical and suggest that under certain conditions laminar forms of a particular species developed, while under other conditions a domical shape was produced. A set of ecophenes therefore exists but the underlying controlling factors are not readily discernible. The shapes can be explained by a number of factors and these could include sediment-shedding capability, responses to current activity, variations in food, and oxygen supply. Variations in substrate consistency may also have affected shapes.

Stromatoporoids in the Upper Visby Beds do not show direct evidence of any of these possibilities but consideration of the sort of responses they might have made is worthwhile since little information is available on stromatoporoid palaeoecology.

A sediment-shedding capability is important for benthic organisms and developing a profile suitable for rejecting sediment landing on the growing surfaces is clearly desirable. Domical forms of all four species would have shed sediment from the apical areas, allowing growth to continue. Sediment interdigitations in stromatoporoid margins may well contain sediment shed from topographically higher parts of coenostea, and the stromatoporoids could clearly survive if the lower parts were smothered. If a domical growth style is a response to sedimentation then this suggests that sediment was continually settling on coenostea and would also suggest that laminar forms of any species grew in times (or areas) of little or no sedimentation. Unfortunately, the evidence of a low

sedimentation rate discussed earlier is compelling and laminar and domical forms do occur near each other on approximately the same horizons (text-fig. 2). The Upper Visby sea bed was probably uneven (Kershaw 1980) and a different interpretation is possible; a laminar form growing on a slightly raised area may have developed into a domical form had it settled as a larva in a lower area.

Differences in shape could have been a response to sedimentation, but could alternatively be due to a response to current activity for respiration and feeding. Although there is no evidence of strong current flow across the sediment surface, bottom currents must have been sufficiently aerated to allow the benthos to develop and this suggests the presence of at least gentle currents. Laminar organisms on a sediment surface in relatively deep environments live in water travelling slowly due to bed friction; the oxygen and food supply rates to them are consequently less than even a few centimetres higher up in the water column. The apices of domical organisms are not only higher in the water column, but because they interrupt the water flow they create eddies around them and keep the water well mixed in their vicinity. Since most stromatoporoids are domical in the Upper Visby Beds, they would have caused such local disruptions of water flow across the surface. It may be significant that tabulates and heliolitid corals also show a range of shapes from laminar to high domical which may be a response to the same stimuli.



TEXT-FIG. 8. Schematic vertical sections of stromatoporoid morphotypes from the Upper Visby Beds showing variations in the arrangements of laminae. See text for explanation.

Variation of substrate consistency is unlikely to have governed stromatoporoid morphology in these beds. Laminar forms would have been stable on an unconsolidated muddy substrate since coenosteal weight was low and evenly spread. Domical forms, with a higher mass per unit area of base, would have been better suited to firmer substrates. However, laminar forms are found not just on the substrate surface but also encrusted on skeletons of other organisms.

The four species do nevertheless show a different response to substrates. *C. simplex* is significantly more abundant as an encruster on the skeletons of other organisms than on the muddy substrate (Table 1B), suggesting a preference for harder and possibly topographically higher settling points. *D. pexisum*, *P. hesslandi*, and *S. impexa*, however, show a tendency to grow directly on the muddy substrate.

The pattern of accretion of laminae on the upper (growing) surfaces of these stromatoporoids described earlier may be indicative of shape-controlling factors. Significantly, laminae in upper parts of nearly all domical forms typically do not envelop earlier laminae completely. This feature may represent a mechanism by which growth was concentrated in the topographically higher central area of a coenosteum to cause local turbulence by interfering with water flow across the sediment and thereby feed more efficiently. By limiting growth to the central portion, metabolic energy would also have been saved if sedimentation affected the stromatoporoids since sediment clearly collected on and choked the topographically lower marginal areas. Whether this could be taken to imply that the presence of laminar and domical forms of the same species in these beds is due to variations of interplay between water flow and sediment deposition (from suspension) is open to conjecture, but the possibility nevertheless exists.

That *D. pexisum* is the most abundant of the four species studied could be explained by its generally taller profile than in the other three (text-figs. 5, 6). An upstanding shape is optimized for collecting food and oxygen and for shedding sediment, but also notable is that *D. pexisum* is generally less

ragged than *P. hesslandi* and *S. impexa* (Table 1) when horizontal raggedness is considered. The average value of RH/B of *D. pexisum* is lowest indicating that less of the upper surface area was covered by sediment in ragged forms. However, similarity of the RV/V values for the three species which have ragged forms means that, on average, the sediment wedges in *D. pexisum* are thicker due possibly to the steeper sides causing sediment to collect on a smaller marginal area than in flatter stromatoporoids. *D. pexisum* also has the smallest number of ragged forms of the three. No ragged forms of *C. simplex* were found in the sample. This species forms small coenostea (text-fig. 7). Its profile ranges from laminar to high domical but generally has a low profile (text-fig. 5); it may have been unable to thrive on the muddy sea floor. Its small size and lack of raggedness suggest a slow growth rate and a possible inability to shed sediment effectively; it may have been killed very easily by sedimentation.

The overall impression is that *D. pexisum* is the most abundant due to its height above substrate although the precise reasons as to why this should be so are as yet unclear.

CONCLUSIONS

This analysis of level-bottom stromatoporoids from the Upper Visby Beds on Gotland suggests that in a relatively poor, low diversity assemblage, different species developed alternative growth strategies and a variety of responses to the environmental pressures. Composite specimens reflect current activity across the surface of these sediments which resulted in overturning.

In a wider context, overturning and sedimentation are probably the two most important physical factors affecting the generation of stromatoporoid shapes and their effects have also been observed by the author in Ordovician and Silurian forms from Norway, Silurian forms from England and elsewhere on Gotland, and Devonian forms from England and Belgium in a variety of reef and non-reef environments. Most literature on stromatoporoid morphology also shows that these factors are common (e.g. Noble 1970; Kapp 1974; Cornet 1975). This study has documented the variety of their effects for a small assemblage and detailed examinations of these should be carried out elsewhere too.

An interesting parallel exists between the Upper Visby stromatoporoids and those from an almost identical environment in the Hemse Marls (Ludlow) in south-west Gotland. The most abundant species in the latter, *Pycnodictyon densum* (Mori 1970), has a similar internal structure to *D. pexisum* and is also usually low to high domical, also commonly with a smooth non-enveloping growth form. This could reflect the occupation of a similar ecological niche by two species at different times.

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A LATE UPPER TRIASSIC SPHENOSUCHID CROCODILIAN FROM WALES

by P. J. CRUSH

ABSTRACT. The fossil material of a 760 mm long crocodylian, *Terrestri-suchus gracilis* gen. et sp. nov., from a late upper Triassic fissure filling in the Carboniferous limestone of the old Pant-y-flynon quarry near Cowbridge, Glamorgan, is described. The quadratojugal is parallel sided and the squamosal lacks a descending process. A hard secondary palate is formed by the maxillae and premaxillae. A fenestra pseudorotundum is present but the pterygoids were not sutured to the braincase. The Eustachian tubes were ramified. A prearticular is present. The teeth are recurved, flattened, and bear serrations. The ischium projects posteriorly and the pubis, bearing an obturator foramen, borders the open acetabulum. The postero-ventrally extended coracoid joins the ossified sternum. The carpals and tarsals are crocodylian. The fifth metatarsal is reduced but bears two phalanges. The dorsal vertebrae are primitive. A paired row of leaf-shaped dorsal scutes were present. The earliest crocodyles are placed in three suborders—Protosuchia, Sphenosuchia, and Triassoestia. The genus *Pedeticosaurus* is included in the Protosuchia which were ancestral to the Mesosuchia. *Dibothrosuchus*, *Hesperosuchus*, *Hemiprotosuchus*, *Pseudohesperosuchus*, and *Sphenosuchus* form part of the Sphenosuchia. *Saltoposuchus* and *Terrestri-suchus* belong in a new family Saltoposuchidae. *Triassoestes* and *Hallopus* are included in their own suborders. The Hallopada, Sphenosuchia, and Triassoestia have no known descendants.

THE matrix-bearing *Terrestri-suchus*, and five other species of reptile, was found by Professor K. A. Kermack and Dr. P. L. Robinson in the spring of 1952 (Kermack 1956; Robinson 1957a). The material was discovered on a tip in the old Pant-y-flynon quarry, near Cowbridge, Glamorgan. The fossils came from a fissure, of unknown location, in the Carboniferous limestone of the quarry. The finely preserved and abundant material of *Terrestri-suchus* consists primarily of a number of blocks bearing associated and, sometimes, articulated bones but, in addition, there are a large number of individual bones that have been entirely freed from the matrix. The referral of the individual bones to *Terrestri-suchus* can be easily done on the basis of the articulated material. The fossils were prepared out mechanically using a needle mounted in a pin chuck and sharpened with a fine-grade oilstone. The bone was strengthened with dilute poly-butyl-methacrylate lacquer.

Age of the Welsh crocodile. Robinson (1957a, b) split the vertebrate-bearing fissures of the Bristol Channel area into two groups. The first group yielded mammals or mammal-like reptiles and she aged these as Rhaetic or lower Liassic. The second group, including Pant-y-flynon, lacked these animals and were believed to be Triassic and pre-Rhaetic. In making this distinction she assumes the older fissures to have been covered by the marine transgression of the Rhaetic. Robinson aged the older fissures on the basis of: a theoretical consideration of the mechanism of formation and filling of the fissures, a detailed consideration of the structure of the fissure at Emborough quarry, and the lack of mammals. Her general interpretations cannot be proven but the fauna of Emborough is shown to have been pre-Rhaetic as Rhaetic deposits covered this quarry. Robinson (1971) aged the Pant-y-flynon fissure as upper Norian because she assumed it to have passed through the conglomerate that lies above the Carboniferous limestone, which she regarded as Norian. The relationship of the fissure that contained *Terrestri-suchus* to the conglomerate is unknown as, in the new quarry, fissures both pass through and start below the conglomerate. Furthermore there is no evidence that the conglomerate is of Norian age, it could be Rhaetic or even lower Jurassic. There is no Rhaetic covering at Pant-y-flynon. Faunal correlations between Robinson's Triassic fissures suggest that they are contemporaneous, if the reptiles are assumed to have been evolving rapidly, except for Highcroft

whose fauna is too poorly known. Furthermore, elements of the fauna of the Triassic fissures are closely related to *Trilophosaurus* (Case 1928a, b; Gregory 1945), *Icarosaurus* (Robinson 1962; Colbert 1965), and *Saltoposuchus*. *Trilophosaurus* comes from the Dockum beds, *Icarosaurus* from the Locatong facies of the Newark group, and *Saltoposuchus* from the Stubensandstein. *Trilophosaurus* and *Icarosaurus* are usually considered upper Triassic and the Stubensandstein as upper Triassic but pre-Rhaetic. Thus these correlations, and Robinson's age determination of Emborough, imply that *Terrestrisuchus* was upper Triassic and pre-Rhaetic in age.

SYSTEMATIC PALAEONTOLOGY

Class REPTILIA

Order CROCODYLIA

Suborder SPHENOSUCHIA

Family SALTOPOSUCHIDAE fam. nov.

Terrestrisuchus gen. nov.

Type species. *Terrestrisuchus gracilis*. sp. nov.

Diagnosis. Small terrestrial crocodylian; skull bones unornamented; skull table rounded; supratemporal and antorbital fenestrae elongated; frontals excluded from supratemporal fenestrae; squamosal large and convex laterally; frontals and parietals paired; postorbital bar superficial; otic notch formed; quadrates bear conchae, slope anteriorly, and buttress under the squamosals; quadratojugal parallel sided; nineteen maxillary teeth; maxillae and premaxillae form a secondary palate; anterior palatal fenestrae present; interpterygoid vacuities present; basipterygoid articulations movable; pterygoids not sutured to the braincase; pterygoid flanges formed; Eustachian tubes ramified; fenestra pseudorotunda formed; external but no internal mandibular fenestra present; prearticular present; no pronounced retroarticular process; articular fenestrated and possessing a dorsally directed, medial, process; teeth thecodont, recurved, flattened, bearing anterior and posterior cristae and serrations; vertebrae platycoelous; neural spines low; about twenty-four presacrals; two sacrals; about seventy caudals; all presacrals bear free ribs; costal articulations fuse only on the last presacral; dorsal ribs bear only anterior flanges; double row of dorsal, ornamented, leaf-shaped scutes; pectoral girdle lacks clavicles; ossified sternum present; slender interclavicle present; coracoids extended postero-ventrally; supracoracoid foramen present; scapula expanded into points anteriorly and posteriorly; limb bones hollow; humerus with a well-developed deltopectoral crest; ulna bears a slight olecranon; carpus crocodylian; only one distal carpal; ilium with pre- and post-acetabular processes; supra-acetabular crest well developed; acetabulum perforated; pubis entered acetabulum; obturator foramen present; ischium projected posteriorly; pelvic symphysis present; femur with a fourth but no lesser trochanter; tarsus crocodylian; metatarsal five reduced but bearing two phalanges; metatarsals one to four subequal in length.

Etymology. The generic name has been chosen in order to emphasize the terrestrial nature of the early crocodiles.

Terrestrisuchus gracilis. sp. nov.

Diagnosis. As for genus. The specific name refers to the light graceful build of this animal.

Holotype. Specimen P. 47/21 and its counterpart P. 47/22. These blocks bear the remains of a single, partially articulated, virtually complete individual. Some bones have been prepared out of these blocks and are labelled P. 47/21a, b, c and P. 47/22a, i. Department of Zoology and Comparative Anatomy, University College, London.

Paratypes. Associated and individual bones. Department of Zoology and Comparative Anatomy, University College London.

Locality and horizon. Fissure filling in the Carboniferous limestone of the old Pant-y-ffynon quarry, about three miles east of Cowbridge, Glamorgan, Wales; late upper Triassic.

DESCRIPTION: SKULL

The identifications of the skull bones were based on the semi-articulated specimen P. 78/1a, the closely associated skull elements on the holotype, and the associated bones on P. 79/1 and P. 147/1. The cranial bones of *Terrestrisuchus* are abundant in the material but unfortunately there are no laterospheroids, prefrontals, premaxillae, or vomers preserved and there is no certain basisphenoid. Of the other elements, there are, on average, between four and five examples of each. There is no evidence for the presence of a dermo-supraoccipital. The restorations are based on an analysis of how the bones articulated with each other. The semi-articulated specimen (P. 78/1a) was of little use in reconstructing the skull as it is incomplete and crushed. The illustrations (text-figs. 1-6) show what is actually known of the bones, their reconstructed form, and their postulated articulations. The basisphenoid was not reconstructed in lateral view (text-fig. 4D, E) and no attempt was made to reconstruct the laterospheroids. The remains of the quadratojugal have been omitted from text-fig. 1B, the remains of the quadratojugal, parietal, and frontal from text-fig. 2B, and the parietal from text-fig. 4C.

Cranium. The cranium was wedge-shaped in dorsal and lateral views and approximately square in occipital view. The skull table was convex across its longitudinal axis, and the large, flat squamosals sloped strongly ventro-laterally. The postorbital bar was inclined posteriorly. The large, almost centrally positioned, orbit was oval in dorsal view and almost circular in lateral view. The antorbital fenestra, formed by the maxilla and lacrimal, was long and narrow as was the supratemporal fenestra. The infratemporal fenestra, bordered by the broad, parallel-sided quadratojugal, was triangular in outline. The post-temporal fenestrae were large and had a complex shape. The palatal vacuities were approximately oval and long interpterygoid vacuities remain. The basipterygoid articulations were movable. The choanae were elongate oval-shaped openings and a short secondary palate was formed by the premaxillae and maxillae. In life this was possibly extended by soft tissue, across the palatines, to shift the function choanae posteriorly. The quadrate was inclined anteriorly and the otic notch was well developed. The skull did not possess postfrontals or interpterygoids.

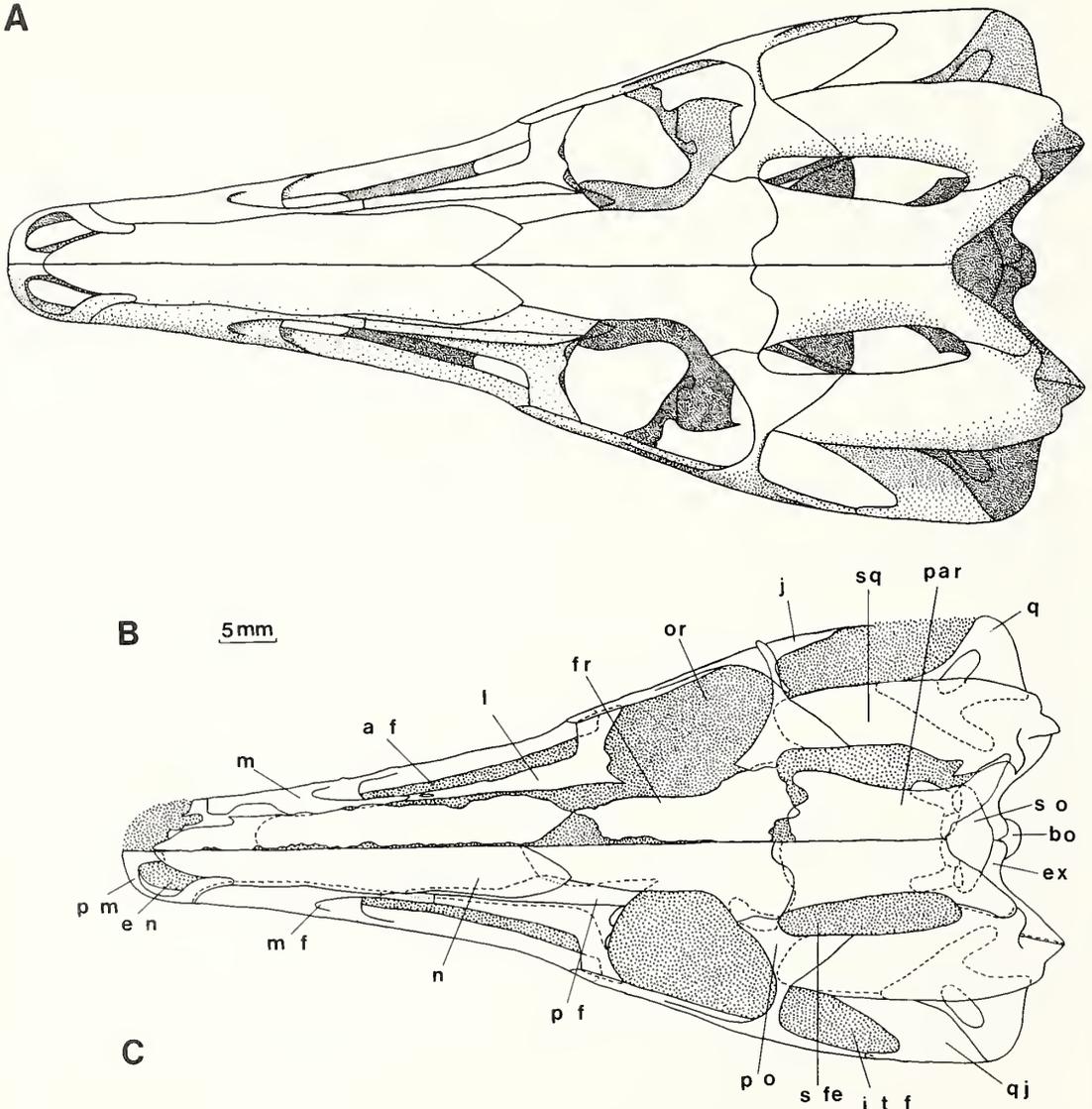
Frontal. Eight specimens of the frontals are preserved allowing their complete reconstruction. These bones are paired unlike those of the modern crocodylians which fuse before the animal leaves the egg. The frontals were flat and smooth dorsally with straight medial edges where they sutured together. Anteriorly the dorsal surfaces bear recessed articulations where they were overlapped by the nasals and prefrontals. Posteriorly there were overlapping articulations with the parietals and postero-laterally flanges extended into notches within the postorbitals. There were no articulations between postorbitals and parietals. The ventral surface of each frontal bears a well-developed crista cranil frontale. The anterior part of the orbital surface of the frontal, lateral to this ridge, bore a groove for articulation with the prefrontal. A process was present at the anterior end of the orbital surface which also articulated with the prefrontal.

Jugal. Three examples of this bone are preserved and those on P. 78/1a and P. 79/1a allow this element to be completely reconstructed except for the distal part of the dorsal process. This element is triradiate and consists of anterior, posterior, and dorsal processes. The lateral surface of the bone is smooth. The dorsal process of the jugal is long, slender, slightly tapering, swept back at a small angle to the vertical, and inclined slightly medially. No articular facets for the postorbital are preserved. The postorbital bar was not recessed below the level of the skull surface. The posterior process tapers distally. There is no evidence as to how this bone articulated with the quadratojugal. The anterior process of the jugal is pointed and is constricted centrally. The lateral surface of this process is convex across its length. As only a small amount of the medial surface of the jugal is visible, on P. 78/1a, its articulations with the maxilla, lacrimal, and ectopterygoid, as reconstructed, are purely suppositions.

Lacrimal. Five lacrimals are preserved and together they allow the whole bone to be described. The lacrimal consists of an approximately triangular facial plate and a descending maxillary process. The ventral edge of the facial plate and the anterior edge of the maxillary process bounded the antorbital fenestra. The posterior edge of the maxillary process is slightly concave where it formed the antero-ventral edge of the orbit. The medial surface of the lacrimal is smooth. The postero-dorsal corner of this surface is hollowed out into an approximately triangular recess in which the prefrontal articulated. The prefrontal also fitted within a groove that runs along the dorsal margin of this surface. The medial side of the maxillary process is built up centrally into a low ridge. The opening into the lacrimal duct is positioned just dorsal to the termination of the maxillary process. The lateral surface of the lacrimal was smooth. The anterior end of this surface of the facial plate bore a strong ridge, dorsally, that fitted medial to the maxilla. Details of the ventral articulations with the jugal and maxilla are unknown.

Maxilla. Seven maxillae have been referred to *Terrestrisuchus* and the structure of this bone is almost completely known. The basal portion of the maxilla consists of a long, horizontally orientated, tooth-bearing ramus the

ventro-lateral edge of which is nearly straight. Rising dorsally from the anterior half of the basal ramus is an ascending lamina consisting of a facial plate and a postero-dorsally directed projection. The anterior part of the basal portion of the bone is extended medially to form a palatal process. The lateral surface of the maxilla is smooth except for a number of small blood and nervous foramina that run along its ventral margin. A conical fossa is present in the facial plate anterior to the antorbital fenestra. This fossa is directed antero-ventrally and is of moderate depth. The lateral surface of the postero-dorsal projection turns sharply medially and then ventrally where it borders the antorbital fenestra. Articular facets for the nasals are not preserved but it is assumed that they overlapped the dorsal edge of each maxilla. There is no evidence for the mode of articulation with the premaxilla or for a notch between premaxilla and maxilla such as has been figured in *Sphenosuchus* (Walker 1970). The palatal process is rather narrow; it articulated medially with its pair and probably also with the



TEXT-FIG. 1. *Terrestrialisuchus gracilis* gen. et sp. nov. A-C, cranium in dorsal view: A, reconstruction; B, structure of the preserved material; C, restoration of the articulations. For explanation of abbreviations, see page 155.

vomers. The posterior edge is concave and formed the anterior border of the internal nares. The maxilla forms the posterior portion of the anterior palatal foramen which opens out from the bottom of a pit that would have been originally formed by maxilla and premaxilla. Specimen P. 144/1 bears oval alveoli for fifteen thecodont teeth and three more were inserted into a common alveolar groove at the back of the maxilla. Specimen P. 147/1a displays the structure of the medial surface of the anterior part of the maxilla. It shows that there was a second ridge running dorsal to the palatal process and separated from the ventral edge of the bone by a groove. It is suggested that this groove bore the chaonal tube and that at least the anterior part of the internal nares were covered by a soft palate.

Maxillary teeth are well preserved on P. 147/a. They have well-developed oval roots and laterally compressed crowns. These teeth are pointed and recurved and bear anterior and posterior cristae which are finely serrated.

Nasal. This bone is well represented in the material and P. 108/1 bears a fine specimen that shows its original outline. The medial edge of the bone is straight where it butt-jointed to its pair. The nasals are pointed anteriorly and posteriorly. The frontals wedged in between them posteriorly and were overlapped by them dorsally. No articular surfaces are preserved for the prefrontals and maxillae. A small process from the anterior end of the bone formed a notch that housed a process of the premaxilla. The dorsal surface of the bone is smooth and whilst it is flat posteriorly anteriorly it becomes strongly convex across its length.

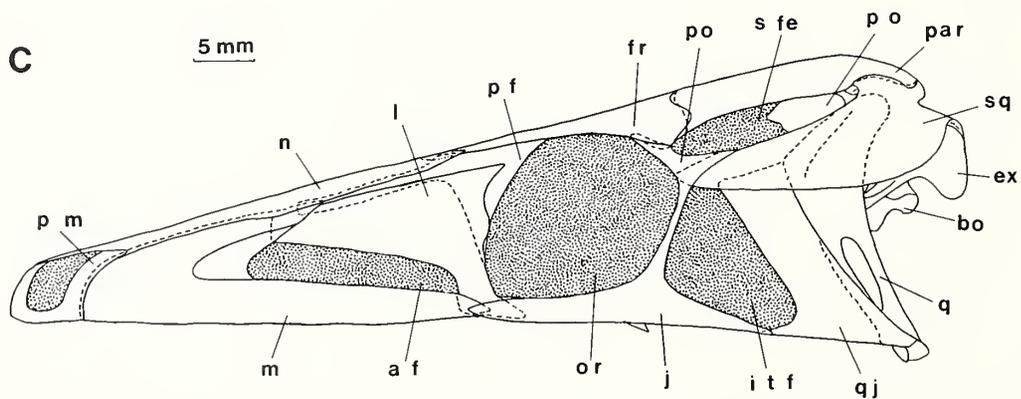
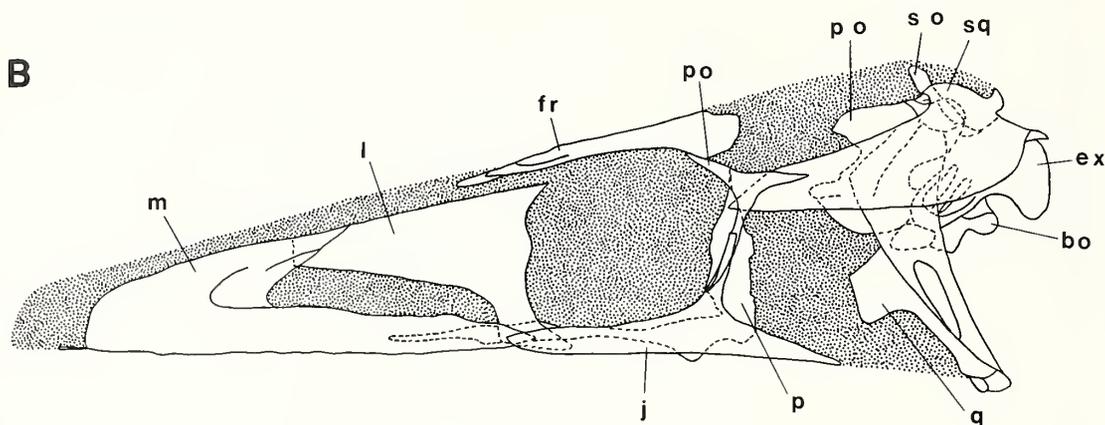
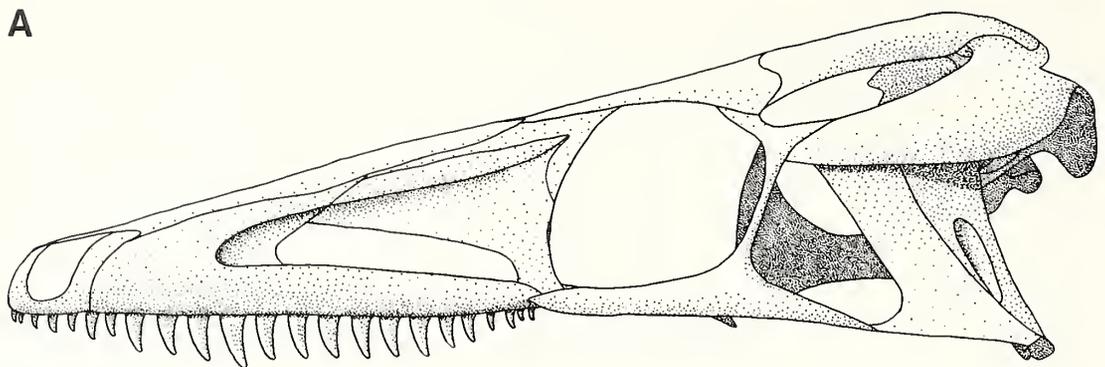
Parietal. Although the six preserved parietals are all in poor condition there is sufficient material to allow this element to be fully described. The parietal is a long narrow bone that articulated with its pair along the midline. Details of this articulation are not preserved but it appears that the bones were simply butt-jointed together. The anterior portion of the lateral edge of this bone formed the gently concave margin of the supratemporal fenestra. The postero-lateral corner of the parietal is extended into a process that articulated with the squamosal and medial to this articulation the bone is deeply notched. It is thought that the supraoccipital joined to the posterior edge of this notch and its anterior processes buttressed against the ventral surface of the parietal but no defined articular facets for the supraoccipital are present. The details of the squamosal articulation are not clear but it is apparent that the postero-lateral process of the parietal fitted into a notch formed for it on the postero-medial edge of the squamosal. The dorsal surface of the parietal is smooth. The centre of the bone is strongly convex across its longitudinal axis which results in the skull table being arched between the supratemporal fenestrae. The edge of the bone dipped steeply into the fenestra and its posterior margin was bent downwards on to the occipital surface.

Postorbital. Only two postorbitals are preserved but the example on P. 79/1c is in excellent condition. This element is a triradiate bone consisting of posterior, lateral, and medial processes. The posterior ramus which overlapped the squamosal is approximately triangular in dorsal view and antero-medially formed part of the margin of the supratemporal fenestra. The lateral process is slender and tapers towards its tip where it articulated with the jugal. The medial process is excavated by a deep groove which housed a process of the frontal.

Prefrontal and premaxilla. No prefrontals or premaxillae have been identified in the material. They have been reconstructed on the basis of the articulations, preserved for them, on the other cranial bones and on the structure of this element in *Sphenosuchus* (Walker 1972). No restoration of the portion of the prefrontal within the orbit has been attempted.

Quadratojugal. The quadratojugal is a very thin, fragile bone and is thus poorly preserved. Two specimens display parts of this element and from these parts, and knowledge of the adjacent bones, the whole can be reconstructed. The quadratojugal has been restored as an approximately parallelogram-shaped bone that increases in width ventrally. The posterior, dorsal, and ventral edges of the bone were straight but the anterior edge was concave. The dorsal edge buttressed under the squamosal but no details of this articulation are preserved. Postero-ventrally the quadratojugal overlapped the lateral edge of the quadrate whilst dorsally it articulated with the thin anterior edge of that bone.

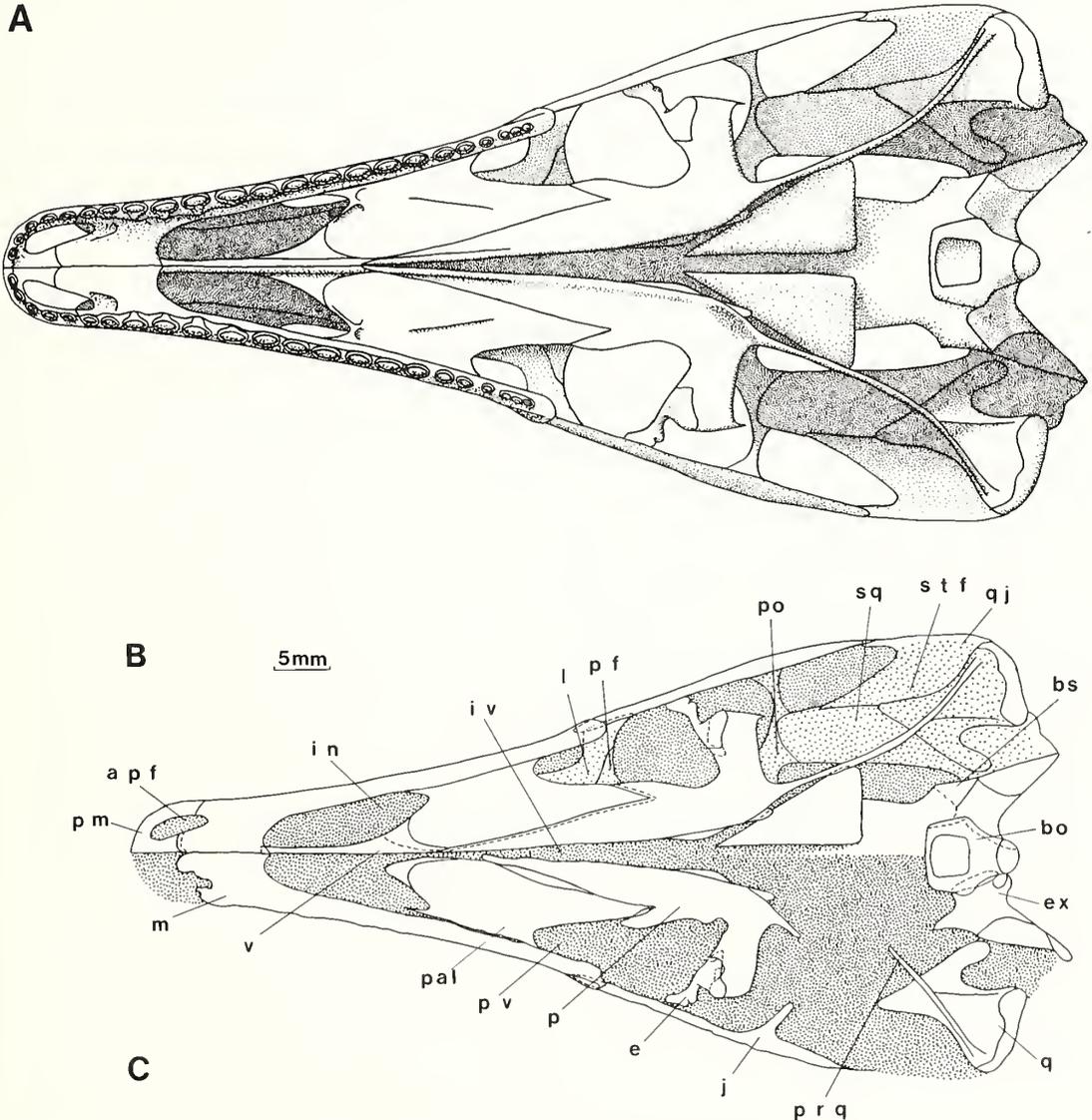
Squamosal. Eight examples of this bone are preserved and its structure is completely known. When viewed directly, the squamosal is approximately flat and kidney-shaped with three posteriorly placed projections. In life its dorsal surface sloped strongly ventro-laterally. This surface is smooth and slightly convex across its length. The lateral edge of the squamosal is convex whilst the medial is concave where it bordered the supratemporal fenestra. The bone surface dipped very steeply into the fenestra. A number of shallow, longitudinal grooves are present on the region of the bone which was overlapped by the postorbital. The largest of the processes of the squamosal extended posteriorly and slightly ventrally. This process articulated with the exoccipital but it is not known how. Medial to this exoccipital process are two more that formed a notch for the postero-lateral process of the parietal.



TEXT-FIG. 2. *Terrestriisuchus gracilis* gen. et sp. nov. A-C, cranium in left lateral view: A, reconstruction; B, structure of the preserved material; C, restoration of the articulations.

Ectopterygoid. Two of these bones have been identified and one, on P. 79/1a, is almost perfect. The ectopterygoid is triradiate and consists of a jugal process and lateral and medial palatal processes. The palatal processes both taper distally and diverge at about 80° . The lateral process overlapped the transverse process of the pterygoid ventrally. The lateral part of the medial process also articulated with the ventral surface of the pterygoid but its tip passed through a notch in that bone and then fitted against its dorsal surface. The jugal process, which curves antero-dorsally, is oval in cross-section where it joins the palatal processes. Laterally this process expands and divides to form a pair of articular surfaces for the jugal.

Palatine. The palatines are large bones that covered much of the ventral surface of the snout. Each articulated medially with the pterygoid and vomer and laterally with the maxilla. The lateral edge of the palatine was horizontally orientated and, as the medial edge lay dorsal to the lateral, the palate was vaulted. Four good



TEXT-FIG. 3. *Terrestriisuchus gracilis* gen. et sp. nov. A-C, cranium in ventral view: A, reconstruction; B, restoration of the articulations; C, structure of the preserved material.

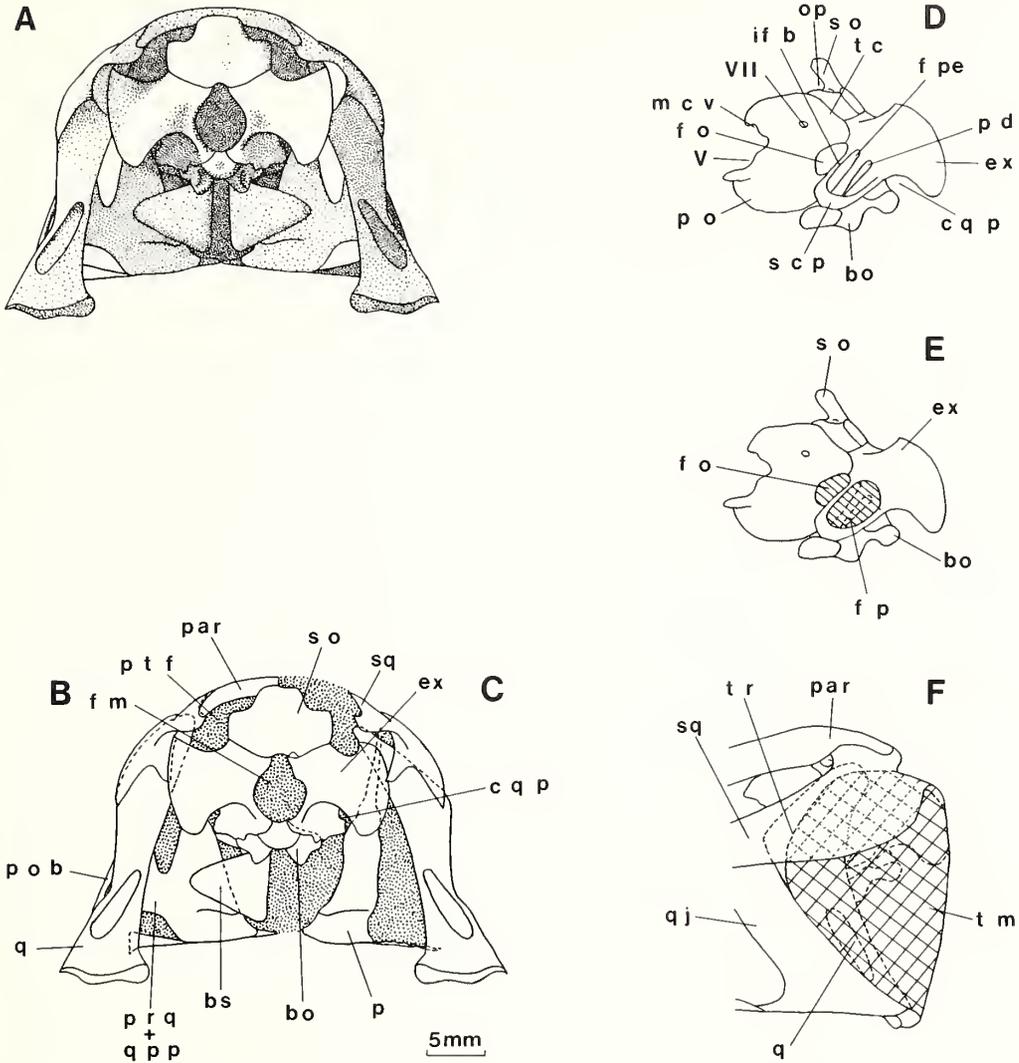
specimens of the palatine are preserved. This element is basically a flat plate of bone whose medial outline is convex anteriorly and slightly concave posteriorly. The lateral outline is straight centrally but notched anteriorly and posteriorly. The bone is thickened where it butt-jointed to the maxilla. No details of the articulations with the pterygoid are preserved. A facet for articulation with the vomer is present on the anterior margin of the ventral surface. The ventral surface of the palatine is smooth and approximately flat. Antero-laterally it bears a pair of hollows and an intervening ridge and in addition it was traversed by a step-like change in height that runs in a line directed postero-medially. These features imply that a soft palate may have extended over the palatines and that the functional choanae may have lain behind them.

Pterygoid. The pterygoid is well known from one almost complete specimen (P. 112/1) and others that are well preserved but incomplete (P. 78/1a and P. 47/22). The pterygoid is composed of three processes: palatal, transverse, and quadrate. The palatal process is a long, tapering plate of bone that extended anteriorly along the palate adjacent to its pair across the midline. The process is straight medially but did not suture to its counterpart and thus they were separated by a narrow interpterygoid vacuity. The lateral margin of the palatal process is also straight except for a small, tapering, antero-laterally directed palatine process. The tip of the palatine fitted into the notch that lies anterior to this process. The palatal process is strengthened medially by a low ridge. A deep, conical hollow is formed at the posterior end of the palatal process where it intersects with the transverse process. The posterior edge of the transverse process is concave whilst the lateral is slightly convex. The postero-lateral tip of this process was extended into a point. The anterior edge bears a notch for articulation with the ectopterygoid and longitudinal grooves mark the position of articulation of the lateral palatal process of that bone. The transverse process is twisted along its length so that its antero-lateral corner lies dorsal to its postero-lateral corner. The quadrate ramus of the pterygoid is approximately triangular in outline and its main surface faced postero-medially. The original outline of this process is uncertain and it is not known how it articulated with the pterygoid ramus of the quadrate. The posterior surface of the quadrate ramus is traversed by a ridge towards its ventral end and just dorsal to this the bone is deeply hollowed out. This hollow formed a cotyle for articulation with the basiptyergoid process of the basisphenoid. This articulation was probably moveable. A small hook of bone, visible in palatal view, extends from the medial end of the ridge.

Vomer. No examples of this element are present but its outline can be reconstructed with fair certainty. The details of its structure are based on the vomer of *Sphenosuchus*.

Quadrate. There are seven quadrates preserved and, although none is perfect, in combination they give an almost complete picture of the structure of this bone except for some uncertainty as to the extent of the pterygoid process. The quadrate is a pillar-like bone that sloped strongly antero-dorsally. It consists of a triangular dorsal part with an approximately rectangular ventral extension that expands slightly towards its distal end. The bone is twisted centrally so that the external surface of the dorsal part faced laterally and very slightly posteriorly whilst the ventral part faced postero-dorsally and slightly laterally. The mandibular condyle faced postero-ventrally; this surface is expanded medially but narrows towards its lateral edge. A deep cavity or conch is present in the posterior surface of the bone in the same position as that of a lizard. The lateral edge of the ventral portion of the bone is broad and dorsally it merges with the lateral surface of the pterygoid ramus. The quadratojugal articulated with this edge of the bone. The dorsal edge of the quadrate is almost straight and sloped anteriorly, ventrally, and laterally. This edge is thin anteriorly but thickens posteriorly where it buttressed under the squamosal. The lateral surface of the dorsal part of the bone is smooth and slightly concave. A faint ridge runs along its dorsal margin diverging anteriorly from the dorsal edge. This ridge formed the antero-dorsal margin of the tympanic membrane. The pterygoid ramus is very thin and its outline is not fully known. As preserved, this projection has straight, parallel, dorsal, and ventral edges and its distal margin is slightly convex. The process was inclined ventrally and antero-medially.

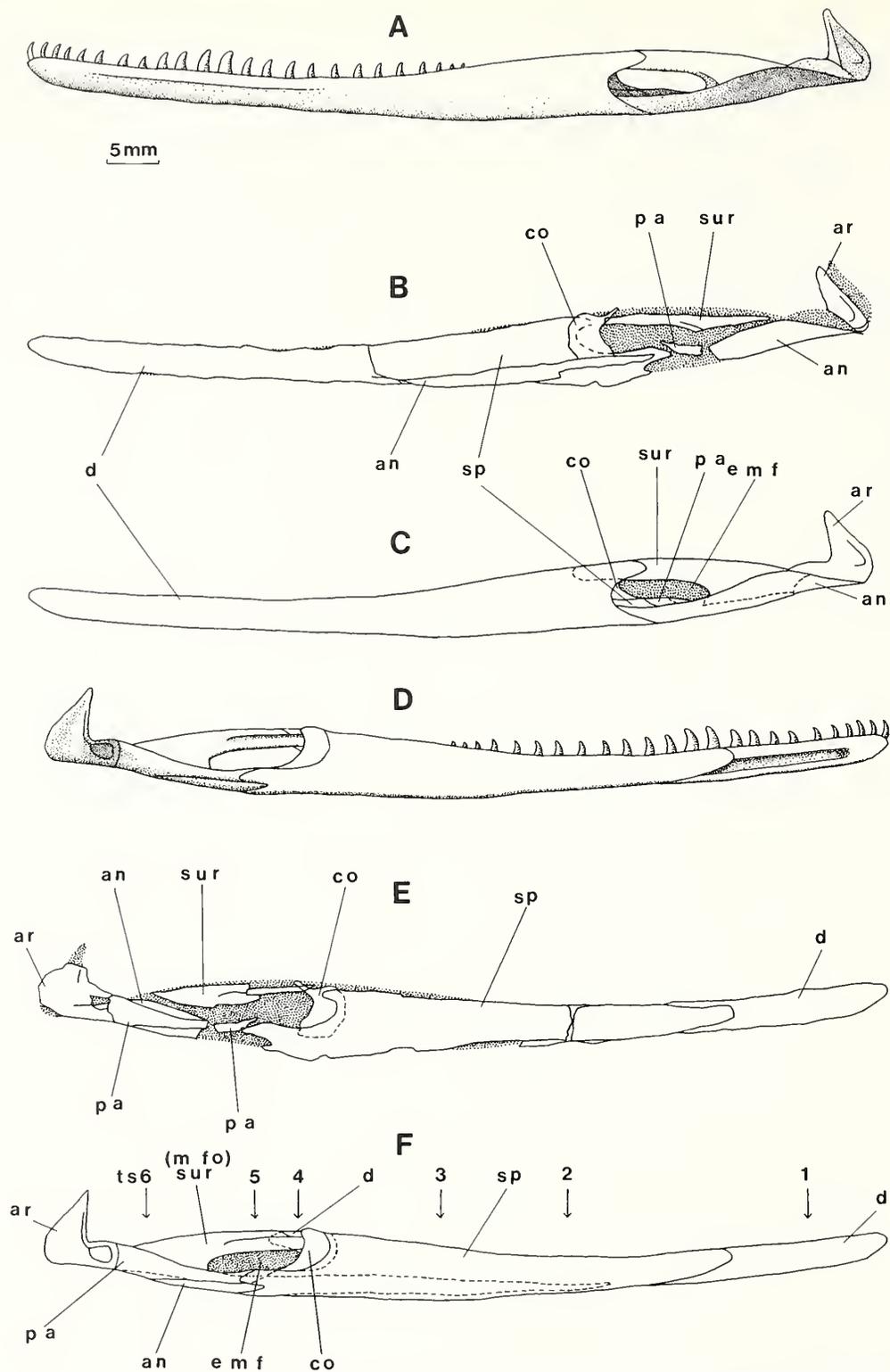
Basioccipital. The structure of this bone is well displayed by an articulated specimen on P. 78/1a, and a second, individual bone (P. 62/20) freed from most adhering matrix. The basioccipital consists of an approximately square body connected by a narrow neck to a swelling that formed the occipital condyle, the posterior end of which is depressed to form a small notochordal pit. The dorsal surface of the basioccipital formed the posterior part of the floor of the cranial cavity. This surface is smooth and slightly concave across its length. Flanking this surface are two articular facets: one for the exoccipital and a second, more anterior, facet for the basisphenoid. The anterior edge of the basioccipital also articulated with the basisphenoid. The basioccipital is hollow and this cavity opens into an approximately square foramen on the ventral surface of the bone. This basioccipital fossa is presumed to be part of the ramifications of the Eustachian tube system. Basioccipital tuberculi are present posteriorly and the lateral surfaces of these projections are hollowed out into shallow cavities that faced posteriorly and slightly laterally. These cavities were for insertion of the subvertebral muscles.



TEXT-FIG. 4. *Terrestriusuchus gracilis* gen. et sp. nov. A-C, cranium in posterior view: A, reconstruction; B, restoration of the articulations; C, structure of the preserved material; D, reconstruction of the braincase; E, position of the fenestrae ovalis and pseudorotunda; F, reconstruction of the tympanum.

Basisphenoid. No element has been satisfactorily identified as a basisphenoid and thus this element has been reconstructed like that of *Sphenosuchus*.

Exoccipital. The exoccipitals can be completely described as six examples of this bone are preserved. The left exoccipital, comprising specimen P. 65/67, was used as the basis of this description as it is in excellent condition and is freed from nearly all adhering matrix. The 'exoccipital', as described, is composed of the fused exoccipital and opisthotic. The paraoccipital processes were swept backwards and expand dorso-ventrally towards their distal ends. The concave, thickened, dorsal edge of each process formed the ventral margin of the post-temporal fenestra. The distal end of the paraoccipital process articulated with the squamosal. The supraoccipital



TEXT-FIG. 5. *Terrestriuchus gracilis* gen. et sp. nov. Left mandible in A-C, lateral, and D-F, medial views; A, D, reconstructions; B, E, structure of the preserved material; C, F, restorations of the articulations.

articulated with the dorsal margins of the anterior portions of the exoccipitals and also with flanges that they sent out above the foramen magnum. Anteriorly the exoccipital articulated with the prootic. A subcapsular process is present antero-ventrally and the lateral surface of this articulated with basisphenoid. The fenestra ovalis was formed at the junction with the prootic. Postero-ventral to this foramen is the foramen perilymphaticum separated from the ovalis by a narrow interfenestral bar. The perilymphatic duct opened posterior to the foramen perilymphaticum. This duct is confluent medially with the rest of the metotic fissure that served for the exit of nerves IX-XI.

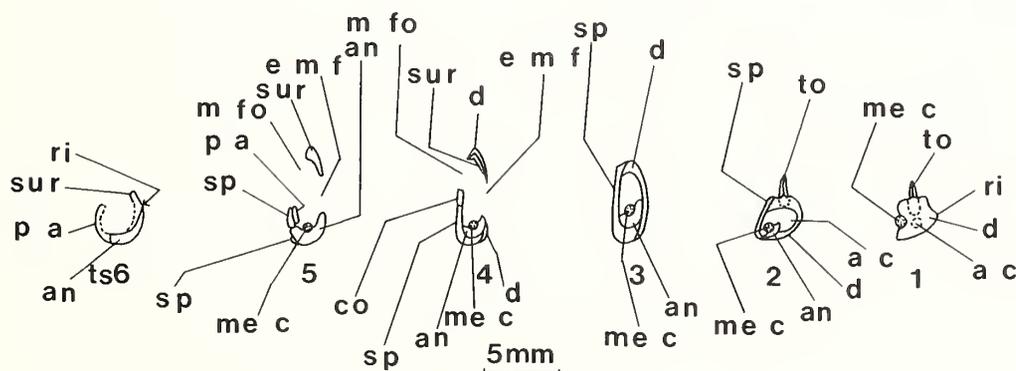
Laterosphenoid. No examples of the laterosphenoid have been identified but the structure of the prootics suggests their original presence. They were certainly present in *Sphenosuchus*.

Prootic. Only a single specimen of the prootic is preserved and unfortunately even this bone is in poor condition. It lies in lateral view, partially articulated with the exoccipital, on P. 47/22. The postero-dorsal edge of the prootic attached to the supraoccipital and the dorsal edge, which is straight and was horizontally orientated, articulated with the parietal. The prootic met the laterosphenoid anteriorly where it formed the posterior margin of the foramen ovale for the exit of the fifth cranial nerve. A notch, dorsal to the foramen ovale, could be part of a foramen for the middle cerebral vein. The ventral edge of the prootic articulated with the basisphenoid.

Supraoccipital. Two examples of this bone are preserved: one of these, on P. 47/22, is complete but has only its posterior and right aspects exposed whilst the second, P. 31/11, has been freed from matrix but is incomplete ventrally. The posterior part of the supraoccipital forms an occipital plate that sloped antero-dorsally at about 45°. The ventral edge of the bone articulated with the exoccipitals. The lateral margins of the occipital plate bear parallel-sided, roughened surfaces that, by analogy with the modern crocodile, were for the attachment of cartilages that partly filled the post-temporal fenestrae. The dorso-lateral edges of the plate are concave and formed parts of the margins of the post-temporal fenestrae. The dorsal edge of the occipital plate articulated with the ventral surface of the parietal by means of two oval articular facets. The posterior surface of the occipital plate is smooth and flat except for a low, centrally positioned, dorso-ventrally directed ridge. The supraoccipital sends projections anteriorly, from the lateral sides of the occipital plate, and these house segments of the osseus labyrinth.

Mandible. As reconstructed (text-figs. 5 and 6) the mandible is long and slim with a very long dentary and well-developed splenial. The angular is also large but, in contrast, the other bones are rather small. The articular is a fragile bone with medial and dorsal foramina. A dorsal process extends, from the articular, medial to the quadrate cotyle. The symphyseal area is small and the splenials do not reach the ends of the dentaries.

Angular. Five angulars are preserved and together they give a complete picture of the structure of this bone. The angular is long and slender and whilst it formed much of the lateral wall of the posterior end of the mandible it was only slightly exposed medially. The bone is rod-like anteriorly but posteriorly it is flattened; it tapers to a point anteriorly and posteriorly. The anterior portion of the bone is rounded off ventro-laterally and is hollowed



TEXT-FIG. 6. *Terrestri-suchus gracilis* gen. et sp. nov. Transverse sections of the left mandible, for positions of the sections see text-fig. 5F.

out medially forming the Meckelian canal. The anterior portion of the angular lay against the dentary and fitted into a groove in the splenial. More posteriorly the bone articulated dorsally with the surangular and medially with the prearticular. More posteriorly still it fitted against the articular.

Articular. Only two of these elements are preserved and both are on P. 78/1a in articulation with the other skull bones. The left of these is well preserved but has only its ventral surface exposed. The lateral, medial, and posterior aspects, and part of the dorsal surface, of the right are visible but the bone has been crushed latero-medially. The articular is a thin walled, hollow bone and foramina open into it on its dorsal and medial surfaces. The medial foramen is large and oval but only a portion of the dorsal opening is visible. The articular surface for the quadrate lay posterior to the medial foramen. The bone supporting the deep cotyle for the quadrate is thin and, unexpectedly, interrupted by the dorsal foramen. Posterior to the articulation for the quadrate the medial part of the articular is expanded dorsally into a tapering process. This element articulated laterally with the angular and anteriorly with the prearticular. Unlike this bone in the modern crocodile, the articular had, at the most, only a very small contact with the surangular.

Coronoid. A single, right coronoid is contained, in lateral view, on P. 63/8. This bone is in very poor condition and was only identified because of its association with a splenial. The specimen is crushed and, as preserved, its surface is slightly convex. The complete posterior edge is concave where this element would have bordered the mandibular fossa. Anteriorly the bone is convex where it fitted into the coronoid notch of the splenial. No articular facets for the splenial are preserved.

Dentary. This element is better represented than the other bones of the lower jaw as there are six examples preserved. The dentary is a long slender bone whose distal end curves slightly dorsally. Anteriorly the ramus of the dentary is parallel sided but posteriorly it increases in height. The lateral edge of the bone is smooth and, anteriorly, bears a low ridge that runs parallel to its dorsal margin. The medial surface is traversed by the Meckelian canal. This canal terminates in a small hollow anteriorly where it was joined to its pair on the opposing dentary. The area of the symphysis is smooth. The dentary articulated medially with the splenial and postero-ventrally with the angular. More posteriorly still it articulated with the surangular.

Dentary teeth. The alveoli of the dentary are positioned along its lateral side. When preserved the teeth are fairly even in their development although there is evidence of a slight increase in height centrally. The dentary has been restored with twenty-four teeth although this may be slightly more than were originally present. The posterior end of the dentary has been restored without any teeth. There is no direct evidence for this unusual condition and it is postulated because of the length of the mandible and the sizes of the other bones. The anterior dentary teeth bore anterior and posterior cristae; they were slim, pointed, and recurved. The roots were oval in cross-section. The more posterior teeth were laterally compressed although otherwise they were pointed, bore anterior and posterior cristae, and were recurved like the anterior teeth. They differ from the latter in bearing serrations on their posterior edges. These are only visible ventrally but it is probable that they extended all along the posterior cristae.

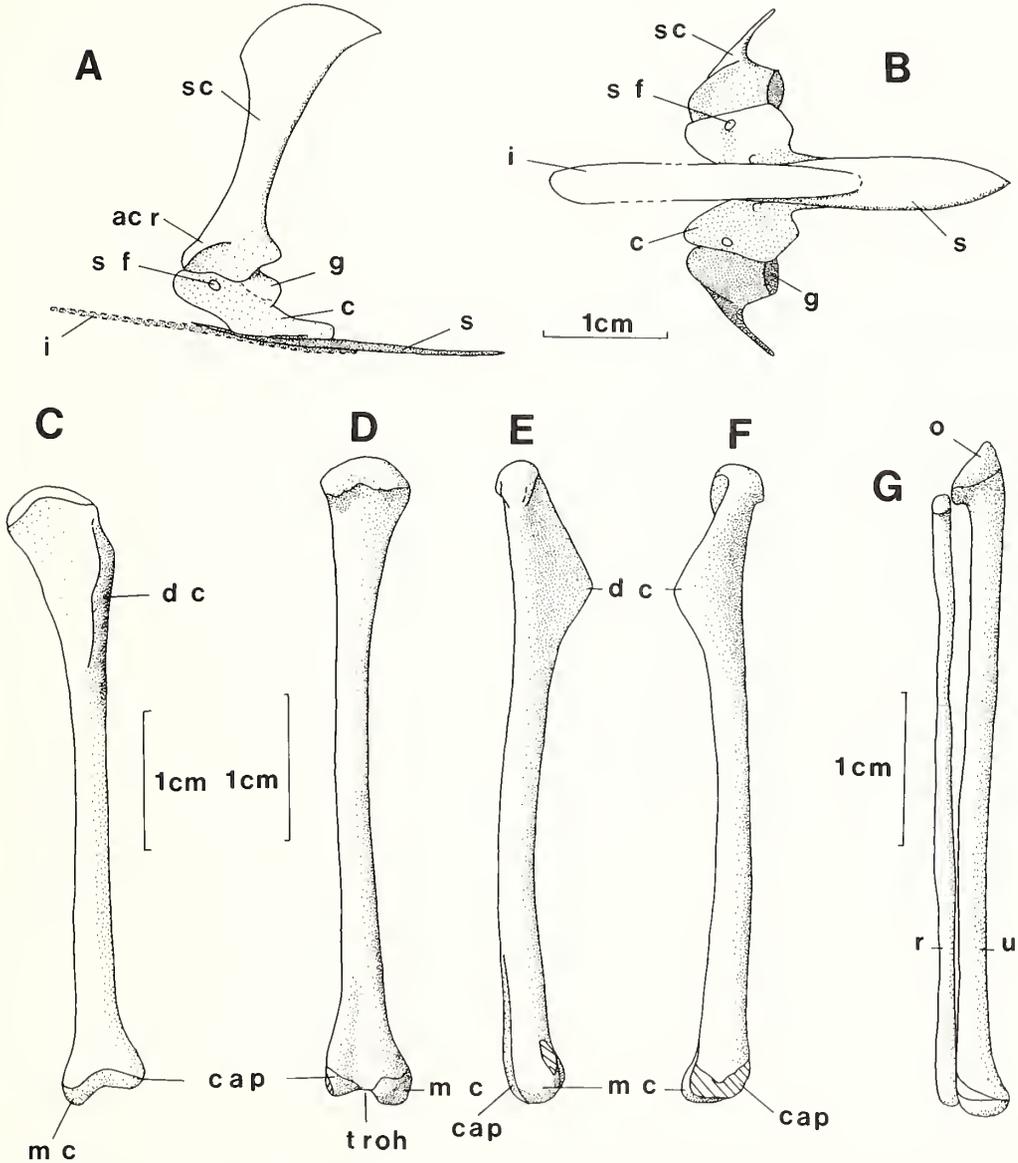
Prearticular. A single, right prearticular is preserved on P. 78/1a, and it is exposed in medial and lateral views. This bone expands posteriorly and whilst its ventral edge is almost straight its dorsal edge is slightly concave. The postero-medial surface is strongly convex but anteriorly the bone is flattened. Posteriorly it articulated with the articular and anteriorly it fitted lateral to the splenial. Postero-ventrally it fitted against the medial edge of the angular but more anteriorly it shifted its articulation on to the dorso-medial edge of that bone.

Splenial. Five splenials are preserved and the right on P. 63/8 is almost complete. The dorsal edge of this element is very slightly concave anteriorly and very slightly convex posteriorly. The posterior margin of the bone is incised by a large notch that articulated with the coronoid and a smaller, ventrally placed notch against which the angular fitted. The ventral edge of P. 63/8 is poorly preserved and has been reconstructed as slightly convex. The medial surface of the bone, as preserved, is flat. The ventro-lateral margin of the bone forms a groove which formed an articular surface for the angular.

Surangular. A single surangular is present on P. 78/1a and, unfortunately, this bone has been fractured centrally and its anterior end has been lost. The posterior part of the bone is approximately triangular and it has an antero-dorsal extension that runs above the external mandibular foramen. Anteriorly the dorsal edge of the bone projects medially so that it has an inverted V-shape in cross-section. This anterior process of the surangular fitted within the dentary. The lateral surface of the bone is convex across its longitudinal axis. Postero-ventrally a ridge is visible running parallel to the posterior part of the external mandibular foramen. Posteriorly this crest turns to run postero-dorsally and the angular buttressed under it. Below this ridge the ventro-lateral surface articulated with the medial surface of the angular.

DESCRIPTION: POSTCRANIAL SKELETON

Pectoral girdle. The material contains nine specimens of the scapula, eleven of the coracoid, three of the ossified sternum, but only one of the interclavicle. These allow a reconstruction of the pectoral girdle (text-fig. 7A, B) where only the shape of the interclavicle is in doubt. The scapula is waisted with a flattened dorsal portion drawn out into a point anteriorly and posteriorly. The convex dorsal edge of the blade is poorly finished and it is likely that it bore a cartilaginous suprascapula. The bone has an oval cross-section at its narrowest point and thickens ventrally. The ventral part of this element bears a distinct acromial ridge and its posterior edge is thickened to



TEXT-FIG. 7. *Terrestriusuchus gracilis* gen. et sp. nov. A-B, reconstruction of the pectoral girdle in left lateral and ventral views; C-F, left humerus, P. 47/22, in anterior, posterior, medial, and lateral views; G, left radius and ulna, P. 47/22, in lateral view.

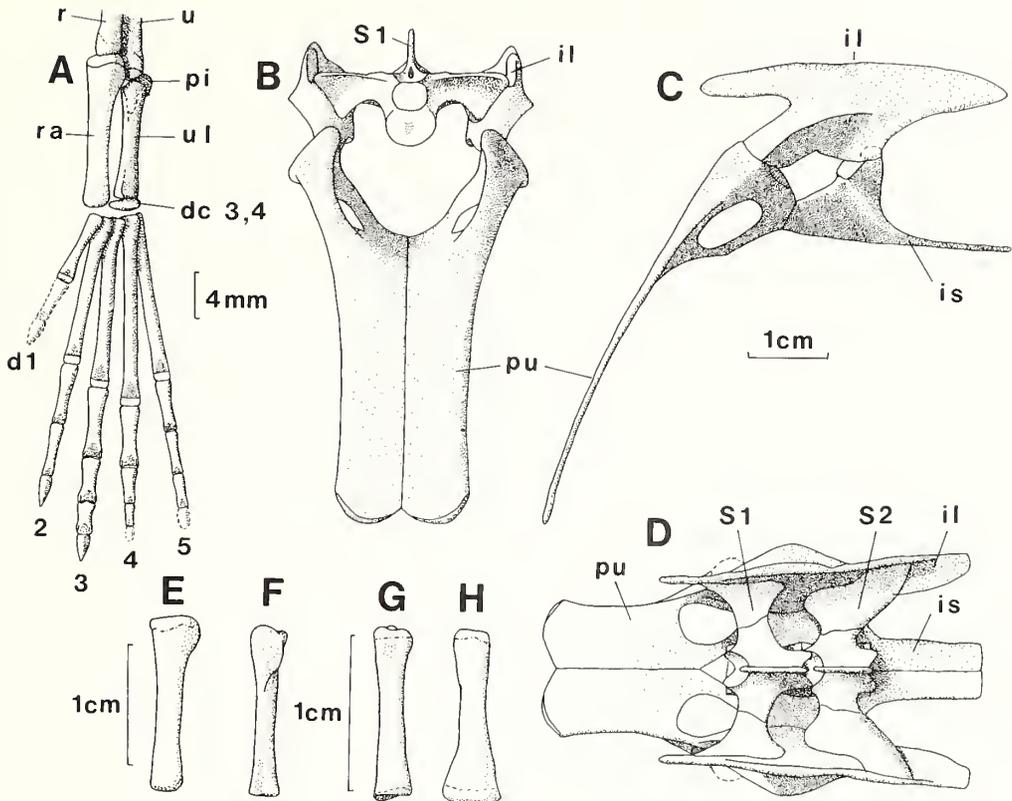
support the glenoid articular surface. This articulation is oval and slightly concave; it faced posteriorly, ventrally, and slightly medially. The medial surface of the ventral part of the bone lacks the process found in *Sphenosuchus*. The coracoid consists of a thickened central region supporting the glenoid articulation, and a much thinner anterior plate perforated by the supracoracoid foramen. The anterior plate is approximately triangular in outline. Posteriorly the bone is drawn out into a long tapering extension. The ventral surface of this process bears a deep trough bounded dorsally by a horizontally directed ridge. This ridge is homologous with the biceps tubercle in *Sphenosuchus* (Walker 1972). The edges of the sternum fitted into these troughs as shown by the articulated girdle of *Pseudohesperosuchus* (Bonaparte 1971*b*). The portion of the glenoid articular surface supplied by the coracoid is oval in outline and flat. This facet faced posteriorly, dorsally, and laterally. The coracoid is very similar to the problematical bone of *Hesperosuchus* (Colbert 1952). The preserved specimen of the interclavicle is very damaged and its original shape and length are uncertain. As preserved, this bone is elongated, flattened, and has parallel edges. The sternum is a thin, fragile bone. This ossification is smooth on both surfaces, its lateral edges are convex, and it is pointed anteriorly and posteriorly. The interclavicle fitted against its antero-ventral surface.

Humerus. There are sixteen humeri preserved and text-fig. 7 C-F shows the most complete of these which is only slightly damaged distally. The humerus is a long, slender bone that was held vertically (text-fig. 14). The head extends about a third of the way along the length of the bone and is set off at a small angle to the direction of the shaft. This means that the centre of the thickened, proximal, articular surface is slightly medial to the line of the shaft. The deltopectoral crest is well developed; its surface is convex laterally and concave medially. In lateral view the crest has a triangular outline and rises to a point just over half-way along its length. The central region of the shaft is thin walled and has a circular cross-section. The capitellum, or radial condyle, and medial convexity are well developed. They are separated by a groove or trochlea that articulated with the olecranon of the ulna. In life the distal articular surfaces faced downwards which implies that the forearm was held in an extended position.

Antebrachium. The ulna is a slender bone with a long shaft but only slight proximal and distal expansions (text-fig. 7G). The proximal part of the bone is formed into an olecranon. The head of the bone is approximately triangular in proximal view with a concave anterior edge that fitted against the flattened proximal end of the radius. The ulna has a double flexure giving it a very slight S-shape in lateral view. The shaft is circular in cross-section and thin walled. The distal end of this element is slightly expanded posteriorly giving it a tear-drop outline in distal view and its medial surface is flattened anteriorly where it fitted against the distal end of the radius. The distal articular surface is slightly concave. The radius is also a slender bone with poorly developed proximal and distal expansions. The proximal end is flattened antero-posteriorly, whilst the distal expansion is oval in distal view. The shaft of the radius is straight and parallel sided; it is hollow with a slightly oval cross-section.

Carpus and manus. The carpus is fully crocodylian and is composed of just four ossifications: the radiale, ulnare, pisiform, and the fused remains of distal carpals three and four (text-fig. 8A, E-H). In addition, although the proximal carpals are relatively longer, their articular surfaces can be homologized with those of the modern crocodile. Specimen P. 72/1 includes an almost perfect set of these bones completely freed from matrix. Thus on the reconstruction only the details of the articulations and the terminal phalanges on digits one, four, and five are conjectural. The radiale is a slender bone with a slight distal expansion and a more pronounced proximal one where it contacted the radius and ulna. The articular surface for the radius is oval in shape whilst that for the ulna is triangular. The lateral surface of the distal portion of this bone bears a trough for muscular insertion. The ulnare is more expanded distally than proximally. The proximal articulation for the ulna is approximately triangular whilst the distal for the fused distal carpals is tear-drop shaped. The pisiform is an irregular pear-shaped bone. It is small relative to those of *Protosuchus* and the modern crocodiles suggesting that the wrist was less flexible in *Terrestriisuchus*. The bone representing the distal carpals is flattened and triangular in proximal view. The manus has been reconstructed as digitigrade. The preserved ungual phalanges are curved, pointed, and bear grooves on their lateral and medial surfaces. It would thus appear that digits two and three at least terminated in a claw.

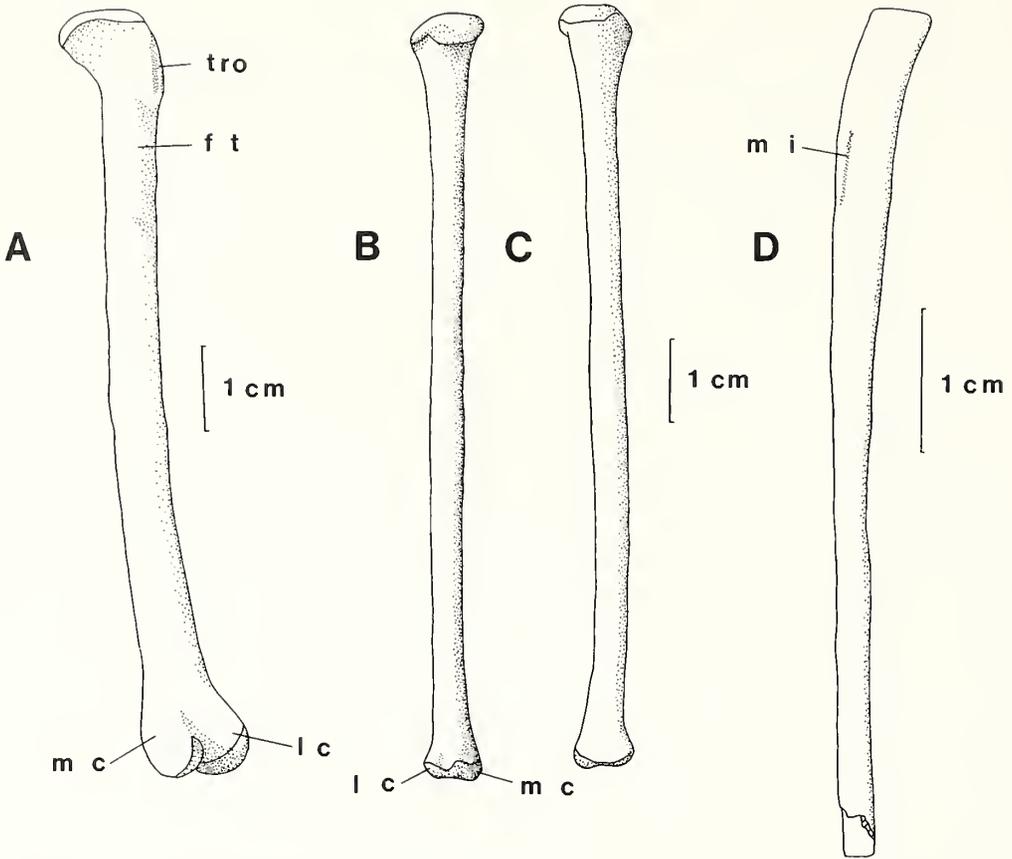
Pelvis. Eleven specimens of the ilium are preserved, sixteen of the pubis, and six of the ischium. The fine quality of these bones allows the pelvic girdle to be completely reconstructed (text-fig. 8B-D). The iliac blade, which is rather low, extends anteriorly into a long, laterally compressed process whilst the posterior projection is deeper anteriorly but tapers distally. Part of the rib of the first sacral vertebra attached to the ventral edge of the anterior projection whilst the rest attached to the base of the ilium (text-fig. 13A). The rib of the second sacral vertebra attached to the base of the ilium and also fitted around a strong ridge that runs along the ventral edge of the



TEXT-FIG. 8. *Terrestrisuchus gracilis* gen. et sp. nov. A, reconstruction of left carpus and manus in anterior view; B-D, reconstruction of pelvis, based on P. 72/1, in anterior, left lateral, and dorsal views (in B the second sacral vertebra and ischia are not included); E-F, left radiale, P. 72/1, in anterior and lateral views; G-H, left ulnare, P. 72/1, in posterior and lateral views.

medial surface of the posterior projection. The ventral edge of the ilium is notched where it bordered the acetabular foramen. The bone forming the medial wall of the acetabulum is thin and the supra-acetabular ridge is strongly developed. The ilium is thickened where it supports the articulations for the pubis and ischium. The pubes are well developed and their anterior ramii were joined medially although it seems likely that there was a break in the symphysis below the acetabulum. Each pubis bears a well-developed, oval, obturator foramen. The ischia bore flattened posterior projections that joined along the midline. The dorsal part of the ischium is thickened where it buttressed against the ilium. The anterior edge is thin and straight for articulation with the pubis. The antero-dorsal margin of the ischium is rounded off where it bordered the acetabular foramen.

Femur, tibia, and fibula. Although fourteen specimens of the femur are preserved, none is quite perfect. Text-fig. 9A shows the best example which is on block P.24/39a. The femur is a slender bone with a slightly developed head which is flattened and twisted on the shaft such that it was directed antero-medially. In this position it would have buttressed under the supra-acetabular ridge of the ilium if the femur were, as reconstructed, held vertically. There is no greater or lesser trochanter but the proximal part of the shaft bears a weakly developed fourth trochanter. The proximal end of the femur bears another trochanter which takes the form of a low ridge running along the posterior margin of the head. The shaft has a slight sigmoid flexure that is much less apparent than in the modern animal. The medial and lateral condyles are well developed for articulation with the tibia. The fibula articulated with a facet on the lateral edge of the lateral condyle. The tibia is a slender bone (text-fig. 9B, C) that was slightly longer than the femur. There is no complete fibula present and the illustrated specimen, P. 130/1

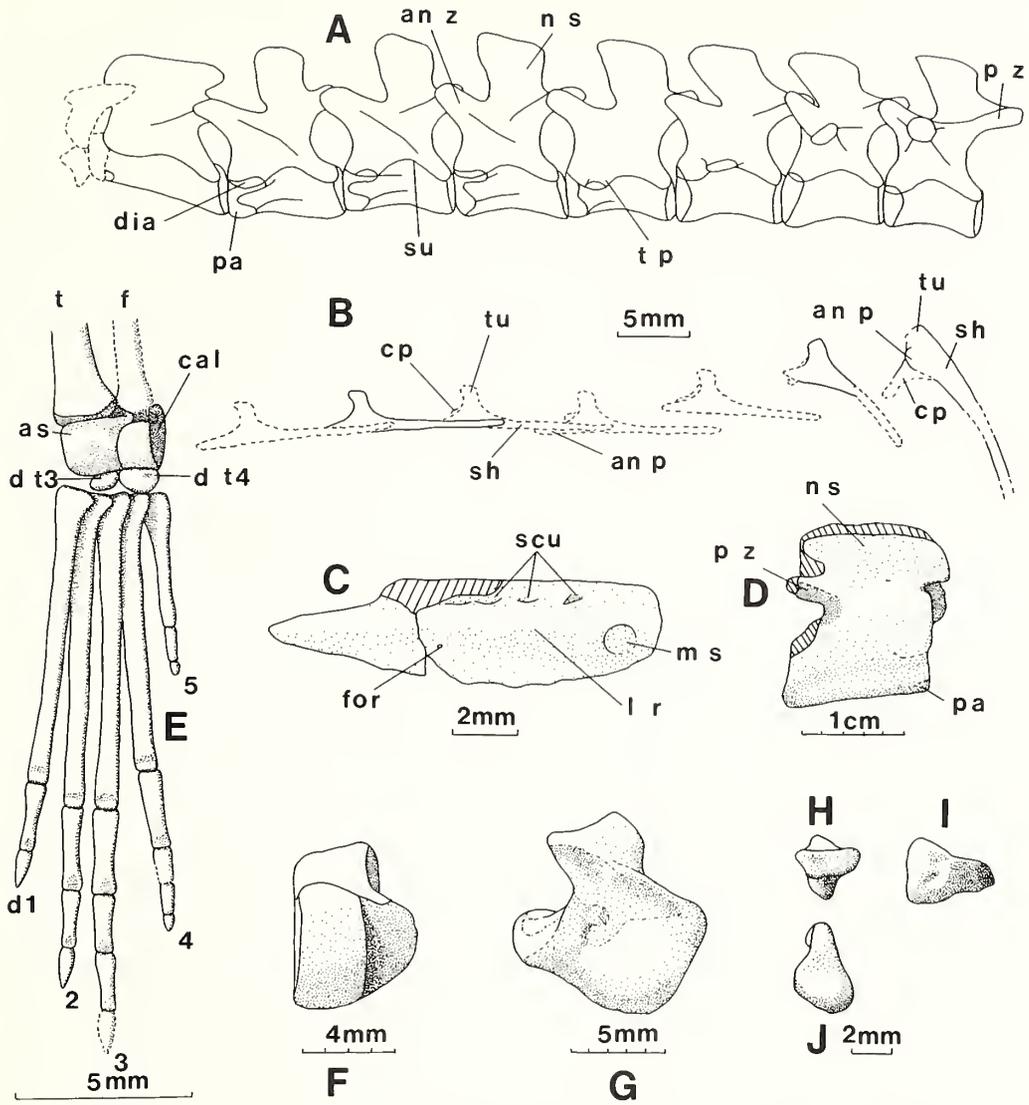


TEXT-FIG. 9. *Terrestriisuchus gracilis* gen. et sp. nov. A, restoration of right femur, based on P. 24/39a, in postero-medial view; B-C, left tibia, P. 11/1, in posterior and anterior views; D, left fibula, P. 130/1, in lateral view.

(text-fig. 9D), is incomplete distally. This element is a slender bone that is flattened proximally and bears a slight crest, for muscle insertion, on the lateral surface of its anterior edge. The distal expansion of the bone is slight.

Tarsus and pes. There are just four bones in the tarsus: the astragalus, calcaneum, and distal tarsals three and four (text-fig. 10E-I). The proximal tarsals articulated together by a ball and socket joint, with the astragalus functionally part of the crus whilst the pes, distal tarsals, and calcaneum moved as a unit on the astragalus and fibula. The calcaneum bears a well-developed tuber. The reconstruction of the tarsus is based on specimen P. 47/21a which comprises a virtually perfect set of tarsals completely freed from matrix. The medial surface of the calcaneum bears a circular socket, which accepted the peg of the astragalus, and a projecting lip of bone that lay posterior to the peg. Distal tarsal three, as preserved, is approximately cylindrical in shape. Distal tarsal four is larger than the other distal tarsal and consists of two expansions set at right angles to each other. The anterior of these lay horizontally whilst the posterior lay vertically and both were triangular in outline. The first four metatarsals are long and were approximately equal in length whilst the fifth is reduced. The fifth is primitive for a crocodile in that it is still about half the length of metatarsal four and bears two phalanges although these have been reduced to two small nubbins of bone. The proximal expansion of metatarsal five is bulbous and it bears a flange that fitted behind the proximal expansion of metatarsal four. The phalangeal formula is 2, 3, 4, 4, 2.

Armour and gastralia. A single row of scutes was present on each side of the dorsal midline but there is no evidence of any ventral or dorsal paramedial scutes. The armour is not shown in the reconstruction. The thoracic



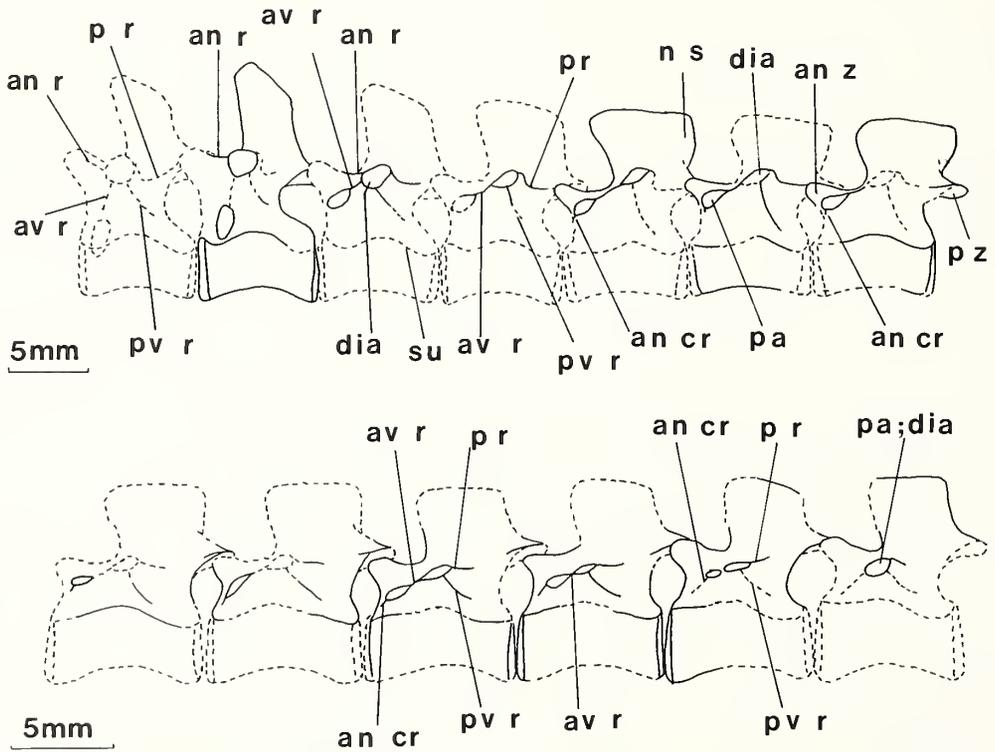
TEXT-FIG. 10. *Terrestrisuchus gracilis* gen. et sp. nov. A, reconstruction of cervical vertebrae, based on P. 79/1; B, reconstruction of cervical ribs; C, left scute, P. 123/1, in dorsal view; D, axis, P. 47/22a, in right lateral view; E, reconstruction of left tarsus and pes in anterior view; F, right calcaneum, P. 73/1, in anterior view; G, right astragalus, P. 110/1, in anterior view; H-J, right distal tarsal four, P. 47/21a, in anterior, dorsal, and lateral views.

scutes are basically leaf-shaped (text-fig. 10C) with an anterior peg that fitted into a triangular groove on the ventral surface of the adjacent plate. Each scute bears a prominent ridge along its midline and is sculptured medial to this ridge. A muscle scar is present postero-laterally. The gastralia, which are single ossifications, are broad, flattened, and V-shaped. The lateral projections of these elements curved slightly dorsally.

Atlas-axis complex. The atlas intercentrum, pro-atlas, and axis rib are not present in the material and the other atlantal elements are poorly preserved. The axis is in good condition on F. 47/22a (text-fig. 10D). The remains of the atlas neural arch show that it consisted of a dorsal flange that lay nearly horizontally and protected the dorsal

part of the spinal cord, and a crescentic ventral part that articulated with the atlas intercentrum, the basioccipital condyle, the odontoid, and the axis centrum. The atlas rib was a cylindrical rod of bone. Only a damaged nodule of bone is preserved representing the odontoid which was sutured, not fused, to the axis centrum. The figured specimen of the axis lacks an anterior zygapophysis. Specimen P. 78/1a shows this to have been an oval facet that faced dorso-laterally. There is only a single articular surface for the axis rib.

Cervical vertebrae and ribs. The cervical vertebrae have been reconstructed (text-fig. 10A) on the basis of an articulated, although damaged, cervical series on P. 78/1 and individual examples of V2-6, V8, and V9 which are well preserved on P. 79/1. The only doubtful parts of this restoration are the exact shapes of the neural spines which show some variation. A slight hypapophysis is present on V3 but such a flange is not found on the axis or on any of the more posterior vertebrae. The parapophyses on V3 and V4 are approximately oval in outline whilst more posteriorly they become triangular. On Vertebrae V3-5 the articular surface of the parapophysis merges with that of the diapophysis but posteriorly they are distinct. On the anterior vertebrae the parapophysis is supported by a strong ridge but this has faded out by V7. The structure of the transverse process, bearing the diapophysis, changes markedly along the sequence V3-9. On V3 the transverse process is just a slight protuberance with a ridge running back from it but the diapophysis moves progressively postero-dorsally along the series V3-9 and the transverse process increases in length. On V6 and V7 the transverse process is dorso-ventrally flattened and bears two ridges running along its anterior and posterior margins. On V8 a third ridge is developed postero-ventrally and on V9 a fourth antero-ventral ridge is present. The neural spines are flattened without trace of any dorsal thickening. A deep pit is present at the base of the posterior edge of the neural spine whilst a shallower one is present below its anterior edge. The anterior and posterior zygapophyses are well developed. The suture between the neural arch and centrum runs through the transverse processes on V3-5 and just below it on V7.

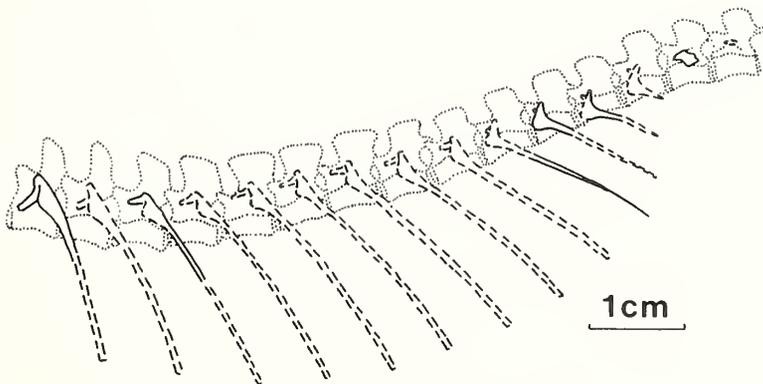


TEXT-FIG. 11. *Terrestrisuchus gracilis* gen. et sp. nov. Reconstruction of dorsal vertebrae, V10-16 and V19-24.

The cervical ribs are generally poorly preserved but P. 79/1a bears a well-preserved rib of V4 and P. 78/1b shows the structure of those of V8 and V9. It is thus possible to reconstruct the cervical ribs with confidence (text-fig. 10). The ribs of V3 to V7 are all similar and each extends anteriorly into a pointed, tapering process and posteriorly into a shaft that projected parallel to the vertebral column. The tuberculum and capitulum diverge at about 45° to one another. The rib of V8 possesses a pointed anterior process but the shaft is now longer and extends ventro-laterally. The anterior projection of V9 has been converted into a thin, rounded flange and the shaft now extends to curve around the body. There is no evidence for the presence of a cartilaginous uncinat process on any of the ribs.

Dorsal vertebrae and ribs. Specimen P. 78/1b bears V10–18 in association but these vertebrae are not well preserved. Block P. 72/1 contains the last seven presacrals, in better condition, in articulation with the two sacrals. There are some fine examples of individual vertebrae (P. 30/1, P. 80/1) and the dorsal column can be reconstructed (text-fig. 11) although not with quite the same confidence as the cervicals. The number of presacral vertebrae has been taken as twenty-four as this is the number present in *Protosuchus* and *Orthosuchus*. The material of *Terrestrisuchus* only allows a minimum number of twenty-three to be established. There is no distinction between thoracic and lumbar subregions as even the final presacral vertebra bears a free rib. The structure of the centrum is basically unchanging along the dorsal series except that it becomes relatively longer posteriorly. The articular surfaces of the centra are platycoelous but the anterior is more deeply hollowed out than the posterior. The parapophysis moves dorsally within this vertebral series and by V12 has migrated to just antero-ventral to the transverse process. At the posterior end of this series it moves closer to the diapophysis and finally merges with it on V24. Posterior to V13 this articulation is supported by a crest anteriorly. Unlike the situation in the modern crocodile the parapophyses are never borne on the transverse processes. The ridges supporting the transverse process are the same on V10 and V11 as those on V9, however by V13 the anterior ridge has disappeared and the antero-ventral ridge joins to the parapophysis. The three remaining ridges are present all the way back to V23. The structure of the neural spines is well preserved on V14 and V16, on P. 78/1b, and there is no trace of any dorsal thickening. The zygapophyses of V10 and V11 are like those of the cervical vertebrae but by V15 they have come to lie more horizontally. Pits were present at the bases of the neural spines of all the dorsal vertebrae.

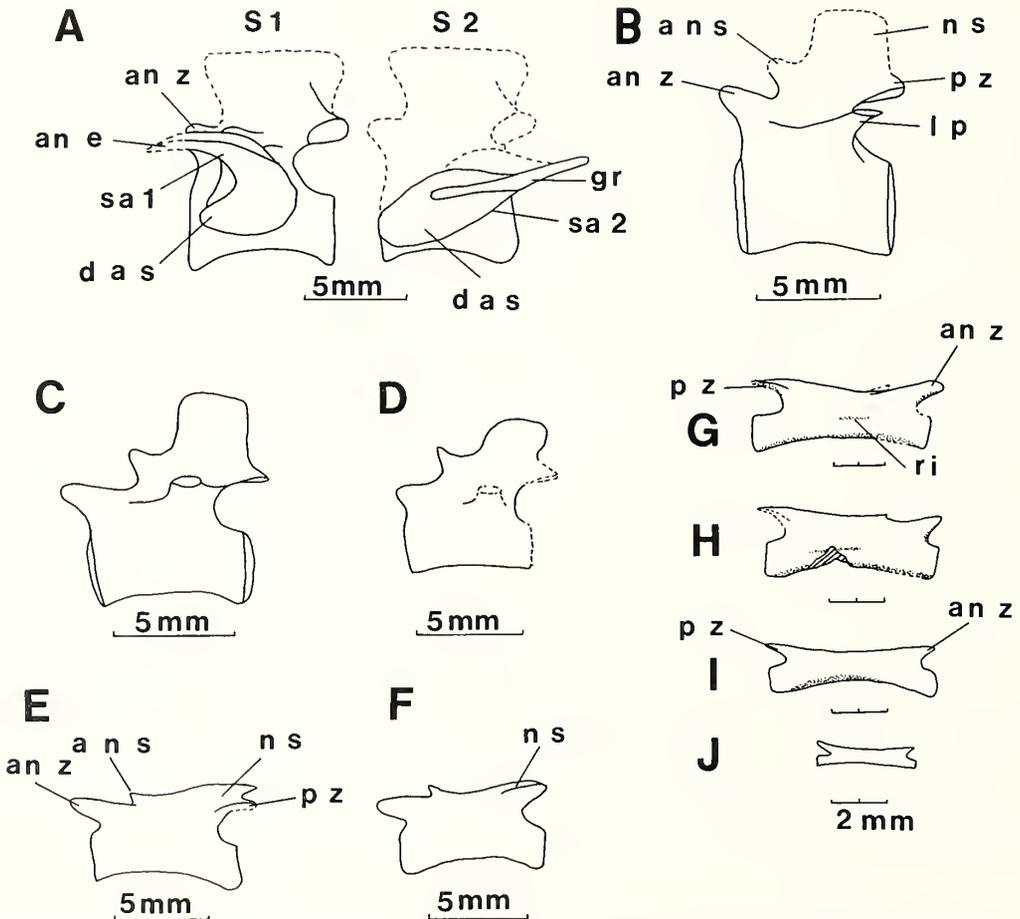
A fairly large number of dorsal ribs are preserved but few are in good condition. Text-fig. 12 shows what is believed to be an accurate restoration of these bones. The only significant reconstruction has been in the lengths of their shafts. All the ribs are dichocoelous except for that of V24 which is holocephalous. Rib ten on P. 78/1a is well preserved. The tuberculum is broad and flattened whilst the capitulum is circular in cross-section. The anteriorly projecting flange lies at about 45° to the plane of the articular processes. Rib sixteen, on the same specimen, is in fine condition. The tuberculum has now become just a small projection but the capitulum is well developed. The anterior flange is now triangular in outline and lies in the same plane as the heads of the bone. The ribs reduce posteriorly until that of V23 is just a flattened piece of bone with no shaft and barely distinguishable articular facets. The rib of V24 is exceptional in that it extended horizontally; it is flattened and has an approximately rectangular outline.



TEXT-FIG. 12. *Terrestrisuchus gracilis* gen. et sp. nov. Reconstruction of dorsal ribs, V10–24.

Sacral vertebrae. The first sacral vertebra is represented by four specimens one of which, P. 1/1, has been completely freed from matrix and is in excellent condition. The second sacral vertebra is less well represented in the material, but there is a fine specimen showing the centrum and rib in ventral view (P. 24/39c). The reconstruction of the sacrum on text-figs. 8B, D and 13A is thus considered to be accurate. The ribs of the first sacral vertebra are short and stout and they attach to transverse processes that arise from the complete dorso-ventral extent of the pedicels. Their distal articular surfaces for the ilia consist of a large ventral portion that faced ventrally, laterally, and slightly posteriorly, and a long tapering anterior extension. The transverse processes of the second sacral vertebra also originate from the whole height of the pedicels. The distal articular surfaces of these ribs are expanded anteriorly but taper posteriorly. Each articular surface bears a deep groove for articulation with the ilium.

Caudal vertebrae. The tail of *Terrestrisuchus* was very long and the number of caudal vertebrae has been estimated at about seventy. The tail can be split into two regions, 1 and 2, on the basis of the presence or absence of lateral processes (text-fig. 13B-J). These processes consist of ribs sutured to transverse processes. The proximal vertebrae of region 1 have short, stout centra and the main part of the neural spine is short and square. There is a small antero-dorsally directed accessory spine developed at the base of the anterior edge of the main neural spine.

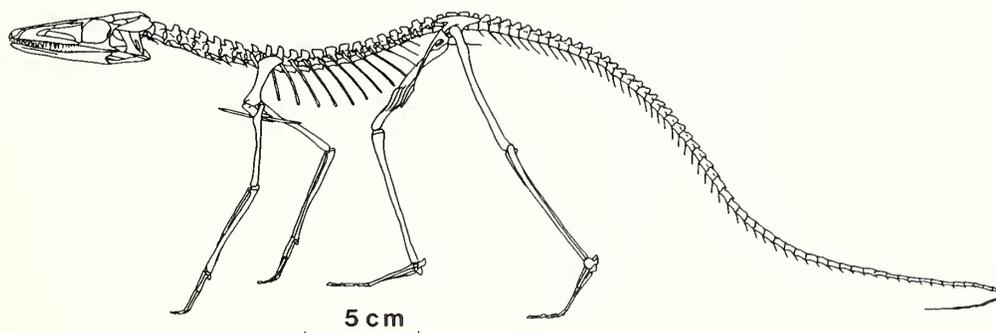


TEXT-FIG. 13. *Terrestrisuchus gracilis* gen. et sp. nov. A, reconstruction of sacrum in left lateral view; B-F, reconstruction of caudal vertebrae, in left lateral view, proximal region 1, medial region 1, distal region 1, proximal region 2, and medial region 2; G-J, distal region 2, P. 47/21, in right lateral view.

The lateral processes of these vertebrae exceed the length of the centrum and are swept back posteriorly and slightly dorsally. The centra of the vertebrae of the medial part of region 1 are more laterally compressed than those of the proximal region. The lateral processes project more directly laterally and are shorter than those on more anterior vertebrae. The distal vertebrae of region 1 show some change in the shape of the neural spine which now slopes posteriorly but the accessory spine is still present. The centrum is now more laterally compressed than those of the medial vertebrae and is relatively shorter. The lateral processes are further shortened. The more posterior of these vertebrae bear a small boss placed centrally on the lateral surface of the centrum. The proximal vertebrae of region 2 have centra that are relatively longer than those of the anterior vertebrae. There is still an accessory spine but the main neural spine is now very low and extended into a point posteriorly. The only difference in the medial vertebrae of this region is that the neural spine is rounded off posteriorly. More distally the bones become relatively longer and first lose all trace of neural spines and then zygapophyses.

Haemal arches. The extent of the haemal arches is uncertain although it is known that they were present anteriorly but did not continue to the end of the tail. They are basically rods of bone with a dorsal expansion that is pierced by a foramen. This expansion becomes relatively smaller towards the distal end of the tail. There is no evidence for the regional differentiation found in the chevrons of the modern crocodile.

Reconstruction and size. As restored *Terrestrisuchus* has a short trunk, long upright limbs, and a very long tail (text-fig. 14). The pelvis was held high above the pectoral girdle and both the manus and pes were digitigrade. The total length has been estimated to lie between 490 and 770 mm. It is not possible to be certain but it seems most likely that this material represents a small species rather than a collection of juveniles.



TEXT-FIG. 14. *Terrestrisuchus gracilis* gen. et sp. nov. Reconstruction based upon P. 47/21, 22.

DISCUSSION

Crocodylian affinities. *Terrestrisuchus* is considered to be a crocodile because of the presence of an elongated radiale and ulnare, whose structure can be homologized with those bones of the modern crocodile. Other apomorphic characters for the order Crocodylia, present in this genus, are the absence of a descending process from squamosal to quadratojugal and the presence of a parallel-sided quadratojugal. (The quadratojugal of *Pseudohesperosuchus* is assumed to be specialized.) *Terrestrisuchus* has other character states considered by Langston (1973) and Nash (1975) to be diagnostic of the Crocodylia: external nares terminal in position; some development of a secondary palate; choanae posterior to the external nares; quadrate inclined and bordered by a long slender quadratojugal; pterygoids wide with deep wings; advanced crurotarsal joint; femur without a marked fourth trochanter and no development of a greater trochanter; external surfaces of the dorsal scutes sculptured.

A proposed classification of the crocodiles:

Order Crocodylia Gmelin 1788

Suborder Triassolestia nov.

Family Triassolestidae Bonaparte 1970

Genus *Triassolestes* Reig 1963

Suborder Sphenosuchia nom transl., ex. infraorder Sphenosuchia, Bonaparte 1971 *incertae sedis*:

Dibothrosuchus Simmons 1965

Family Saltoposuchidae nov.

Genera *Saltoposuchus* Huene 1921, *Terrestrisuchus* gen. et sp. nov.

Family Hemiprotosuchidae nov.

Genus *Hemiprotosuchus* Bonaparte 1969

Family Sphenosuchidae Huene 1922

Genera *Pseudohesperosuchus* Bonaparte 1969, *Sphenosuchus* Houghton 1915, *Hesperosuchus* Colbert 1952

Suborder Protosuchia Mook 1934

Family Protosuchidae Brown 1933

Genera *Erythrochamps* Houghton 1924, *Notochamps* Broom 1904, *Pedeticosaurus* Van Hoepen 1915, *Protosuchus* Brown 1933, *Orthosuchus* Nash 1968, *Stegomosuchus* Huene 1922, *Eupneumatosuchus* Crompton and Smith 1980

Family Platygognathidae Simmons 1965

Genus *Platygognathus* Young 1944

Suborder Hallopoda Marsh 1881

Family Hallopodidae Marsh 1881

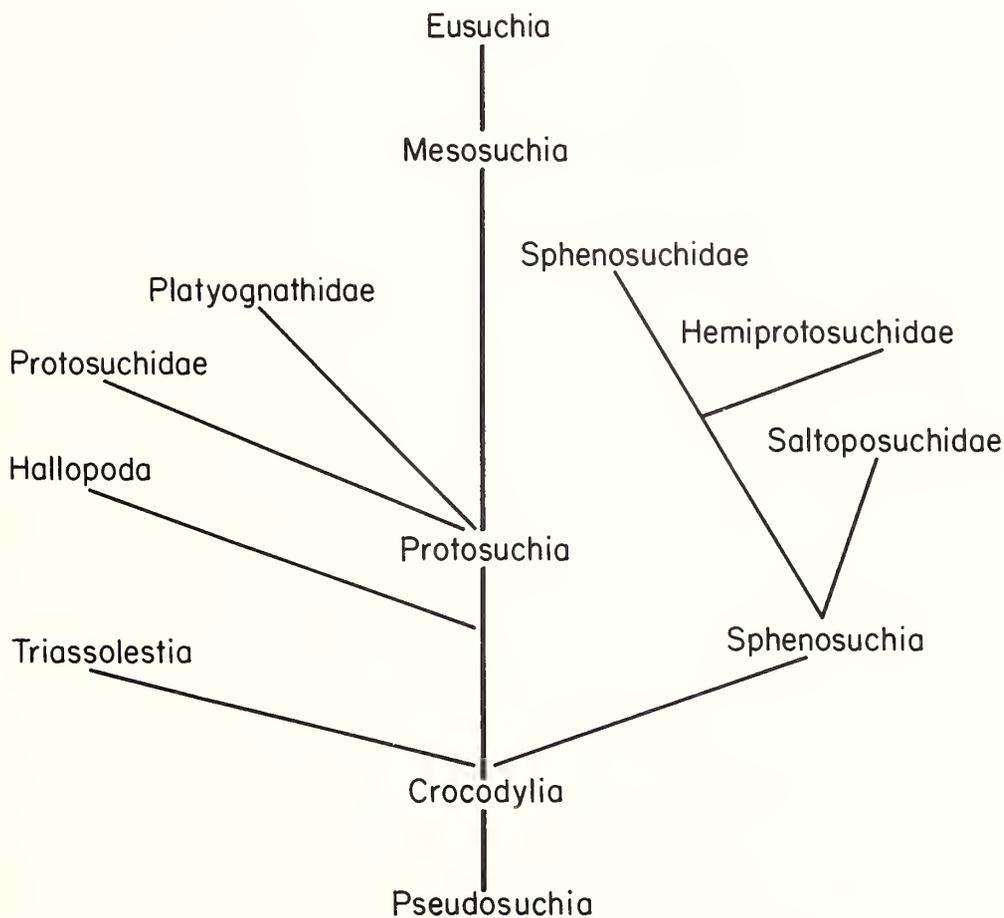
Genus *Hallopus* Marsh 1877

Suborder Mesosuchia Huxley 1875

Suborder Eusuchia Huxley 1875

The order Crocodylia is conventionally split into three suborders: Eusuchia, Mesosuchia, and Protosuchia. These are retained but an additional suborder is proposed, Triassolestia, for *Triassolestes*. This, the suborder Hallopoda, for *Hallopus*, and the suborder Sphenosuchia are all included in the Crocodylia. The suborder Triassolestia contains only *Triassolestes* in its own family, Triassolestidae. *Triassolestes* (Reig 1963; Bonaparte 1971a) is very tentatively included in the Crocodylia because of the presence of elongated carpals but otherwise it differs from the other crocodiles in having a coracoid without a dorso-ventral or postero-ventral projection and a non-crocodylian tarsus. In addition to these primitive characters it has some specialized features in that it has a reduced metatarsal one and the pes is functionally tridactyle. The suborder Sphenosuchia has been divided into three families: Saltoposuchidae, Hemiprotosuchidae, and Sphenosuchidae. These are linked by the presence of: a caracoid with a postero-ventral projection, a quadrate conch, and an ossified sternum (this character state is paralleled in *Hallopus*). The Hemiprotosuchidae and Sphenosuchidae, although distinct, are more closely related to each other than either is to the Saltoposuchidae. They are linked by the following character states: interpterygoid vacuities closed; frontals entering the supratemporal fenestrae; fused parietals; and scutes square or rectangular. All of these character states were developed in parallel in the Protosuchia. *Terrestrisuchus* and *Saltoposuchus* are classified together on the basis of the presence of a kidney-shaped squamosal. Additionally, a comparison of the skull, mandibular, and postcranial remains reveals many similarities in detail and argues strongly for their close relationship. The animals do differ in certain skull features sufficiently to separate them generically. For instance, the maxilla of *Saltoposuchus* lacks the fossa found in this bone of *Terrestrisuchus*. The Hemiprotosuchidae is a monotypic family specialized in that the supraorbital is incorporated into the skull roof (Bonaparte 1969, 1971). The members of the Sphenosuchidae are linked by the possession of: a reduced squamosal overlapped postero-laterally by the opisthotic, a longitudinal crest on the parietals, and a depression on the frontals (the latter two character states have been independently developed in the Protosuchia). The

suborder Protosuchia is split into two families: the Protosuchidae with seven members and the Platyognathidae that contains only *Platyognathus*. The Protosuchia are a group that have many apomorphic characters: two supraorbital elements; absence of an obturator foramen in the pubis; entry of the frontals into the supratemporal fenestrae; midline fusion of the parietals (the last two character states are variable in this suborder and are also found in the Sphenosuchia); dorso-ventrally expanded coracoid and ischium; rod-shaped pubis partly or fully excluded from the acetabulum; the absence of an obturator foramen in the pubis; dorsal ribs flanged anteriorly and posteriorly; metatarsal five without phalanges; ventral scutes present (this character is variable); immovable basiptyergoid articulations; quadrate and pterygoid fused to the braincase; straight groove on squamosal for ear flap; rectangular squamosals; square or rectangular scutes; and loss of interptyergoid vacuities (the last two character states were developed in parallel in the Sphenosuchia). The members of the Protosuchidae are united by having conical teeth that are unserrated. The posterior teeth of *Eupneumatosuchus* are flattened, however. The teeth of the South American sphenosuchid genera also lack serrations. The new material, recently described by Crompton and Smith (1980), of *Protosuchus* and *Eopneumatosuchus* has helped to confirm the close relationships of the Protosuchidae. *Eopneumatosuchus* itself clearly belongs in the suborder Protosuchia. *Platyognathus* (Young 1944; Simmons 1965) has a number of specializations which indicate that



TEXT-FIG. 15. Phylogeny of the Crocodylia.

it belongs in a family of its own: fused mandibular ramii (*Sphenosuchus* has developed this character state in parallel); procoelous vertebrae; teeth with a polygonal transverse section; terminal and confluent external nares; and anterior mandibular teeth projecting forward (this character state may also be present in *Notochampsia*). Although the classification presented here postulates much parallel evolution in the early crocodiles it is believed to have reduced it to a minimum. It is recognized that with better information on the less well-known genera the classification would probably alter.

Interrelationships of the suborders. There appears to have been a radiation of the Crocodylia represented by the Protosuchia, Triassoestia, and Sphenosuchia at the end of the Triassic (text-fig. 15). The upper Jurassic Hallopoda may have had a common ancestry with the Protosuchia as although *Hallopus* is specialized (Walker 1970, 1972) in having a functionally tridactyle pes, and a posteriorly rotated pubis has three characters otherwise only found in the Protosuchia—a dorso-ventrally expanded ischium and a rod-shaped pubis that is fully excluded from the acetabulum. These suborders, the Sphenosuchia and the Triassoestia, are proposed to have had a common pseudosuchian origin. The Sphenosuchia cannot be ancestral to the Protosuchia, as has often been thought, because of the presence of the quadrate conch and the structure of the coracoid. It is not considered possible to derive the coracoid of *Protosuchus* from those of the sphenosuchids. Furthermore, the secondary palate of the latter, as evidenced by those of *Terrestriuchus* and *Sphenosuchus*, are not homologous with that of *Orthosuchus* but are convergent with the type found in birds (Walker 1972). *Sphenosuchus* itself is further removed from a protosuchian ancestry by its functionally tridactyle pes. The supraorbital of *Hemiprotosuchus* bars it from a protosuchian ancestry. The specialized structure of *Triassolestes* means that the Triassoestia cannot be the ancestral group of the protosuchids. The terrestrial, cursorial, quadrupedal crocodiles represented by the Hallopoda, Sphenosuchia, and Triassoestia have no known descendants and seem to have been a relatively short-lived phenomenon. These forms are diverse when they first appear at the Triassic-Jurassic boundary and by the end of the Jurassic are only represented by one highly specialized genus, *Hallopus*. Other terrestrial crocodiles evolved within the Mesosuchia but they never attained the same degree of cursorial adaptation. The early forms may have been outcompeted by the coelurosaurs as the latter became more highly adapted for a bipedal, cursorial mode of life. The Protosuchia diverged ecologically from the Sphenosuchia and adopted a way of life similar to that of the modern crocodiles.

Origin of the Crocodylia. The thecodonts have long been considered ancestral to the later archosaurian groups including the crocodiles and thus membership of this order was investigated in the light of knowledge of the structure of *Terrestriuchus*, in an attempt to trace the early crocodylian suborders back to a common ancestor. The thecodonts were reviewed by Romer (1972) who divided them into four suborders. The first suborder Proterosuchia contains three families Proterosuchidae, Erythrosuchidae, and Prestosuchidae which are primitive groups showing no crocodylian affinities. The fourth family Proterochampsidae has specializations excluding it from a crocodylian ancestry as do the next two suborders Aetosauria and Phytosauria. The final suborder Pseudosuchia contains a wide variety of forms some of which have been classified here as crocodiles. Some of the pseudosuchids are specialized, and some are primitive, but no species gives any indication of the origin of the crocodiles.

Dibothrosuchus. This animal is poorly preserved and consists only of cranial fragments, a number of articulated vertebrae, and parts of a forelimb. Simmons (1965) considered it to be similar to *Hesperosuchus* which suggested a crocodylian affinity. It is tentatively included in the Sphenosuchia because of the presence of a postero-ventral projection on the coracoid.

Saltoposuchus. This genus was first described by Huene (1921) who divided it into two species *Saltoposuchus connectens* and *S. longipes*. Study of the material reveals that the remains are of four individuals of only one species. Within those numbered 12596 and 12597 the individual called *S. longipes* is simply a larger specimen of *S. connectens*. Furthermore, the material attributed to *Procompsognathus*, on find number 12597, is also of *Saltoposuchus*. In these remains there was an

angular, identified by von Huene as a clavicle of *S. connectens*, from find 12597 which did not form part of the other two individuals. There are therefore the remains of three animals, all of the species *S. connectens*, on the two numbered finds from Heugelschen. The individual identified as *S. longipes* from Burrenschen is also *S. connectens*. Knowledge of the material of *Terrestriusuchus* has made possible some reinterpretations of the material of *Saltoposuchus*. In find 12596 Huene's pterygoid is a left squamosal in dorsal view, his palatine a left quadrate in antero-lateral view, and his metatarsal an ulna. In find 12597 Huene's humerus fragment is a left frontal; his clavicle is a left angular in medial view; the pterygoids are squamosals in ventral view; the prefrontal is a left jugal in lateral view; the quadratojugal is a left quadrate and the right quadrate is a left quadrate. Walker (1968, 1970) was correct in assigning this genus to the Crocodylia. He correctly reidentified the 'lacrymal' as a jugal, but was mistaken in suggesting that the ischium was a coracoid. He suggested that the pubes belong to *Procompsognathus* but this is not the case.

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Explanation of abbreviations used in text-figs.

a n s	accessory neural spine	e n	external nares	op	opening into cranial cavity
ac r	acromial ridge	f o	fenestra ovalis	or	orbit
a c	alveolar canal	f p	fenestra pseudorotunda	p v	palatal vacuity
an	angular	f	fibula	pal	palatine
an cr	anterior crest	for	foramen	pa	parapophysis
an e	anterior extension	f m	foramen magnum	par	parietal
an r	anterior ridge	f pe	foramen perilymphaticum	p d	perilymphatic duct
av r	antero-ventral ridge	f t	fourth trochanter	pi	pisiform
a f	antorbital fenestra	fr	frontal	p r	posterior ridge
a p f	anterior palatal foramen	g	glenoid	p z	posterior zygapophysis
an p	anterior process	gr	groove	pv r	postero-ventral ridge
an z	anterior zygapophysis	il	ilium	po	postorbital
ar	articular	i t f	infratemporal fenestra	p o b	postorbital bar
as	astragalus	i	interclavicle	p t f	post-temporal fenestra
bo	basioccipital	if b	interfenestral bar	p a	prearticular
bs	basisphenoid	i n	internal nares	p f	prefrontal
cal	calcaneum	i v	interpterygoid vacuity	p m	premaxilla
cap	capitellum	is	ischium	p o	prootic
cp	capitulum	j	jugal	p	pterygoid
c	coracoid	l	lacrimal	p r q	pterygoid ramus of the quadrate
co	coronoid	l c	lateral convexity	pu	pubis
c q p	cranio-quadrate passage	l p	lateral process	q	quadrate
d c	deltpectoral crest	l r	longitudinal ridge	q p p	quadrate process of the pterygoid
d	dentary	m fo	mandibular fossa	q j	quadratojugal
dia	diapophysis	m	maxilla	ra	radiale
d 1-5	digits one to five	m f	maxillary fossa	r	radius
d a s	distal articular surface	me c	Meckelian cartilage	ri	ridge
dc 3, 4	distal carpals three and four	m c v	middle cerebral vein	S 1, 2	sacral vertebrae one and two
dt 3, 4	distal tarsals three and four	m c	medial convexity	sa 1, 2	sacral ribs one and two
e	ectopterygoid	m i	muscle insertion	sc	scapula
ex	exoccipital	m s	muscle scar	scu	sculpturing
e m f	external mandibular foramen	n	nasal		
		n s	neural spine		
		o	olecranon		

sh	shaft	sp	splenia	troh	trochlea
s	sternum	sq	squamosal	tu	tuberculum
s c p	subcapsular process	t c	temporal canal	t m	tympanic membrane
s t f	subtemporal fenestra	t	tibia	t r	tympanic ridge
s f	supracoracoid foramen	to	tooth	u	ulna
s o	supraoccipital	t p	transverse process	ul	ulnare
s fe	supratemporal fenestra	ts 1-6	transverse sections one to six	v	vomer
sur	surangular				
su	suture	tro	trochanter		

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THE AFFINITIES OF THE CRETACEOUS AMMONITE *NEOSAYNOCERAS* BREISTROFFER, 1947

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ABSTRACT. The cryptic micromorph ammonite *Neosaynoceras* Breistroffer, 1947 is redescribed and shown to be a Cenomanian offshoot of *Salaziceras* Breistroffer, 1936 of the Flickiidae. *Salaziceras* and *Neosaynoceras* are separated from the remaining Flickiidae as Salaziceratinae subfam. nov.

THE Albian–Cenomanian marls of Algeria and Tunisia, Madagascar and Tanzania, and Texas and northern Mexico are well known for their rich faunas of diminutive pyritic ammonites (Pervinquière 1907, 1910; Collignon 1928–1929, 1931, 1964; Böse 1928; Adkins 1928; Young 1979). Some of these are no more than nuclei of larger species, but others are genuinely diminutive, frequently paedomorphic taxa, unknown for reasons of preservational potential or environmental preferences in other facies (Kennedy and Hancock 1971; Kennedy and Wright 1981). The affinities of genera and subgenera *Euhystriocheras* Spath, 1933, *Prionocycloides* Spath, 1925, and *Sakondryella* Collignon, 1964, among these dwarfs, with the Mortoniceratinae were demonstrated by Kennedy and Wright (1981), and the origins of the Flickiidae in Lyelliceratidae by Wright and Kennedy (1979). We deal here with the diminutive and highly distinctive genus *Neosaynoceras* Breistroffer, 1947 (p. 76), type species *Saynoceras gazellae* Pervinquière, 1907 (p. 115, pl. 5, figs. 1–6), which is known only from the lower Cenomanian of Algeria, Tunisia, and Madagascar. The largest known specimens are less than 15 mm in diameter and show modification of ornament suggestive of maturity (crowded sutures, and excentric coiling). When introducing *S. gazellae* in 1907, Pervinquière placed it between *Holcodiscus* Uhlig, 1882 and *Scaphites* Parkinson, 1811 and regarded it as a perisphinctid; Roman (1938, p. 391) concurred with this assignation, but Breistroffer (1947, p. 76) regarded it as a degenerate acanthoceratid. In the *Treatise* Wright (1957, p. 414), following Breistroffer, assigned it to the Acanthoceratinae without comment. It is argued below that *Neosaynoceras* is a Cenomanian offshoot of *Salaziceras* Breistroffer, 1947 of the Flickiidae.

SYSTEMATIC PALAEOONTOLOGY

Repositories of specimens. The following abbreviations are used to indicate the repositories of specimens cited: GPIT—Geologisches und Paläontologisches Institut, Tübingen; OUM—University Museum, Oxford; SP—Collections of the Sorbonne, now in the Université Pierre et Marie Curie, Paris. The Collignon Collection is now housed in the Université de Dijon.

Family FLICKIIDAE Adkins, 1928 Genus *Neosaynoceras* Breistroffer, 1947

Type species. *Saynoceras gazellae* Pervinquière, 1907 p. 115, pl. 5, figs. 1–6, by the original designation of Breistroffer (1947, p. 76).

Diagnosis. Small: largest known specimens less than 15 mm diameter. Phragmocone a globose cadicone, smooth or with faint radial folds and shallow furrows at first which develop into primary ribs with bullate inner and outer ventrolateral tubercles linked across the venter by riblets or striae.

The outer ventrolateral tubercles are opposite or alternate on the venter, more commonly the latter. Body chambers are strongly ribbed and tuberculate and markedly scaphitoid with the inner edge occluding part of the umbilicus; tubercles become spinate and the shell resembles a Horse Chestnut (*Aesculus*) seed case. The suture line is simple with rounded terminations to the constituent elements of lobes and saddles; E/L is narrow and asymmetrically bifid, L broad with few incisions, L/U₂ small and little subdivided.

Discussion. Few genera resemble *Neosaynoceras*, and this is a major factor in the difficulty experienced in deciding its affinities. The most obvious comparison is with the Scaphitaceae, especially given the obviously scaphitoid coiling of the body chamber of some specimens (Pl. 21, figs. 1, 4, 20) and the looping of ribs between outer ventrolateral tubercles (Pl. 21, figs. 3, 12), a style of ornament shown by several *Scaphites* (e.g. Wiedmann 1965, pl. 57, figs. 1–7) of essentially the same date. The test of scaphitid affinities lies in the suture line. Scaphitids have quadrilobate early sutures, after a quinquilobate primary suture (see Doguzhaeva and Mikhailova 1982) and also ‘pseudolobes’ in the saddle L/U, resulting from the widening of this saddle and the deepening of its central lobule (Wiedmann 1965; Kullman and Wiedmann 1970). Unfortunately the preservation of the Madagascar material of *Neosaynoceras gazellae* available to us has not allowed the exposure of the early sutures. The mature suture lines, however, show no trace of development of ‘pseudolobes’, which are manifest in contemporary Scaphitaceae. Consequently we dismiss the idea of affinities with this group, despite the scaphitoid body chambers.

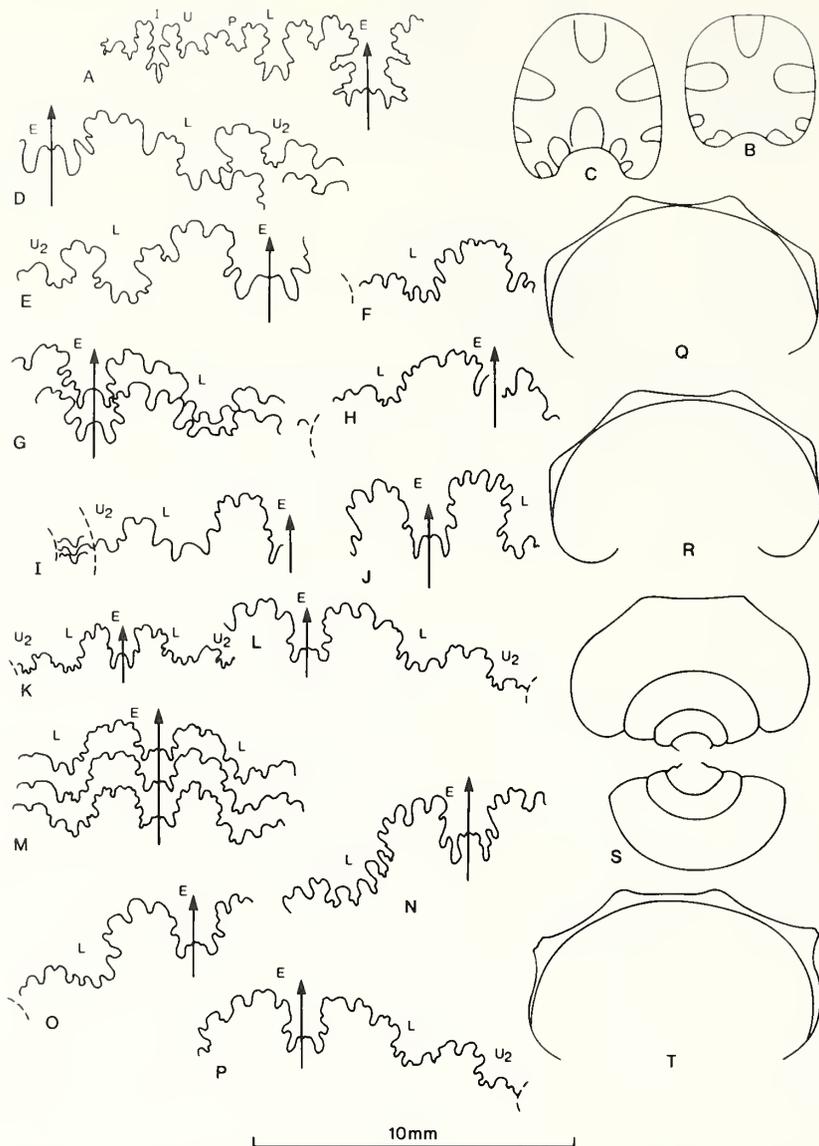
Affinity with the Acanthoceratidae is suggested because these are the only contemporary group in which strong ventrolateral tuberculation commonly develops, as in lower Cenomanian genera *Mantelliceras* Hyatt, 1903, *Sharpeiceras* Hyatt, 1903, and *Graysonites* Young, 1958 of the Mantelliceratinae, or *Acompsoceras* Hyatt, 1903 of the Acanthoceratinae. Study of the early development of these taxa shows that their early ontogeny (well shown in similarly sized specimens figured by Pervinquière 1907, 1910 and Collignon 1928–1929, 1931) involves early acquisition of umbilical, inner, and outer ventrolateral tubercles, plus in some lateral or even siphonal tubercles (e.g. *Acompsoceras*), and ribs at a stage where *Neosaynoceras* is almost smooth. These early Cenomanian acanthoceratids also lack constrictions or furrows and looping of ribs between ventral tubercles.

The closest analogues to *Neosaynoceras* lie in the late Albian *Salaziceras* Breistroffer, 1936 (p. 64, type species *Ammonites salazacensis* Hébert and Munier-Chalmas, 1875, p. 114, pl. 5, fig. 6). Scholz (1979) illustrates the ontogeny of the genus in detail and, although the taxonomic treatment may be questioned, specimens named *Salaziceras salazacense peyrolasense* Scholz, 1979 (p. 93, pl. 21, figs. 16, 18–20; text-figs. 25, 26B, 27C–G, K, N–Q) have nuclei with furrows and folds like those of *Neosaynoceras* nuclei (e.g. Scholz 1979, pl. 21, figs. 18–20), while specimens described as *Salaziceras breistrofferi pseudonodosa* Scholz, 1979 (p. 96, pl. 21, figs. 23, 24, 26; text-fig. 27R) develop a single ventral tubercle linked across the venter by a looped rib (text-fig. 10–Q). Scholz also introduced a subgenus *Salaziceras (Noskytes)* Scholz, 1979, type species *S. (N.) bakonyense* Scholz, 1979 (p. 97, pl. 22, figs. 1–5; text-figs. 27S, 28) for species with a transient juvenile stage with siphonal tubercles and an adult body chamber with strong ventral tubercles linked across the venter by looped ribs (text-fig. 1G–H, K–N, R–S), the adult aperture developing a remarkable constriction and ventral rostrum (text-fig. 1H, L, M). Examination of casts of the types of *S. (N.) bakonyense* throws doubt on the existence of a true siphonal tubercle. In one paratype it is displaced from the siphonal line, while in the other it is visible on a few ribs only and is likely to be a malformation.

It also appears possible that *Noskytes*, which has a highly specialized aperture, is the microconch of *Salaziceras*. In any case, the common morphological features of these tuberculate upper Albian *Salaziceras* and lower Cenomanian *Neosaynoceras* suggest close affinity, and that *Neosaynoceras* is a descendant of *Salaziceras* in which the single ventrolateral tubercle of *S. breistrofferi pseudonodosa* and of ‘*Noskytes*’ body chambers has been replaced by inner and outer ventrolateral tubercles. The suture lines of both genera are simplified, but this is no strong indicator of affinity, rather reflecting their small size.



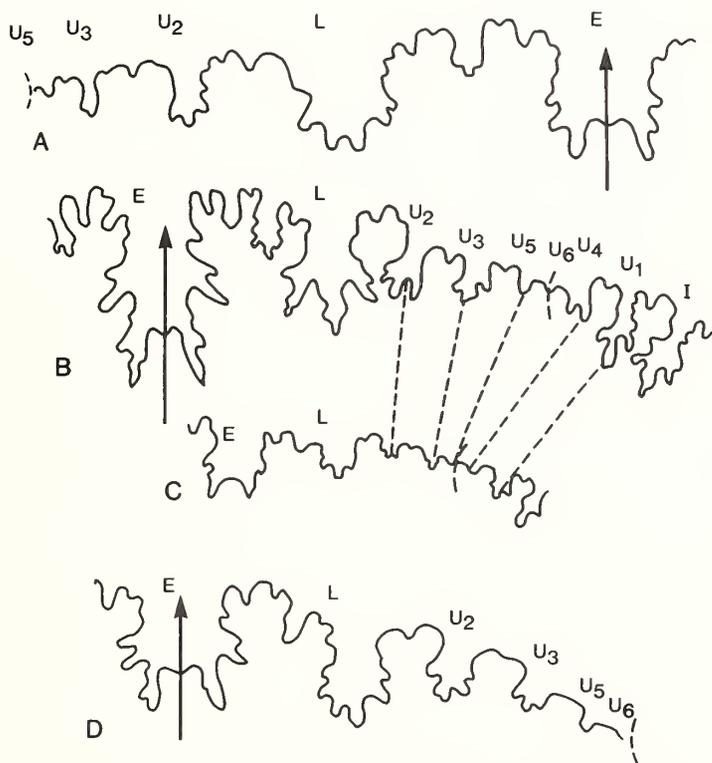
TEXT-FIG. 1. A-D, *Metascaphites thomasi* (Pervinquière, 1907), holotype, the original of Pervinquière 1907, pl. 4, figs. 30, 31, from Djebel Mrhila, Tunisia. Sorbonne Collections, now in the Université Pierre et Marie Curie, Paris. E-F, *M. thomasi* (Pervinquière, 1907), GPIT 1486/243, the original of Scholz 1979, pl. 22, fig. 6. G-H, K-N, R-S, *Salaziceras* ('*Noskytes*') *bakonyense* Scholz, 1979. G-H, GPIT 1426/240, a paratype, the original of Scholz 1979, pl. 22, fig. 3; K-M, GPIT 1486/238, a paratype, the original of Scholz 1979, pl. 22, fig. 1; N, GPIT 1486/241, inner whorls of the holotype, the original of Scholz 1979, pl. 22, fig. 4; R-S, GPIT 1486/242, a paratype, the original of Scholz 1979, pl. 22, fig. 5. I-J, T-U, *S. (Salaziceras) breistrofferi breistrofferi* Scholz, 1979. I-J, GPIT 1486/237, a paratype, the original of Scholz 1979, pl. 21, fig. 28; T-U, GPIT 1486/236, the original of Scholz 1979, pl. 21, fig. 27. O-Q, *S. (S.) breistrofferi pseudonodosa* Scholz, 1979, GPIT 1486/235, a paratype, the original of Scholz 1979, pl. 21, fig. 26. The originals of E-U are from the upper Albian of the Bakony Mountains, Hungary. All figures are $\times 2$.



TEXT-FIG. 2. Suture lines and whorl sections. A-B, *Metascaphites subthomasi* Wiedmann, 1962, GPIT Ce 1162/76, holotype, the original of Wiedmann 1962, pl. 13, fig. 8, text-figs. 57, 58, from the upper Albian of Izurdiaga, Navarra, Spain. C, *Scaphites (Scaphites) peroni* var. *inornata* Pervinquière, 1910, the original of Pervinquière 1910, pl. 2, fig. 15, from Berrouaghia, Algeria. Sorbonne Collections, now in the Université Pierre et Marie Curie, Paris. D, E, *M. thomasi* (Pervinquière, 1907), holotype, the original of Pervinquière 1907, pl. 4, figs. 30, 31, from Djebel Mrhila, Tunisia. Repository as for C. F-T, *Neosaynoceras gazellae* (Pervinquière, 1907). F, the lectotype, the original of Pervinquière 1907, pl. 5, fig. 2, from Pont du Fahs, Tunisia; G, T, the original of Pervinquière 1907, pl. 5, fig. 4; H, the original of fig. 6, both from Guern er Rhezal, Tunisia. Repository as for C. I, OUM KX1604; J, OUM KX1614; K, OUM KX1611; L, P, Q, OUM KX1609; M, OUM KX1606; N, R, OUM KX1610; O, OUM KX1607; S, OUM KX1613. All specimens from the lower Cenomanian of Beraketa-sur-Sakondry (Manera), Madagascar.

A further diminutive taxon with ventral tubercles is *Metascaphites* Wiedmann, 1962 (p. 212), proposed as a subgenus of *Scaphites*, with *Scaphites? thomasi* Pervinquière, 1907 (p. 121, pl. 4, figs. 30, 31; text-fig. 39) as type species. The holotype by monotypy, and a specimen from the upper Albian of Hungary, are shown in text-fig. 1A–F. When introducing this genus, Wiedmann also included a second species *Metascaphites subthomasi* Wiedmann, 1962 (p. 218, pl. 13, fig. 8; text-figs. 57, 58) for a fragment of only three camerae from the mid-upper Albian of Irzudiaga, Navarra, Spain. *M. subthomasi* has a basically quadrilobate suture with well-developed ‘pseudolobe’ (text-fig. 2A) and is a scaphitid. In contrast, *M. thomasi* shows only a part of the external suture (text-fig. 2D, E), which complements that of the other known specimen (text-fig. 3D) from Hungary. These closely recall the sutures of *Salazicerias* (*Salazicerias*) and *S. (Noskytes)*, and indeed Scholz included *M. subthomasi* in *Noskytes*. This is nomenclatorially irregular, and those who believe *Noskytes noskensis* and *M. thomasi* to be congeneric must use the latter generic name, which has priority. The Spanish *M. subthomasi* is a *Scaphites* allied to *Scaphites peroni* Pervinquière, 1910 (p. 26, pl. 2, figs. 10–16), especially the variety *inornata* which has a similar whorl section and suture. Irrespective of the relationship between *Noskytes* and *Metascaphites*, the latter is easily separated from *Neosaynoceras* by its possession of only one row of ventrolateral tubercles.

Occurrence. Lower Cenomanian of Algeria, Tunisia, and Madagascar.



TEXT-FIG. 3. Sutures. A, *Salazicerias (Salazicerias) salazacense* (Hébert and Munier-Chalmers, 1875) at a whorl height of 8.7 mm. B, C, *S. ('Noskytes') bakonyense* Scholz, 1979. B at a whorl height of 5.5 mm; C at 2 mm. D, *Metascaphites thomasi* (Pervinquière, 1907) at a whorl height of 8 mm. A–D are copies of Scholz (1979, text-figs. 27B, sb, sa, t).

Neosaynoceras gazellae (Pervinquière, 1907)

Plate 21, figs. 1–22; text-fig. 2F–T

- 1907 *Saynoceras gazellae* Pervinquière, p. 115, pl. 5, figs. 1–6.
 1925 *Saynoceras gazellae* Pervinquière; Diener, p. 96.
 1931 *Saynoceras gazellae* Pervinquière; Collignon, p. 77 (37).
 1938 *Saynoceras gazellae* Pervinquière; Roman, p. 391.
 1947 *Neosaynoceras gazellae* (Pervinquière); Breistroffer, p. 92 (76).
 1947 *Neosaynoceras gazellae* (Pervinquière) var. *globosa* Breistroffer, p. 92 (76).
 1957 *Neosaynoceras gazellae* (Pervinquière); Wright, p. L414, fig. 534: 1a, b.
 1964 *Neosaynoceras gazellae* (Pervinquière); Collignon, p. 26, pl. 323, figs. 1430–1432.

Types. Pervinquière (1907, p. 115) based this species on eight specimens, of which three were figured. We have traced four of these in the Collections of the Sorbonne, Paris (now housed in the Université Pierre et Marie Curie, Paris), including the lectotype designated by Breistroffer (1947, p. 76) (the original of Pervinquière 1907, pl. 5, figs. 2a, b, 3) and the holotype of var. *globosa* Breistroffer (1947, p. 76) (the original of Pervinquière 1907, pl. 5, figs. 4a–c, 5a, b) from the lower Cenomanian of Pont du Fahs and Guern er Rhezal, Tunisia.

Other specimens studied. More than a hundred specimens from the lower Cenomanian of Beraketa-sur-Sakondry, Madagascar, including the originals of Collignon (1964, pl. 323, figs. 1430–1432).

Description. The smallest specimens we have seen are 4.5 mm in diameter. At this size, the shell is a globose cadicone, with a deep conical umbilicus and very depressed whorls, the whorl breadth to height ratio ranging from 1.56 to 1.73. The umbilical wall slopes outwards, with a rounded shoulder and very broad, rounded venter. Moulds are either smooth or bear low radial folds from a diameter of 3–4 mm onwards; these are stronger on the flank, but weaken and may disappear on the venter. Some specimens also bear occasional shallow transverse furrows or constrictions. As size increases, the lateral folds strengthen progressively, and develop into distinct ribs (Pl. 21, figs. 15, 17) of which there may be up to sixteen per whorl in the largest specimens, although there is wide variation (Pl. 21). As the ribs strengthen, inner and outer ventrolateral tubercles develop, elongated parallel to the ribs and generally blunt. There is again wide variation in the relative development of both tubercles and ribs. In general, the outer ventrolateral tubercles are slightly offset and linked across the venter by low riblets or striae (Pl. 21, figs. 3, 12), which either loop or occasionally zigzag between them.

Few specimens have any part of the adult body chamber preserved but, of those that do, most show sutural crowding at a phragmocone diameter of 7–9 mm, with a single Madagascar example septate at 14 mm diameter. At this diameter, ribs are well developed for the preceding whorl and tubercles for the preceding quarter of a whorl (generally from 6 to 7 mm onwards) (Pl. 21, figs. 14, 18). The whorl section remains depressed at the end of the phragmocone with a whorl breadth to height ratio of 1.47 to 1.89, but it becomes markedly polygonal in costal section as a result of the development of ribs and tubercles (Pl. 21, figs. 2, 16).

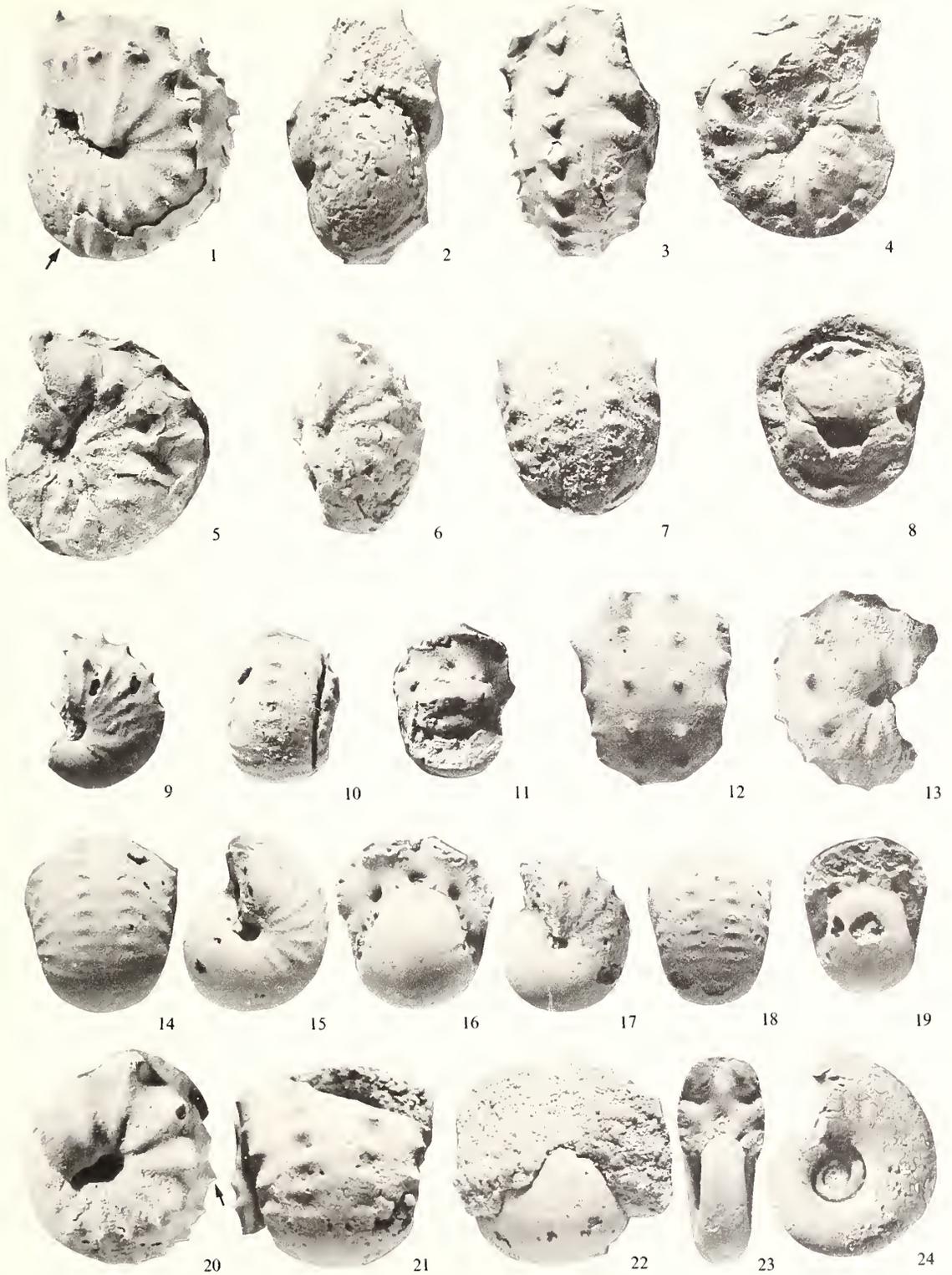
Body chambers have been seen to extend for up to two-thirds of a whorl, but none is complete. Coiling becomes markedly scaphitoid (Pl. 21, figs. 1, 4, 20) with the umbilicus partly occluded; the body chambers have

EXPLANATION OF PLATE 21

Figs. 1–22. *Neosaynoceras gazellae* (Pervinquière, 1907). 1–3, lectotype, the original of Pervinquière 1907, pl. 5, figs. 2, 3; 4, 5, paralectotype, the original of Pervinquière 1907, pl. 5, fig. 1; 6–8, paralectotype, the original of Pervinquière 1907, pl. 5, figs. 4, 5; 9–11, paralectotype, the original of Pervinquière 1907, pl. 5, fig. 6. 1–3, from Pont du Fahs, Tunisia; 4–11, from Guern er Rhezal, Tunisia. All specimens are from the Sorbonne Collections, now in the Université Pierre et Marie Curie, Paris. 12, 13, OUM KX1608; 14–16, the original of Collignon 1964, pl. 323, fig. 1430; 17–19, the original of Collignon 1964, pl. 323, fig. 1431; 20–22, the original of Collignon 1964, pl. 323, fig. 1432. 12–22, from Beraketa-sur-Sakondry (Manera), Madagascar.

Figs. 23, 24. *Scaphites* (*Scaphites*) *peroni* var. *inornata* Pervinquière, 1910, the original of Pervinquière 1910, pl. 2, fig. 15, from Berrouaghia, Algeria. Repository as for figs. 1–11.

All figures $\times 3$. Arrows indicate where septation ceases.



KENNEDY and WRIGHT, *Neosaynoceras* and *Scaphites*

flattened sides; the section remains depressed (whorl breadth to height ratio up to 1.8) and polygonal. Tubercles strengthen into finger-like spines (Pl. 21, fig. 2), ventral and ventrolateral ribbing declines, and the mould resembles a miniature Horse Chestnut seed case.

Typical suture lines are shown in text-fig. 2F–P. Although there is variation in detail, E is broad with a large median element, and E/L broad and asymmetrically bifid with a large incision adjacent to L. L is broad and shallow with more or less uniform simple lobules, and L/U smaller, simple, and bifid. The preservation precludes development of I, but septal faces (Pl. 21, fig. 16) show it to have been narrow.

Discussion. The generic discussion outlines features which differentiate *N. gazellae* from the most closely comparable species of *Salaziceras*, *Noskytes*, and *Metascaphites*. Separation of inflated forms as var. *globosa* Breistroffer, 1947 is unnecessary. *Saynoceras boulei* Collignon, 1931 (p. 76 (36), pl. 7 (3), fig. 22) is probably not a species of *Neosaynoceras*. It differs from *N. gazellae* in having relatively well-developed umbilical tubercles which give rise to single or paired ribs with conical inner ventrolateral tubercles, three times as numerous as the umbilical and feeble outer ventrolateral tubercles that disappear on the body chamber, with occasional siphonal tubercles on a siphonal ridge. These all suggest that it is an acanthoceratine, perhaps allied to some species of *Protacanthoceras*, e.g. *P. arkelli* Wright and Kennedy, 1980 (figs. 24–26) or *P. proteus* Wright and Kennedy, 1980 (figs. 50, 52).

Occurrence. Lower Cenomanian pelagic marl facies of Algeria, Tunisia, and Madagascar.

DISCUSSION

Wright and Kennedy (1979) included *Salaziceras* in Flickiidae, since there was good evidence of a phyletic line from *Salaziceras* to *Ficheuria* and thence to the rest of the family, and since *Salaziceras* was already a dwarf form with simplifying suture line. Scholz's (1979) demonstration of the morphological range within *Salaziceras* and the present linking of *Neosaynoceras* to *Salaziceras* shows that within Flickiidae there were two trends: one to forms with smooth shells and simple sutures, the other to strongly ornamented forms with tuberculate venters and more normal sutures. It is reasonable to distinguish these as subfamilies and we therefore group *Salaziceras* (including *Noskytes* and *Metascaphites*) and *Neosaynoceras* in Salaziceratinae subfam. nov., distinguished by strong ornament and normally frilled sutures, leaving *Ficheuria*, *Flickia*, and *Adkinsia* in Flickiinae *sensu stricto*.

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A NEW SUBFAMILY OF THE PTERASPIDIDAE (AGNATHA, HETEROSTRACI) FROM THE UPPER SILURIAN AND LOWER DEVONIAN OF ARCTIC CANADA

by D. K. ELLIOTT

ABSTRACT. New Pteraspidae from the upper Silurian and lower Devonian of arctic Canada differ from established members of the family in possessing a single orbito-cornual plate and a pineal plate enclosed by the dorsal disc. A new subfamily of the Pteraspidae, the Anchipteraspinae, is raised to accommodate five species of the new genera *Anchipteraspis*, *Ulutitaspis*, and *Rhachiaspis*. Consideration of the growth and structure of the shields of the Anchipteraspinae indicates their close relationship to both the Cyathaspinae and early members of the Pteraspinae. It is proposed that the Pteraspidae were developed from the Cyathaspinae by processes both of fusion and subdivision of the shield and that the Psammosteida developed from the Pteraspinae by similar processes.

LARGE numbers of heterostracans have been collected from Silurian and Devonian strata in the Yukon, British Columbia, and Northwest Territories and in recent years much of this material has been described (Denison 1963, 1964; Dineley 1964, 1968, 1976; Broad 1973; Broad and Dineley 1973; Dineley and Loeffler 1976; Loeffler and Jones 1976, 1977; Elliott 1983; Elliott and Dineley 1983). These descriptions have provided valuable information on the evolution of the Heterostraci, and indicate that the Canadian arctic was probably a centre of early development and radiation for this group. Evidence from these faunal descriptions indicates that anaspids, thelodonts, cyathaspids, and amphiaspids probably developed earlier there than elsewhere (Thorsteinsson 1967; Broad 1973), and more recent work (Elliott and Dineley 1983) has recorded the earliest known occurrence of *Protopteraspis* suggesting that pteraspidinids also evolved initially in this area. Further evidence for this view is provided in this work in which three new genera and five new species of heterostracans are described. These new genera are grouped as a new subfamily of the Pteraspidae and provide a link between that family and the Cyathaspidae, indicating an evolutionary connection.

The fauna is Upper Silurian and Lower Devonian in age and comes from the Peel Sound and Somerset Island Formations of Prince of Wales and Somerset Islands, Northwest Territories. Collections were made by the author in 1976 and by Bristol and Ottawa University parties in 1966, 1967, and 1974.

MATERIALS AND METHODS

The specimens described were preserved in slightly calcareous sandstones or calcareous siltstones. Both matrices allowed preparation by the transfer method of Toombs and Rixon (1950) in which the specimens were embedded in clear plastic and the matrix then removed with a dilute solution of acetic acid. This process enables the lateral line sensory canal system to be traced when the shields are viewed by transmitted light.

The measurements and ratios employed (Table 1) follow very closely those used by Denison (1964) when describing cyathaspids, except that the post-branchial length was not employed due to the difficulty of deciding the precise position of the branchial opening in pteraspids. The specimens are the property of the National Museum of Canada, Ottawa, and bear their catalogue numbers (prefixed NMC).

TABLE 1. Statistical comparison of dorsal shields of members of the Anchipteraspidinae. (Parameters selected for measurement are those used by Denison 1964.)

Dimensions (mm)					Ratios				
Med. length	Max. width	Orb. width	Orb. length	Pineal length	Max. width	Orb. width	Orb. length	Pineal length	
					Med. length	Med. length	Med. length	Med. length	
<i>Anchipteraspis crenulata</i>									
Range	26.0-28.5	20.0-23.0	9.5-10.5	3.0-3.5	4.5-5.0	0.78-0.81	0.35-0.39	0.11-0.14	0.15-0.19
Average	26.8	21.2	10.0	3.2	4.8	0.79	0.37	0.12	0.17
N=	4	4	4	4	4	4	4	4	4
<i>Ulutitaspis notidana</i>									
Range	32.5-35.0	22.0-23.0	12.0-13.5	4.0-5.5	6.5-7.5	0.63-0.71	0.34-0.40	0.12-0.15	0.19-0.21
Average	33.5	22.3	12.6	4.8	7.0	0.67	0.37	0.14	0.20
N=	4	6	6	6	5	4	4	4	4
<i>Ulutitaspis truncata</i>									
Range	20.0-21.5	18.5-19.0	9.5-10.5	3.0-4.0	4.5-6.5	0.93-0.97	0.45-0.53	0.15-0.20	0.23-0.32
Average	20.1	18.8	9.7	3.3	5.1	0.95	0.48	0.17	0.26
N=	4	4	4	4	4	4	4	4	4
<i>Ulutitaspis aquilonia</i>									
Range	25.5-29.0	21.5-24.0	11.5-13.0	3.0-4.5	4.0-6.5	0.80-0.84	0.42-0.45	0.11-0.15	0.19-0.22
Average	28.6	23.3	12.3	4.4	6.0	0.82	0.43	0.14	0.20
N=	4	4	4	4	4	4	4	4	4
<i>Rhachiaspis pteriga</i>									
Range	32.5-34.0	25.0-27.0	11.0-12.5	4.0-4.5	6.0-6.5	0.74-0.82	0.32-0.39	0.12-0.14	0.19-0.20
Average	32.6	25.6	11.6	4.1	6.2	0.78	0.35	0.13	0.19
N=	4	4	4	4	4	4	4	4	4

STRATIGRAPHY

The heterostracans described here were collected from the lower member of the Peel Sound Formation on Prince of Wales Island and the Somerset Island Formation on Somerset Island (text-fig. 1).

Rocks of the Peel Sound Formation occur over much of Prince of Wales Island and in gentle synclines in the Cape Anne-Pressure Point and Creswell Bay areas of Somerset Island. Originally named by Thorsteinsson and Tozer (*in Fortier et al.* 1963) the formation consists of red sandstones and siltstones, grading upwards into oligomict conglomerates and pebbly sandstones, deposited over a large delta system as subaerial alluvial fans prograding from the rising Boothia Uplift. On Prince of Wales Island, Miall (1970) separated the formation into lower and upper members. The lower, consisting of interbedded limestone, siltstone, sandstone, and oligomict conglomerate, is exposed only as a narrow band along the flank of the Boothia Uplift and has yielded large numbers of ostracoderms (Broad 1973; Broad and Dineley 1973; Loeffler and Dineley 1976; Elliott and Dineley 1983). The upper member is characterized by the disappearance of virtually all but conglomerate in the succession (Miall 1970). The Transition Bay localities on Prince of Wales Island all occur in the lower member of the Peel Sound Formation. This member is transitional between the marine Read Bay Formation and the upper member of the Peel Sound Formation.

On Somerset Island the localities occur in the Somerset Island Formation (Miall *et al.* 1978) which has been erected to include the transition beds between the Peel Sound sandstones and conglomerates and the underlying Read Bay limestones. It comprises a lower member consisting of grey and mottled planar-bedded limestones, and an upper member consisting of interbedded grey laminated dolostone and limestone, red quartzose siltstone, red dolosiltstone, and minor nodular limestone. The original

Read Bay–Peel Sound contact, defined (Thorsteinsson and Tozer 1963) at the occurrence of the oldest red siltstone unit, has been retained as the boundary between the two members of the Somerset Island Formation. The formation was deposited in predominantly intertidal and supratidal environments as the lowest part of a regressive sequence culminating in the conglomerate of the Peel Sound Formation. This unit is considered to be an age equivalent to the lower member of the Peel Sound Formation on Prince of Wales Island (Miall *et al.* 1978), both units representing the lowermost beds of a prograding clastic wedge, though separated by the Boothia Uplift and showing differences in lithology.

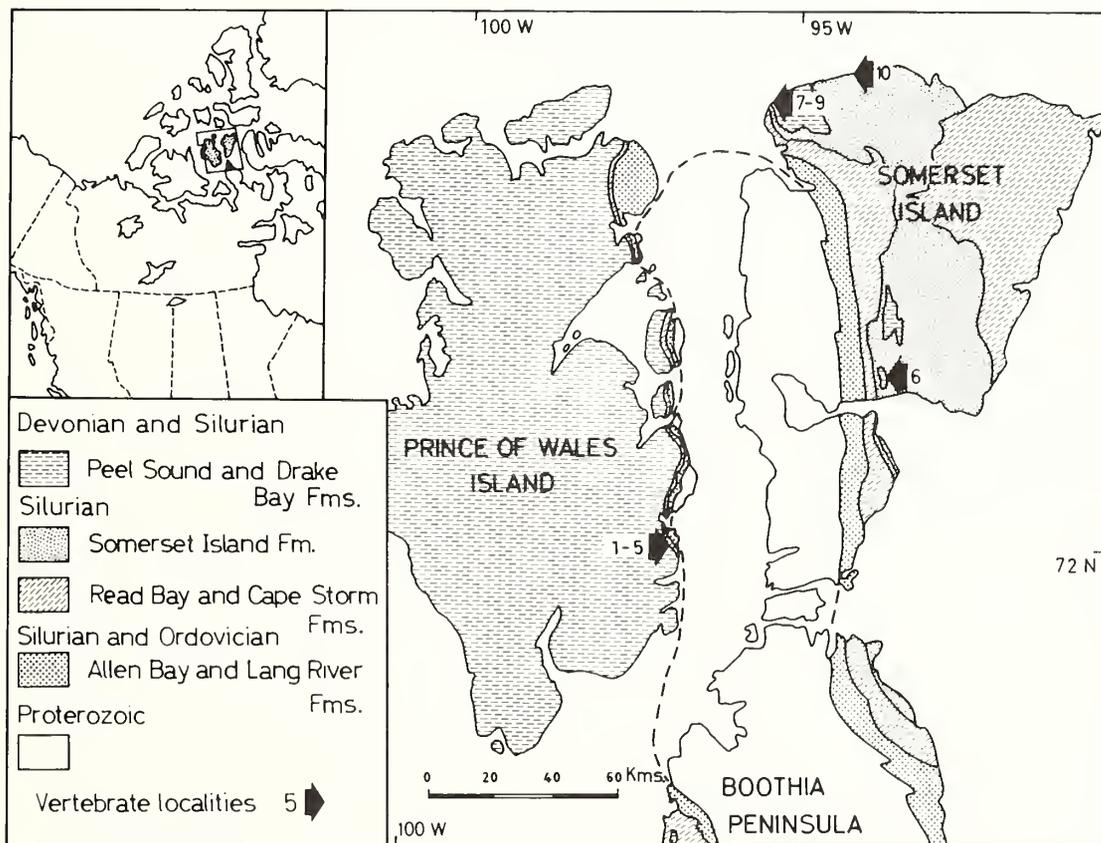
LOCALITIES

Prince of Wales Island

Locality 1. 96° 32' W, 72° 11' N. Gorge 26.4 km north of Transition Bay. 15 m above base of Peel Sound Formation. Grey, medium-grained sandstone grading up into poorly sorted conglomerate. Fauna: *Torpedaspis elongata*; *Corvaspis*; ?*Traquiraspis* sp.; cyathaspidids indet.; *Ulutiaspis notidana* gen. et sp. nov.

'Unnamed gorge' of Broad (1973); Broad and Dineley (1973). 22.5 km north of Transition Bay. 96° 28' W, 72° 10' N.

Locality 2. North side of gorge, 10.5 m above top of Read Bay Formation. Medium-grained grey sandstone with quartz clasts at base. Heterostracans concentrated at base where shields are stacked and current aligned.



TEXT-FIG. 1. Collecting localities and geology of Prince of Wales and Somerset Islands and Boothia Peninsula.

(Locality 7 of Broad (1973); Broad and Dineley (1973); G.S.C. locality C-10045.) Fauna: *Boothiaspis alata*; *B. angusta*; *B. ovata*; *Torpedaspis elongata*; *Poraspis* cf. *P. polaris*; *Corvaspis* sp.; ?*Traquairaspis* sp.; *Ulutitaspis truncata* gen. et sp. nov.

Locality 3. North side of gorge, 95.6 m above top of Read Bay Formation. 1 m thick medium to fine-grained sandstone, red at base and showing desiccation cracks. Fish occur throughout. (Locality 7 of Broad (1973); Broad and Dineley (1973); G.S.C. locality C-10046.) Fauna: *Torpedaspis elongata*; *Boothiaspis* sp.; *Corvaspis* sp.; ?*Traquairaspis* sp.; cyathaspidids indet.; acanthodian spines; *Ulutitaspis notidana* gen. et sp. nov.

Locality 4. North side of gorge. 60.3 m above top of Read Bay Formation (Broad, pers. comm. 1977). Probably equivalent to locality 3. 7 m of grey-green, fine-grained sandstone with dolomitic matrix. All ostracoderm material is black. Fauna: *Lingula* sp.; *Poraspis* cf. *P. polaris*; *Corvaspis* cf. *C. kingi*; ?*Traquairaspis* sp.; *Ulutitaspis* sp., gen. nov.

Locality 5. South side of gorge. 80.7 m above top of Read Bay Formation. 1.3 m of red medium-grained, finely laminated sandstone. Matrix dolomitic and calcareous. Fauna: *Corvaspis* cf. *C. kingi*; ?*Traquairaspis* sp.; *Ulutitaspis notidana* gen. et sp. nov. (*Listraspis* sp. in Broad (1973); Broad and Dineley (1973)).

Somerset Island

Locality 6. 93° 45' W. 72° 52' N. Kanguk Gorge, 8 km north of Creswell Bay. Upper member of Somerset Island Formation. Fauna: *Corvaspis* sp.; ?*Traquairaspis* sp.; *Rhachiaspis pteriga* gen. et sp. nov.

Locality 7. 95° 17' W. 73° 58' N. Cliffs on the north-east side of Pressure Point. Locality approximately 45 m below the top of the lower member of the Somerset Island Formation. (Locality 5 (part) of Broad (1973); Broad and Dineley (1973); G.S.C. locality C-10049.) Fauna: *Torpedaspis elongata*; *Boothiaspis ovata*; *Pionaspis acuticosta*; ?*Traquairaspis* sp.; Acanthodii indet.; *Ulutitaspis notidana* gen. et sp. nov.; *Rhachiaspis pteriga* gen. et sp. nov.

Locality 8. 95° 14' W. 73° 59' N. Stream valley 1.6 km east of Pressure Point. 15.2–31.4 m above the base of the upper member of the Somerset Island Formation (Gibling pers. comm. 1977). Grey, white, and buff, coarse to fine-grained, crossbedded sandstone. (Locality A of Dineley (1968); locality 5 (part) of Broad (1973), Broad and Dineley (1973); *Corvaspis* locality of Dineley and Loeffler (1976); G.S.C. locality C-10050.) Fauna: *Torpedaspis elongata*; *Boothiaspis alata*; *Corvaspis arctica*; *Hemicyclaspis murchisoni*; ?*Traquairaspis* sp.; Acanthodii indet.; *Ulutitaspis aquilonia* gen. et sp. nov.

Locality 9. 95° 14' W. 73° 57' N. Small bluff on the north-east side of the stream draining the north side of the coll 4 km south-east of Pressure Point. Reported (Broad and Dineley 1973) as being 260' above the base of the Peel Sound Formation. Remapping by Miall (Miall and Kerr 1977) places this locality in member 1 or 2 of the redefined Peel Sound Formation. Slightly calcareous, white, crossbedded sandstone. (Locality 5 (part) of Broad (1973), Broad and Dineley (1973); G.S.C. locality C-10052.) Fauna: *Torpedaspis elongata*; *Corvaspis* sp.; *Pionaspis* sp.; ?*Traquairaspis* sp.; olbiaspid indet.; Cyathaspidids indet.; *Rhachiaspis pteriga* gen. et sp. nov.

Locality 10. 94° 09' W. 74° 08' N. Near sea level in small graben 8 km west of Cunningham Inlet. 21.3 m above the base of the upper member of the Somerset Island Formation. Blue, slightly calcareous sandstone. (Locality F of Fortier *et al.* (1963); locality 5 (part) of Broad (1973), Broad and Dineley (1973); G.S.C. locality C-10053.) Fauna: *Torpedaspis elongata*; *Corvaspis* sp.; *Pionaspis* sp.; ?*Traquairaspis* sp.; Acanthodii indet.; *Anchipteraspis crenulata* gen. et sp. nov.

SYSTEMATIC PALAEOLOGY

Order HETEROSTRACI Lankester 1868

Family PTERASPIDIDAE Claypole 1885

Diagnosis. (Amended after Denison 1970.) Heterostraci with dorsal shield composed of rostral and pineal plates, a dorsal disc with a dorsal spine attached to its posterior margin, and paired branchial, orbito-cornual, or orbital and cornual plates, the latter occasionally reduced or absent. Ventral shield formed by a large ventral disc, variably developed paired lateral, oral, and sometimes postoral plates, and in *Doryaspis* a pseudorostrum. Branchial openings more or less posteriorly placed at or near the lateral margin of the dorsal shield, typically at the posterior ends of the branchial plates and commonly bounded posteriorly by cornual plates. Sensory canals of dorsal disc arranged in two

longitudinal pairs connected on each side by three commissures, normally radially arranged. Ornamentation fine and commonly crenate. Scales small, numerous, and rhomboid.

Remarks. The family Pteraspidae was divided into two subfamilies by Denison (1970), the Doryaspidinae containing the aberrant pteraspidid *Doryaspis*, and the Pteraspinae containing all other forms. A further subfamily, the Anchipteraspidinae, is established in this work to include forms that possess a single orbito-cornual plate and a pineal plate enclosed by the dorsal disc.

Subfamily ANCHIPTERASPIDINAE subfam. nov.

Diagnosis. Dorsal shield composed of rostral and pineal plates, a dorsal disc with posterior dorsal spine and paired branchial, dorsal, and orbito-cornual plates. Pineal plate totally enclosed by the dorsal disc. Branchial openings more or less posteriorly placed and bounded dorsally by the orbito-cornual plate. Narrow pre-oral surface ornamented by dentine ridges. Dorsal sensory canal system composed of paired lateral and medial longitudinal canals joined by three pairs of lateral commissures. Inter-orbital canal forming posteriorly directed loop on the dorsal disc, median longitudinal canals not contacting inter-orbital canal. Ventral shield formed by a large ventral disc.

Genera assigned. *Anchipteraspis* gen. nov., *Ulutitaspis* gen. nov., *Rhachiaspis* gen. nov.

Remarks. In the complement of plates the Anchipteraspidinae shows most similarity to the Pteraspinae though in some features the relationship to the Cyathaspididae can still be clearly seen. The main points of difference are that the pineal plate in the Anchipteraspidinae is still totally enclosed by the dorsal disc whereas that of the Pteraspinae is situated on the margin between the dorsal disc and the rostral plate; also the orbital and pineal plates of the Pteraspinae are represented by one plate, the orbito-cornual, in the Anchipteraspidinae.

An enclosed orbit is characteristic of the Pteraspidae though this feature is also found in a number of cyathaspidids, notably in the Ctenaspidinae and in *Listraspis*. Denison (1964) has shown that in the cyathaspidid *Listraspis* this enclosure is due to the fusion of a sub-orbital plate to the dorsal shield. There is no clear evidence as to the method of enclosure of the orbit in the Anchipteraspidinae though there is disruption to the ornamentation below the orbit in several specimens which may indicate fusion of a sub-orbital plate.

Fusion of the branchial plate to the dorsal shield is likewise a pteraspidid feature. In the Cyathaspididae the simple, notched plate is normally separate though in *Listraspis* a plate of typically cyathaspidid type is fused to the dorsal shield and in the Ctenaspidinae the branchial plate appears to have become incorporated in the dorsal shield as a lateral lamina and ventrolateral plate.

The pattern of the dorsal lateral line canals in the Anchipteraspidinae is very close to that found in the primitive pteraspidid *Protopteraspis*, showing two pairs of longitudinal canals joined by three sets of commissures, a posterior loop of the inter-orbital canal, and no contact between the medial dorsal canals and the inter-orbital canal. No cyathaspidid shows as regular and complete a pattern.

The separate dorsal spine is not a cyathaspidid feature. Though spines are present in such forms as *Cyathaspis* and *Listraspis* there is no evidence that they are more than an outgrowth of the dorsal shield (Kiaer 1932; Denison 1964).

Classification within the Cyathaspididae and the Pteraspidae is based on characters derived almost entirely from the dorsal shield, and the most important of these is the mode of formation of the shield. In the Pteraspidae the plates comprising the dorsal shield were initiated at a juvenile stage, remained separate during the life of the animal while increasing in size by peripheral accretion, and fused only at maturity (White 1935, 1958, 1973; Heintz 1938; Denison 1973). In the Cyathaspididae the shield formed at maturity (Denison 1964) though in some forms the epitega functioned as separate units in the growth of the superficial layer (Dineley and Loeffler 1976). Evidence from a specimen of *Ulutitaspis aquilonia* gen. et sp. nov. (NMC 13844, Pl. 2, fig. 3; text-fig. 7B) shows that the animal continued growing after development of the dorsal disc had been initiated. This effectively separates the Anchipteraspidinae from the Cyathaspididae and shows that their affinities lie with the Pteraspidae.

Genus *Anchipteraspis* gen. nov.

Type species. *A. crenulata* gen. et sp. nov.

Name. Greek 'anchi' meaning almost and *Pteraspis*, the type species of the subfamily Pteraspidae.

Diagnosis. Dorsal shield small and broad, and with a very blunt rostrum. Ornamentation of extremely fine ridges (17/mm) with well-developed alternating lateral projections at the base. Narrow orbito-cornual plates with smooth lateral margins indented at the level of the branchial openings. Inter-orbital canal forming posteriorly directed loop on dorsal disc.

Anchipteraspis crenulata gen. et sp. nov.

Plate 22, figs. 1-3; text-fig. 2

Name. Latin 'crenulata' meaning minutely crenate, referring to the ornament of very fine crenate ridges.

Type material. Holotype NMC 13854, dorsal shield; Plate 22, figs. 1, 3; from locality 10, Peel Sound Formation, Somerset Island.

Other material. NMC 13853, 13855, 13856, 13857, dorsal shields.

Diagnosis. As for genus, the type being the only species. For dimensions see Table 1.

Locality. 10.

Description. The rostrum is broad and very short with a rounded anterior margin. The dorsal surface is convex and a conspicuous groove separates it from the convexity of the dorsal disc (NMC 13854; Pl. 22, fig. 1). Laterally the plate margins form deep pre-orbital lobes (Pl. 22, fig. 3) bounding the ventral pre-oral surface. The posterior margin of the ventral pre-oral surface is slightly concave, no median lobe is developed. The surface is very narrow, only 0.75 mm wide, and is little more than a maxillary brim similar to that found in *Listraspis* (Denison 1964) and ornamented with fine transverse dentine ridges.

The dorsal disc is domed anteriorly with parallel lateral margins and an almost transverse posterior margin, slightly concave to either side of the median process. In NMC 13855 a median ridge is present anterior to the dorsal spine. The pineal plate is large and oval and ornamented with ridges parallel to the plate margins.

The dorsal spine is only seen in NMC 13855 where it is incomplete and distorted. Anteriorly the median ridge of the dorsal disc appears to merge with the spine through an area of short irregular ridges, a feature common in the subfamily. Laterally the plate junction is demarcated by a distinct groove. Only the base of the spine is preserved but the ridge pattern suggests that it would have been backswept.

The large orbits are laterally placed, and the orbito-cornual plates form laminae with smooth lateral margins that maintain a constant width of about 2 mm to a point just past the branchial openings where they are constricted (NMC 13854; Pl. 22, figs. 1, 3). Posteriorly the laminae flare out to form posterolateral points similar in shape to the cornual plates of Pteraspidae. The ornamentation is generally longitudinal and continuous on both dorsal and ventral surfaces indicating that this is one plate, but in the holotype the ornamentation is

EXPLANATION OF PLATE 22

Fig. 1. *Anchipteraspis crenulata* gen. et sp. nov. NMC 13854. Dorsal view, $\times 3$.

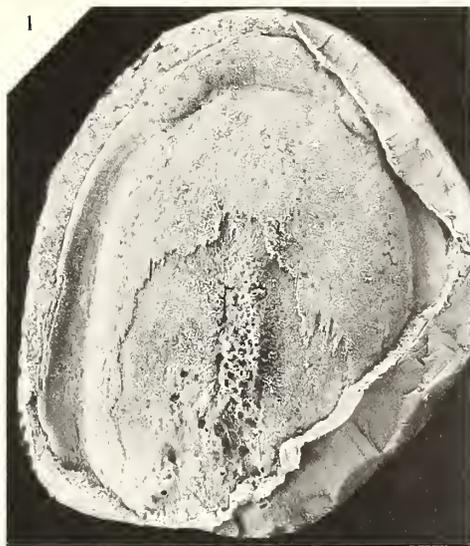
Fig. 2. *Anchipteraspis crenulata* gen. et sp. nov. NMC 13853. Lateral view, showing branchial plate and branchial opening, $\times 3$.

Fig. 3. *Anchipteraspis crenulata* gen. et sp. nov. NMC 13854. Internal view of dorsal shield showing posterior part of orbito-cornual plate and impressions of internal organs, $\times 3$.

Fig. 4. *Ulutitaspis truncata* gen. et sp. nov. NMC 13835. Dorsal view, $\times 4$.

Fig. 5. *Ulutitaspis truncata* gen. et sp. nov. NMC 13836. Ventral pre-oral surface, $\times 10$.

Fig. 6. *Ulutitaspis truncata* gen. et sp. nov. NMC 13838. Dorsal view showing internal mould with impressions of internal organs, $\times 4$.



disrupted at the level of the branchial constriction suggesting the incipient development of separate cornual and orbital plates. Below the orbit the ornamentation is also disrupted and broken into short ridges (NMC 13854; Pl. 22, figs. 2; text-fig. 2A). This almost certainly indicates the final stage of enclosure of the orbit either by the fusion of a sub-orbital plate as occurs in *Listraspis* (Denison 1964), or by the growth of the orbital plates ventrolaterally around the orbits.

The branchial plate is attached dorsally to the medial edge of the ventral surface of the orbito-cornual plate, and is directed slightly medioventrally. The anterior end of the plate is blunt and the posterior margin, terminating at the base of the cornual extension of the orbito-cornual plate, is gently convex (Pl. 22, fig. 2; text-fig. 2A). The branchial opening is large and elongated and occurs about a third of the way from the posterior margin of the shield. The upper margin of the opening is damaged in NMC 13853 which shows it in lateral view, but in NMC 13854 it is clearly roofed by the ventral surface of the orbito-cornual plate.

A small plate is fused to the anterior margin of the branchial plate in NMC 13853 (Pl. 22, fig. 2; text-fig. 2A). A similar plate occurs in the same position in *Listraspis* (Denison 1964) and is certainly a lateral plate that has become fused to the dorsal shield.

The dorsal sensory canal system is visible only in NMC 13855 (text-fig. 2B). The pattern is very similar to that found in *Protopteraspis*, the most primitive genus of the subfamily Pteraspidae. Two pairs of longitudinal canals, medial and lateral, are joined by three pairs of transverse commissures. The medial canals terminate anteriorly before reaching the loop formed on the dorsal disc by the inter-orbital canal. The lateral canals join the inter-orbital canals behind the orbits before continuing ventrally.

No ventral shields are known for this genus.

Remarks. This genus is separated from *Rhachiaspis* gen. nov. by its smaller size and narrower orbito-cornual plates. It differs from *Ulutitaspis* gen. nov. chiefly in the smooth lateral margins present on the orbito-cornual plates.

The canal system shows considerable similarity to that found in *Protopteraspis* in having the same complement and arrangement of canals. However, it retains a certain rectangularity of arrangement that is closer to the pattern normally developed in the Cyathaspididae than to the radiating pattern found in the Pteraspidae.

Anchipteraspis is very similar in some aspects to the cyathaspidinid *Listraspis canadensis* (Denison 1964). The overall proportions are very similar as is the shape and relationships of the branchial plates. The orbito-cornual plate of *Anchipteraspis* is also very similar superficially to the laterally extended lateral epitegum of *Listraspis*. However, there is no separate pineal plate in *Listraspis* though a large pineal prominence is developed. There is also no indication of a posterior dorsal spine in *Listraspis*; a distinct postero-median process is developed but the ridges of the central epitegum curve into it showing that it is part of this epitegum and not a separate spine.

Genus *Ulutitaspis* gen. nov.

Type species. *U. notidana* gen. et sp. nov.

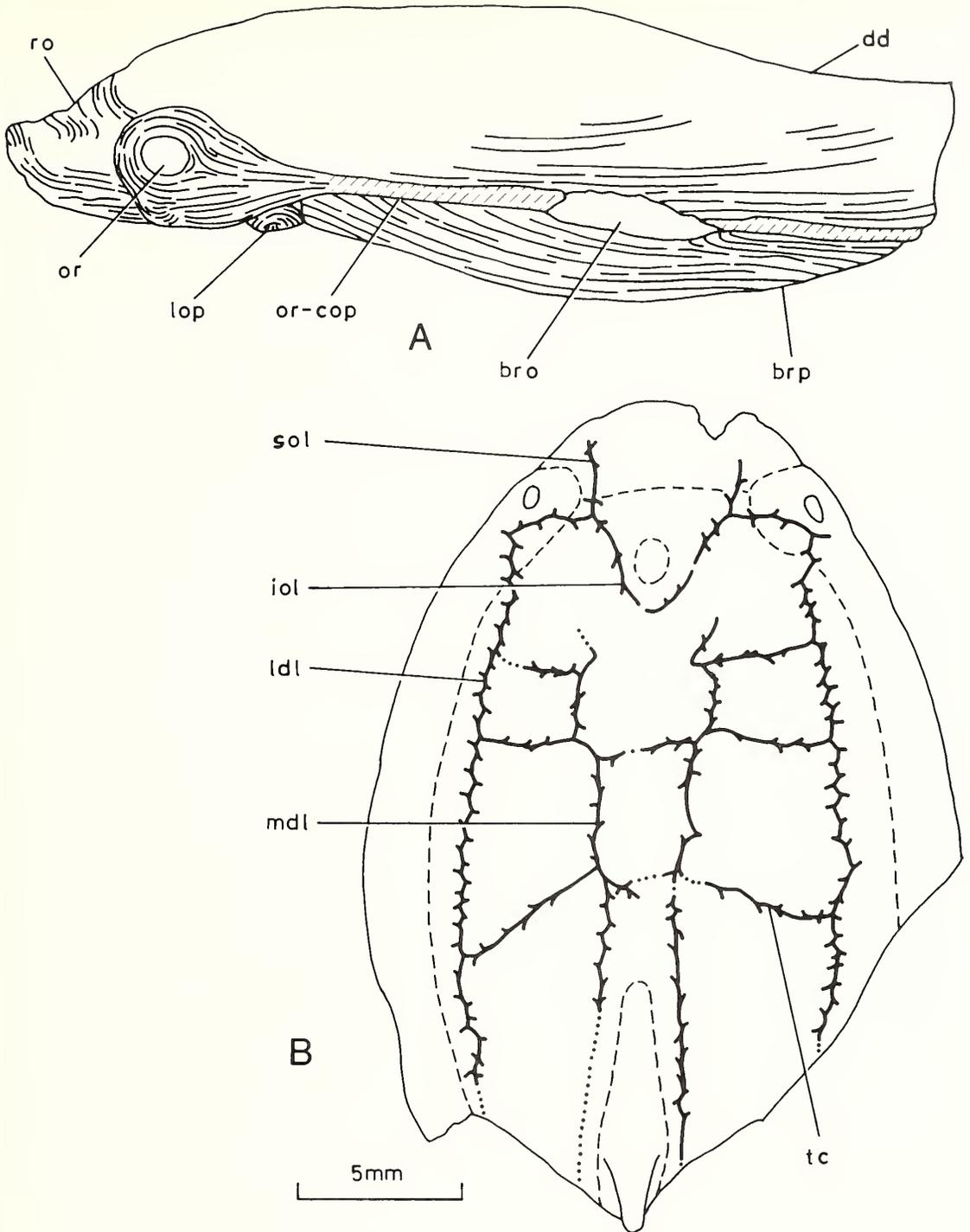
Name. Eskimo 'ulutit' meaning a saw, and Greek 'aspis' meaning shield referring to the serrated lateral margins of the dorsal shield.

Diagnosis. Dorsal shield small and gently arched, with generally high width ratio. Rostrum blunt, with well-developed median rostral process and broad ventral pre-oral surface ornamented with dentine ridges. Lateral margin of the orbito-cornual plate serrate for two-thirds of its length, the serrations increasing in size posteriorly. Cornual extension following deep notch at the level of the branchial opening. Well-developed, slender, posterior dorsal spine. Ornamentation of fine crenate ridges, becoming coarse and smoothly rounded at the lateral margins of the rostral and orbito-cornual plates.

Ulutitaspis notidana gen. et sp. nov.

Plate 23, figs. 1, 2; Plate 24, fig. 1; text-figs. 3, 4

Name. Greek 'notidanos' meaning with pointed dorsal fin, referring to the pointed dorsal spine.



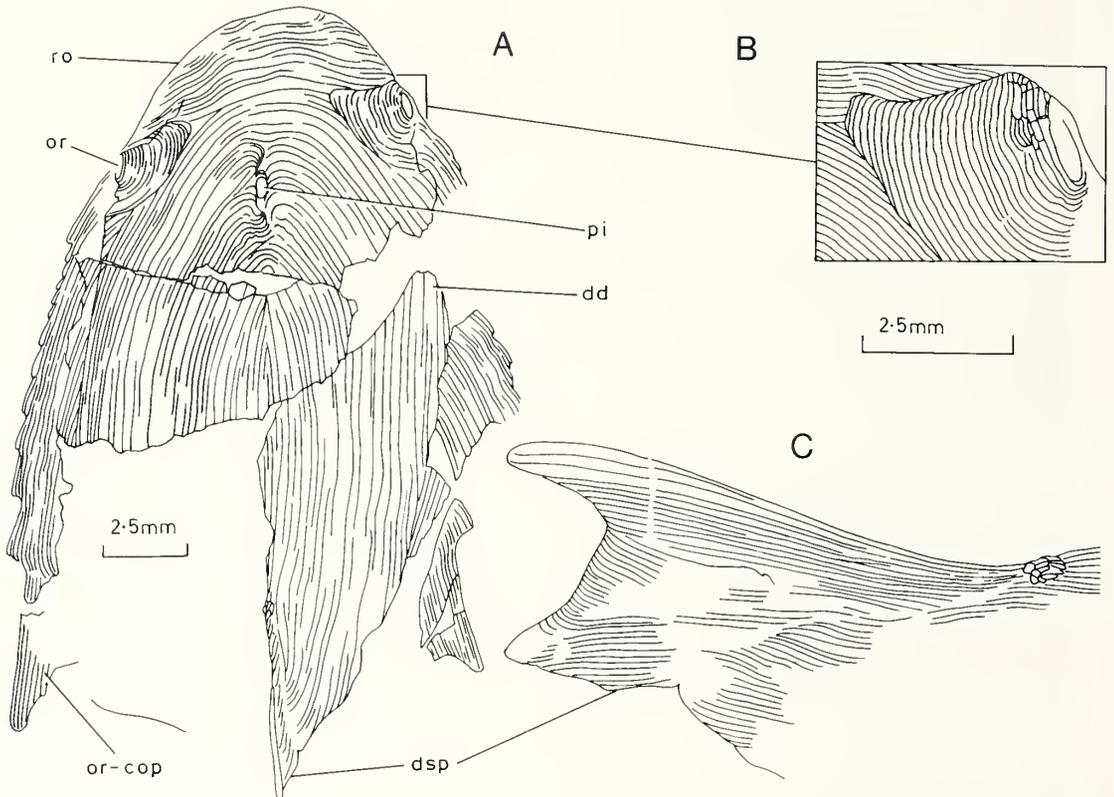
TEXT-FIG. 2. *Anchipteraspis crenulata* gen. et sp. nov. A, lateral view of dorsal shield, NMC 13853. B, dorsal sensory canal system, NMC 13855. Explanation of abbreviations for this and subsequent text-figs.: bro, branchial opening; brp, branchial plate; cep, central epitegum; cop, cornual plate; dd, dorsal disc; dsp, dorsal spine; gl, growth line; iol, interorbital canal; ldl, lateral dorsal canal; lep, lateral epitegum; lop, lateral oral plate; mdl, medial dorsal canal; mdr, median dorsal ridge; or, orbit; orp, orbital plate; or-cop, orbito-cornual plate; pa, pineal macula; pi, pineal plate; rep, rostral epitegum; ro, rostral plate; sol, supraorbital canal; sop, suborbital plate; tc, transverse commissure; vps, ventral pre-oral surface.

Type material. Holotype NMC 13823, dorsal shield; Plate 23, figs. 1, 2; from locality 3, lower member of the Peel Sound Formation, Prince of Wales Island.

Other material. NMC 13824–13832, 13834, dorsal shields; NMC 13833, ventral shield.

Diagnosis. Shield relatively slender (width ratio 0.63–0.71) with blunt almost transverse margin to rostrum. Dorsal spine slender and backswept. Small pineal plate. Straight lateral margin to cornual extension. Inter-orbital canal forming particularly deep narrow posteriorly directed loop on the dorsal disc. For dimensions see Table 1.

Localities. 1, 3, 5, 7.



TEXT-FIG. 3. *Ulutitaspis notidana* gen. et sp. nov. NMC 13823. A, dorsal view. B, detail of orbital area. C, dorsal spine in lateral view. For explanation of abbreviations see text-fig. 2.

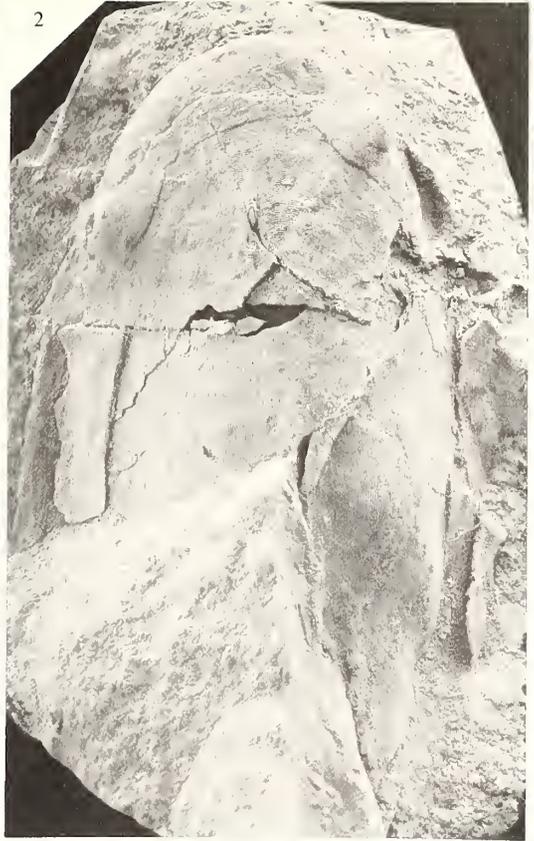
EXPLANATION OF PLATE 23

Fig. 1. *Ulutitaspis notidana* gen. et sp. nov. NMC 13823. Internal mould of dorsal shield showing impressions of internal organs, $\times 3$.

Fig. 2. *Ulutitaspis notidana* gen. et sp. nov. NMC 13823. Dorsal view, $\times 3$.

Fig. 3. *Ulutitaspis aquilonia* gen. et sp. nov. NMC 13844. Dorsal view showing growth lines, $\times 4$.

Fig. 4. *Ulutitaspis aquilonia* gen. et sp. nov. NMC 13840. Dorsal view, $\times 4$.



ELLIOTT, *Ulutitaspis*

Description. *U. notidana* has a gently arched dorsal shield and is narrower than the other members of the genus, having a width ratio of only 0.67 on average. The ornamentation is of crenate ridges but these are coarser than in *Anchipteraspis crenulata*, averaging 11/mm on the dorsal disc, and decreasing to 7/mm on the lateral margin of the orbito-cornual plate where they become broad and rounded and lose the lateral projections at the base.

The rostral plate is short and broad and bears transverse dentine ridges. Posteriorly the ridges are parallel to the plate margin, anteriorly they break up into short ridges and denticles which extend on to a ventral laminae formed by the downturning of the anterior and lateral edges of the rostrum. This laminae forms a deep pre-orbital lobe and a shallow median lobe. Ventrally the pre-oral surface is ornamented with transverse dentine ridges, it is up to 2 mm deep and bears a slight posterior median projection (Pl. 24, fig. 1).

The broad elliptical ridge pattern of the dorsal disc is interrupted anteriorly by the small pineal plate. Centrally the ridges run almost longitudinally, meeting at a slight angle over a low median crest, variably developed before the dorsal spine.

The dorsal spine is long and gently sloping, its posterior point reaching a height of 4 mm above the dorsal shield in the holotype. The spine is ornamented with longitudinal dentine ridges, coarse and broadly rounded on the dorsal edge, fine and serrate on the lateral margin where they meet those of the dorsal disc at a sharp angle. Anteriorly there is an area of short irregular ridges spreading from the dorsal disc and obscuring the margin with the dorsal spine.

The orbito-cornual plates have oblique ridges meeting those of the dorsal disc at a slight angle. As in the other members of the subfamily there is an area of disrupted ornamentation below the orbit, indicating that the process of orbital enclosure has not yet reached the final stage seen in the Pteraspidae. Above the orbits the plates are expanded to form medial projections indicating development towards the pineal plate. The lateral laminae of the plates have a serrated margin, the serrations increasing in size posteriorly and in the holotype reaching a final depth of 1.5 mm and length of 2.5 mm (Pl. 23, fig. 1; text-fig. 3A). At the level of the branchial opening the laminae narrow abruptly and in some specimens a break in ornamentation is present at this point. The cornual part of the plate has a straight lateral margin and a rounded point projecting past the posterior margin of the shield.

The branchial plate is known only from two partial specimens. In NMC 13826 the internal aspect of the opening can be seen, showing it to have an abrupt, vertical anterior margin and a chamber that is triangular in cross-section. The branchial plate is fused to the ventral surface of the orbito-cornual plate which also roofs the branchial opening.

The dorsal sensory canal system is well preserved in the holotype and in NMC 13830 (text-fig. 4). It follows the pattern normal for the subfamily, though the loop formed on the dorsal disc by the inter-orbital canal is very narrow and extends further back than in any other species. In the holotype the lateral longitudinal canals are well within the lateral margins of the dorsal disc. In NMC 13830 the lateral canals are close to the plate margins but the similar areal extent of the canal systems in the two specimens suggests that further growth has taken place in the holotype after enclosure of the canals.

The one ventral shield is an internal cast and shows nothing of the dentine ridge pattern or the canal system. The shield is gently arched and has a blunt anterior border with a slight median concavity and a strongly convex posterior border.

Remarks. *U. notidana* is separated from *U. truncata* and *U. aquilonia* by its larger size and more slender form. *Rhachiaspis pteriga* is similar in size but possesses broader orbito-cornual plates with smooth lateral margins, and a vertical dorsal spine. *A. crenulata* is smaller, lacks a serrated margin to the orbito-cornual plate, and has a more curved lateral margin to the cornual extension.

Ulutitaspis truncata gen. et sp. nov.

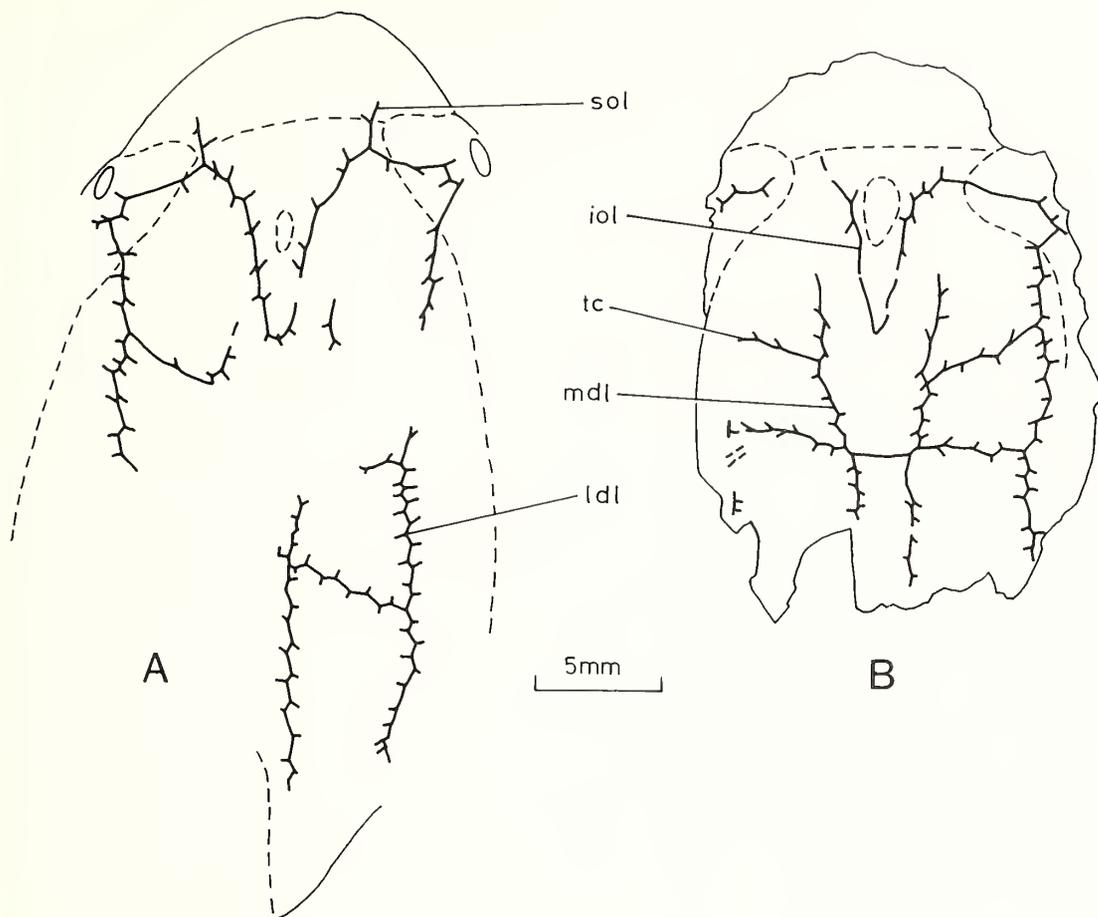
Plate 22, figs. 4–6; text-fig. 5

Name. Latin 'truncare' meaning to shorten, referring to the shortness of the dorsal shield.

Type material. Holotype NMC 13835, dorsal shield; Plate 22, fig. 4; from locality 2, lower member of the Peel Sound Formation, Prince of Wales Island.

Other material. NMC 13836–13839, dorsal shields.

Diagnosis. Dorsal shield small, strongly arched, and with a very high width ratio (0.93–0.97). Dentine ridges on rostrum curve round two centres on the anterior margin. Well-developed ventral pre-oral surface. For dimensions see Table 1.



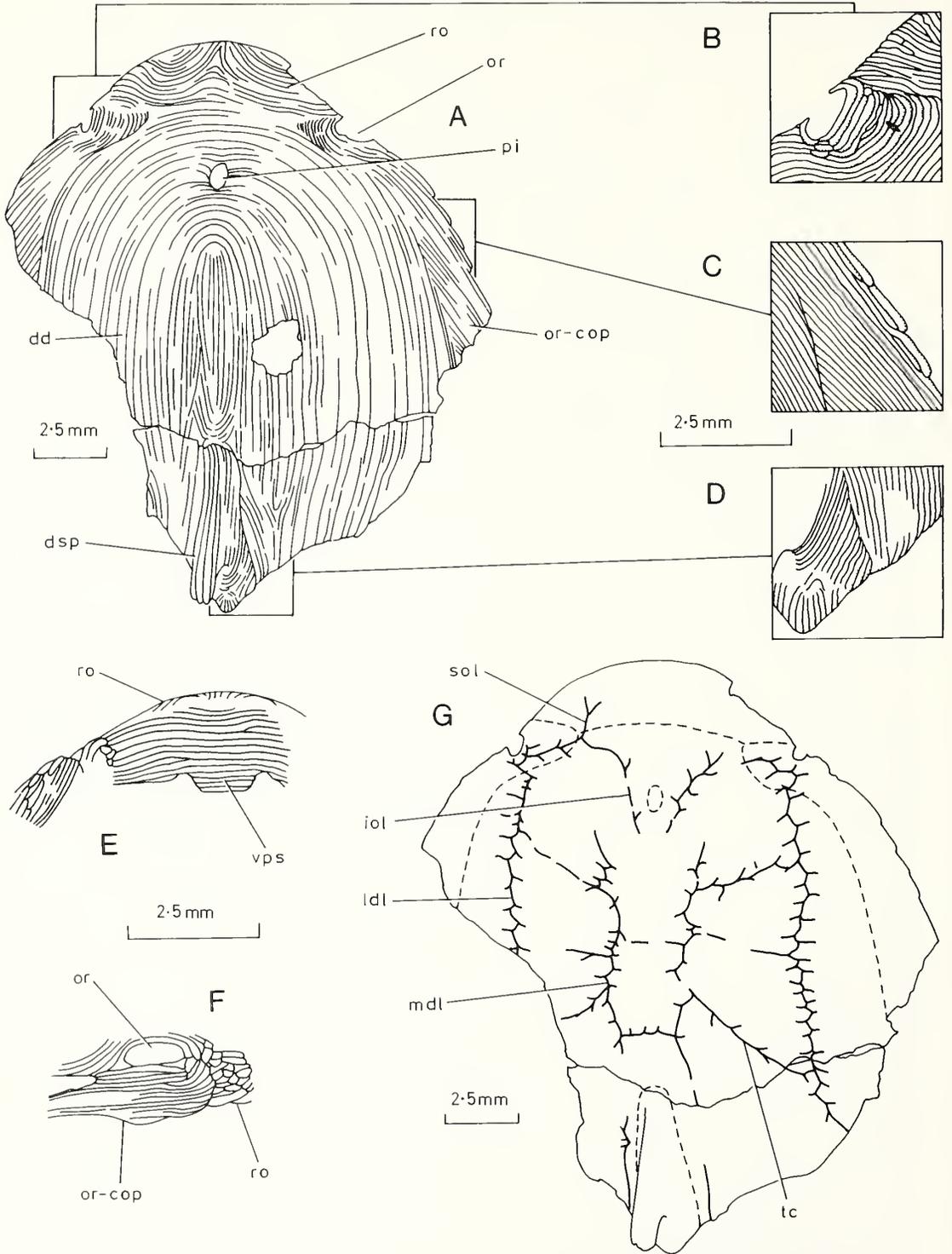
TEXT-FIG. 4. *Ulutitaspis notidana* gen. et sp. nov. Dorsal sensory canal system. A, NMC 13823. B, NMC 13830. For explanation of abbreviations see text-fig. 2.

Locality. 2.

Description. This is an extremely broad form with a width ratio greater than any other member of the Pteraspidae and rivalled only by *Ctenaspis* and *Listraspis* among the Cyathaspidae.

The broad rostrum has a rounded anterior margin and the dentine ridges curve around two anterolateral centres so that medially the ornamentation is longitudinal (Pl. 22, fig. 4; text-fig. 5A). The ridges coarsen in this area to 7/mm from 15/mm on the posterior margin of the plate, and also break up into short ridges and denticles running on to the ventral lamina. The ventral pre-oral surface is deeper and broader in this species than in the other members of the genus. In the holotype it is 2 mm deep and ornamented with transverse dentine ridges averaging 9/mm (Pl. 22, fig. 5; text-fig. 5E).

The dorsal spine is present in the holotype where it is slender and slopes back at a shallow angle, reaching 3 mm above the dorsal shield though the tip is broken. Laterally the ridges of the spine meet those of the dorsal disc at a sharp angle and a shallow sulcus is formed at the plate junction. Anteriorly the plate boundary is indistinct owing to the presence of an area of short irregular ridges. On the posterior point of the median process in the holotype two small scale-like areas are delineated by the ornamentation (text-fig. 5D). These probably indicate the presence of small scales absorbed into the posterior margin of the shield.



TEXT-FIG. 5. *Ulutispis truncata* gen. et sp. nov. A, dorsal view; B, C, D, details of orbit, orbito-cornual plate and dorsal spine; NMC 13835. E, ventral pre-oral surface; F, detail of orbit; NMC 13836. G, dorsal sensory canal system, NMC 13835. For explanation of abbreviations see text-fig. 2.

The orbito-cornual plates are similar to those found in the other members of the genus, differing only in their greater width. The posterior point is blunt and the outline of the cornual part of the plate is similar to that of *U. notidana*. In this species the ornamentation below the orbit is not broken into short lengths as is the case in the type species and in *Anchipteraspis crenulata*. This may indicate that in this species the process of orbital enclosure has been completed.

The branchial plate is generally similar to that of *A. crenulata* though there is no fused lateral plate on the anterior termination. The branchial opening is set well back under the cornual part of the orbito-cornual plate and is posteriorly directed.

The dorsal sensory canal system is similar to that found in the other members of the genus (text-fig. 5G). The only difference lies in the proportions, due to the shortness of the shield in *U. truncata*.

There are no specimens of the ventral shield.

Remarks. The presence of orbito-cornual plates with serrated lateral margins confine this species to the genus *Ulutitaspis*. It is distinguished from the other members of the genus by its small size, very high width ratio, and details of rostral ornamentation.

The change in ornamentation on the posterior point of the posterior median process in the holotype probably indicates the attachment of small scales, a feature that is not infrequently found on the posterior margin of dorsal shields in the Pteraspidae. It has been suggested by Denison (1960, 1964) that the dorsal spine in the Pteraspidae originated by this process. A large median dorsal scale becoming incorporated into the dorsal disc and subsequently developing to form a spine whilst maintaining its status as a separate plate. The Anchipteraspidinae provide no information to support this view, rather they indicate that the dorsal spine originated as an outgrowth of the dorsal shield that subsequently developed as a growth centre and became a separate plate.

Ulutitaspis aquilonia gen. et sp. nov.

Plate 23, figs. 3, 4; text-figs. 6, 7

Name. Latin 'aquilonaris' meaning north and referring to the area in which it was discovered.

Type material. Holotype NMC 13840; Plate 23, fig. 4; from locality 2, upper member of the Somerset Island Formation, Somerset Island.

Other material. NMC 13841–13844, dorsal shields.

Diagnosis. Dorsal shield oval in outline and gently arched, between 25.5 and 29.0 mm long and with a width ratio of 0.80 to 0.84. Rostrum short and rounded, posterior extension of the orbito-cornual plate long and curved. For dimensions see Table 1.

Locality. 8.

Description. The specimens of this species are generally poorly preserved. In the holotype (Pl. 23, fig. 4; text-fig. 6A) the posterior median process is missing and the length has been estimated with information from NMC 13844.

The rostrum is broad and rounded, with transverse ornamentation. There is a broad ventral pre-oral surface, ornamented with transverse dentine ridges and up to 2.5 mm deep in the centre where the posterior margin bears a low median lobe.

The pineal plate is larger than in the other members of the genus and in the holotype is ornamented with short longitudinal ridges. The longitudinal ornamentation in the midline of the dorsal disc breaks up into an area of short ridges in front of the dorsal spine, but in NMC 13844 (Pl. 23, fig. 3; text-fig. 7A) the dorsal disc is marked by growth lines, indicated by irregularities in ridge pattern. Two almost complete growth lines can be traced and the first of these shows an anterior notch for the pineal body. The later growth line curves round the margin of the pineal plate, however, and between the pineal plate and the notch in the first growth line is an area of short irregular ridges. This appears to show that the organism increased in size between the development of the two growth lines as the pineal organ clearly moved forward in that time. The dorsal spine is known from two specimens (NMC 13840 and 13844, text-fig. 7C) both incomplete. The shape, however, appears to be very similar to that in the other members of the genus.

The orbito-cornual plates are incomplete in the holotype but they are sufficiently well preserved to show the lateral serrations. The posterior termination to the plate is preserved in NMC 13841 (text-fig. 6C) which shows it to be a sharply pointed projection with a convex outer margin and straight inner margin. This contrasts with the shorter blunt terminations to the plate in *U. notidana* and *U. truncata*.

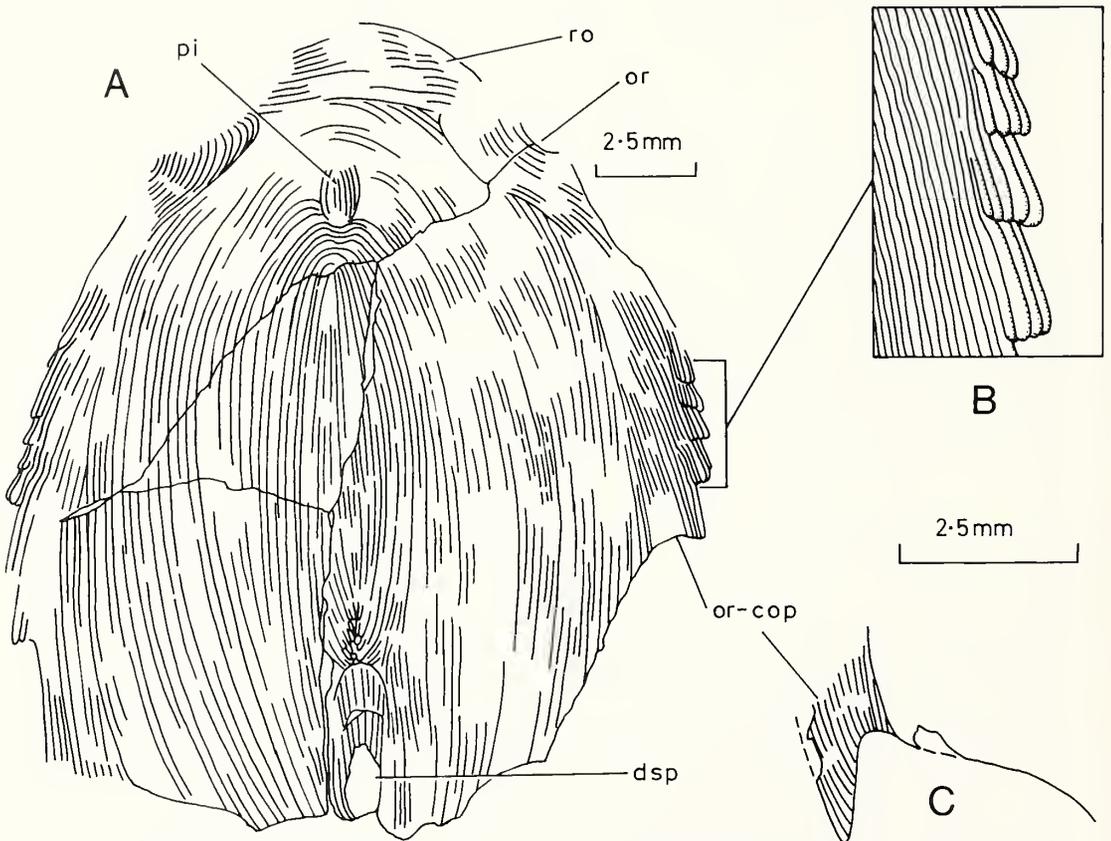
The branchial plate is known only in internal view (NMC 13841) and is relatively short with a large branchial opening.

The dorsal sensory canal system is essentially the same as that found in the other members of the genus (text-fig. 7A).

There are no specimens of the ventral shield.

Remarks. This species is separated from the others in the genus by the width ratio of the dorsal shield, which lies between that of the other two species, and by the slender, pointed posterior terminations to the orbito-cornual plates which differ from the short blunt terminations found in the other forms.

The evidence provided by the growth lines on the dorsal disc of NMC 13844 is of the greatest importance. These lines record the mode of growth of the shield and not only show that the dorsal disc was initiated at a median growth centre and developed by peripheral accretion but also that the animal continued growing during the early stages of this process. This is indicated by the fact that though the first growth line shows a notch for the pineal plate the final position of the plate is further forward showing an increase in size of the organism between the formation of the two growth lines.



TEXT-FIG. 6. *Ulutitaspis aquilonia* gen. et sp. nov. A, dorsal view; B, detail of lateral serrations; NMC 13840. C, posterior termination of left orbito-cornual plate, NMC 13841. For explanation of abbreviations see text-fig. 2.

This mode of growth of the shield is unlike that in the Cythaspidinae, in which growth of the animal had ceased when the shield started forming, and more like that found in the Pteraspida, where the plates were initiated at an early stage in the growth of the animal and remained separate, though increasing in size by peripheral accretion, until the adult stage was reached.

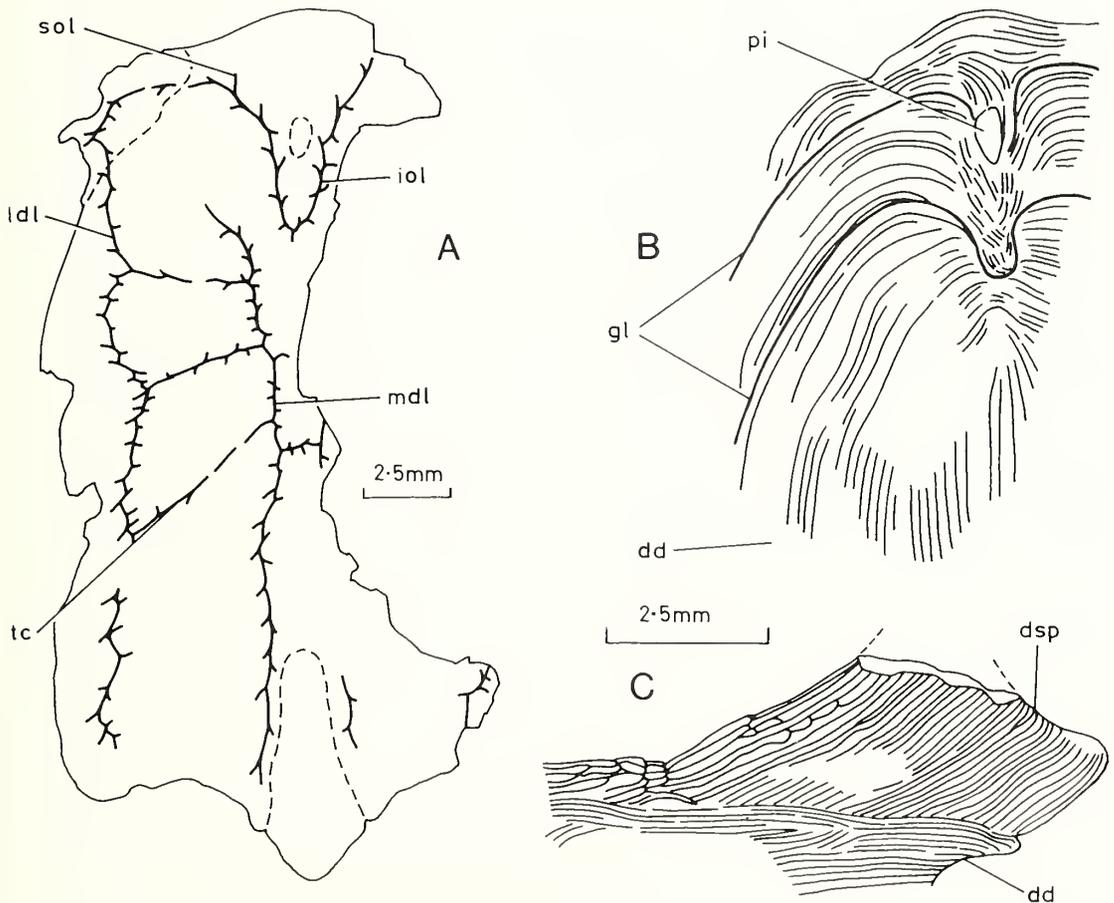
Ulutitaspis sp. indet.

Plate 24, fig. 2

Material. NMC 13846, dorsal shield.

Locality. 4.

Description. The dorsal shield is estimated to have been about 26 mm long and 17 mm wide. It is crushed and the posterior and left side are missing. The ornamentation is in all respects similar to that found in *Ulutitaspis* and the plate margins can be clearly seen. The anterior part of the orbito-cornual plate is present on the right side and the margin is serrated. The posterior part of the plate is missing, however, as is the dorsal spine. The bone is black and opaque and hence it is not possible to see any details of the dorsal sensory canal system.



TEXT-FIG. 7. *Ulutitaspis aquilonia* gen. et sp. nov. A, dorsal sensory canal system; B, detail of growth lines on dorsal shield; C, dorsal spine; NMC 13844. For explanation of abbreviations see text-fig. 2.

Remarks. This specimen shows enough of the features of the genus to be attributed to *Ulutitaspis*. It occurs at a locality within the stratigraphic range of *U. notidana* and most resembles that species, its width ratio of 0.65 and orbital width ratio of 0.38 falling within the size range for that form. It is very much smaller than any of the specimens of *U. notidana*, however, with a length of 26 mm and width of 17 mm compared with an average of 33.5 mm and 22.3 mm for *U. notidana*. As the specimen is incomplete no definite relationship can be determined and it is therefore referred merely to *Ulutitaspis* sp.

Genus *Rhachiaspis* gen. nov.

Type species. *R. pteriga* gen. et sp. nov.

Name. Greek 'rhachis' meaning backbone or ridge and 'aspis' meaning shield, referring to the prominent median dorsal ridge.

Diagnosis. Dorsal shield large and strongly vaulted, dorsal disc elongated and bearing a sharp median dorsal crest. Posterior margin deeply excavated between the median process and a pair of lateral processes. Spinal element waisted, the anterior part occupied by a spine with a vertical anterior margin, the posterior part with a median groove. Narrow ventral pre-oral surface with ornament of transverse dentine ridges. Orbito-cornual plates broad, upswept anteriorly and with broad curved cornual extensions.

Rhachiaspis pteriga gen. et sp. nov.

Plate 24, figs. 3-6; text-fig. 8

Name. Greek 'pteron' meaning wing and 'megas' meaning large, referring to the very broad orbito-cornual plates.

Type material. Holotype NMC 13851, dorsal shield; plate 24, figs. 4-6; from locality 7, lower member of Somerset Island Formation, Somerset Island.

Other material. NMC 13847, 13848, 13850, dorsal shields; NMC 13849, 13852, ventral shields.

Diagnosis. As for genus, the type being the only species. For dimensions see Table 1.

Localities. 6, 7, 9.

Description. The dorsal shield is large and broad with a short rostral plate. The ventral pre-oral surface forms a narrow band only 1 mm deep, ornamented with transverse dentine ridges and with a slight median lobe on the posterior margin.

The dorsal disc is elongated, rounded anteriorly, and almost parallel sided. It bears a conspicuous median crest extending from the centre of growth to the dorsal spine. In NMC 13847 this crest is extremely narrow and vertical and appears to merge with the dorsal spine, though in the holotype they are clearly separate. The posterior margin of the disc is very deeply excavated between the well-developed posterior median process and a pair of smaller posterolateral processes. The pineal plate is small and cannot be clearly seen in any specimen. In the holotype it interrupts the anterior ridge pattern of the dorsal disc and appears to be ornamented with short longitudinal ridges.

EXPLANATION OF PLATE 24

Fig. 1. *Ulutitaspis notidana* gen. et sp. nov. NMC 13828. Dorsal shield in internal view, $\times 2.5$.

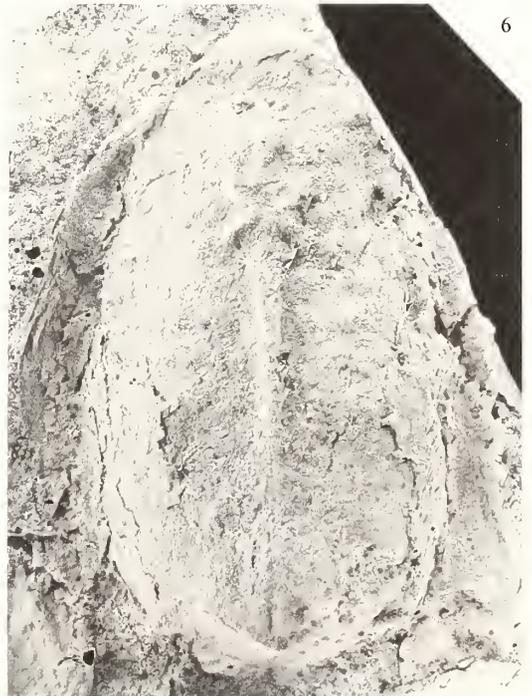
Fig. 2. *Ulutitaspis* sp. gen. nov. NMC 13846. Dorsal view, $\times 3$.

Fig. 3. *Rhachiaspis pteriga* gen. et sp. nov. NMC 13849. Ventral shield, $\times 3$.

Fig. 4. *Rhachiaspis pteriga* gen. et sp. nov. NMC 13851. Dorsal shield in lateral view, $\times 3$.

Fig. 5. *Rhachiaspis pteriga* gen. et sp. nov. NMC 13851. Dorsal view, $\times 3$.

Fig. 6. *Rhachiaspis pteriga* gen. et sp. nov. NMC 13851. Dorsal view of internal mould showing impressions of internal organs, $\times 3$.



The spine is characteristic in this genus. The base is divided into anterior and posterior parts by a median constriction, the anterior part bearing the dorsal spine which has an almost vertical leading edge and slopes posteriorly (Pl. 24, fig. 4). The spine is broken in the holotype and neither its total height nor the shape of its termination are known. Posteriorly the plate expands to the margin of the shield and in the holotype has a median sulcus ornamented with longitudinal ridges, separating a pair of lateral prominences ornamented with transverse ridges. This feature can only be seen in the holotype, where the surface detail is poor, but may indicate the presence of fused dorsal ridge scales.

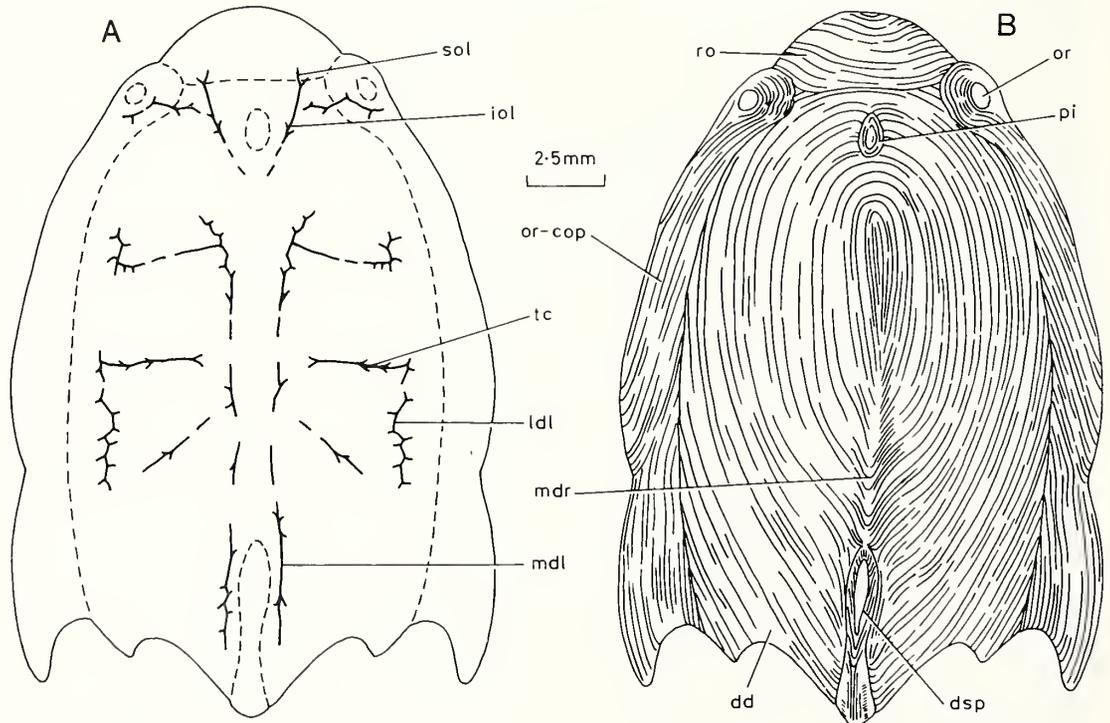
The orbits are prominent and laterally directed and there is no disruption of ornamentation below them. The lateral laminae of the orbito-cornual plates are very broad, and are very much upswept just behind the orbits. This feature can be seen in all the specimens and is not a distortion produced during preservation, it results in a concave dorsal surface to the plate anteriorly which fades away towards the middle of the plate.

The branchial plate is known only from internal casts and is similar to those found in other members of the subfamily.

The dorsal sensory canal system is not well preserved and it has been reconstructed (text-fig. 8A) based on NMC 13847 and 13851. It appears to show a pattern similar to that found in other members of the Anchipteraspinae, though it is not possible to see if a complete loop is formed by the inter-orbital canal, nor if the median dorsal canals terminate before meeting the inter-orbital canal.

Of the two ventral shields known NMC 13849 is the best preserved (Pl. 24, fig. 3), and shows the ventral dentine ridge pattern and sensory canal system. Its shape is very similar to that found in the Pteraspinae, with anteriorly a median depression, probably the site of attachment for sub-oral and oral plates, and posteriorly a slight median process. The generally elliptical ornament is interrupted anteromedially, the longitudinal median ridges meeting the transverse anterior ridges in an area of swirls and whorls.

The canal system is incomplete but appears to follow the pteraspidid pattern with an anterior median loop and paired lateral canals giving rise to a number of lateral transverse commissures.



TEXT-FIG. 8. *Rhachiaspis pteriga* gen. et sp. nov. A, dorsal sensory canal system (based on NMC 13847 and 13851). B, reconstruction of dorsal shield. For explanation of abbreviations see text-fig. 2.

Remarks. This distinctive form is separated from the other members of the Anchipteraspidinae by its large size, broad upswept orbito-cornual plates, and vertical dorsal spine.

The keel-like median dorsal ridge, merging with the vertical dorsal spine, and the broad orbito-cornual plates are probably developments to aid the stability of the animal in swimming, as are the greatly extended cornual plates and tall dorsal spines developed in some pteraspids. The upswept anterior to the orbito-cornual plates would also have helped to give uplift to the anterior part of the body by increasing the area of the anterior bearing surface. These developments suggest that *R. pteriga* was an active and capable swimmer.

The waisted shape of the spine base is unknown elsewhere in the Pteraspidae. The posterior part of the plate is unfortunately not clear in the only specimen that shows it; it may represent included dorsal ridge scales as are present in the type specimen of *Utuittaspis truncata*.

AGE OF THE FAUNA

The Somerset Island localities occur almost exclusively within the Somerset Island Formation. Localities at West Creswell Bay and Cape Anne have been dated as early Pridolian (Miall *et al.* 1978) based on conodont faunas including *Ozarkodina confluens* and *Pelekysgnathus* sp. The base of the formation becomes younger eastwards across northern Somerset Island (Jones and Dixon 1977) and in the north-east part of the island the underlying Read Bay Formation is Pridolian. A fauna including *O. confluens* has been reported from the Leopold Formation in this area (Loeffler and Jones 1976, 1977) in association with ostracodes and ostracoderms, and dated (Uyeno *in* Loeffler and Jones 1977) as late Ludlow or early Pridolian. Thorsteinsson (1980) considers that the basal beds of the Somerset Island Formation on Boothia Peninsula are latest Ludlovian in age, on the basis of the presence of *Pedavis* sp. aff. *P. thorsteinssoni* (Uyeno 1980). The cyathaspidid *Torpedaspis elongata* occurs with this conodont on Boothia Peninsula and also occurs in the lower part of the Somerset Island Formation in north-western Somerset Island indicating a similar age there.

A number of the vertebrates provide independent evidence of age. *Boothiaspis alata* occurs in both members of the Somerset Island Formation at Pressure Point and also in the lower member of the Peel Sound Formation at Transition Bay. It also occurs in the Devon Island Formation on Ellesmere Island where it is associated with a monograptid dated as Pridolian by Thorsteinsson on Cornwallis Island (Broad 1973). *Ariaspis ornata* is known from the lower member of the Somerset Island Formation at Pressure Point but it has also been reported from Beaver River (Denison 1963) and the Delorme Formation (Dineley and Loeffler 1976). Though originally assigned an early or middle Ludlovian age on the basis of associated invertebrates, the age could range from Wenlockian to Pridolian (Dineley and Loeffler 1976) as *Monograptus dubius* which occurs above the Beaver River fauna is now known to extend from the Llandoveryan to the Pridolian (Broad and Lenz 1972).

Hemicyclaspis murchisoni, which occurs in the upper member of the Somerset Island Formation at Pressure Point, is regarded as an index fossil for the lowest Downtonian of Britain (White 1950), now considered to be equivalent to the early Pridolian (Loeffler and Dineley 1976). It therefore appears that the whole of the Somerset Island Formation is latest Ludlovian or Pridolian in age.

On Prince of Wales Island only the Transition Bay localities can be dated and correlated with those on Somerset Island. Invertebrate dating of the sequence through the lower member of the Peel Sound Formation has yielded upper Silurian ages (Bolton and Copeland *in* Broad and Dineley 1973; Bolton, pers. comm. 1976) for the whole of the sequence. Thorsteinsson (1980) concludes that the age range of the lower member of the Peel Sound Formation on Prince of Wales Island is late Ludlovian to early Pridolian, based mainly on the presence of *Hemiarges bigener* towards the top of the lower member. This trilobite is found at widely separated localities within the arctic archipelago, but wherever it can be related to diagnostic fossils it appears to be confined to beds of Pridolian age (Thorsteinsson 1980). Miall *et al.* (1978) consider the lower member of the Peel Sound Formation on Prince of Wales Island to be equivalent in age to the Somerset Island Formation though the rock types differ.

GROWTH AND DEVELOPMENT OF THE DERMAL SHIELD

The lack of a universally agreed interpretation of the mode of growth of the heterostracan shield has resulted in the development of many divergent views on the evolution of the order. The Anchipteraspidae show several features that are of value in illustrating the growth of the heterostracan shield and the evolutionary relationships between the heterostracan families. They show superficial similarity to both the Cyathaspididae and the Pteraspidae; however, both these groups have been shown to possess dissimilar modes of growth.

Growth of the Cyathaspididae. The cyathaspidid dorsal shield is divided into rostral, lateral, and central areas termed 'epitega' (Stensiö 1958), delineated by dermal ridge patterns and originally thought to be merely superficial divisions (Kiaer 1932; White 1935). The view that in some genera at least the epitega were distinct plates (Kiaer and Heintz 1935; Moy-Thomas 1939; Obruchev 1945; Stensiö 1958) was supported by Denison (1964), who showed that the superficial layers developed first, possibly in separate epitegal units, and that the subsequent formation of the deeper layers may have occurred as one unit. It has now been demonstrated (Dineley and Loeffler 1976) that in some cyathaspidids the superficial layer not only grew independently in the epitegal areas but that growth took place incrementally. In *Pionaspis amplissima* (text-fig. 9A) successive growth lines indicate that formation of the shield did not start until the individual reached full size, and then continued by peripheral accretion from centres within each epitegum until the edges met and fused.

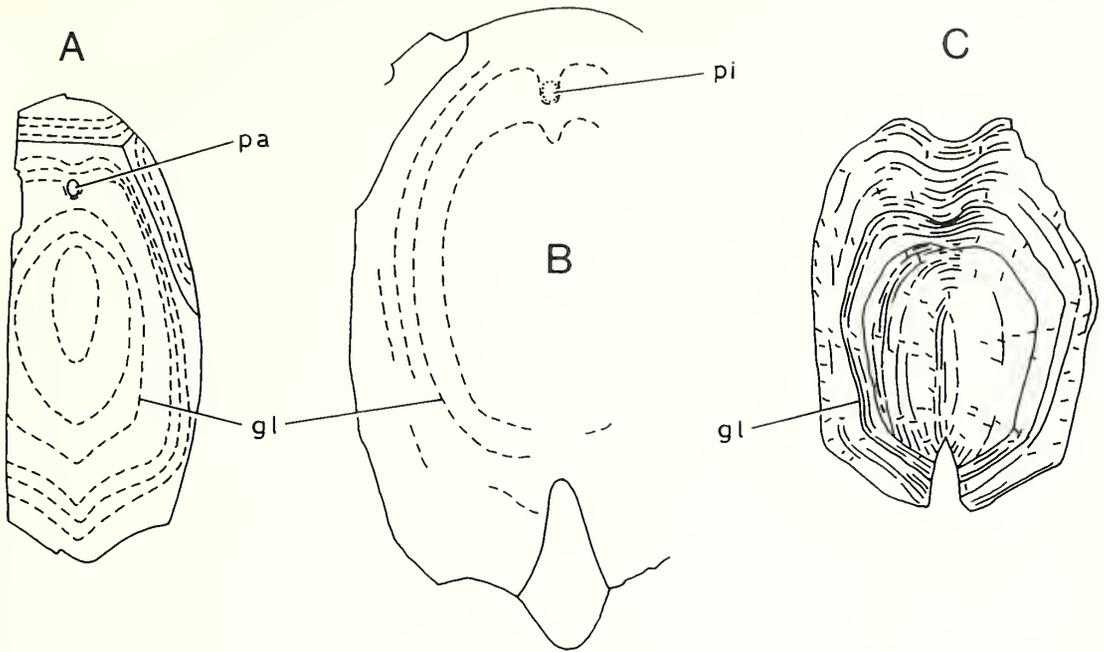
Growth in the Pteraspidae. Though it was originally thought (Zych 1931; White 1935) that development of the pteraspidid shield was not initiated until the individual had reached almost full size, as in the cyathaspidids, study of growth stages (Heintz 1938; White 1958) has demonstrated that after an early unarmoured stage the plates developed separately though remaining in contact peripherally (text-fig. 9C). Growth of the shield appears to have been initiated at a total length of about 23 mm (Denison 1973; White 1973), and ultimate fusion of the plates was delayed for a progressively longer period of time as the family evolved (White 1958). Evidence from thin sections shows that, as in the cyathaspidids, growth of the superficial layer preceded that of the cancellous and basal layers (Denison 1973; White 1973).

Growth in the Anchipteraspidae. In the Anchipteraspidae growth lines are visible on a number of specimens but only on one are they complete enough to throw any light on the process of growth in the subfamily. A specimen of *Ulutitaspis aquilonia* (NMC 13844, Pl. 23, fig. 3; text-fig. 9B) shows a series of growth lines on the dorsal shield, the first of which has a clear anterior notch for the pineal body (text-fig. 7B). The pineal body is further forward, however, and a further growth line curves round it indicating that the animal continued growing after the initiation of shield formation. The second growth line appears to mark the stage at which growth of the animal ceased; however, it is still inside the lateral dorsal canals and indicates that they had not been invested by the shield at this point.

From this evidence it appears that the Anchipteraspidae had developed the ability to continue growth once the shield had started to form but that the ability was still limited, comparable to the stage reached in the primitive pteraspidid *Protopteraspis* in which the shield fused shortly after investing the lateral dorsal canals of the sensory canal system.

EVOLUTIONARY RELATIONSHIPS OF THE PTERASPIDIDAE

Various authors have derived the Pteraspidae from a number of different heterostracan families. Tarlo (1962, 1967), Obruchev (1967), and Halstead (1973) agreed in deriving the Pteraspidae from the Traquairaspididae, a view followed by Broad (1971) and more recently by Dineley and Loeffler (1976). Stensiö (1958) believed that the ancestors of the Pteraspidae were forms like the psammosteids in which belts of smaller scales separate the larger plates. Obruchev (1945) believed that the Pteraspidae evolved from the Cyathaspididae and Denison (1964, 1973) followed this view.



TEXT-FIG. 9. Growth stages in heterostracan dorsal shields. A, *Pionaspis amplissima* (from Dineley and Loeffler 1976). B, *Ulutitaspis aquilonia*, NMC 13844. C, *Belgicaspis crouchi* (from White 1973). For explanation of abbreviations see text-fig. 2.

The discovery of the subfamily Anchipteraspidae provides new and stronger evidence in favour of the development of the Pteraspidae from the Cyathaspidae. Evidence from the arrangement of plates in the dorsal shield shows that evolutionary development was not totally by a process of fusion or of subdivision of dermal elements but by a combination of the two processes, thus supporting the views of Denison (1964) and Westoll (1967).

Denison (1964, pp. 465-466) set out the arguments in favour of the derivation of the Pteraspidae from the Cyathaspidae and this plan was also followed by Broad (1971) and Dineley and Loeffler (1976) in their argument for a derivation from the Traquairaspidae. I have used the same headings in the following assessment of the contribution of the Anchipteraspidae towards a solution of the problem.

1. The known geological record of the two groups was cited as favouring the derivation of the Pteraspidae from the Cyathaspidae by Denison (1964); however, Dineley and Loeffler (1976) showed that this was equally true for a derivation from the Traquairaspidae which range from the Wenlockian to the early Dittonian. Recent work on *Protopteraspis* from the Canadian arctic (Elliott and Dineley 1983) suggests that they are Pridolian in age in this area which may therefore be an evolutionary centre for the genus. In many localities they are preceded in the same stratigraphic sections by members of the Anchipteraspidae. The cyathaspid *Listraspis canadensis* which shows most similarity to the Anchipteraspidae and is probably the most closely related form is known only from British Columbia. It was dated as late Downtonian by Denison (1964); however, this date has been questioned by Dineley and Loeffler (1976) who do not feel so precise an estimate can be gained given the present level of knowledge on the cyathaspids and traquairaspids on which it is based.

2. Denison viewed the epitega, branchial plates, and ventral shield of the Cyathaspidae as comparable to the plates of the pteraspid shield; however, Dineley and Loeffler (1976) considered

that these were more closely comparable to plates in the traquairaspidid head shield. The Anchipteraspidinae appear to occupy an intermediate position in which the plates can be directly compared with those found in both the Cyathaspididae and the Pteraspididae.

In cyathaspidids the branchial plate is usually flat, elongated, and notched on the dorsal margin to form the branchial opening. It is also generally separate, though in *Listraspis* it is fused to the dorsal shield and in the Ctenaspidinae it has also been incorporated into the dorsal shield. The branchial plate of pteraspidids is fused to the dorsal shield, and even in the earliest representatives is enfolded to form a branchial duct. Though in the Anchipteraspidinae the plate is normally flat and fused to the dorsal shield, in *U. truncata* a branchial duct is formed by the partial enfolding of the branchial plate. This plate would require little change to form a branchial plate of pteraspidid type.

The orbito-cornual plates of the Anchipteraspidinae can also be directly compared with the separate orbital and cornual plates of the Pteraspididae and the orbital and lateral epitega of the Cyathaspididae. In the Anchipteraspidinae the plate is clearly demarcated into an orbital and a cornual part by an abrupt narrowing, and in the holotype of *Anchipteraspis crenulata* the ornamentation of the plate is disrupted at this point, possibly indicating the incipient development of separate plates. Denison (1964) has suggested that the cornual plates of pteraspidids were derived from a pair of scales attached to the posterolateral corners of the dorsal shield, a view apparently supported by the scale-like posterior cornual plates present in juvenile specimens of *Lampraspis tuberculata* (Denison 1973). However, the earliest members of the Pteraspidinae, the genus *Protopteraspis*, have in all cases well-developed cornual plates, and on functional grounds it also seems more likely that an outgrowth of the dorsal shield, initially developed as a control surface, would be retained and developed into separate plates. Such outgrowths have developed independently in the Cyathaspididae, *Listraspis* and *Ctenaspis* showing well-developed lateral laminae, and have been reported in the Traquairaspididae (Broad 1971).

Enclosed orbits are not a normal feature in the Cyathaspididae though they are present in the Ctenaspidinae and in *Listraspis*, a feature explained by Denison (1964) as being the result of fusion of a suborbital plate. Such plates have been described in articulated cyathaspidids by Kiaer (1932) and Dineley and Loeffler (1976). In *A. crenulata* disruption of the ornamentation below the orbit may be due to the incorporation of a suborbital plate or to the growth of the orbital plate down and around the orbit.

The pineal area in the advanced Cyathaspidinae probably remained naked longer than adjacent areas of the shield (Dineley and Loeffler 1976), thus the pineal plate of pteraspidids could have developed as a new centre of ossification in the postrostral field of cyathaspidids. *Listraspis* has a large pineal prominence and the members of the Anchipteraspidinae also have large pineal areas covered by separate plates.

The dorsal spine is a separate element in the Pteraspidinae and its development has been attributed (White 1935; Denison 1960, 1964) to the attachment of a dorsal ridge scale to the posterior margin of the dorsal disc and its gradual incorporation into the disc. The particularly scale-like dorsal spines of *Pteraspis rostrata* (White 1935) and *P. carmani* (Denison 1960) have been cited as evidence to support this view. Scale-like dorsal spines seem, however, to have been developed for functional reasons in flat-bodied forms, particularly protaspids, which may have been bottom dwellers and as such may not have required strongly functional keels. For this reason scale-like dorsal spines are seen as a later development in the Pteraspidinae, a view supported by the fact that the early members of the subfamily possess well-developed dorsal spines as do the Anchipteraspidinae.

In the Cyathaspididae a scale-like dorsal spine has been identified in *Ariaspis* (Denison 1964; Dineley and Loeffler 1976). In the specimen illustrated by Dineley and Loeffler the scale is less obviously demarcated from the rest of the shield and appears to be part of a band of scale-like elements forming the posterior margin of the dorsal shield. A similar band is present in a specimen of *Archegonaspis* cf. *A. schmidtii* illustrated by Loeffler and Jones (1976). If these elements are scales they appear to have been totally incorporated into the shield and there is no evidence to suggest that they would retain their identity within the shield to the extent of developing as separate plates.

The crest on the central epitegum in *Cyathaspis* has been described as a real dorsal spine

comparable with that of *Pteraspis* (Kiaer 1932). Similar crests are developed in *Ctenaspis* and *Listraspis* among the cyathaspidids, and erect dorsal spines are also present in two traquairaspidids described by Broad (1971). In none of these forms is there any indication that the spine was anything more than a development of the dorsal disc.

In the Anchipteraspidinae the dorsal spine is a discrete element, separated from the dorsal disc. In several specimens the anterior margin is obscured by the development of short, irregular ridges which may indicate that the process of total separation of the spine was not yet complete. This suggests that the first stage in the development of the pteraspimid dorsal spine was not the attachment of a scale to the posterior margin of the dorsal shield but the development of a posterior median crest, an adaptation of functional value to the animal. Once the crest had developed it would have separated to form a discrete element by the development of a new centre of growth and as part of the process of separate development of the epitegal areas taking place in the Cyathaspidinae at this time (Dineley and Loeffler 1976, pp. 104–107).

3. The microstructure of the shield of the Anchipteraspidinae is too poorly preserved to shed any light on the closeness of its relationship to the Cyathaspidinae and Pteraspidae.

4. The lateral line canal system of Pteraspidae is easily derivable by minor modification of the simple pattern of cyathaspidids (Denison 1964, p. 465), though Broad (1971) and Dineley and Loeffler (1976) have suggested that this is more easily derived from that of certain traquairaspidids. In the Anchipteraspidinae the system is similar in all respects to that found in *Protopteraspis*; however, in *Anchipteraspis crenulata* the system still displays a rectangular appearance strongly reminiscent of the cyathaspidid type, normally an almost diagrammatically simple combination of longitudinal canals and transverse commissures. However, Kiaer and Heintz (1935) have noted an evolutionary trend towards a more regular and complete dorsal pattern in *Poraspis*. The anchipteraspidinid-pteraspidinid type of canal system could be developed from the basic cyathaspidid system by a process of fusion, and just such a system is found in *Ctenaspis*, a specialized cyathaspidid thought (Denison 1964) to have been derived from the Cyathaspidinae. In fact the resemblance is strong enough to have led Kiaer (1930) to suggest that the pteraspids were derived from *Ctenaspis*.

5. The dentine ridges of pteraspids are typically narrow crested and crenulate. This type of ridge is also found in *Listraspis* and is characteristic of the Anchipteraspidinae. It is not considered that the traquairaspidid type of ornament could easily give rise to the pteraspimid ridge as suggested by Broad (1971).

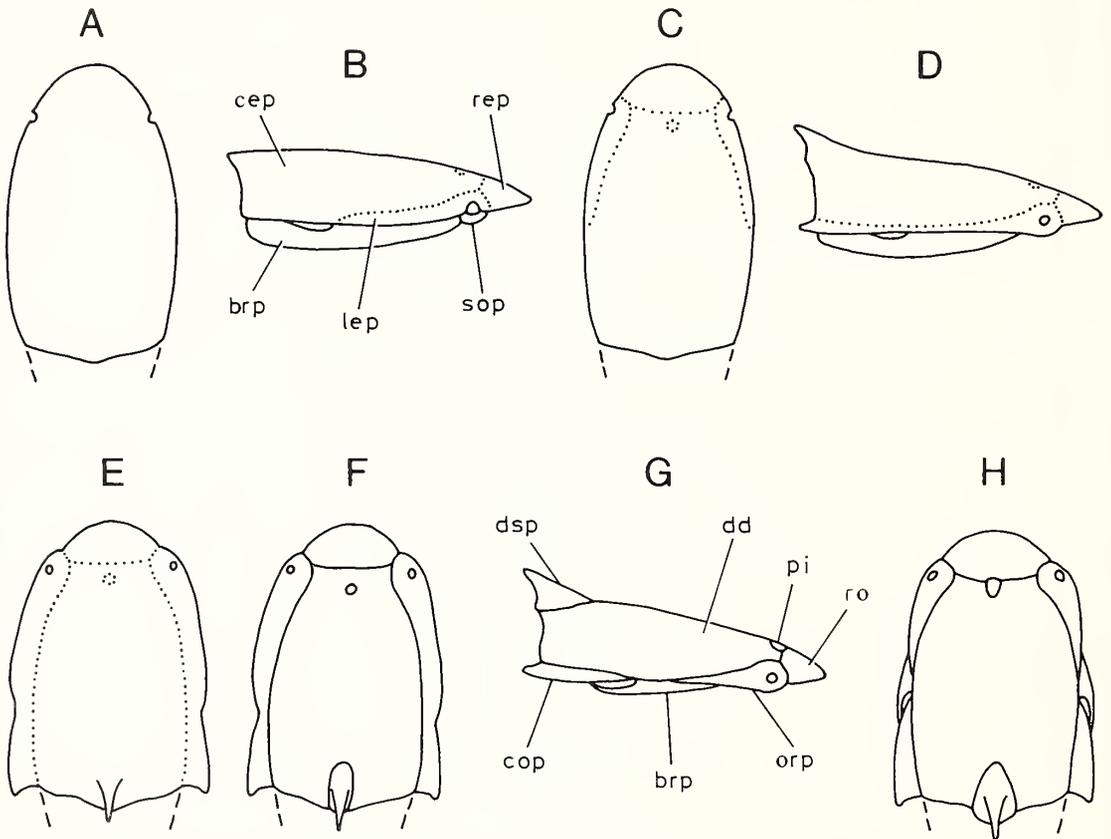
6. The narrow ornamented pre-oral surface typical of *Protopteraspis* is found in a primitive condition in the maxillary brim of *Listraspis* (Denison 1964) and other cyathaspidids. The Anchipteraspidinae also show this feature, *A. crenulata* bears only a narrow ornamented area but in *U. truncata* it is well developed. No feature of this type has been reported in the Traquairaspididae.

Interpretations of the relationships of the most well-known heterostracan groups, the Pteraspidae, Cyathaspididae, Psammosteida, and Traquairaspididae, has been dependent to a very great extent on views on the way in which the dermal shield developed. The Lepidomorial Theory of Ørvig (1951) though originally based on the development of elasmobranch scales was applied by Stensiö (1958) to growth in the Heterostraci and provided support for the evolutionary development of the shield by a process of fusion. This view was embodied in the evolutionary scheme of Halstead (1973), which begins with the fully tessellated *Eriptychius* and *Tesseraspis* and leads to two major groupings of heterostracans which progress from partially tessellate to non-tessellate forms. One group passes through the partially tessellated *Kallostrakon*, *Corvaspis*, and *Cardipeltis* to produce the non-tessellated Cyathaspididae and Amphiaspididae; the other progresses via *Weigeltaspis*, the Psammosteida, and the Traquairaspididae to produce the non-tessellate Pteraspidae. However, as noted by Janvier (1981), the recent discoveries of lower Ordovician remains (Ritchie and Gilbert-Tomlinson 1977), showing no indication of tesserae, make this scheme less than satisfactory, and the independent derivation of the Pteraspidae and Cyathaspididae is unlikely as the shape and distribution of the dermal plates in both groups is similar.

Halstead (1973) considers the psammosteids to be ancestral to the pteraspids; however, there is much stronger evidence to suggest that the reverse is true (Obruchev 1947, 1967; Westoll 1967). The

main plates of the early psammosteids are homologous with those of pteraspids, though an additional postorbital plate is present and the large plates are separated by a scale mosaic. This latter innovation may demonstrate a further advantage in growth, permitting a longer growth period in this family. Young stages of early forms such as *Drepanaspis* are very pteraspid in appearance (Gross 1963) and show most similarity to the dorsoventrally depressed early Devonian pteraspids such as *Protaspis* in which the cornuals are small and the branchial plates are large and have posterior branchial openings (Miles 1971). It was probably from among these forms that the drepanaspids were evolved.

It seems that more complex processes than simple fusion or subdivision may have been at work in the development of the shield (Obruchev 1943; Denison 1964; Westoll 1967) and evolutionary advancement within the Heterostraci should not be gauged automatically by the degree to which fusion of the shield has progressed.



TEXT-FIG. 10. Stages in the development of the heterostracan dorsal shield from the Cyathaspidae to the Pteraspidae. A, cyathaspid with undivided dorsal shield and separate branchial plate. B, C, cyathaspid with dorsal shield divided into epitega. D, E, cyathaspid in which the lateral epitega are developed to form laminae, the orbit is enclosed, the branchial plate fused, and the dorsal spine developed as an outgrowth of the dorsal disc. F, anchipteraspid in which separate growth centres initiated in pinal and dorsal spine areas, and development of shield occurs before maturity. G, H, pteraspid in which peripheral growth of plates continues through ontogeny. For explanation of abbreviations see text-fig. 2.

CONCLUSIONS

It is proposed here that the Pteraspidae evolved from the Cyathaspididae during the Pridolian via the new subfamily Anchipteraspididae. This may have been a rapidly occurring event in a restricted area as there have been no other reports of forms attributable to the Anchipteraspididae though *Protopteraspis*, the earliest pteraspidid, has a wide distribution (Blicek 1981; Elliott and Dineley 1983).

The processes taking place in the dorsal shield are initially the development of rostral, dorsal, and lateral epitega in a cyathaspidid (text-fig. 10A-C). Growth would be initiated at maturity from separate growth centres in the epitega and fuse peripherally on contact, though the branchial plate would remain separate. *Pionaspis* is an example of this stage (Dineley and Loeffler 1976). Subsequently the lateral epitega would be developed to form lateral laminae and the orbit would be enclosed by the fusion of a sub-orbital plate (text-fig. 10D, E). The dorsal spine would be developed as an extension of the dorsal disc and fusion of the branchial plate would take place; however, growth of the shield would still be initiated at maturity. *L. canadensis* is an example of this stage (Denison 1964). The next stage is that reached in the Anchipteraspididae and requires merely the initiation of growth centres in the pineal area and at the dorsal spine, and the initiation of shield development before maturity to allow limited growth before the final fusion (text-fig. 10F). The final stage, embodied in *Protopteraspis*, requires shield growth to be initiated early allowing separate development of the plates by peripheral growth through ontogeny with fusion occurring at maturity (text-fig. 10G, H).

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THE LOWER JAW OF *SUNOSUCHUS THAILANDICUS*, A MESOSUCHIAN CROCODYLIAN FROM THE JURASSIC OF THAILAND

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ABSTRACT. A nearly complete lower jaw is described of the longirostrine mesosuchian crocodylian *Sunosuchus thailandicus* Buffetaut and Ingavat (1980), from the Phu Kradung Formation (early Jurassic) of north-eastern Thailand, and the affinities of the genus are discussed. The jaw is large and robust, with a long symphysis, and each dentary contains about thirty teeth. Despite the unusually elongated mandibular symphysis the genus is referred to the Goniopholididae rather than to the Pholidosauridae, on the basis of the skull characters present in the Chinese species *S. miaoi* Young (1948). *Sunosuchus*, however, is in some respects morphologically intermediate between the Goniopholididae and the Pholidosauridae.

IN 1979 the posterior part of the right ramus of the lower jaw of a large crocodylian was collected from the Jurassic Phu Kradung Formation by Mr. Nares Sattayarak (Department of Mineral Resources, Bangkok), near the town of Nong Bua Lam Phu in north-eastern Thailand. The specimen was subsequently described by us (Buffetaut and Ingavat 1980) and referred to a new species of the genus *Sunosuchus* Young 1948, *S. thailandicus*. In November 1980 a Thai-French party visited the locality under the guidance of Mr. Sattayarak, and could excavate most of the remaining parts of the mandible of the same individual. The purpose of this paper is to describe the lower jaw of *S. thailandicus* on the basis of the nearly complete specimen now available, and to discuss the affinities of *Sunosuchus* more fully than was possible in 1980.

GEOLOGICAL SETTING

The specimen was found in a road-cut at km 80+800 on the highway between Udon Thani and Nong Bua Lam Phu. It was embedded in a reddish claystone containing calcareous nodules which give it a conglomeratic appearance, belonging to the Phu Kradung Formation. The Phu Kradung Formation belongs to the lower part of the Khorat Group (see Ramingwong 1978, for a review of the Khorat Group). Although it was first considered to be largely Triassic (Ward and Bunnag 1964), the Phu Kradung Formation is now usually referred to the early Jurassic (Hahn 1982), which is in accordance with recent magnetostratigraphic data (Bunopas 1981; Maranate 1982). Recent discoveries of land vertebrates in the Khorat Group (Buffetaut 1982*a*) have allowed a better dating of its formations, and these biostratigraphic data are in agreement with an early Jurassic age for the Phu Kradung Formation (Buffetaut and Ingavat, in press), although very few vertebrate fossils have been found in this formation itself. The best specimen discovered so far is the crocodylian jaw described in this paper, and it does not provide accurate biostratigraphic information (except that it has to be younger than the Triassic). At the moment, it is still impossible to refer the Phu Kradung Formation to any definite stage of the early Jurassic.

The Khorat Group, which occupies a vast area of north-eastern Thailand, is interpreted as an essentially freshwater molasse deposit resulting from the erosion of mountains created by the collision of the Thai-Chan, Indochina, and South China blocks (Indosinian orogeny) sometime in the middle or late Triassic (Bunopas 1981). The Phu Kradung Formation, which contains

non-marine bivalves, is supposed to have been deposited in a fluvio-lacustrine environment (Hahn 1982). Teeth from this formation which have been referred to marine reptiles (Kobayashi *et al.* 1963; Ward and Bunnag 1964) in all likelihood actually belong to crocodylians (Buffetaut and Ingavat 1980), and cannot be used as evidence of marine influences.

PRESERVATION OF THE SPECIMEN

The lower jaw of *S. thailandicus* from Nong Bua Lam Phu is kept in the collections of the Department of Mineral Resources, Bangkok, under no. TF 1370. When found, the specimen was already broken within the sediment, and had been further damaged by roots, especially in its posterior parts. The dentaries were separated along the symphyseal suture. Many teeth are missing, and their alveoli are filled with matrix; in some of them the tips of replacement teeth are visible. All the erupted teeth still preserved in their alveoli are broken; a number of tooth fragments were found in the sediment around the jaw, but only a few could be fitted back to it. The edges of the alveolar openings are often poorly preserved, so that in some parts of the dentaries it is difficult to count the alveoli. The left ramus of the mandible is broken at the level of the most posterior teeth, and roots have damaged this region, which is now difficult to reconstruct. On the right side, a section comprising the back part of the symphysis (posterior to the seventeenth tooth) and the anterior part of the ramus could not be found (see Pl. 25) despite a thorough search of the outcrop, which also failed to reveal any other skeletal elements of this crocodylian.

DESCRIPTION

The mandibular symphysis is long, reaching the level of the twenty-fifth tooth, and represents about 42% of the total length of the lower jaw, but it is also robust and relatively wide, with an anterior spoon-shaped expansion followed by a constriction (Pl. 25, figs. 1, 2). More posteriorly, the sides of the symphysis diverge only slightly towards the rear. In lateral view (Pl. 25, fig. 3) the toothed part of the jaw is seen to be slightly curved, its dorsal side being concave and its ventral side convex. Posterior to the symphysis, the mandibular rami diverge gradually. The medial side of the left ramus makes an angle of 30° with the longitudinal axis of the symphysis. The *fenestra mandibularis externa* is elongated and both its ends are pointed.

Measurements

Total length of lower jaw (as reconstructed)	1140 mm
Length of symphysis (dorsally)	475 mm
Maximum height of symphysis (at the level of the twenty-second tooth)	56 mm
Maximum width of left dentary (at the level of the fourth tooth)	80 mm
Length of splenial symphysis	170 mm

Dentary. The dentaries are elongated and joined together at the symphysis for a considerable part of their length. Twenty-eight alveoli are visible on the left dentary, the posterior part of which is damaged, and it is likely that there were actually thirty teeth in each dentary. Anteriorly, the dentaries are widened to form the above-mentioned spoon-shaped expansion, the dorsal surface of which is slightly concave transversally and convex longitudinally. The maximum width of the symphysis is at the level of the fourth alveoli, the edges of which are projecting laterally. Posterior to the expansion, the jaw becomes narrower up

EXPLANATION OF PLATE 25

Figs. 1-5. Lower jaw of *Sunosuchus thailandicus* Buffetaut and Ingavat 1980, from the early Jurassic Phu Kradung Formation near Nong Bua Lam Phu, north-eastern Thailand, Collection of the Department of Mineral Resources, Bangkok, no. TF 1370 (holotype). 1, dorsal view. 2, ventral view of symphysis and left ramus. 3, left lateral view. 4, lateral view of anterior part of right dentary. 5, medial view of anterior part of left dentary. All figs. $\times \frac{1}{6}$. Photographs by C. Abrial.



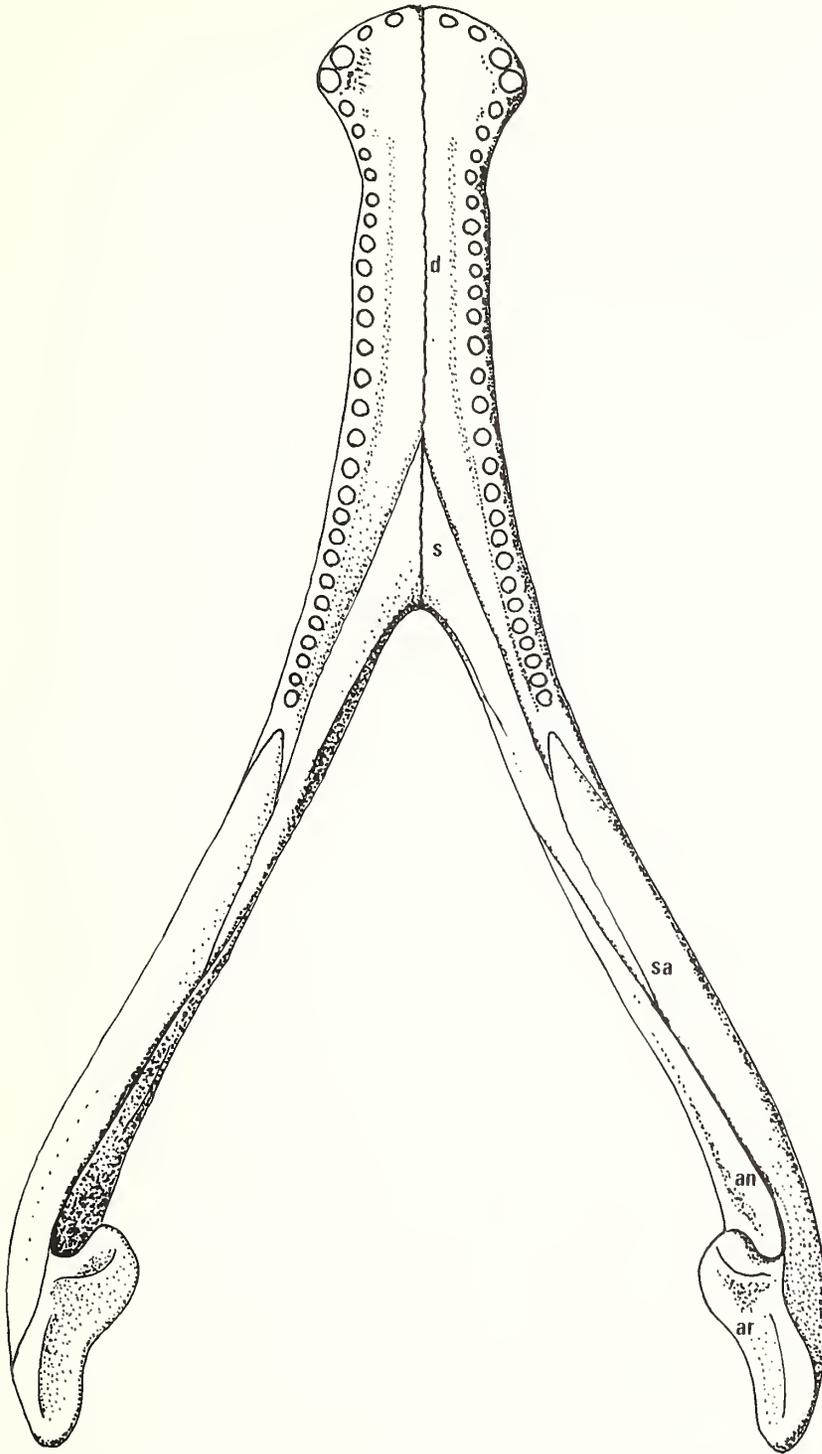
BUFFETAUT and INGAVAT, *Sunosuchus*

to the level of the seventh tooth, the symphysis being narrowest at the level of the interval between the seventh and eighth teeth. Further posteriorly, the symphysis becomes slightly wider again. The two most anterior alveoli (with diameters of 12 and 15 mm respectively) open upwards and towards the front. At this level, the anterior edge of the symphysis is regularly rounded. The third and fourth alveoli are very large (diameters: 20 and 23 mm) and contiguous; they open upwards and outwards. The fifth alveolus is much smaller (diameter: 10 mm) and separated from the fourth by a fairly long space (20 mm). More posteriorly, the diameters of the alveoli are difficult to measure accurately because their edges are not perfectly preserved. Up to the ninth alveolus, the alveoli are small, with diameters between 10 and 13 mm, and separated by short spaces (5 to 10 mm). The lateral edges of the alveoli protrude in dorsal view, more so on the right side than on the left, a condition which may well be abnormal. Further posteriorly, the alveoli are almost contiguous, separated by spaces only a few millimetres long. Posterior to the end of the symphysis, the walls between the alveoli are not very distinct, which gives the impression that the teeth were set in a groove. The diameter of the teeth does not seem to decrease much towards the rear. In lateral view, on the left side (Pl. 25, fig. 3), the lateral edge of the alveolar row is regularly curved, with the concavity facing upwards. On the right side (Pl. 25, fig. 4), the outline is more irregular. Medial to the tooth rows, the buccal floor is nearly flat, sloping only slightly from the midline towards the sides. There is no sagittal ridge, and only slight longitudinal depressions on both sides. From the level of the seventeenth alveolus rearwards, a weak ridge is visible immediately medial to the tooth rows. At the level of the sixteenth alveolus on the right side, and medial to it, there is a distinct rounded pit, with no symmetrical depression on the left side. Generally speaking, the teeth on the right side show a more irregular implantation, which may be pathological. The medial face of the dentaries is a sutural surface (Pl. 25, fig. 5) longitudinally crossed by the Meckelian canal, which ends anteriorly at the level of the sixth tooth. Grooves and ridges diverge on both sides of this canal. The ventrolateral surfaces of the dentaries are ornamented with irregular deep grooves, which become more loosely arranged anteriorly, where their longitudinal orientation disappears. Just below the tooth rows, a series of vascular foramina is visible.

The teeth are poorly preserved. They are strong, conical, and slightly recurved. There are very stout recurved fangs in the third and fourth alveoli. The apex of the teeth is rarely preserved. However, in the seventeenth alveolus of the left dentary, the rounded tip of an unworn replacement tooth is visible, with irregular ridges and wrinkled carinae. The teeth bear numerous fine ridges, separated by grooves with a concave floor. The carinae are poorly marked.

Splenial. The splenials taper to a point between the dentaries, thus taking part in the mandibular symphysis. Ventrally, the right splenial is seen to reach the level of the thirteenth tooth. Dorsally, the splenial was apparently somewhat shorter; to judge from the poorly preserved anterodorsal end of the left splenial, it reached the level of the seventeenth or eighteenth tooth. In posterior view, the left splenial shows a deep pit overhung by the posterodorsal part of the bone. Posteriorly, in the jaw rami, each splenial forms a kind of low ridge medial to the tooth row. Still further back, the splenial becomes a relatively thin bony plate adhering to the more lateral bones of the jaw and reaching the anterior extremity of the *fenestra mandibularis externa*, but these regions are poorly preserved and few details can be seen.

Mandibular rami. In the posterior parts of the mandibular rami, the sutures between the bones are usually difficult to trace, so that it is not convenient to describe each bone separately. On the lateral surface, the dentary is fork-shaped posteriorly and thus forms the anterior border of the *fenestra mandibularis externa*. Along the ventral edge of this opening, it tapers to an elongated point. More ventrally, the anterior end of the angular also forms a point, below the posterior end of the dentary. Above the *fenestra mandibularis externa*, the suture line between the surangular and the dentary is poorly visible. The *fenestra mandibularis externa* is roofed over by the surangular, which forms a smooth bony plate, convex dorsally and concave ventrally. The ventral limit of the *fenestra* is a more robust bony bar formed by the angular; its ventrolateral surface is covered with grooves, while the medial and the concave dorsal surfaces are smooth. Posterior to the *fenestra mandibularis externa*, the surangular and the angular meet along a hardly discernible suture to form, on the lateral side, a vast bony surface ornamented with deep irregular pits separated by strong ridges. This surface is limited dorsally by a distinct ridge borne by the surangular. This bone does not take part in the glenoid surface for articulation with the quadrate. The glenoid surface is formed by the articular alone; it is large, tongue-shaped, with a strong rounded medial expansion, which overhangs the medial surface of the bone. The retroarticular process is moderately long (170 mm on the left side), not much recurved, with a slight upward concavity. It is built mainly by the articular, the angular and the surangular being included in it along part of its length only, on the lateral side.



TEXT-FIG. 1. Reconstruction of the lower jaw of *Simosuchus thailandicus*, based on specimen TF 1370 (holotype), in the collection of the Department of Mineral Resources, Bangkok. Dorsal view. Abbreviations: an, angular; ar, articular; d, dentary; s, splenial; sa, surangular. $\times \frac{1}{6}$.

AFFINITIES OF *SUNOSUCHUS THAILANDICUS*

The additional data now available about the mandible of the Nong Bua Lam Phu crocodylian justify a further discussion of its affinities (Buffetaut and Ingavat 1980).

Affinities with Sunosuchus miaoi. The type species of the genus *Sunosuchus* is *S. miaoi* Young 1948, based on various remains including an incomplete skull and lower jaw from the Jurassic Hokou series of Kansu, in north-central China (see Young 1948, Buffetaut and Ingavat 1980). Comparisons between *S. miaoi* and *S. thailandicus* are relatively difficult, because most of the mandibular symphysis (the anterior part) of the Chinese specimen is missing, while nothing is known about the skull of the Thai form. However, the parts known in both specimens are very similar. The resemblances in the general shape of the mandibular rami and of the *fenestra mandibularis externa*, and in the morphology of the teeth, have already been mentioned in our previous paper. It now appears that the posterior part of the symphysis is also similar in both forms, but so little is preserved of the symphyseal region in the Chinese fossil that this comparison is not very revealing. In any case, knowledge of the complete lower jaw of the Thai crocodylian by no means precludes its inclusion in the genus *Sunosuchus*. Distinction from the Chinese form at the species level is justified by size and proportional differences (Buffetaut and Ingavat 1980).

Affinities of the genus Sunosuchus. The discovery that *S. thailandicus* is a very long-snouted crocodylian prompts a new discussion of the systematic position of the genus *Sunosuchus*. Young (1948) classified *S. miaoi* among the Pholidosauridae because he assumed that its snout was long and relatively narrow. Although this was not exactly obvious on the basis of the Chinese specimen, the discovery of the jaw from Thailand now shows that Young was right in considering *Sunosuchus* as a longirostrine crocodylian. In 1980 we defended the view that *Sunosuchus* should be included in the Goniopholididae, because of several features of the skull of *S. miaoi*, viz. small supratemporal fenestrae, anterior palatal openings, and the possible presence of maxillary depressions. Although, as we already pointed out, some Goniopholididae had relatively long snouts, the very long mandibular symphysis of *S. thailandicus* is at first sight more reminiscent of the consistently long-snouted Pholidosauridae (although it is rather different from *Pholidosaurus* itself, in which the jaws are much more slender). As mentioned above, the mandibular symphysis of *S. thailandicus* reaches the level of the twenty-fifth tooth, while it reaches the level of the sixth or seventh alveoli in *Goniopholis*, and that of the eleventh tooth in *Vectisuchus leptognathus*, a relatively long-snouted goniopholidid from the Wealden of England (Buffetaut and Hutt 1981). The shape of the symphysis of *S. thailandicus*, and especially of its anterior end, is also reminiscent of some pholidosaurids, notably the very large *Sarcosuchus*, from the lower Cretaceous of Niger and Brazil (see Buffetaut and Taquet 1977) in which, incidentally, the symphysis reaches at least the level of the twenty-third tooth. Although the rather conspicuous constriction at the level of the interval between the seventh and eighth teeth in *S. thailandicus* is not so marked in *Sarcosuchus*, in both instances there is a noticeable anterior expansion, the widest part of which corresponds to the large third and fourth alveoli. However, some short-snouted Goniopholididae, such as *Goniopholis crassidens* from the Purbeck and Wealden of England, are also very similar to *S. thailandicus* in this respect, although they have a short symphysis (see the lower jaw figured by Owen 1878, pl. I). The main difficulty about assessing the affinities and systematic position of *Sunosuchus* is that the Goniopholididae and the Pholidosauridae are two closely related mesosuchian families. Actually, the question is whether *Sunosuchus* should be considered as a primitive pholidosaurid, with small supratemporal fenestrae, or as a specialized long-snouted goniopholidid, and in this respect the length of the symphysis is probably not of prime importance, all the more so that elongation of the jaws is known to have occurred independently in many crocodylian lineages. There remains the already mentioned skull characters that we used (Buffetaut and Ingavat 1980) to support the inclusion of *Sunosuchus* in the family Goniopholididae. The presence of a maxillary depression in the posterior part of the maxillae (about the definition and significance of this feature, see Buffetaut 1982b) would be important evidence in favour of this inclusion, but it needs to be checked on the actual

specimen whether the depression shown on Young's figures is really natural, and not an artefact of preservation. Maxillary depressions are known only in the Goniopholididae. Anterior palatal openings in the palatines and maxillae, like those of *S. miaoi*, have been reported only in some North American Goniopholididae (Mook 1967; Langston 1973) of the late Jurassic, and this may also be a character restricted to some goniopholidids. However, these openings may actually represent a primitive condition retained from Triassic crocodylians in which the palate was not as well developed as in the Mesosuchia (Buffetaut 1982*b*). In this case they may have also been present in primitive representatives of several mesosuchian families, including possibly the Pholidosauridae. The problem cannot be solved at the moment for lack of relevant evidence (it should be remembered that extremely little is known about the early representatives of most families of freshwater or terrestrial Mesosuchia prior to the late Jurassic; see Buffetaut 1982*b*). As to the small size of the supratemporal fossae, it is also a primitive feature for all Mesosuchia. The question is whether a pholidosaurid-like crocodylian with small supratemporal fossae should be included in the Pholidosauridae.

In the absence of data about some crucial parts of the skull, such as the premaxillae, which are hook-shaped in the Pholidosauridae (Buffetaut 1982*b*), it is obviously difficult to reach a definite conclusion about the systematic position of *Sunosuchus*. We think the best attitude at the moment is to consider it as a long-snouted, specialized goniopholidid, while keeping in mind that the Pholidosauridae probably have their origin among the Goniopholididae (Buffetaut 1982*b*), and that *Sunosuchus* is in some ways morphologically intermediate between these two families.

A NOTE ON PALAEOBIOGEOGRAPHY

There is little to add to the remarks on the palaeobiogeographical significance of *S. thailandicus* which were made in our 1980 paper. On the basis of its morphology and of the depositional environment of both the Phu Kradung Formation in Thailand and the Hokou series in China, *Sunosuchus* can be considered as a presumably piscivorous freshwater crocodylian, which should be used as a continental faunal element in palaeobiogeographical reconstructions. In the context of the hypothesis of the northward drift of South-East Asia and its subsequent collision with mainland Asia (see Ridd 1980), the occurrence of the genus *Sunosuchus* in Thailand and in China (and, so far, nowhere else) does suggest that in the Jurassic the fauna of north-eastern Thailand already had Laurasian affinities. Recent palaeontological discoveries in Thailand actually indicate that colonization of north-eastern Thailand by Laurasian continental vertebrates had already taken place earlier: the late Triassic, probably Norian, vertebrate fauna from the Huai Hin Lat Formation, which includes lungfishes, stegocephalian amphibians, turtles, and phytosaurs, shows striking Laurasian affinities (review in Buffetaut 1982*a*). This in turn indicates that collision of the Indochina block (which includes north-eastern Thailand) with South China occurred no later than the late Triassic.

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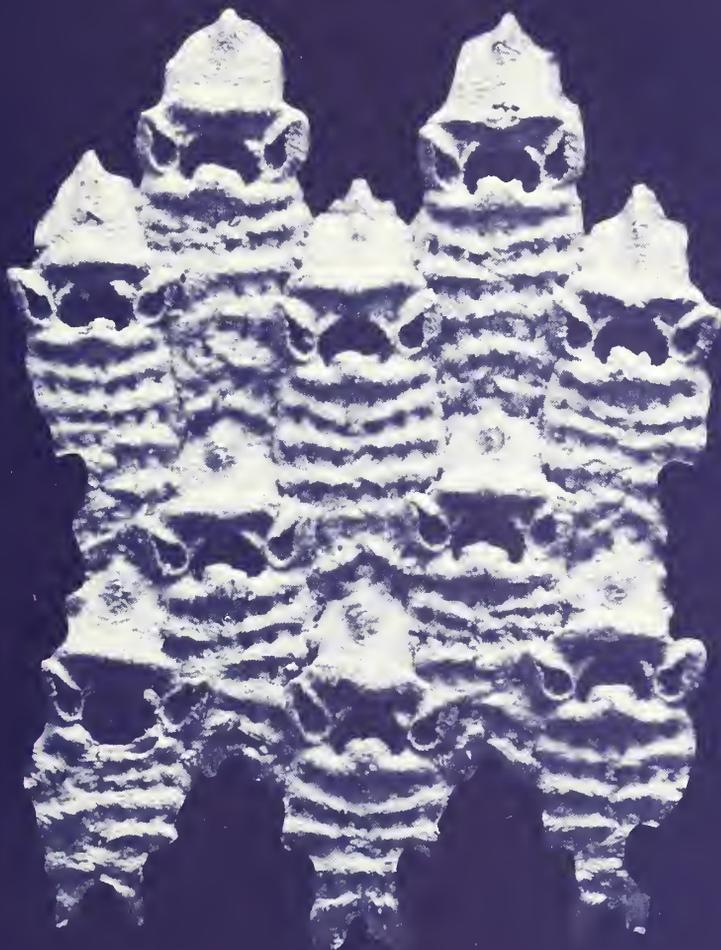
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Cover: The Coralline Crag (Pliocene) bryozoan *Cribritina* sp. showing a group of ten feeding zooids each with an ovicell and paired adventitious avicularia on either side of the orifice. This specimen was figured as *Leprealia punctata* Hassall in G. Busk's Palaeontographical Society monograph of *Crag Polyzoa* (1859, pl. 4, fig. 1). It is reillustrated here by means of a new technique, scanning electron microscopy of the uncoated specimen using back-scattered electrons. × 75.

Grant

CONSTRUCTIONAL MORPHOLOGY OF BIVALVES: EVOLUTIONARY PATHWAYS IN PRIMARY VERSUS SECONDARY SOFT-BOTTOM DWELLERS

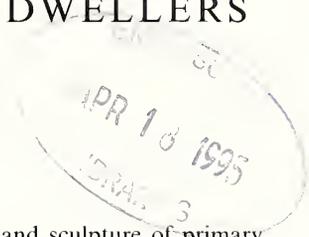
by A. SEILACHER

(Twenty-fourth annual address, delivered 10 March 1983)

ABSTRACT. In contrast to the minor within-habitat improvements in shell shape and sculpture of primary soft-bottom dwellers, the transition of fixosessile rock dwellers back to soft substrates has resulted in fast and drastic morphological changes. They were facilitated by the available ecologic stepping stones that caused morphogenetic programmes—first to ‘derail’ (rock habitats), then to be shortened (to fit the size of dead shell habitats), and finally to extend again (in order to increase mechanical stability on soft bottoms). The third step allows only a limited number of adaptational strategies (flat, outriggered, and edgewise recliners; mud stickers; ‘pickabacks’) that led to convergent shell forms in different groups of bivalves. Within groups, however, phylogenetic and morphogenetic constraints, as well as the adaptational landscape, channel evolution to such a degree that it becomes difficult, at least in the fossil record, to resolve the multitude of parallel and iterative lineages.

EVOLUTIONARY discussions in modern times have often been discussed in terms of theoretical models, with the result that they become more and more detached from the everyday experience of palaeontologists engaged in stratigraphical and morphological problems. This development has forced us into divided camps: neutralists versus adaptationists, gradualists versus punctuationalists, and so on. This appears unnecessary to me. The present study builds on the conviction that evolution is an ecological process and that it is basically opportunistic. Thus I do not expect evolution to subscribe to any particular principle, but to follow the one or the other as fits the situation. In order to understand a given situation in morphological evolution, we must learn the licences, i.e. the options and constraints that are imposed on established bauplans by morphogenetic mechanisms in their approximation of an appropriate functional design, or paradigm. This is the approach of *constructional morphology*. We consider it as a method of research rather than a theoretical framework, so that it makes sense only if applied to a certain group of organisms. Nevertheless the resulting case histories are not irrelevant for theoretical evolutionary considerations. By extending our view from specific cases to larger groups, we can expect to find general patterns—not in the sense of built-in rules (because the steps are stochastic in principle), but as a reflection of the adaptive landscape and its changes in time, by which evolution is ultimately moulded.

In this approach our curiosity focuses on the familiar phenomena of convergence (if we deal with disparate origins) and of parallelism and iteration (within one group). Classical convergences, such as aberrant ‘coralliform’ types—including top-shaped rudist bivalves, richthofeniid brachiopods, hipponicid gastropods—are not randomly distributed in ecospace, but are concentrated in an ecological group that is here called ‘secondary soft-bottom dwellers’. By this we understand forms that acquired a sedentary mode of life, usually attached to hard substrates, in a previous evolutionary step and have secondarily switched to life on areas of marine soft bottoms (sands and muds). In this new habitat they found enough food as suspension feeders, but faced the critical problem of their inherited immobility. Only very few groups, such as the swimming pectinids and limids (perhaps similarly some strophomenacean brachiopods), the burrowing actinians, and some corals managed to develop a new mode of mobility, sufficient to escape from predators and to reorient themselves.



Others went into 'pickaback' symbiosis with a mobile partner such as a hermit crab. But the vast majority solved the problem by stabilizing themselves through stable shapes and/or heavy and commonly oversized skeletons.

From the different phyla and classes included in the project, I select here the bivalves, because they are well-known and have made the transition from soft to hard substrates and back several times during their long history, such that we can hope to sample most of the different solutions. Bivalves also allow us to compare form changes in secondary soft-bottom dwellers with those in primary ones, particularly with changes that improved the ability to burrow.

This project (D 60, 'Substratwechsel im marinen Benthos') is part of the Tübingen special research group (SFB 53) supported by the Deutsche Forschungsgemeinschaft. The contribution largely draws upon published results of temporary members of the group and discussions with them through the years, in particular A. Hoffmann (Madison, Wisc.), H. Röder (Seelberg), H. Schmalfuss (Stuttgart), P. Signor (Davis), E. Savazzi (Uppsala), G. McGhee (New Brunswick). Figured specimens are deposited in the collections of the Institut für Geologie und Paläontologie of the Tübingen University under the catalogue numbers GPIT 1604/1-42. This is Nr. 163 of the series 'Konstruktionsmorphologie' (Nr. 162 see: Hemleben and Spindler, *Utrecht Micropal. Bull.*, in press).

PRIMARY SOFT-BOTTOM DWELLERS

Molluscs probably had their origin on hard bottoms, where they could crawl in a limpet-like fashion with a broad-soled foot and protect themselves by pressing the dorsal shell against the substrate. From such ancestors, bivalved forms evolved probably with the transition to soft substrates, where the gills needed an extra protection (Vogel and Gutmann 1980). The change from a univalved to a bivalved state required only a minor change in the ontogenetic programme of calcification (Bayer 1978). Since the univalved ancestors in this case had not lost their mobility, the foot could become adjusted in the new habitat to become an effective burrowing organ. Thus, bivalves as a group can be considered primary soft-bottom dwellers that largely use the gills as a food-filter and have therefore lost typical mollusc attributes such as primary eyes and the radula.

In the molluscs, bivalved form has evolved more than once (rostroconchs, bertheliniid gastropods, bivalves); but in each case (as also in bivalved arthropods) the two valves remained connected by a less-calcified zone that acts as an elastic ligament. This is in marked contrast to the brachiopod valves, whose articulation probably evolved secondarily from two separate shells protecting the gills of a worm-like ancestor (Vogel and Gutmann 1980). Since this option has led to a crucial constraint in the further modification of the bivalve bauplan, we must first discuss the properties and modifications of the bivalve ligament.

Ligaments

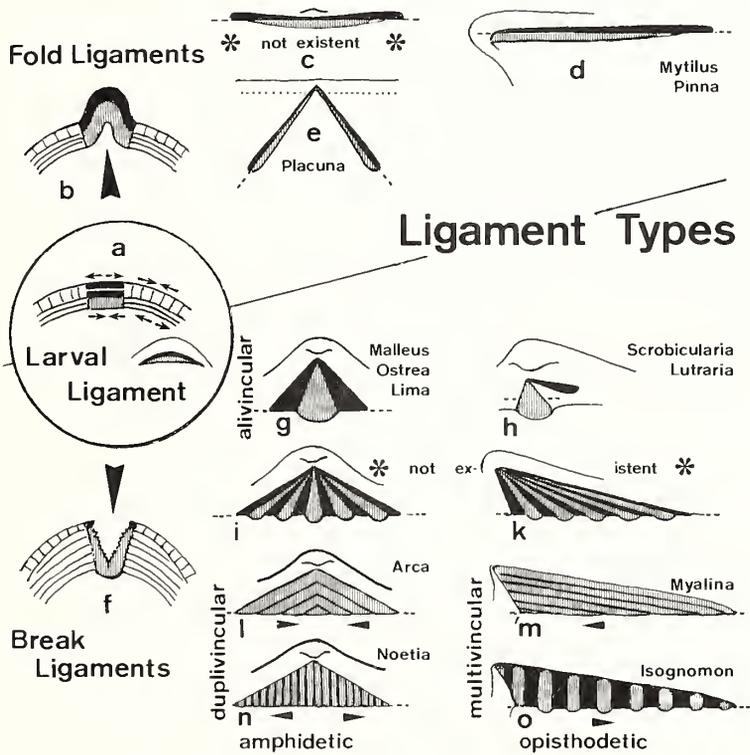
As an antagonist of the adductor muscles, the ligament elegantly serves the function of opening the valves. This problem could not be solved by hydraulics alone, because for such a function the mantle sac would have to remain closed in the open-valve position, which is incompatible with feeding. The alternative, namely opening the valves by diductor muscles, was secondarily achieved by the pholads. In this group the valves have become drilling devices, while their protective function is taken over by the hard substrate in which they bore (Röder 1977). Therefore it was possible to attach part of the anterior adductor muscle on the outside of the hinge, where it could act as a diductor and control the complicated movements of the valves much better than a lifeless ligament, which has become obsolete in this case.

The other major group in which the ligament has become reduced or lost are the rudists. Here the delegation of the opening function to parts of the adductors seems to have been attained through tooth-like projection of the myophores, with the advantage that the diductor parts remained inside the shell. This construction would approach that of articulate brachiopods, but its functional details and the possible pathways into it are not yet clear.

Returning to the structure and properties of the ligament, it should be remembered that we deal with a less calcified part of the shell that grows primarily in a similar way, i.e. with an outer layer

(apart from the periostracum) formed near the margin and an inner layer thickening the ostracum from the inside. The structure of the two layers corresponds to the stress to which they are exposed; it is fibrous (or prismatic) on the compressive and lamellar (or nacreous) on the tensional side, with the expected inversion in the ligament versus the shell. But the ideal design, in which the two layers should have corresponding thicknesses throughout the shell so that their boundary remains in the neutral zone, is impossible to produce in a growing structure, in which only the inner layer can be secondarily thickened. In the calcified shell, this defect can be compensated by overdesigning. In the ligament, however, it becomes critical. A second constraint stems from the fact that the ligament consists of non-living material. Thus its elastic properties do not change with the dimensions of the growing shell and they may also deteriorate by ageing.

Text-fig. 1 shows ways in which the two constraints are coped with in various types of ligaments. Major 'tricks' are (1) the breaking of the outer layers, with fresh material being continuously produced in the functional zone and (2) the regular introduction, or maintenance, of separate generative zones for the outer layer apart from the outer shell margin. Text-fig. 1 also demonstrates that the new generative zones do not grow as predicted by the model of spiral shell growth (text-fig. 11-κ), but in ways that allow to maintain, at all stages, the same absolute distances between them along the hinge line. We assume that these distances are optimized against the constant elastic properties of the two ligament materials. The ligament also imposes strong constraints on shell geometry. For instance, *fold ligaments* limit not only the secondary thickening of the shells, but also

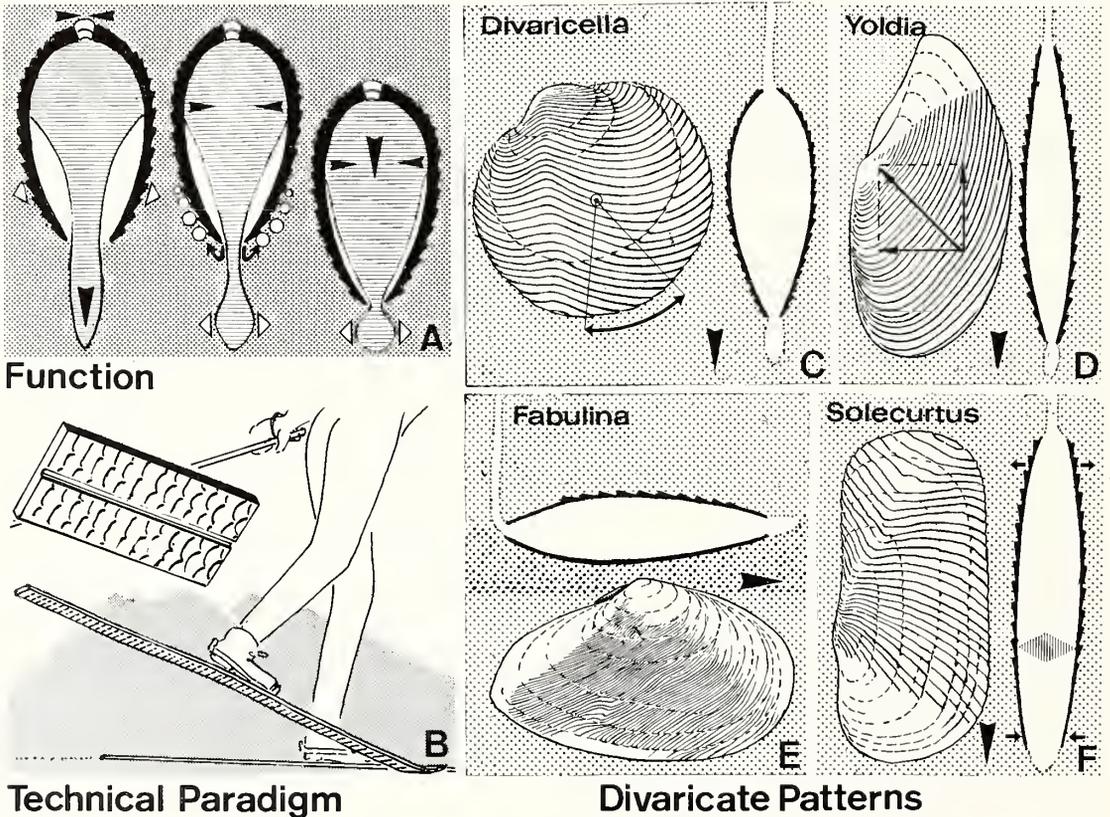


TEXT-FIG. 1. Only fold ligaments remain functional throughout their lengths; in break ligaments the functional parts of the two layers alternate along the hinge. Note that seemingly straightforward solutions (C, G, H) are not represented because of geometrical or mechanical constraints (from Seilacher 1981, modified).

shell curvature. In the theoretically simplest case, in which this type of ligament would extend amphidetically on both sides of the umbo (text-fig. 1C), shell curvature would be reduced to zero. It is therefore not represented. Also, the evolution of inequilateral, prosogyre shells in this group has probably as much to do with the space conflict between the two umbones in the case of a non-expandable ligament, as with an endobenthic, burrowing mode of life.

It should be noted that seemingly non-breaking ligaments are nevertheless affected by growth deformation. This is most obvious in modern *Pinna* (text-fig. 8), where the cross-sectional angle of the hinge becomes widened beyond the yield of the ligament during ontogeny. As a result the ligament is broken in the apical part of all specimens and the separated apices become scissored in a regular way (the left apex always slips dorsally over the right one), with internal flexible septae compensating for the inevitable damage. In this case the ligament will start to break from the inside—an interesting analogue to the rostroconch hinge. It would be interesting to study whether in this case the animal is able to repair the damage by deposition of new ligament material from the inside.

BURROWING SCULPTURES



TEXT-FIG. 2. Ratchetted sculptures reduce back slippage while the shell acts as a penetration anchor for the probing foot. Deviations from the paradigm of the cross-country ski reflect the rocking and opening of the valves (C-E) and their pivoting in F. In horizontal burrowers (E) burrowing sculptures are stronger on the upper valve to compensate for reduced resistance of the sediment layer on top (A from Trueman and Ansell 1969, C-F from Seilacher 1972, modified).

Break ligaments, on the other hand, are split from the outside. They not only allow, but require a certain amount of shell thickening and also permit the growth of highly vaulted valves. Nevertheless inequivalvity is common, because it reduces the space problem of the opposed umbones and because it agrees with the pleurothetic mode of life, which is common in epibenthic species. Inequivalves are also limited by the requirement that an equal amount of ligament should break on both valves. Another way out of the umbonal space problem is the transition, during ontogeny, from convex to concave curvature in the flatter valve of inequivalves such as *Gryphaea*.

An obviously successful compromise is the ligament design found in many heterodonts (text-fig. 1H). Here the two ligament layers are widely separated for increased lever on both sides of the hinge axis and breakage is not excessive. The resulting limitation of shell curvature also agrees with the streamlining required by a burrowing mode of life, while umbonal collision can be avoided by a prosogyrous growth programme. Another possibility to avoid this collision is an ontogenetic switch to higher curvatures in both valves after a flattened umbo has been produced in the early stages (*Circe*).

We shall come back to ligamental problems in our discussion of secondary soft-bottom dwellers.

Shell adaptations to burrowing

On soft bottoms the ability to burrow has a major bonus, because it reduces predation pressure, while allowing for various modes of nutrition such as suspension feeding, epistratal and intrastratal sediment feeding, and even carnivorous habits. The mechanical principles of soft-substrate burrowing have been analysed by Trueman and Ansell (1969). The most effective design is represented by worm-like organisms. As primary soft-bottom dwellers in the strictest sense they have evolved a cylindrical hydraulic body that combines ideal streamlining with the possibility to glide through the sediment almost as easily as along its top. Here, the peristaltic thickening and contraction of body sections transform the push-and-pull action into a seemingly continuous process. In bivalve burrowing, however, functions are divided between the different parts of the body (text-fig. 2). The foot, as a hydraulic structure, alternatively thins into a probe and thickens into a protraction anchor. Correspondingly, the shell is expanded as a penetration anchor during the probing of the foot and becomes partly closed when it is pulled behind. In this phase friction can be further reduced by the ejection of water from the front end and the resulting fluidization of the sediment around the shell.

This mode of burrowing was so successful that it has been maintained by all bivalves that remained in soft substrates. They also have never reduced the shell, because it serves not only for protection, but also supports the necessary filter chamber. In boring bivalves, however, these two functions were taken over by the hard substrate, so that the shell could be transformed into a boring instrument without being constrained by additional tasks (Röder 1977).

In burrowing bivalves evolutionary trends in shell morphology are thus limited to minor modifications that improve the burrowing function. For instance, *shell geometry* tends to become more streamlined and elongated as species burrow deeper and reach more compacted sediment (Stanley 1970).

Another common trend is the evolution of *burrowing sculptures* (Jefferies *et al.* 1981; Savazzi *et al.* 1982) in shallow burrowers (text-fig. 3). Like the profiles of cross-country skis, they reduce back slippage of the shell while it serves as a penetration anchor and produce minimal friction while it is being pulled forward. The effectiveness of such ribs obviously depends on their profile, which should be ratcheted. But experiments (Savazzi 1981*b*) have shown that their dimensioning is also important. If the ribs are too low, sediment grains will be little affected; if they are too high, grains in the grooves will slip as a whole against the outside sediment, so that effectivity diminishes again.

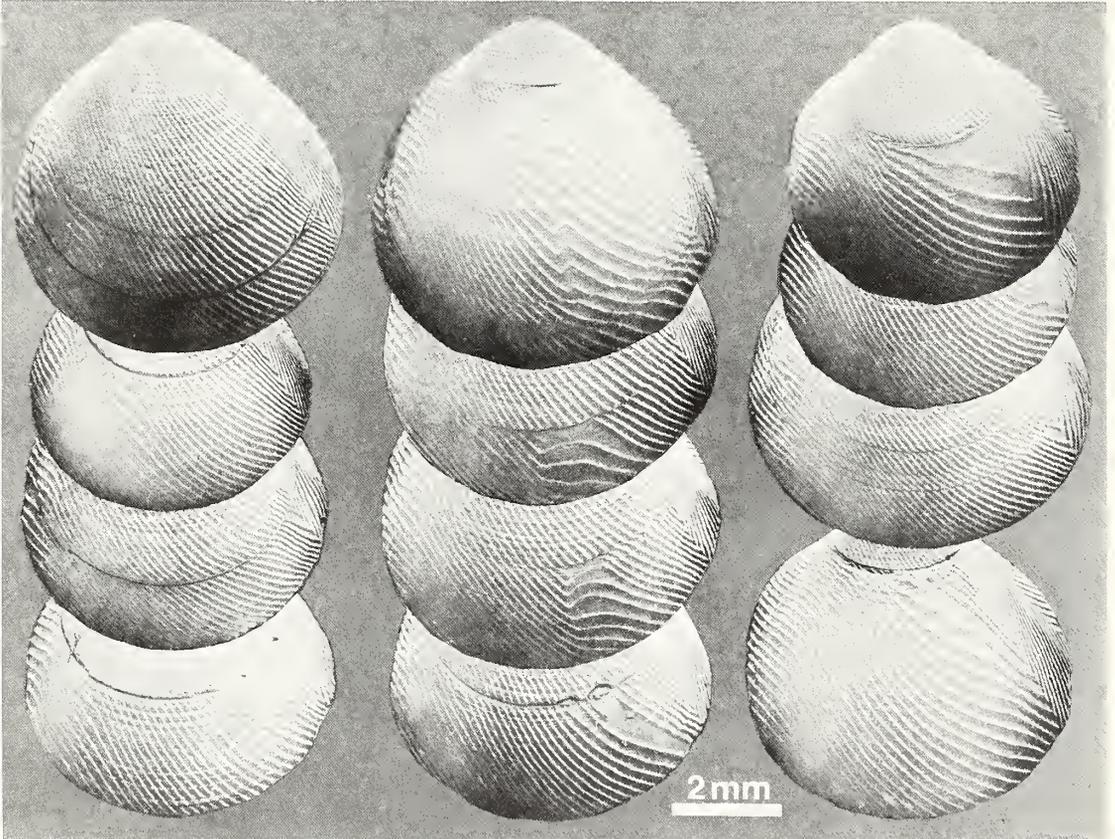
On this basis one can formulate the paradigm for burrowing ribs in the following way (Seilacher 1973):

1. They should be ratcheted with the gentle slopes in burrowing direction.
2. Their strike should be at right angles to burrowing direction.
3. Their height should correspond to the grain size of the burrowed sediment.
4. In highly vaulted bodies the profile may be smoothed in the most projecting surfaces, where forward friction is most critical.

The approximation of this paradigm has been studied in many groups of burrowers (bivalves, gastropods, crustaceans, trilobites, lingulid brachiopods, calcichordates; see Jefferies *et al.* 1981 for a summary). In the view of constructional morphology, these examples are interesting not only because of their palaeobiological and palaeoenvironmental implications. They may, by significant deviations from the physical paradigm, also reveal the constraints imposed by a particular bauplan or morphogenetic program.

In bivalves the major constraint is implied in their accretionary mode of shell growth. In the theoretical model of spiral shells (Raup 1966), growth conformable sculptures are either radial or concentric. None of the two can have the same strike relative to burrowing direction all over the shell. This dilemma can be lessened by emphasizing radial or concentric ribs, or both, in the parts of the shell, in which they happen to run in the right direction (Seilacher 1973, fig. 2). More difficult is the task to maintain the same rib dimensions during growth.

Thus it is not surprising that many bivalves programme their burrowing ribs with a principle (Waddington and Cowe 1969; Meinhardt, in preparation) that is dependent on a time function rather than being dictated by the geometry of spiral growth (text-fig. 3). This 'divaricate principle' (Seilacher 1972), familiarly expressed in mollusc colour patterns, but also in arcoïd ligaments, is better suited for the task at hand. First, it provides not only one, but two coordinate strike directions in a V-shaped fashion. Secondly, the asymmetry is also provided, as seen in corresponding colour patterns. Thirdly,



TEXT-FIG. 3. Shell outline and divaricate rib pattern of *Strigilla pisiformis* from Miami (Florida) correspond to the *Divaricella* Type (text-fig. 2C). The regular fashion in which traumatic gaps in the pattern regenerate indicates that this pattern is formed by a diffusive inhibitor/activator system (SEM photos by H. Hüttemann).

the spacing (and consequently rib height) is largely growth-independent, so that a near-optimal scale can be maintained with less difficulty. Thus the alternative, but less efficient solution of allometrically reducing the height of the ribs relative to their distance (Savazzi 1981*a*, 1982*a, b*) is not necessary in this case.

In spite of their fabricational flexibility, actual divaricate burrowing ribs *deviate* in significant ways from the cross-country ski paradigm. The rib distance, for instance, is negatively allometric, but still increases with growth in absolute measure (Seilacher 1972, fig. 6). This indicates that the underlying morphogenetic principle is not completely growth-independent. More surprising is the fact that these ribs do rarely run truly perpendicular to burrowing direction. This has to do with the fact that bivalve shells are not used like cross-country skis. Shells with a rounded outline (*Divaricella* type, text-fig. 2C), perform a rocking movement (Stanley 1969), which is also reflected in their V-shaped rib pattern. The dividing line between the two sets of ribs, however, does not run in burrowing direction, but is rotated from it counter-clockwise in left view. An analogous rotation is observed in the more elongated shells of the *Yoldia* type (text-fig. 2D), in which only one set of divaricate ribs is developed. This rotation makes sense, if we consider the opening of the valves during the probing phase: the observed rib direction corresponds to the resultant of the opening and the backslippage vector. A third group (*Macoma* type, text-fig. 2E) resembles the previous one in outline and rib pattern, but is sculpturally inequivalve. It comprises species that burrow along horizontally in a flat position as they graze the sediment surface with their ingestion siphons. Their reduction or omission of burrowing sculptures on the lower valve compensates for the higher friction exerted by the sediment below the shell as compared to the thin and less compacted sediment cover on top of it.

The occurrence of divaricate burrowing ribs in most groups of endobenthic bivalves indicates that the underlying morphogenetic principle is generally available. All the more it is surprising that not all burrowing species make use of this possibility. Instead, we find smooth, radially or concentrically ribbed and tuberculated forms in the same niche. Obviously, there are alternative solutions to the adaptational problem as well as constraints related to other functions that exclude one standard interpretation.

It might be mentioned that the case of divaricate burrowing ribs has been repeatedly cited by modern neutralists (e.g. Gould and Lewontin 1979) in their critique of the traditional adaptationist camp. In fact, I am still inclined to believe that most divaricate colour patterns are primarily neutral, or non-functional features in the sense that any other arrangement would do as well. This is suggested by the fact that in life the patterns remain hidden in the sediment or under a thick periostracum and that they are extremely variable in contrast to the few species, in which such patterns demonstrably have a mimetic function. A similar evolutionary relationship was assumed in the sculptural expression of divaricate morphogenetic programmes. I see this switching into a more rigorously selected function of a pre-existing, or pre-disposed structure as an interesting mechanism, but not as a general or even predominating mode of evolutionary change.

SECONDARY SOFT-BOTTOM DWELLERS

Bivalves were extremely successful as soft-bottom filter feeders. Nevertheless, many groups have left the soft bottom to become hard-bottom dwellers again; but since the burrowing foot could not evolve back into a crawling sole, they became sedentary. The pathway into a fixosessile niche was wide open to bivalves due to their mode of nutrition and the general presence of byssus as an organ for larval attachment (Stanley 1972). The pedomorphic retention of this attachment (and in some instances its replacement by cementation of the shell to the hard substrate) throughout life led to the reduction of the foot. It also led to the high intraspecific variability in shell shape that is characteristic of oyster-like, cemented forms and for species whose byssal attachment to rocky substrates is similarly rigid.

It is the evolution of such fixosessile rock dwellers back to soft-bottom habitats that I address here. This step is particularly interesting for a number of reasons:

1. The major adaptational problem implied is straightforward: to make up for the inherited loss of the foot in an environment devoid of adequate anchoring ground.

2. This evolutionary habitat change has happened in so many instances among bivalves as well as in other sessile groups, that we have a good chance to do comparative studies and to sample a wide variety of possible pathways.

3. It is in this group (for which we use the terms 'secondary soft-bottom dwellers') that we find the largest number of bizarre forms—quite in contrast to the primary soft-bottom dwellers discussed in the previous paragraph.

Thus our first question will be, what allowed the extreme and rapid changes of established bauplans in this particular situation? This question is relatively easy to answer. It has primarily to do with the ecological stepping stones that facilitate this change. Corresponding to the rule that an established system tends to adapt to changing conditions first by developing a cover under which the old functions can continue, the pioneer species will attach to hard substrates that are available on soft bottoms, i.e. to dead shells of other organisms. The only morphological change (the 'cover') necessary is progenetic reduction of adult size by shortening the life cycle ('miniaturization stage'). This stepping stone remains to be used during early ontogenetic stages by most of the species that do become independent of such anchoring grounds as they grow up. This makes it difficult, in the fossil record, to distinguish the miniaturized pioneers from juvenile stages of secondary soft-bottom dwellers in the strict sense.

The miniaturization stage is critical, because the following evolutionary step implies a considerable change of selection pressure and also a switch from an *r*- to a *K*-strategy. Independence from an adequate anchoring ground can be gained in three different ways:

1. By developing a *new mode of mobility*, such as the ability to swim up (pectinids, limids, and possibly some Strophomenacea), to crawl (certain corals and bryozoans), and to burrow (soft-bottom sea anemones; *Penicillus*, fig. 11). Among the pelecypods, only attached Arcacea seem to have been able to re-activate the foot for this purpose (Thomas 1976).

2. By establishing symbiotic 'pickaback' relationship with a mobile partner. The shelter-building associates of hermit crabs and of some worms are familiar examples.

3. By mechanically stabilizing the body by shape, weight, and size.

Among bivalves the third solution has been the one predominantly used. Therefore we will focus our discussions on this 'strategy'. In doing so, we first deal with the forms that were originally cemented, then discuss byssally attached forms, and finally borers.

CEMENTED STOCKS AND THEIR SOFT-BOTTOM DERIVATIVES

Most cemented bivalves are monomyarian (oysters, spondylids, *Placunopsis*, plicatulids); but the dimyarian Chamacea, Rudists, and fresh-water 'oysters' (*Etheria*) show that this is not a necessary relationship. We shall here use the Ostreacea for reference, because this is the most varied group. Thus the principal adaptational strategies can be discussed in oyster examples and analogous adaptations in other groups be listed as convergences.

Morphogenetic consequences of cementation

Since cementation is the task of the growing mantle edge, the commissure has to fit snugly to the substrate. This means that the relief of the substrate is moulded on the outside not only of the attached valve ('immuration', Voigt 1968), but also of the free valve—in this case as a positive transformed by the spiral growth geometry ('xenomorphism'). The control of substrate topography on growth is also expressed in the outlines of cemented shells, which tend to be irregular and highly variable. This ecotypic 'derailment' of a regular growth programme may facilitate a subsequent switch to novel programmes.

Cemented growth may continue in this fashion throughout life; but in many cases the commissure will eventually lift-off the substrate in order to facilitate water circulation, to widen the shell cavity, and to defend against overgrowth. This is also the case in the miniaturized soft-bottom pioneers growing on other shells. The mode in which the attached valve lifts the commissure, predetermines

the general geometry of growth during subsequent soft-bottom adaptations (text-fig. 4). Thus elevation of the posterior margin induces an helicospiral exogyrid form, of the ventral margin the planispiral gryphaeid growth, and of the whole shell including the hinge the saccostreid cone shape. Other modifications during the lift-off include the alctryoniid plication of the commissure and retarded calcification giving the free valve a higher flexibility.

These differences can be observed in juvenile stages of advanced forms, but also in minute ancestral forms. It is probably no coincidence that small and thin-shelled epizoic versions appear stratigraphically below the large free forms in *Lopha* (Middle Triassic; Seilacher 1954) and in *Exogyra* (Lower Toarcian; Seilacher 1982a). The same is true for *Plicatula* (*P. spinosa*; Domerian). A systematic search should also document the miniaturized epizoic ancestors of other groups such as rudists.

Recliners versus 'mud stickers'

Among the possible strategies of mechanical stabilization two groups should be distinguished, although they may be not sharply separated. In the first and more common case ('recliners' = Liegeformen; Dacqué 1921) the animal essentially rests on the substrate; in the second the shell itself acts as an anchor in the sediment. In the absence of active burrowing, anchorage inside the sediment must be acquired passively and will therefore evolve preferentially in quiet environments with a relatively high sedimentation rate ('mud stickers'). The difference between the two life forms is expressed in shell shapes and opening mechanisms, but also in shell structures. Only the recliners follow the strategy of heavyweight structures that is so much in contrast to the lightweight skeletons of mobile organisms.

The strategy of 'mud (or sand) stickers', being a response to sedimentation is also valid for living substrates. Therefore it is not surprising to find related forms living in mud and in sponge or coral colonies (*Streptopinna*, text-fig. 9; *Vermicularia*; *Pyrgoma*).

Cup-shaped recliners

Probably no invertebrate has received as much attention in terms of functional morphology and evolution as *Gryphaea* (Hallam 1982). The geometrical inequivalvedness is induced in the juvenile stage, when the attached valve starts to grow up from the initial anchoring ground into a cup, inside which the free right valve nests with a flexible shell margin—a relationship which may also be expressed in adult forms (*Cubitostrea*), whose left valve shows regular radial ribs, while the right valve remains smooth. The resulting gryphaeid curvature of the left valve allows excessive deposition of dense shell material in the umbonal region, which serves as a balance to keep the animal in the right position. The inequivalvedness also permits the umbo of the left valve to expand without getting in conflict with the opposed umbo. The umbonal problem can be even better avoided in the helicospiral exogyrid version, but nevertheless the excessive thickening of the lower valve is maintained.

Convergences. As shown by Stenzel (1971), gryphaeid shells have evolved repeatedly from attached oyster stocks. Similar growth forms can also be observed in other cemented groups, such as *Spondylus* and *Chama*. In all of them it is the attached valve that forms the cup. This is in marked contrast by byssally attached groups (bakevelliids, inoceramids, anomiiids), in which it is the valve originally facing the substrate that becomes the lid in cup-shaped recliners (see below).

Boulder-shaped recliners

Extreme shell thickening in both valves is characteristic for several species of *Crassostrea* (text-fig. 4) in the upper Cretaceous and the Tertiary. During the later part of their lives they continue to thicken the shell without further growth of the soft body, so that the shell cavity is only a small fraction of the whole shell volume. For geometrical reasons, the ligament must also continue to grow during this stage, resulting in a high ligament area with nearly parallel sides. In addition to the excessive shell thickening and unusual size (up to 25 cm in diameter), a very dense shell structure contributes to increase the stabilizing weight of the oysters.

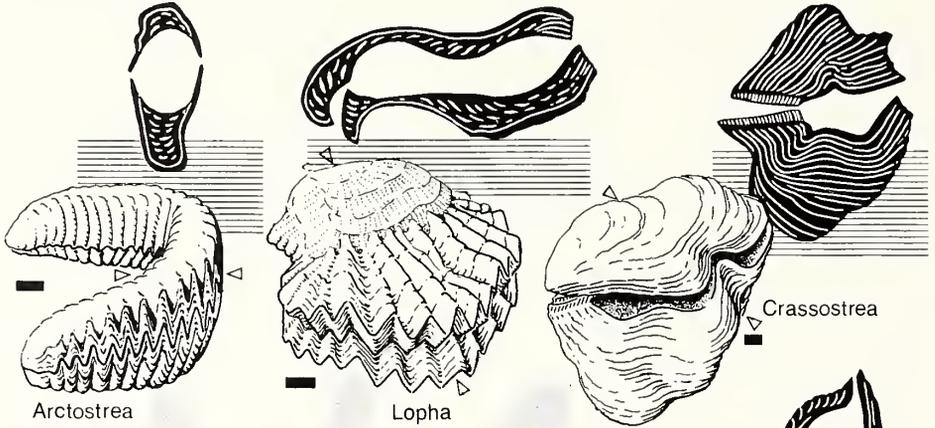
It may be more than coincidence, that the most spectacular 'storm tells' (Seilacher 1983), some of

recliners (heavyweight)

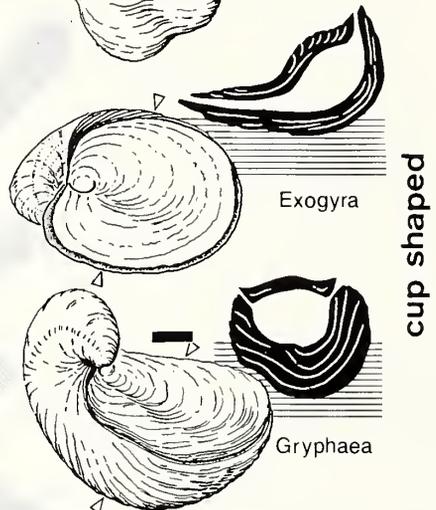
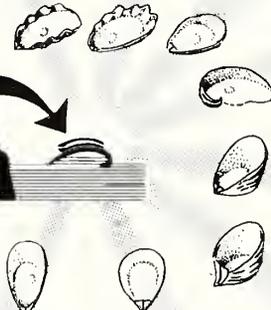
outriggered

fan shaped

boulder shaped



SOFT BOTTOM OYSTERS



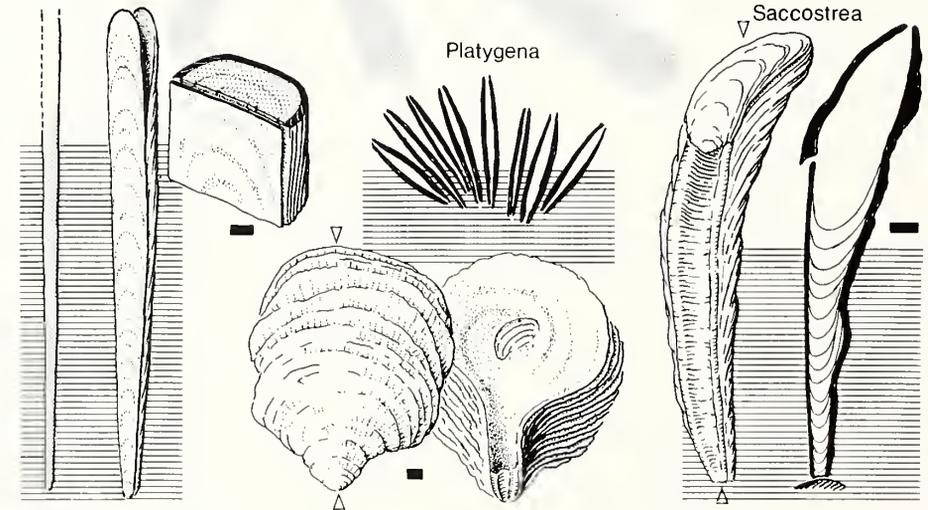
cup shaped

mud stickers (lightweight)

Konbostrea

Platygena

Saccostrea



stick shaped

spoon shaped

cone shaped

them reaching 20 m in thickness (Bender 1968) have accumulated through event condensation during regressive intervals from this type of oyster.

Convergences. Although this seems to be a straightforward strategy, no comparable adaptations can be quoted from other pelecypod groups, which probably could not match the oyster's rate of shell and ligament production.

Fan-shaped recliners

Another possibility to stabilize the shell is its expansion into a flat fan shape. Adhesion to the sediment may be further increased by strong sculptures (radial ribs, spines, foliate concentric ribs). In

TEXT-FIG. 4. Evolution of a wide range of adaptational strategies in soft-bottom oysters was facilitated by a sequence of ecological steps:

(a) The 'derailing' of morphogenetic programmes in fully cemented rock-dwelling oysters.

(b) The progenetic miniaturization in soft-bottom pioneers that used dead shells as stepping stones into the new habitat.

(c) True soft-bottom dwellers use shell substrates only in their early growth stages and become stabilized by size increase, shell thickening, or mud sticking as adults.

Arctostrea sp. (Lower Cretaceous, East Africa; GPIT 1604/1). Horseshoe-shaped elongation stabilizes the shell with the inhaling convex flank facing upcurrent. It is on this anterior side that the zigzag commissure is most pronounced. Since the left valve is excessively thickened and bears lateral outrigger spines in another species (*A. colubrina ricordeana*; see Carter 1968) this was probably the preferred resting surface.

Lopha marshi (Middle Bajocian, Aalen, southern Germany; GPIT 1604/2). After a relatively long encrusting stage that bears the xenomorphic sculpture of pelecypod or ammonite substrates, the shell became fan-shaped, plicate, and very thick, particularly after cessation of radial growth. Epizoans indicate that the species could recline on either valve.

Crassostrea sp. (Upper Eocene, Oriz, Vic Basin, southern Spain; GPIT 1604/3). This large species grew rather irregular throughout life; but the large ligament area, small body cavity, and excessively thick valves as well as a dense shell structure indicate that shell growth had the main purpose of making the animal heavier and continued long after the soft parts had reached their ultimate size.

Exogyra sp. (Upper Cretaceous, Kansas; GPIT 1604/4). Prosogyrous spiral growth was established already in miniaturized epizoic species of the Lower Toarcian. In later reclining species it allowed the umbo of the left valve to become a heavy bottom weight, while the right valve formed a thinner lid. Stabilization was also improved by a gradual evolutionary increase in adult size.

Gryphaea arcuata (Lower Sinemurian, southern Germany; GPIT 1604/5). The almost planispiral growth of this genus is also derived from the way in which epizoic ancestors and juveniles lift off the substrate. It allowed the lower left valve to become even heavier compared to the upper. Narrow species such as this one may also have been passively righted by the principle shown in text-fig. 12.

Saccostrea sp.; East Africa (GPIT 1604/6; reconstructed after specimen courtesy of Dr. D. Nations, Flagstaff). Cone-shaped growth of the lower valve, convergent to rudists and richthofeniid brachiopods, might appear the simplest way to transform a cemented bivalve into a mud sticker, but it creates problems in forms that maintain a functional break ligament with very unequal attachment areas.

Platygena asiatica (Upper Eocene, U.S.S.R.). In this genus a mud-sticking mode of life with the umbones down is documented by field evidence (section of colony, from Hecker 1956). Its valves are relatively thin and very flat. Most characteristic is the internal view (from *Treatise Inv. Pal.* N 1147) with lateral areas of regressive growth lines. They transform the umbonal part of the body cavity into a narrow handle and may have assisted the ligament to open the valves and keep the sediment from entering, if they were provided with flexible brims.

Konbostrea konbo (Upper Cretaceous, Japan; after Chinzei 1982, and in prep. and GPIT 1604/7). Early ontogenetic replacement of the ligament function by the elastic bending of the flat and thin right valve allowed this species to develop a stick-shaped shell, in which the body cavity is restricted to the uppermost part. The rest of the gutter-like left valve is filled with chalky layers, whose upper end forms the fulcrum for the flexible left valve (compare *Lithiotis* in text-fig. 5).

All scales = 1 cm.

contrast to the previous types, however, there is no preference for lying on either the right or left valve. This is indicated by equi-valve shell thickness and can be tested by the statistical distribution of epizoans.

Zigzag folding of the commissure, exemplified by reclining species of *Lopha*, corresponds particularly well to his mode of life. As shown by Rudwick (1964) for brachiopods, it reduces the danger of sediment intake. On the other hand it guarantees that in either position one side of the folded commissure is well above the sediment level. Also it eventually results in the anchoring ribs.

Less sculptured flat oysters may also belong to this type (*Deltoideum delta* in the Upper Jurassic), but their attribution is less certain, because spoon-shaped mud stickers may have similar shapes. Therefore additional evidence (epizoan distribution and slope orientation; observation of life positions in the field) is desirable in these cases.

Convergences. This adaptational strategy is found in Tertiary species of *Plicatula*, an originally cemented recliner, but also in byssal stocks such as many pectinids, the limid *Ctenostreon*, and the anomiiids *Placuma*, *Carolia*, and *Huyella*.

Outriggered recliners

In this case a large resting surface is acquired by deviation from the rounded outline. This can be done by wing-like expansion of the hinge, by finger-like extension of radial ribs, or by elongation of the whole shell into a curved, crescentic outline. The oysters have made use of all three possibilities. *Rastellum* forms a long auricle on the posterior side (much like reclining *Isognomon isognomum*, text-fig. 5). *Lopha quadriplicata* lacks auricles, but in the adult stage it produces strong outriggered ribs by local expansions of the commissure, very much like in the isognomid genus *Mulletia* (text-fig. 5). More common is the third solution (*Arctostrea*, text-fig. 4), combined with a zigzag commissure line. Its curved outline also improves the separation of the inhaling and exhaling currents because the convex inhaling side faces up-current in the hydrodynamically stable position. As in the previous type it makes no difference for outriggered recliners which valve is up; but in *Arctostrea* from the Chalk additional outrigger spines are developed only in the left valve, which must have been down in life position (Carter 1968).

Convergences. Because of the broader range of possibilities, outriggered recliners are more common in some byssate groups (see below), but also among brachiopods.

Cone-shaped 'mud stickers'

The morphogenetic strategy in which the attached valve grows up into a slender cone while the other forms a lid, is well known from rudists as well as richthofeniid brachiopods and seems to be the simplest answer to a rising sediment level. A *Saccostrea* from the East African coast (text-fig. 4) resembles rudists not only in shape, but also by the thin-vaulted septa that obstruct the lower part of the cone as the soft parts move up. But its 'mud-sticking' mode of life is only inferred and needs to be verified by field observations.

In bivalves, however, this mode of growth poses a major problem. In a break ligament the two ligament areas should be of corresponding dimensions, because a break in the middle invalidates equal areas on both valves. Thus the extreme disproportion of ligament attachment on the two valves of *Saccostrea* (text-fig. 4) required a drastic rearrangement in ligament structure, which would deserve a detailed study. In rudists this problem was bypassed by reduction of the ligament and its probable functional replacement by a diductor.

Convergences. Although cone-shaped rudists are commonly referred to as reef-builders (which they may secondarily have become in some cases), their morphology suggests that they originated as 'mud stickers'. This seems also to be the case with the brachiopod *Richthofenia* and other 'coralliform' species, such as the gastropods *Rothpletzia*, in which the operculum, and *Vermicularia*, in which the shell has become tube-like. All these had at some time been cemented to hard substrates. To what extent cone-shaped corals and sponges conform to this model remains to be studied.

Sponges obviously can be 'mud sticking' only with a defunct basal portion, so that the living parts remain washed by water from all sides.

It is probably no coincidence that no cone-shaped forms seem to have evolved from non-cemented bivalves, because they would have no reason to grow up from the substrate by elongation of only one valve.

Spoon-shaped 'mud stickers'

In this type the ligament remains submerged in the sediment. It thus acts against sediment pressure and needs either to be very strong or supplemented in its action by other elastic structures, such as uncalcified shell margins that also keep the sediment from laterally entering the mantle cavity in the open position. The modern *Crassostrea virginica* represents this mode of life, approaching stick- or club-shaped 'mud stickers' with its elongate outline. More characteristic is the Tertiary *Platygena* (text-fig. 4), in which the umbonal part of the body cavity becomes secondarily narrowed to a handle-shaped apsis flanked by broad areas of regressive growth lines. Field evidence (Hecker 1956) shows that they stuck in the sediment as colonies that opened like the pages of a book. Corresponding shell shape suggests a similar mode of life for the extremely flat Upper Jurassic oyster *Delloideum delta*, although this species has not yet been recorded in life position.

Convergences. So far only the Jurassic genus *Lithioperna* can be quoted as a direct analogue (text-fig. 5). It is quite variable in shape, ranging from inequivalve, cup-shaped recliners with thick shells to flat, equivalve forms. In the Calcarei Grigi of northern Italy, some beds consist almost solely of these flat forms, whose imbrication superficially resembles current-induced post-mortem accumulations. But since in these beds all specimens are double-valved, have their umbones pointing downwards, and are unusually elongated, they must be considered as dense beds of 'mud stickers'.

A slightly different version seems to be represented by stacks of the anomiid *Carolia* that T. Aigner found in the Eocene of Egypt. In these stacks, only the first individual closes the byssal notch during ontogeny in the usual fashion. The other ones attach with exactly the same orientation to the convex left valve of their neighbour and secrete on it a calcareous plug that upon retraction of the byssus snugly fits into the persisting byssal notch. These stacks, consisting of up to six individuals, were found in various positions in the rock. They are likely to have been reworked as an aggregate and buried alive during catastrophic events such as storms, while they originally lived in an inclined position similar to *Lithioperna*, with the weight of the byssal plugs adding to keep the umbonal side lowermost.

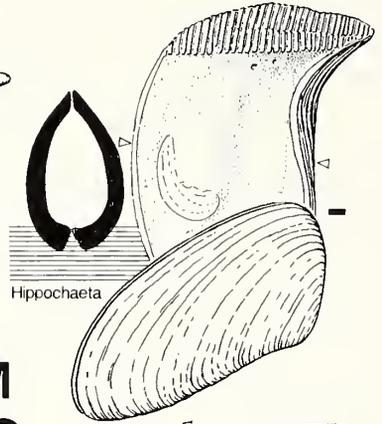
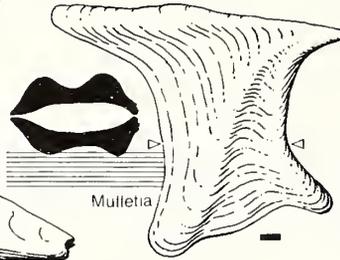
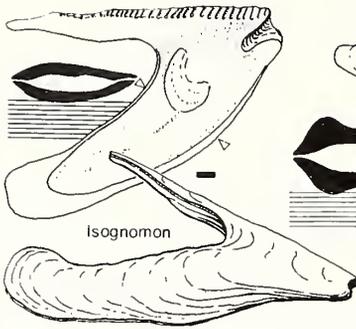
Club-shaped 'mud stickers'

Konbostrea konbo (Chinzei 1982) from Upper Cretaceous mud-flats (text-fig. 4) represents the most extreme deviation from the oyster bauplan. Its elongation, combined with a documented 'mud-sticking' mode of life, was made possible through the early ontogenetic replacement of the ligament function by elastic bending of the right valve, which accordingly remained very thin and completely flat. The left valve, attached only in the juvenile stage, grew in a gutter-like fashion; but its cavity became successively filled by chalky shell material as an alternative to light-weight obstruction by septae, which is possible only in cone-shaped valves. In this way the body and the shifting 'hinge' zone with its fulcrum could move up like an elevator to compensate for the accumulation of mud between the individuals of a colony.

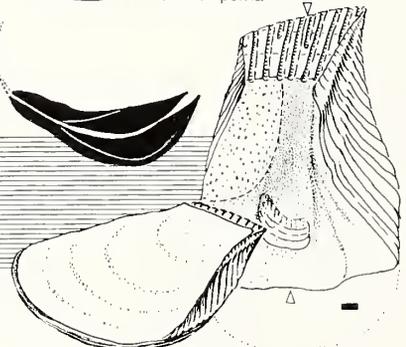
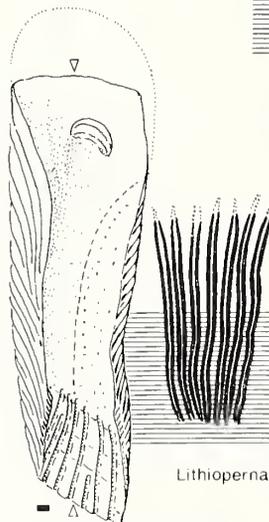
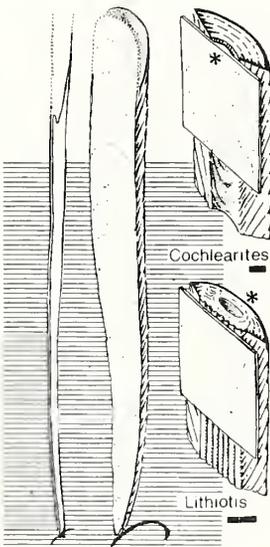
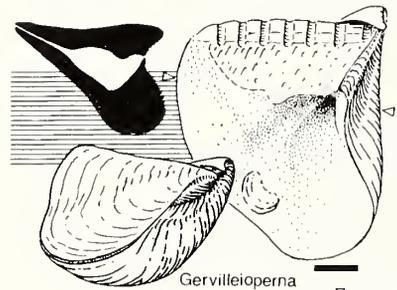
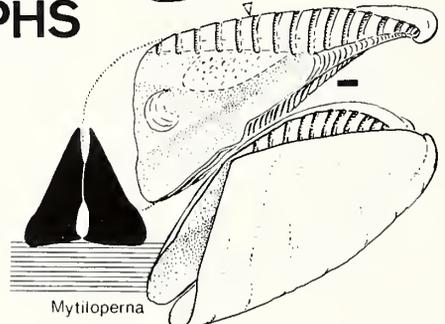
Convergences. The genus *Lithiotis* (text-fig. 5), characterizing a shallow-marine limestone facies in the Lower Jurassic Tethyan realm (Geyer 1977) was convincingly shown to have grown and functioned in an analogous way (Chinzei 1982). This is also true for the associated genus *Cochlearites*, in which it is not the right, but the left valve that provided the fulcrum. Also the fulcral area has a different structure (text-fig. 5). Therefore, Chinzei concluded that the two genera evolved independently, but probably from related stocks. Their taxonomic relationship is still uncertain. Most probably they belong to the bakevelliid stock (*Mytiloperna*, *Gervilleioperna*, *Lithioperna*; text-fig. 5), which shows an unusual radiation in the *Lithiotis* facies. These genera are characterized by a broad-tooth plate

outriggered recliners

edgewise recliners



SOFT BOTTOM
PERNAMORPHS



stick shaped

mud stickers

spoon shaped

cup shaped
recliners

(broken lines in text-fig. 5) that could have evolved into fulcral areas in the elongated forms. Both genera, however, seem to have been cemented to shelly substrates during early ontogenetic stages, *Lithiotis* with the right and *Cochlearites* with the left valve (Chinzei 1982), in contrast to the byssal attachment of other bakevelliids. In fact, cementation might have been necessary to induce their extreme inequivalvedness.

BYSSATE STOCKS AND THEIR SOFT-BOTTOM DERIVATIVES

The adaptational history of byssate bivalves has been treated extensively by Stanley (1972). While I agree with most of his interpretations in terms of functional morphology, I am not so certain about his assumption that most epibyssate forms have evolved, without habitat change, in soft-bottom environments and with the endobyssate stage as an initial step. Stratigraphical evidence does not always support such a sequence (for instance are the first representatives of the bakevelliids and

TEXT-FIG. 5. Secondary soft-bottom dwellers derived from byssate stocks are commonly edgewise recliners that maintain weak byssal attachment in addition to stabilization by shape and weight. Other strategics resemble those in cemented stocks (text-fig. 4); but it should be noted that no cone or stick-shaped mud stickers have evolved from non-cemented rock dwellers.

Modern rock-dwelling isognomonids (*Isognomon* (*Isogonum*) sp.; Langun, Malaysia; GPIT 1604/8) are much more firmly attached than mangrove species (*I. (I.) ephippium*, Philippines; GPIT 1604/9). Therefore they show extreme variability ('morphogenetic derailing') that helped them to evolve extravagant shapes in soft-bottom descendants.

I. (I.) isognonum (Philippines; GPIT 1604/9) is a V-shaped recliner lying either on the right or left valve. It further develops the ventral elongation of rock-dwelling ancestors plus long posterior auricles as outriggers. Increased shell thickness and size also improve stabilization.

Mulletia mulleti (Lower Cretaceous, England, from *Treatise Inv. Pal.* N 325) outriggers by toe-like expansions of the commissure.

Hippochaeta sandbergeri (Oligocene, Weinheim, Germany; GPIT 1604/10) could have been either a flat or an edgewise recliner; but similar forms from the Jurassic (Fürsich 1980) have been found in edgewise life position (see text-fig. 8).

Mytiloperna sp. (Calcarei Grigi, Lower Jurassic; Vajo dell Anguilla, Verona, northern Italy; GPIT 1604/11). Like the following forms, it has a broad tooth plate (broken outline) that indicates affiliation with the Bakevelliidae rather than the Isognomonidae. Triangular cross-section and extreme shell thickening as well as reduced height (compare *Tanchintongia*, text-fig. 8) are typical for edgewise recliners. The posterior gape, the marginal position of the posterior adductor, and the lack of marked growth lines indicate that the shell was originally covered by a less calcified outer layer that formed a flexible flap on the posterior side, much like in the following forms. Note that this is the only edgewise recliner in the bakevelliids. This indicates evolution via mud stickers.

Gervilleioperna sp. (Calcarei Grigi, Lower Jurassic; locality as before; GPIT 1604/12) represents the gryphaeid type of cup-shaped recliners.

Lithioperna (Calcarei Grigi, Lower Jurassic; same locality) occurs in two morphotypes. As isolated recliner, it is found in flat position, with a roundish outline and commonly with very thick and cup-shaped cross-section (GPIT 1604/13). In crowded, book-like colonies, the shells remain flat and thinner-shelled and grow much longer (left specimen, from Accrosi-Benini 1978). If the ventral flexible flange extended to the anterior and posterior sides, it could have prevented lateral penetration of the surrounding sediment when the valves were open (compare similar regressive growth line areas in *Platygena*, text-fig. 4).

Lithiotis and *Cochlearites* (after Chinzei 1982) are perfect homeomorphs of *Konbostrea* (text-fig. 4), though they are certainly not oysters. They are here tentatively affiliated with the bakevelliids, with which they are associated in the Calcarei Grigi, but from which they differ by being monomyarian and cemented as juveniles. Note also that the thin and flat flexible valve is not the same in the two Liassic genera, indicating parallel evolution (asterisk = right valve).

All scales = 1 cm.

inoceramids not modiomorph endobysates?). One should also bear in mind that by their higher fossilization potential 'mud stickers' tend to be well represented compared to rock-dwelling forms, which I would prefer as the initial stage. The main difficulty, however, is the reduction of the foot, which in soft sediments would not have become redundant by the maintenance of byssal attachment throughout life. Certainly, evolutionary pathways between endo- and epibysate forms may have been passable in either direction and one should study each case separately. Still I prefer to consider the majority of byssate 'mud stickers' and recliners as secondary soft-bottom dwellers in the strict sense, i.e. as the result of an evolutionary habitat change from soft to hard bottoms and back again.

As a reference group for byssate bivalves we select here the forms with a multivincular ligament, because they have evolved a great diversity of soft-bottom dwellers both in the Mesozoic and the Recent. In current taxonomy they are grouped under the families of Bakevelliidae and Isognomonidae, which differ in shell structure and in the form of the hinge.

While the mechanical principles of stabilization are the same in cemented and byssate stocks, some general differences should be noted. First, byssate recliners need not be as morphologically stable and thick-shelled as cemented ones, because the byssus may provide an additional means of stabilization throughout life. Secondly, byssate stocks had no access to pathways such as cone-shaped 'mud stickers', but commonly evolved into edgewise recliners, which are conspicuously absent in byssate stocks.

Outriggered recliners

Compared to cemented stocks, outrigger production differs significantly in byssate forms, because their long hinge lends itself to prolongation into a narrow auricle, which may have had a stabilizing function already in rock-dwelling ancestors (Stanley 1972). In truly multivincular species (*Isognomon*, *Mulletia*; text-fig. 5), an auricle forms only on the anterior side, assisted by elongation of the ventral margin at an acute angle.

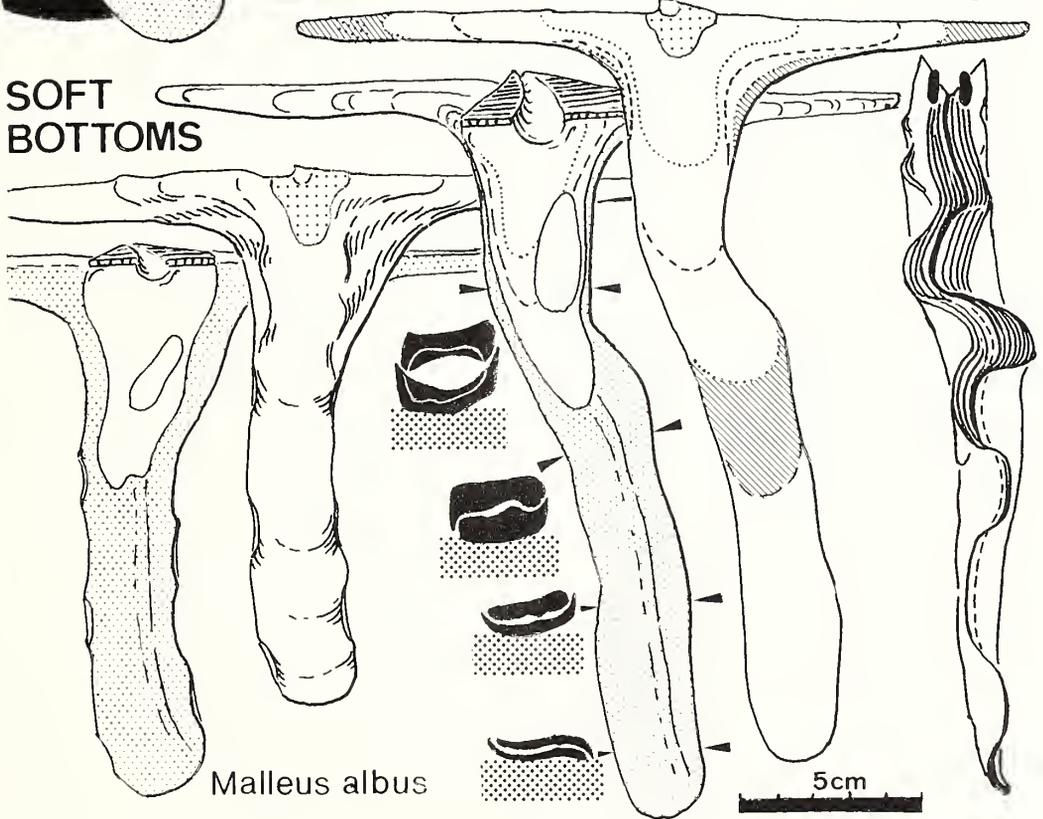
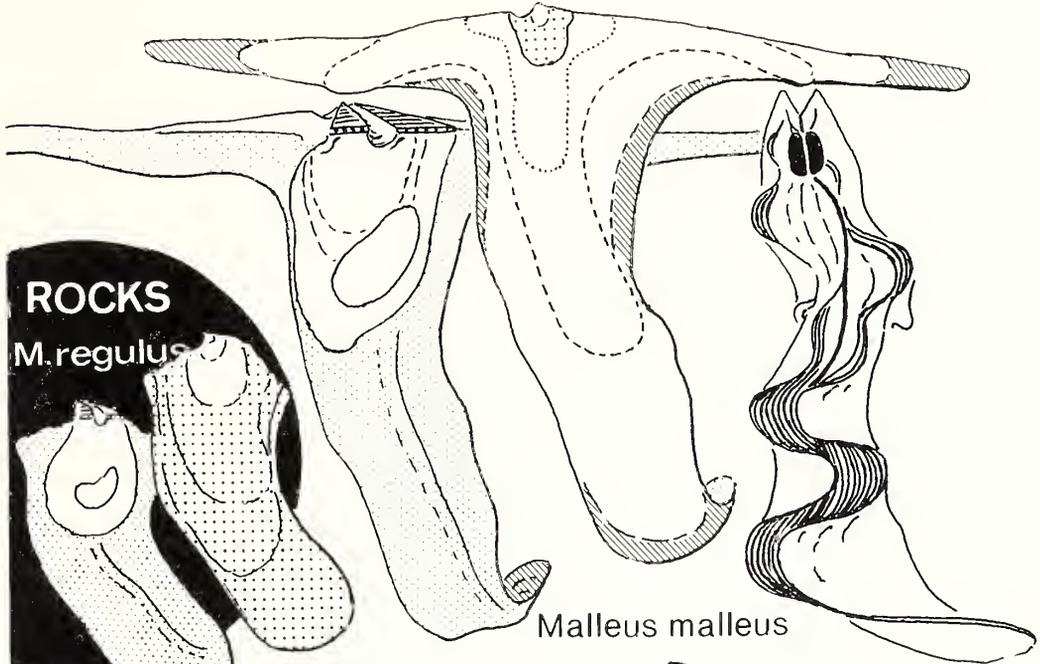
Convergences. *Malleus*, closely related to *Isognomon* in spite of its alivincular ligament, is the prototype of an outriggered recliner (text-fig. 6); but since it evolved an anterior auricle in addition to the posterior one, elongation of the ventral shell margin proceeds at a right angle to the hinge. Secondary shell thickening separates the auricles in later growth stages of *M. albus* (text-fig. 6), so that only the ventral margin can proceed to grow. This also allows the zigzag undulation of the commissure to develop in a more regular fashion with an overlap of the margins at the bends, which keeps the shell from gaping more widely at these points. Epizoan overgrowth shows that *Malleus* reclines ambivalently on the right or left valve (Seilacher 1982*b*) and is no 'mud sticker' as commonly

TEXT-FIG. 6. Although being closely related, the Malleids differ from the isognomonids (top part of text-fig. 5) by having an alivincular ligament and by being byssally attached at the umbo rather than at the anterior flank of the shell. Accordingly they were able to evolve outriggered recliners (not mud stickers, as commonly believed) by developing long auricles on the posterior as well as on the anterior sides of the elongate shell.

The ancestral situation is illustrated by *Malleus regulus* (Cebu, Philippines; GPIT 1604/14) that lives firmly attached to rocks and is relatively small, thin shelled, and highly variable in shape.

Similar stages, first with round outline and then with oriental auricles are also found in the two reclining species; but they are very much reduced in size, indicating that evolution went through a miniaturized stepping stone adaptation. Only in an ontogenetically following outrigger stage does the shell grow hammer shaped, thick, and very large. It also develops a zigzag commissure, in which the absence of secondary shell broadening allows the flanges to overlap and thus to equalize shell gape.

Note also that in comparison to *M. malleus* (Cebu, Philippines; GPIT 1604/15), *M. albus* (Cebu, Philippines; GPIT 1604/16–17) is the more advanced species. It inhabits deeper and finer mud bottoms, is more regular in shape, and has a fourth growth stage, in which only the ventral edge of the shell continues to grow. This is because in this stage the right and left valve auricles become separated and the mantle recedes from them (recessive growth lines on inside of auricles!) in order to allow secondary shell thickening (all specimens drawn to same scale, with the anterior side to the left; from Seilacher 1982*b*).



believed (Yonge 1968). The Pteriacea have probably evolved many pleurothetic recliners, some with pronounced outriggers (*Oxytoma*), but few except the pearl oyster (*Meleagrina*) show extensive shell thickening and excessive sizes.

Edgewise recliners

In equivalved, but thick-shelled species of a generalized outline, such as *Hippochaeta* (text-fig. 5), one might argue whether a pleurothetic or an orthothetic attitude would be most stable—depending on whether or not a byssus was maintained as an additional anchor. In this case, we must rely on field observations, which in the case of Jurassic *Isognomon* species have corroborated an orthothetic life position (Fürsich 1980). Life position is less ambiguous in *Mytiloperna*, whose extremely thickened shell and triangular cross-section provides a stable base on the anteroventral side (text-fig. 5).

Convergences. (a) *Ambonychiacea* (text-fig. 7). Analogous forms have evolved among the Palaeozoic Myalinidae. *Orthomyalina* from the Pennsylvanian, comparable to *Hippochaeta* (text-fig. 5) in outline and shell thickening, may be used to illustrate the difficulties of palaeoecological reasoning. Shell geometry and weighting clearly correspond to a mytiliform edgewise recliner resting on the broad and byssus-bearing anterior surface. On the other hand, a significant inequivalved form with respect to external sculpture and to the inclination of the ligamental area suggests that they were pleurothetic recliners with the more coarsely sculptured left valve facing the sediment (Newell 1942). Field observations clearly support the orthothetic model, but introduce another problem: it is not the byssus-down, but the mechanically less stable hinge-down edgewise position that clearly predominates. A similar dilemma has been recorded by Fürsich (1980) in homeomorph species of *Isognomon* from the Jurassic. He concluded that the morphological evidence is misleading and reconstructed a 'mud sticker' in an apex-down position. As an alternative I suggest that the 'life positions' record a response of the animals when being smothered. By the pull of the byssus they would rotate the shell into an unnatural dying position most likely to be preserved.

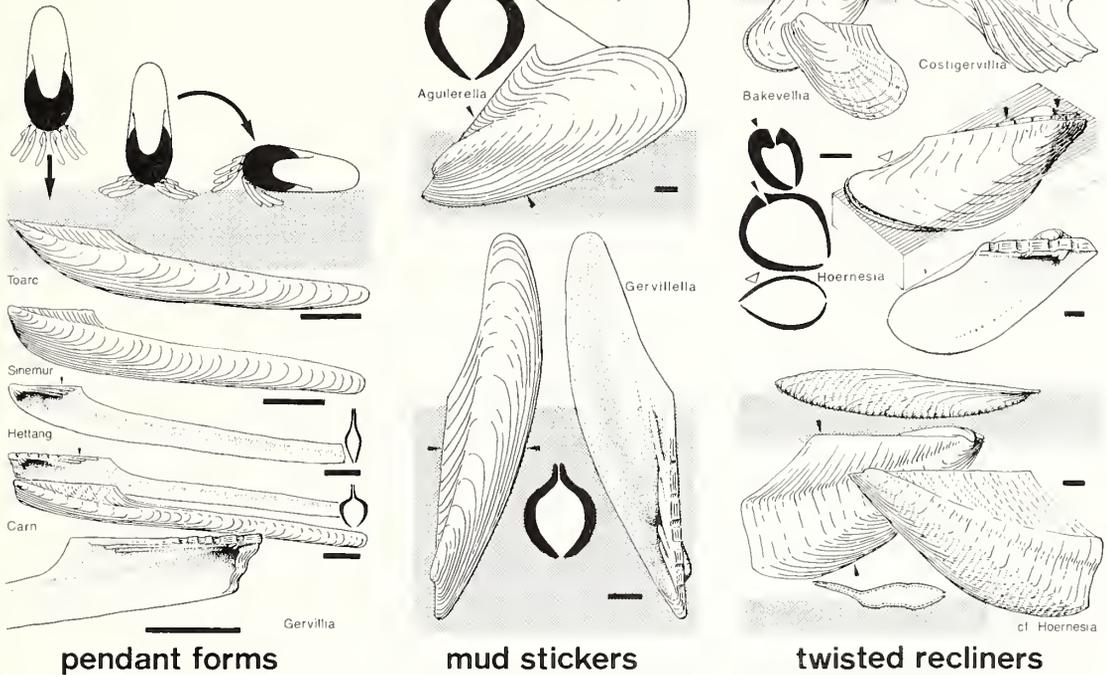
The less ambiguous *Mytiloperna* type is represented in the Ambonychiacea by the giant and thick-shelled *Tanchintongia* that according to Yancey and Boyd (1983) has a myalinid ligament. This genus and other alaticonchiids thrived during the Permian in a facies and climatic zone that seems to correspond to the Lithiotis facies in the Jurassic and the rudist facies in the Cretaceous.

(b) *Mytilacea*. *Congerina*, a thick-shelled relative of the epibyssate fresh-water mussle *Dreissenia*, is broader than *Hippochaeta*, but not as elongate as *Mytiloperna*, with shell-weighting on the recessed anteroventral side. Similar shell thickening is observed in the Jurassic species '*Mytilus mirabilis*' (text-fig. 9) that occurs together with bakevelliid recliners of the Lithiotis facies (text-fig. 5).

All orthothetic recliners discussed so far have probably evolved directly from epibyssate ancestors. The upper Jurassic large- and thick-shelled genera *Trichites* and *Stegoconcha*, however, are derived from endobyssate 'mud stickers' like *Pinna* (text-fig. 9). This derivation is indicated by the fibrous shell structure in both genera and the retention, in *Stegoconcha*, of a keel corresponding to the functional pseudoligament in mud-sticking ancestors (Chinzei *et al.* 1982). The necessity for a thick-shelled pinnid to transform the folding into a breaking ligament may explain why this adaptational pathway has not been used more often in the long history of the pinnids. Derivation from endobyssate ancestors is also indicated for Jurassic Mytilids, in which a square triangular cross-section (*Falcimylithus*, *Arcomylithus*; text-fig. 8) is combined with a rudimentary anterior extension, like in *Modiolus*. A similar cross-section is also found in a Rhaetic species of *Modiolus* (Seilacher 1972, fig. 5B), which was a deep mud sticker with an extremely elongated shell and divaricate, but non-ratcheted rib pattern. Available specimens unfortunately come from rocks in which only the thin calcitic outer layer is preserved, so that the original amount of shell thickening remains uncertain.

Edgewise recliners are also ambiguous because similar forms, even with an extreme triangular cross-section, may have evolved directly from burrowing ancestors and would thus not be secondary soft-bottom dwellers in an evolutionary sense. Examples are the modern cardiid genus *Corculum*, whose shell acts as a light collector for photosymbiotic algae as well as the Jurassic astartiid *Opisoma* (Accorsi Benini 1981) and the Triassic veneroid genus *Dicercocardium*, for which a similar mode of life has been suggested.

BYSSATE BAKEVELLIIDAE

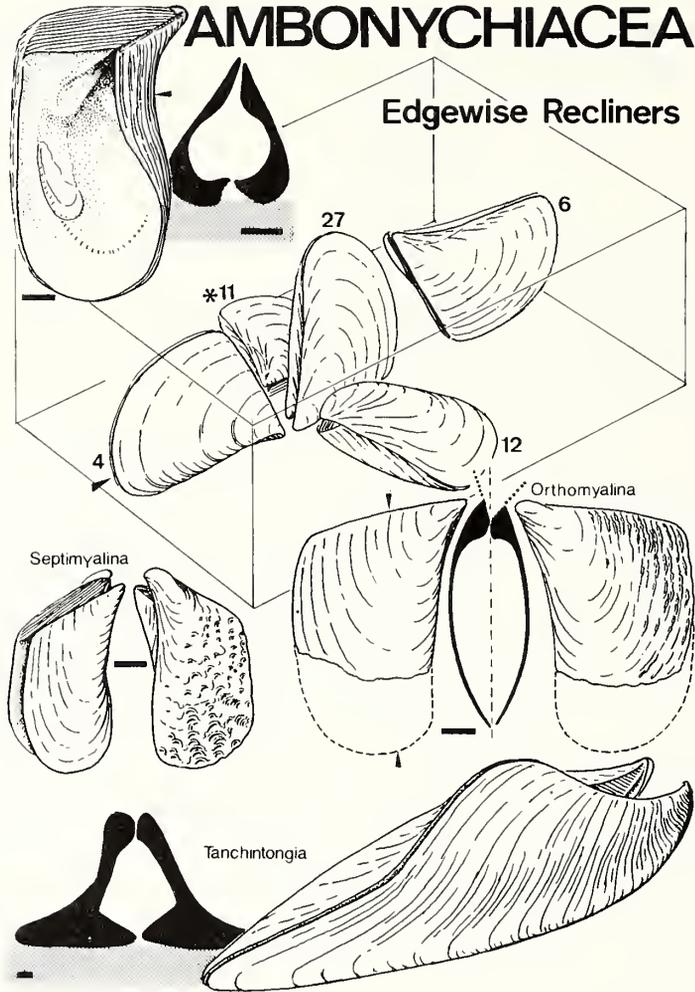


TEXT-FIG. 7. Compared to their more heteromorph derivatives (text-fig. 5), standard bakevelliid genera appear relatively thin-shelled, even if they are not diagenetically reduced to the calcitic outer layer. This indicates that byssal attachment remained an important factor in the stabilization of members living in soft-bottom habitats. Posterior elongation is a general tendency in the group. Because of the possibility of parallel and iterative evolution within the group, no evolutionary pathways can as yet be suggested. Note that mytiliform recliners are not represented except in *Mytiloperna* (text-fig. 5). This and the common occurrence of inequivalvedness indicates pleurothetically attached hard substrate epibyssates as the ancestral stock.

Pendant epibyssate attachment to hard substrates is documented in the saber-shaped *Gervillia lanceolata* of the Lower Toarcian Posidonia Shales (*a*: from Seilacher 1982*a*). This species lived attached to live ammonites and became characteristically oriented when their host died, sank to the bottom, and tipped over in a stagnant basin. By analogy, a similar (but not necessarily pseudoplanktonic) mode of life is assumed for other saber-shaped species (*G. olifex* Quenstedt, Sinemurian oil shales, Dusslingen, GPIT 1604/18; *G. angulati* Quenstedt, Upper Hettangian sandstone, Göppingen, GPIT 1604/19; *G. sp.*, Carnian, Lower Luning Farm, Pilot Mountains, Nevada, GPIT 1604/20).

Endobyssate mud stickers may be either modiolid in shape (*Agulerella pernooides*, Lower Aalenian dark shales, Sondelfingen; GPIT 1604/21–22; compare text-fig. 9) or lance-shaped (*Gervillella aviculoides*, Kimmeridgian limestones, Malagoszcz, Poland; GPIT 1604/23). Note, however, that the hinge is much longer than in similarly elongated epibyssate forms, because the ligament must act against the sediment pressure.

Flatly reclining forms are recognized by various degrees of inequivalvedness and twisting of the commissural plane. All figured species rested on the left valve, which is always more convex and bears stronger sculpture to increase adhesion to the sediment (*Bakevella subcostata*, Trigonodus Dolomite, Middle Triassic, Schwieberdingen, GPIT 1604/24; *Costigervillia crassicoستا*, Bathonian, England, from *Treatise Inv. Pal.* N 307). More elongated forms (*Hoernesia tortuosa*, Aalenian, Gundershofen; internal view from Aalen; GPIT 1604/25–26) have the possibility to grow in a twisted manner, thereby keeping the anterior end in an almost vertical position for endobyssate attachment, while the posterior part reclines flatly on the sediment (see series of cross-sections). A very large undescribed form (*H. sp.*, Sinemurian Limestones, Cerritos Bayos, Chile; GPIT 1604/27) combines twisting by about 30° with divaricate adhesion ribs on the lower valve.



TEXT-FIG. 8. The Ambonychiacea, differing from the isognomonids and the bakeveliids mainly by their ligament pattern, have evolved similar forms of recliners, but seemingly with a narrower range of strategies (no pleurothetic recliners).

In the Permian genus *Tanchitongia* (from Yancey and Boyd, 1983) an edgewise reclining stage is clearly indicated by broad triangular cross-section, extreme shell thickening, and giant size (compare *Mytiloperna*, text-fig. 5).

In *Orthomyalina slocomi* (Upper Pennsylvanian Vinland Shales, Atchinson Co., Kansas) the evidence is more conflicting. Its marked inequivalvity with respect to sculpture (even more pronounced in *Septimyalina*; GPIT 1604/29) and to the dip of the ligament areas (outside views and cross-section in posterior view; GPIT 1604/28) would suggest reclining on the more strongly sculptured left valve (asterisk position). Field measurements (with the kind help of Ron West, Manhattan, Kansas) of isolated bivalved specimens, however, clearly speak for an edgewise attitude—but with the ligament rather than with the byssus side down, as the shell outline and cross-section (GPIT 1604/30) would suggest (arrowed position). The dilemma is solved if we assume that upon irritation the byssus could pull the shell partly into the sediment and rotate it to what would become the preferred burial position.

Cup-shaped recliners

While it is the attached valve that develops into the cup in recliners derived from oysters and other cemented groups (*Spondylus*, *Chama*, *Hinnites*), the relationship is reversed in pleurothetic epibyssates. Here the valve originally facing the hard substrate remains flat and the stronger curvature of the exposed valve (usually the left one) determines the cup of the recliners. If this succession applies also to ontogeny an inversion of the life position is needed. Excessive thickening of the cup-shaped valve, as observed in *Gervilleioperna* (text-fig. 5), may facilitate this change. It is also interesting that *Lithioperna*, which is mostly found as a thin and elongated 'mud sticker', occurs occasionally in a cup-shaped and much thicker shelled ecophenotype (text-fig. 5).

Convergences. *Gervilleioperna* and *Lithioperna*, as well as truly isognomonid recliners, maintain the deep recess on the anterior side, in which the byssus was originally located. In malleids, in contrast, the byssus leaves the shell in an umbonal direction through a notch on the anterior side of the ligament area. It was probably this detail, plus the alivincular ligament, that allowed them not only to develop an anterior auricle (*Malleus*; text-fig. 6), but also rather symmetrical gryphaeid shapes without an anterior recess (*Gryphaeligmus*; Lewy 1982). Cup-shaped forms, but without excessive shell thickening and with a long hinge, have evolved in a number of other pteriomorph epibyssate families (*Cassianella*, *Rhaetavicula*).

Twisted recliners

Shell torsion is another deviation from the standard bivalve bauplan that has received considerable attention recently (McGhee 1978*a, b*; Savazzi 1981*a, b*, and in press *a, b*). It is restricted to groups that are endobyssate in principle and twist the plane of the commissure in the emerging posterior part of the shell in such a way that is more or less parallel to the sediment surface. The twist is counter-clockwise (i.e. in a right-hand screw) in the arcid genus *Trisidos* (McGhee 1978*a*) and clockwise, but less extensive, in species of *Barbatia* (Savazzi 1981*a*). Similarly backvevelliid species (text-fig. 7) may twist either clockwise (*Hoernesia socialis*; *H. tortuosa*; McGhee 1978*a, b*) or counter-clockwise (*Pseudoptera*; Savazzi, in press *b*), while twisting of the present-day mytilid *Modiolus americanus* is ecophenotypically determined and may go in either direction (Savazzi, in press *a*).

All twisted bivalves have in common that they are relatively thin-shelled (particularly if only the calcitic outer layer is preserved), have two adductors, and that the byssus leaves the shell in a ventral or anteroventral direction. Most show also a slight marginal overlap of their more convex valve, which facilitates the development of radial or divaricate ribs in this valve that are suppressed in the other. Since the more convex valve is usually the one that through the twist comes to face the sediment, its inequivalve sculpture may help to stabilize the shell on the mud (text-fig. 7).

Endobyssate 'mud stickers'

'Mud stickers' are much more common in byssate than in cemented stocks of secondary soft-bottom dwellers, probably because a byssal anchor can also be used to pull the shell deeper into the substrate if growth proceeds faster than sedimentation and if the animal is irritated. I prefer to see the endobyssate state in most cases as a secondary step, following epibyssate adaptation to rocky substrates. This view is also supported by the fact that the forms sticking more deeply in the sediment usually show more derived features than shallower endobyssates.

The most striking example is the genus *Pinna*. Its mode of life is commonly modelled after the sand-living Mediterranean species *P. nobilis*, in which only the anterior third of the shell is buried. The vast majority of tropical *Pinna* and *Atrina* species, however, live in mud with the truncated posterior margin level to the sediment surface (text-fig. 9). In this situation, opening of the shell becomes a major problem. It has been solved by making the outer shell layer flexible through a high organic content (therefore it has commonly disappeared during fossilization) and by retarding its enforcement with a nacreous inner layer. The elasticity of this shell aids the ligament in opening the valves in such a way that gaping is restricted to the exposed posterior margin, while the buried ventral

part of the commissure remains closed. Such a shell can be closed by the strong posterior adductor through elastic deformation.

The genus *Pinna*, which appears in the lower Carboniferous, has gone one step further. Here the valves become actively broken along a line that then forms a median carina at some distance from the growing edge. This carina heals on the inside by an elastic shell layer and is not covered by the more rigid nacreous layer except near the umbones. Thus it can act as a pseudoligament that in conjunction with the ligament restores the squarish cross-section after it has been deformed into a rhomb by the adductor (text-fig. 9).

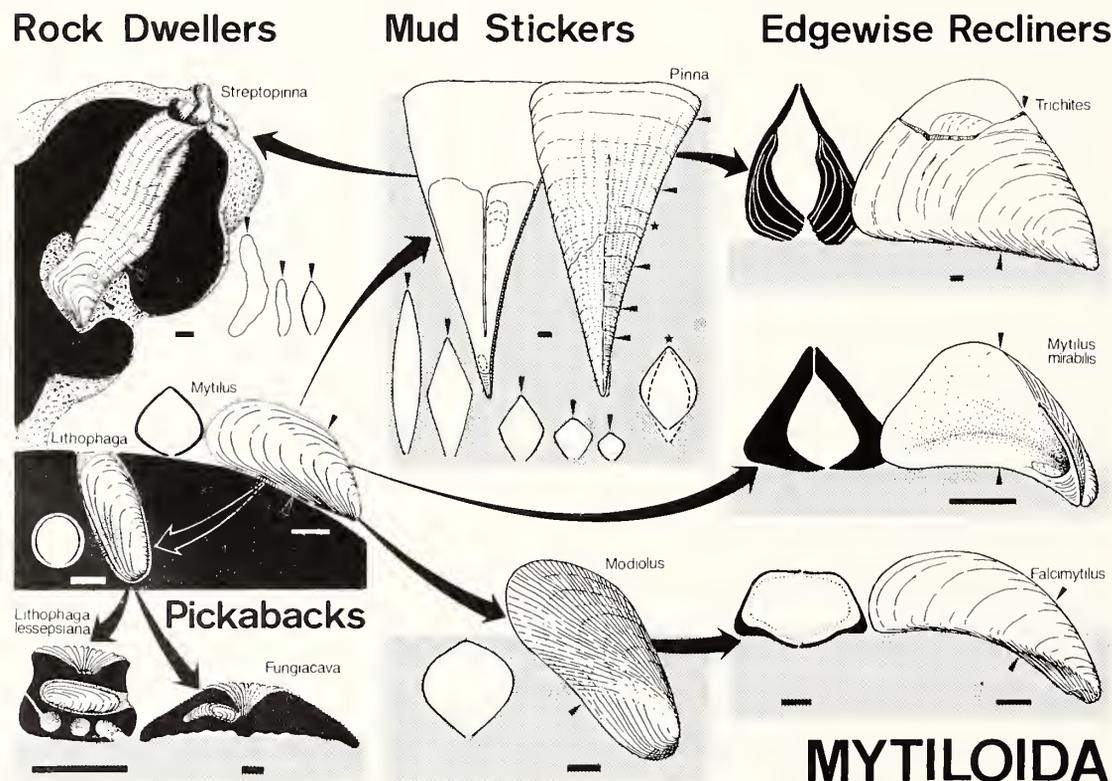
Convergences. While the functional adaptation of *Pinna* seems to have been unique, similarly elongated 'mud stickers' with a near-terminal umbo have evolved in several byssate groups such as the bakevelliids (text-fig. 7). In these cases, however, the shell was only half buried and equipped with a relatively long ligament strong enough to open the valves.

Among the mytilids, a very elongate *Modiolus* from Rhaetian mudstones of the northern Alps (Seilacher 1972, fig. 5B) bears a dense pattern of divaricate ribs that are not ratcheted. This sculpture is similar to that of the borer *Lithophaga* (text-fig. 9) and suggests that this derived species was sticking more deeply in the mud than the *Modiolus* stock.

Swimming bivalves

Although we will not go into the details of bivalve swimming in this context (Thayer 1972) it should be remembered that this secondary mode of mobility has evolved independently in two groups of living bivalves. Both are monomyarian and have an alivincular hinge and both are primarily epibyssate, but with different orientations.

The limids attach to hard substrates in an orthothetic attitude, which they also maintain while



swimming with the umbo ahead. The pectinids, in contrast, are pleurothetically attached and swim accordingly, but in the direction of the ventral margin. Nevertheless the ability to swim is not universal in either group, nor is it unequivocally expressed in shell morphology.

Limidae. *Plagiostoma lineata* from the Lower Muschelkalk is much more highly vaulted than limid swimmers today and has a broad anterior base for reclining. This shape, the common slope-oriented overgrowth by other organisms (Seilacher 1954), the nestling of juveniles in the byssal recess of adults (Jefferies 1960) as well as the common preservation in life position suggest that it was essentially an edgewise recliner. Similarly, the Lower Jurassic *Plagiostoma gigantea* is much too big and thick-shelled to have been an effective swimmer in spite of its flatter shape and smooth surface. Still it can not be excluded that these species were able to swim. An immobile mode of life can be safely assumed, however, for forms like the Middle Jurassic *Ctenostreon*, whose thick shell and anchoring spines suggest a heavy and possibly pleurothetic recliner.

Pectinidae. Similar difficulties arise with the interpretation of fossil scallops. *Pleuronectites laevigatus* from the Upper Muschelkalk was probably not a swimmer. Its left valve is more convex and more commonly overgrown than the right one. Thus the geometry is the opposite of what we find in

TEXT-FIG. 9. The origin of the Mytiloida is here placed in a rocky habitat in order to explain the loss of a burrowing foot. From forms like *Mytilus edulis* they evolved—either directly or via mud stickers—into the niche of edgewise recliners, but also back into the growing rocky substrate of reef corals. Another interesting lineage leads to rock borers and from there to commensalism with corals that had themselves become secondary soft-bottom dwellers.

Mytilus mirabilis (Calcari Grigi, Lower Jurassic, Vajo dell Anguilla, northern Italy; GPIT 1604/31) occurs in association with the recliners *Mytiloperna* and *Gervilleioperna* (text-fig. 5). It became stabilized by differential shell thickening and triangular cross-section.

Modiolus americanus (New Jersey; GPIT 1604/32) represents the adaptation of the mytilid shell shape to mud sticking.

Falcomytilus (Upper Jurassic; from *Treatise Inv. Pal.* N 277; cross-section from *Arcomytilus pectinatus*; GPIT 1604/33) is stabilized mainly by its square cross-section, with some shell thickening in the lower parts of the calcitic outer layer that is only preserved. A vestigial anterior lobe indicates derivation from modiolid ancestors.

Pinna diversicolor (Mindoro, Philippines; modified from Chinzei *et al.* 1982; GPIT 1604/34) is a perfect mud sticker. The opening function of its long and curved ligament is supplemented by the elasticity of the shell, in particular by the pseudoligament (Chinzei *et al.* 1982). This forms on the inside the median carina, where the shell becomes actively broken and is not covered by the internal shell layer. While the series of arrowed cross-sections was made from a plaster cast to show the secondary deformation, the one with a star is drawn from a saw cut through a fresh shell, whose pre-stressing deformed the posterior (broken line) and the anterior side of the cut in the opposite sense.

Trichites giganteus (Upper Jurassic, Schnaitheim, southern Germany; GPIT 1604/35) is one of the rare pinnids that have become edgewise recliners stabilized by triangular cross-section, extreme shell thickening, and giant size.

Streptopinna saccata (Okinawa; GPIT 1604/36) starts its life as a byssate nestler in the crevices of living coral colonies. It then becomes inevitably enclosed by the coral and continues to grow atop of the host. In this stage the two valves become united into a flat tube that can no more be closed. Accordingly, the posterior adductor remains in its juvenile (circle) position to where the soft parts are retracted in defence. On the other hand the loss of bivalvedness allows the tube to grow in a tortuous manner.

Lithophaga lithophaga (Adriatic; GPIT 1604/37) penetrates into calcareous rocks as a chemical borer. This is expressed by the elongate and almost cylindrical shell and fine divaricate ribbing.

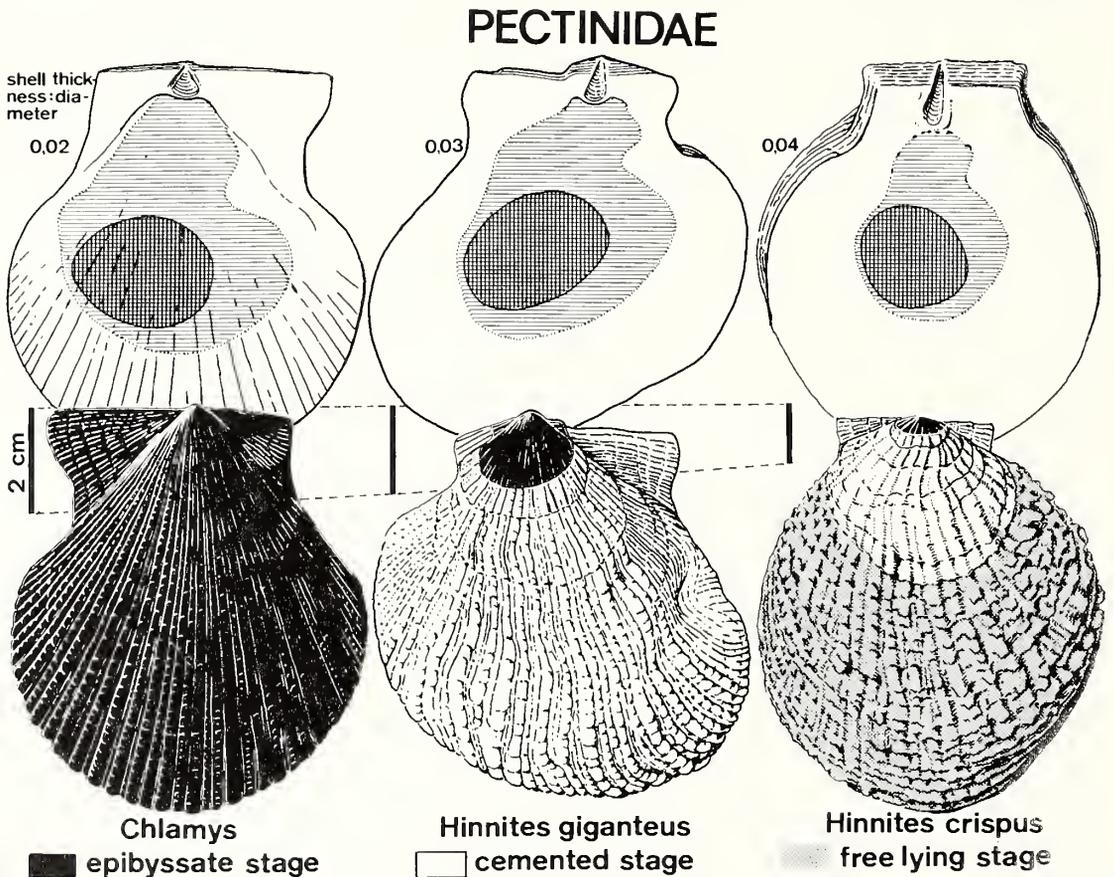
L. lessepsiana and *Fungiacava eilatensis* (from Savazzi 1982d) transfer this habit to live corals. These have themselves become secondary soft-bottom dwellers, either pickabacking with a sipunculid worm (left) or as disk-shaped recliners (right).

All scales = 1 cm.

modern *Pecten jacobaeus*, where the right valve is convex to allow easy take-off and sinking back in the right orientation, while the left valve is flat or slightly concave. Still an inverse life position in *Pleuronectites* is unlikely, because preserved colour bands are restricted to the left valve, like in many modern *Pecten* and *Chlamys* species.

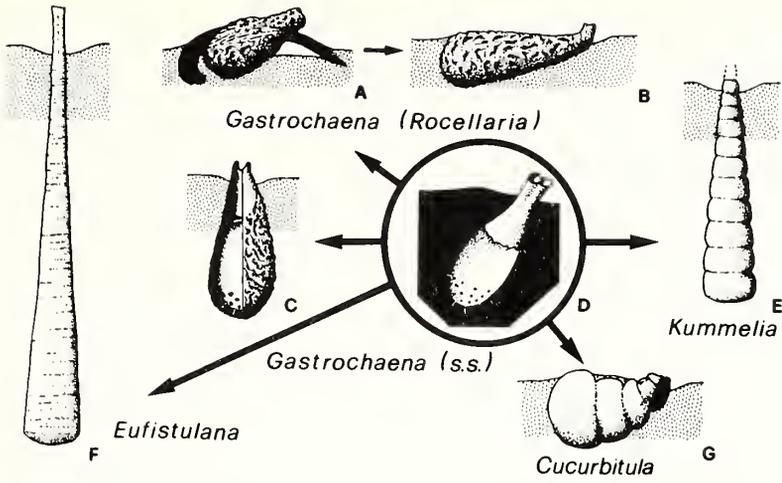
Two pectinid lineages have become sessile again by cementation. The spondylids retain the eyes along the mantle margin (Yonge 1968), while the shell grows thick and irregular as in oysters and allows the introduction of an isodont hinge. Spondylids that became free recliners again in later stages of their ontogeny have already been mentioned as homeomorphs of *Gryphaea*.

More unusual is the life history of *Hinnites giganteus* from the California coast. Here, transition to the cemented state does not occur in early growth stages, but later in ontogeny. Pliocene species went even a step further by becoming soft-bottom dwellers again. Accordingly, their shells record an ontogenetic succession of three adaptational stages (text-fig. 10). The epibyssate and swimming

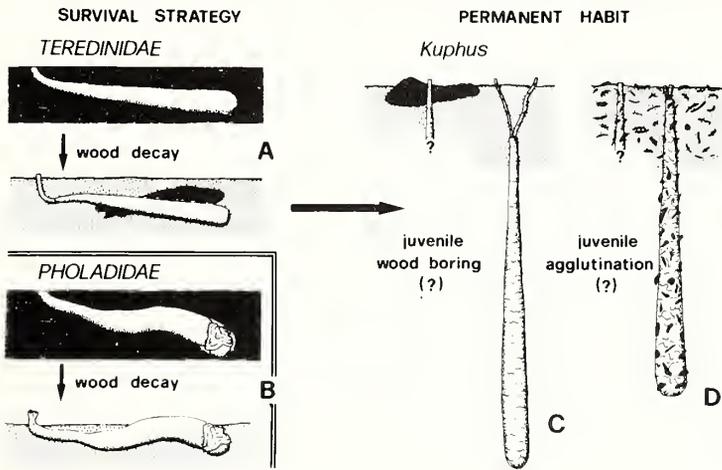


TEXT-FIG. 10. The double strategy of byssal attachment (with the right valve facing the substrate) and free swimming has enabled the scallops to become very efficient secondary soft-bottom dwellers (*Chlamys* sp., Peru; GPIT 1604/38). The return to a rocky substrate in *Hinnites giganteus* (California; GPIT 1604/39) is marked by the transition, after a juvenile *Chlamys* stage (black), to oyster-like cementation and irregular shell growth. Other species (*H. crispus*, Pliocene, N. Italy; GPIT 1604/40, courtesy of E. Savazzi) have again become recliners by adding a third stage, in which the shell grows very large and thick (shaded part). Note that in this stage growth becomes also more regular and that anchorage in the sediment is provided by a new kind of scaly spines.

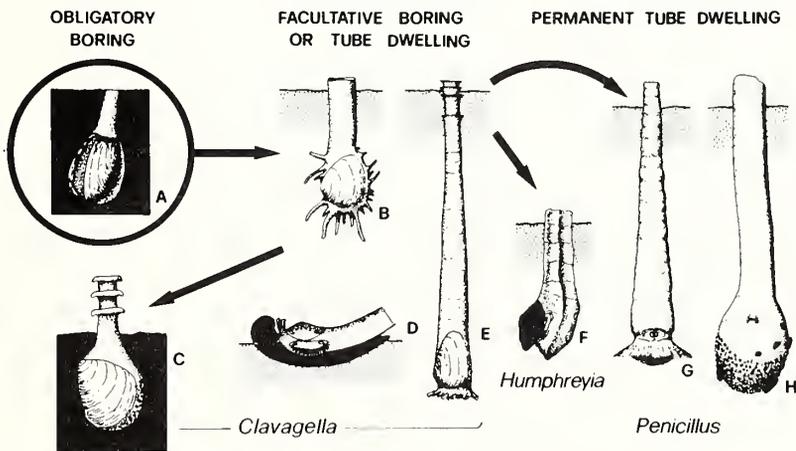
GASTROCHAENACEA



PHOLADACEA



CLAVAGELLACEA



TEXT-FIG. 11. Tube dwelling pelecypods. This unique adaptation to secondary soft-bottom dwelling has evolved only in borers, but independently in three groups and in different genera within them. The two valves remain either free within the bag-like cyst (*Gastrochaenaceae* and *Teredinidae*), or they become incorporated (*Pholadidae*, *Clavagellacea*). Through the tubelets at the lower end of *Clavagellacean* cysts water can be expelled for piston-burrowing (from Savazzi 1982c).

Chlamys stage has a regular shape, while growth becomes irregular and xenomorphic in the following oyster stage. In comparison with the modern, rock-dwelling species, these two stages are reduced in size and relatively thin-shelled in the soft-bottom dwellers in order to fit the unstable substrate of available dead shells. Their third growth stage, in contrast, reflects the mode of life of an immobile recliner, i.e. the shell now grows large and thick for increased stabilization. This evolution transition may have occurred more than once, because one of the two studied species (text-fig. 10) is an ambivalent recliner, while the other (from the Pliocene of New Zealand) is consistently inequivalve with the attached right valve becoming thicker-shelled and cup-shaped in the reclining stage. It is also noteworthy that with the return to a more regular growth in this stage the sculpture does not continue in the *Chlamys*-stage fashion, but attains a new character.

STOCKS BORING IN HARD SUBSTRATES

The comprehensive studies of Enrico Savazzi (1982*c, d*) have shown how boring bivalves returned to soft bottoms. In three groups (Pholadacea, Gastrochaenacea, Clavagellacea) we observe the convergent development of calcareous crypts (with or without inclusion of the valves). These become tube-shaped because further growth is restricted to one or both ends of the closed cylinder (text-fig. 11).

TEXT-FIG. 12. Horn-shaped growth provides secondary soft-bottom dwellers with the possibility to passively become righted-up and replanted in the sediment.

The 'Savazzi effect' (from Savazzi 1982*c*) implies that a washed-out horn-shaped body comes to rest on the sediment in a lateral position with the convex side facing the current and that it then tips into the erosional depression forming on the upcurrent side. This mechanism may be enhanced by differential weighting of the skeleton on the convex side and near the apex. Complete burial may be avoided by expanding structures that keep the open end at the surface like a snow shoe.

The crypt of *Cucurbitula cymbium* (Malaysia; GPIT 1604/41) lacks differential weighting, but the presence of soft-bodied snow shoe expansions (dotted) is suggested by accessory perforations on the concave side near the siphonal opening.

Gryphaea arcuata (Lower Jurassic, southern Germany; GPIT 1604/5), unlike more dilatate species, is most perfectly adapted to the Savazzi effect by its rounded cross-section and weight distribution.

The sessile gastropod *Maoricrypta radiata* (Miocene, Waipara Gorge, New Zealand; GPIT 1604/42; courtesy of D. Mackinnon, Christchurch) resembles *Gryphaea* in shape and excessive shell thickness in the apical part. Still it is doubtful whether it had a similar life position on the soft bottom, because the differential weighting of the apical part is on the concave rather than on the convex side and because soft-bottom species of the related genus *Crepidula* tend to form horn-shaped colonies, to whose stabilization the shell thickening would have also contributed.

In horn-shaped species of *Hippurites* (Gosau, Upper Cretaceous; Reichenhall, *Inst. hist. Geol. Pal.*, Munich; courtesy of R. F. Höfling) the internal pillars of the right valve are situated on the convex side for differential weighting. Tabulate fill structures (shaded, in the studied specimen recrystallized) provide additional weight to the apical part. Horn corals provide many good examples.

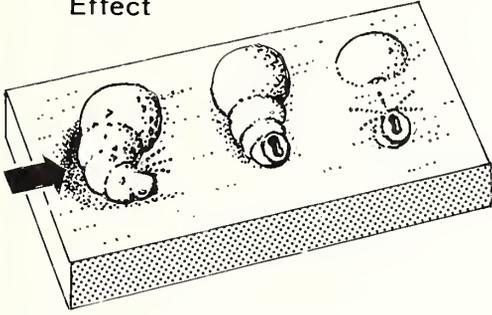
In *Phaulactis* (after Wedekind 1927) differential weighting is obtained by secondary thickening of septa in the apical and convex part of the calyx.

In Archaeocyathid sponges (after *Treatise*) this explanation is more problematic, because the buried parts of the body would be excluded from active feeding. It should be tested whether the horn shape in some figured species is a regular feature.

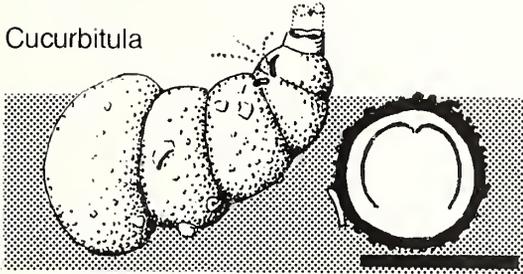
In the lepadomorph barnacle *Euscalpellum zelandicum* (Senonian, Waipara Gorge, New Zealand; reconstruction from Tübingen material) the flexible pedicle is transformed into a solid calcareous body with regular horn shape and root-like scales concentrated on the apical and convex surfaces. The belemnite-like cross-section shows that the central cavity is always excentric, thus providing differential weighting of the convex side.

HORN SHAPED RECLINERS

SAVAZZI
Effect



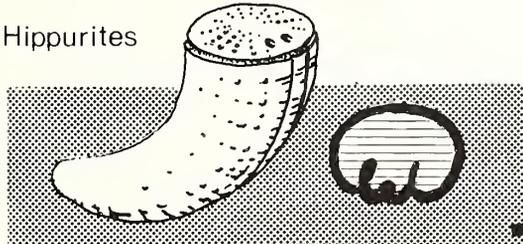
Cucurbitula



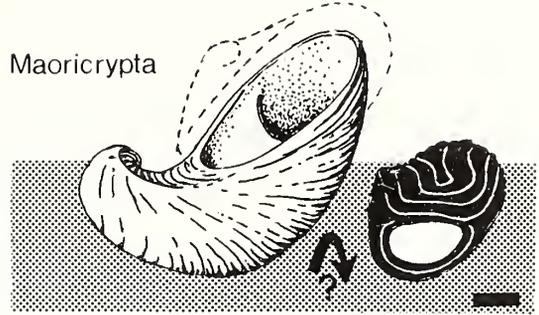
Gryphaea



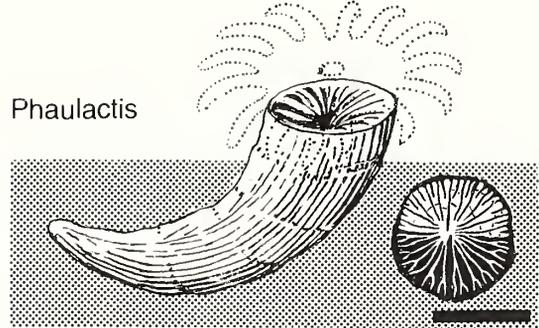
Hippurites



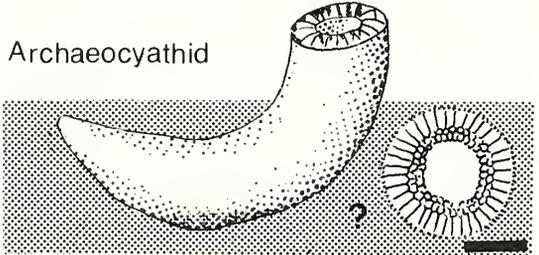
Maoricrypta



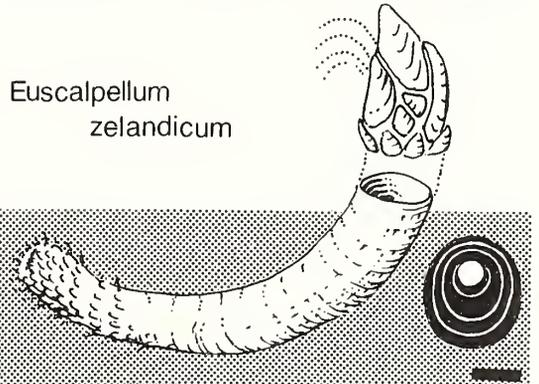
Phaulactis



Archaeocyathid



Euscalpellum
zelandicum



Tube dwellers

The multiple parallel evolution of crypts between and within the three groups (text-fig. 11) becomes understandable if we consider the evolutionary constraints and options involved. All tube dwellers seem to be derived from ancestors that bored in biogenic materials, such as shell, coral, or wood. Such materials, smaller pieces of which are also available on the soft bottoms of low energy environments, favour the formation of calcareous linings that seal the borehole against a porous substrate and allow repair when this substrate has rotted or broken away. Thus cyst formation can be viewed as an extension of former emergency strategies (Savazzi 1982c).

Such tubes could lie simply at the surface; but some species have evolved special mechanisms that allow them to become planted in the way of 'mud stickers'. The most spectacular adaptation is found in some clavagellids, such as *Penicillus*, whose crypt grows only at the posterior (siphonal) end. This allows the lower part of the crypt to develop into an expanded chamber with an elaborate system of perforations and tubelets, through which water can be expelled into the sediment to produce a piston-boring effect (Savazzi 1982c, fig. 15). The gastrochaenid genus *Cucurbitula*, in contrast, becomes passively buried. Its tubes grow consistently in a curved fashion. Exposed to a current, such a horn-shaped cyst will come to rest on its side and orient itself with the convex side upcurrent. In this position eddies will carve out the sediment in front of it, so that the body automatically tumbles into the depression (Savazzi 1982c, fig. 5). This principle which has so far only been tested in the flume (Savazzi 1982c), can also be applied to fossil horn corals, to *Gryphaea*, to horn-shaped rudists, and to the Cretaceous cirriped *Euscalpellum zelandicum* (Withers 1951), in which the convex side of the horn is additionally weighted to facilitate the planting process (text-fig. 12).

Commensals

Another pathway into the soft-bottom habitat is commensal association. For boring bivalves it is favoured by the tendency of other secondary soft-bottom dwellers to develop massive skeletons. If the hosts are molluscs, no special adaptations are necessary other than the selective settlement of the larvae and an adequate miniaturization of the adults. But in the fossil state it may be difficult to distinguish commensal borings from those made in dead shells, except by callus formation and the avoidance of surfaces that were covered by soft parts while the host was alive. Not so in solitary corals, in most species of which the skeleton is covered by living tissue and can grow on the whole external surface. Their infestation requires the ability to penetrate living tissue and to cope with substrate growth and is therefore likely to be more host-specific. Modern (and some fossil) examples, as reviewed by Savazzi (1982d), all involve mytilid borers. Since the mytilid bauplan does not allow the formation of long siphons, this group was not only excluded from the tube-dwelling strategy discussed in the previous paragraph. In a growing coral skeleton, mytilid borers are also forced to keep in contact with the surface by boring backwards and filling the evacuated anterior part of the bore hole with calcareous deposits or septa recognizable in the fossil state.

Mytilid coral borers, which make their excavations mainly by chemical means, also maintain special attitudes and positions with reference to the host. In their horizontal bore holes they lie with the umbones lowermost, so that the inhaling current keeps clear of the sediment. *Fungiacava eilatensis* (text-fig. 8) always settles in the gastrocoel of large mushroom corals so that it can participate (a parasite rather than a commensal) in the host's meals (Savazzi 1982d, figs. 19–20). *Botula cordata* bores Eocene trochiform corals (Savazzi 1982d, figs. 17, 18) from the outside wall, but the opening of its borehole follows the upward growth of the 'mud sticking' host. *Lithophaga lessepsiana* (text-fig. 8) has a similar position on *Heteropsammia*. In this case the host itself has established a symbiotic relationship with a mobile sipunculid worm (*Aspidosiphon*), for which it builds a shelter and in return is held in an upright position and carried around. 'Pickaback' strategies like the last example are much more common and more highly developed in associations of encrusting sponges, hydrozoans, actinians, corals, and bryozoans with hermit crabs.

CONCLUSIONS

1. In contrast to one current view that evolution, being a stochastic process, can produce virtually anything, actual lineages are strongly channelled into a limited number of pathways by the constraints derived from inherited bauplans, fabrication principles, and the adaptive landscape. As a result, adaptational histories appear quasi-deterministic, with convergent, iterative, and parallel evolutions being the rule rather than the exception. This sets a limit to the cladistic analysis within bivalve groups.

2. Tempo and degree of evolutionary change depend largely on the ecological circumstances. While shell forms in the large group of burrowing bivalves have remained conservative (apart from the introduction of burrowing sculptures in some species), they show rapid and sometimes bizarre modification in the small group of secondary soft-bottom dwellers.

3. In the latter group, rapid change was necessary to cope with the problem of passive stabilization on a mobile substrate. It was also facilitated by the 'morphogenetic shunting' induced by miniaturizing stepping stones that pave the way for sessile rock dwellers into the soft-bottom habitat and the following trend towards gigantism for autonomous stabilization.

4. Constructional morphology, if applied to larger groups and used in a comparative way, is a valid tool in evolutionary studies, because it leads to an understanding of evolutionary pathways and thus complements the cladistic reconstruction of phylogenetic relationships.

Acknowledgements. This project was started in 1979 during a sabbatical semester granted by the Tübingen university. Several trips have been supported by the SFB 53; others were provided by a professorship of the University of Kansas (1979) and the invitation as a 'German National Fellow' by the New Zealand Universities (1982). During the years, many colleagues have contributed in the field with their special knowledge of modern and fossil organisms, in particular Dr. B. Rosell (University of the Philippines, Manila), Dr. K. Chinzei (University of Tokyo), Dra. C. Broglio-Loriga (University of Ferrara), Dr. A. Sasekumar (University of Malaya, Kuala Lumpur), Dr. G. Chong-Diaz (University del Norte, Antofagasta, Chile), Dr. H. Wanless (University of Florida, Miami), Dr. R. West (Kansas State University, Manhattan). Others mentioned in the text have kindly loaned specimens from their collections. Without their efforts this study would have been impossible. I thank also my Tübingen colleagues. Earlier versions of the manuscript have been critically read by Dr. W. E. Reif (Tübingen) and Dr. R. Thomas (Lancaster, Pennsylvania). Typing was done by Mrs. H. Wörner, photographic work by Mr. W. Wetzel. I also thank the Palaeontological Association, for committing me, through its annual lecture 1983, to write and draft this paper.

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SILURIAN ODONTOPLEURID TRILOBITES FROM GOTLAND

by LARS RAMSKÖLD

ABSTRACT. Trilobites of the family Odontopleuridae are described from the Silurian of Gotland, Sweden. Twelve species and subspecies (nine named, of which four are new) are assigned to four genera. *Anacaenaspis gotlandensis* Bruton, 1967 is considered to be a junior subjective synonym of *Acidaspis pectinata* Angelin, 1854, which is therefore the type species of the genus. *Primaspis* (*Taemasapis*) Chatterton, 1971 is regarded as a junior subjective synonym of *Dudleyaspis*, which in addition to the nominate subgenus includes *D. (Snoderaspis)* subgen. nov. *Ceratocephala barrandii* (Fletcher in Salter, 1853), *A. pectinata*, *Leonaspis coronata* (Salter, 1853) and *L. crenata* (Emmrich, 1844) are also known outside Gotland. New species and subspecies described are *D. (Dudleyaspis) hamvensis*, *D. (Dudleyaspis) uucifera*, *D. (Snoderaspis) krausi*, and *Leonaspis coronata bufo*.

THE first odontopleurid trilobite described from Gotland was *Odontopleura crenata* Emmrich, 1844, which is now referred to as *Leonaspis*. Angelin (1851, 1854) included a number of additional species in his monograph of Scandinavian trilobites. Lindström (1885) discussed these, but no new species were described by him or other workers until Bruton (1967) revised the Gotland odontopleurids, and gave a modern description of previously known and new species. Since Bruton's study, a wealth of new material has come to light, some from old collections, but most through recent collecting. This material includes previously unknown taxa and more complete specimens of most of the known species. It also provides information for a more satisfactory definition of the genera *Anacaenaspis*, *Dudleyaspis*, and *Primaspis*.

STRATIGRAPHY AND LOCALITIES

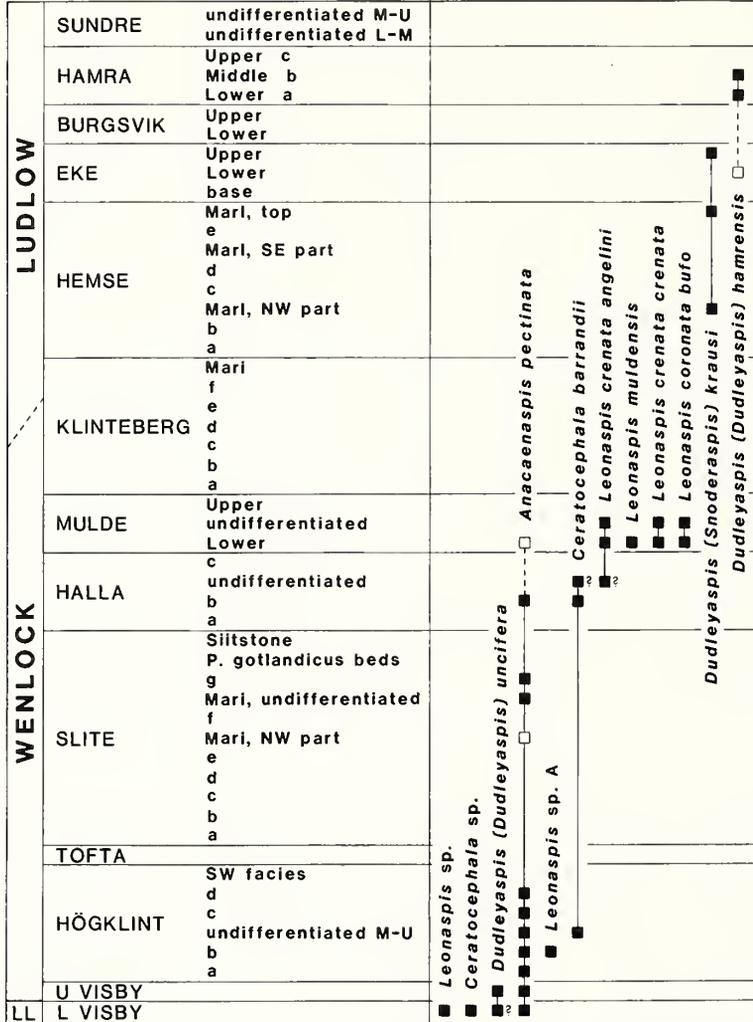
The stratigraphical distribution of the species as plotted in text-fig. 1 follows the same scheme as that in Ramsköld (1983). Again it must be emphasized that this distribution does not necessarily reflect the chronological appearance and disappearance of the various taxa. Locality names followed by numbers are defined in Laufeld (1974*b*), Larsson (1979), and Ramsköld (1983). Two new localities are described here in conformity with this system. DJUPVIKSVÄGEN 1, 635572 164170 (CJ 5512 2873), Eksta parish, *c.* 3950 m SSW of Fröjel church. Topographical map sheet 6 I Visby SO. Geological map sheet Aa 164 Hemse. Ditch exposure along north side of road, from the forest edge and 20 m south-east, *c.* 1100 m north-west of the intersection of road 140 with the road to Djupvik. Mulde Beds, undifferentiated. VALVE 2, 637352 164018 (CJ 7299 2859), Eskelhem parish, *c.* 2800 m NNW of Västergarn church. Topographical map sheet 6 I Visby SO. Geological map sheet Aa 160 Klintehamn. Exposure in ditch running south-east from road, then curving first north then south into the forest. The road/ditch intersection is *c.* 225 m south-east of the house at Valve. Slite Beds, Slite Marl.

For other localities twelve figure grid references are given according to the Swedish National Grid (Rikets nät) system whenever possible.

SYSTEMATIC PALAEOLOGY

The terminology employed here is essentially that of Harrington *et al.* (*in* Moore 1959). Lateral glabellar lobes and furrows are labelled following Jaanusson (1956, p. 37). Terms for the orientation used during photography are those of Whittington and Evitt (1954, p. 11). Specimens are deposited in

Naturhistoriska Riksmuséet, Stockholm (prefixed Ar), in the Type Collection of the Geological Survey of Sweden (SGU), and in the Royal Scottish Museum, Edinburgh (RSM). Unless stated otherwise, illustrations in the plates are of external surfaces of exoskeletons. All specimens were painted with matt black opaque and coated lightly with ammonium chloride prior to photography. Most specimens with numbers beginning Ar51 were collected by the author; other collectors are indicated in the plate explanations when known.



TEXT-FIG. 1. Occurrence of Odontopleuridae in the different stratigraphical units of Gotland. Solid squares represent specimens assigned definitely to a taxon and open squares represent compared forms. A square with a question mark indicates that the horizon is uncertain. The stratigraphical column is a practical way of illustrating the distribution of the species within the mapped units, and is not necessarily a reflection of the chronological appearance and disappearance of various taxa. Diagram modified from Laufeld (1974a, p. 124).

Family ODONTOPLEURIDAE Burmeister, 1843
 Subfamily ODONTOPLEURINAE Burmeister, 1843

Discussion. A re-evaluation of the genera *Anacaenaspis*, *Dudleyaspis*, and *Primaspis* is necessary on the basis of the Gotland material described here (for summary of previous concepts see Chatterton *et al.* 1979, p. 828, and Thomas 1981, pp. 83, 85). When Chatterton (1971) erected *Taemasaspis* as a subgenus of *Primaspis* he noted its close similarity and possible relationship to *Dudleyaspis* (as diagnosed by Bruton 1968). After transferring *Odontopleura portlockii* Hawle and Corda, 1847 (included by Bruton in *Dudleyaspis*) to *Taemasaspis*, Chatterton considered that the subgenus fitted best within *Primaspis*. However, several features indicate that *Taemasaspis* is closer to *Dudleyaspis* than to *Primaspis*, including the straight-eye ridge, the shape, size, and position of the genal spine, the wide thoracic axis, the insignificant fulcral swellings, and the disposition and relative sizes of the pygidial border spines. The widely separated eyes, set in a horizontal plane well below L1 and never overhanging the posterior border furrow due to their rather forward position, are also indicative of affinities with *Dudleyaspis*. Thomas (1981) noted these similarities and regarded *Taemasaspis* as a junior synonym of *Dudleyaspis*; this study confirms these similarities, and Thomas is followed here. A second subgenus of *Dudleyaspis*, *Snoderaspis*, is erected here. When Bruton (1967) erected *Anacaenaspis*, he selected as holotype of the type species *A. gotlandensis* a specimen that is recognized here as belonging to Angelin's (1854) species *pectinata*. The type species therefore becomes *A. pectinata*. This species belongs to a distinct and homogenous group of Silurian odontopleurines, which in addition includes *Acidaspis callipareos* Thomson, 1857, *Anacaenaspis gigantea* Šnajdr, 1978, *A. phasganis* Thomas, 1981, and *Primaspis kruegeri* Schrank, 1969. Generic status for this group seems justified, and *Anacaenaspis* is therefore recognized here. The genus is close to *Primaspis* Richter and Richter, 1917. *Primaspis* species fall into two morphological groups; the type species *P. primordialis* (Barrande, 1846), from the Bohemian Caradoc, and the remainder. Přibyl and Vaněk (1965) erected the subgenera *P. (Primaspis)* and *P. (Meadowtownella)*, respectively, for the groups. These subgenera have rarely been used by subsequent workers. The *Meadowtownella* group is very coherent, and seems in many respects to be related, and perhaps ancestral to *Dudleyaspis*. *P. primordialis*, on the other hand, is similar in some features to *Anacaenaspis*, e.g. in the lengthened occipital ring and the overall shape of the pygidium. However, the free cheek of *primordialis* (figured Šnajdr 1956, pl. 2 (33), fig. 10) is not of *Anacaenaspis* type, but is similar to other *Primaspis* (i.e. the *Meadowtownella* group). Known *primordialis* specimens are not well preserved, but the available material seems to justify retaining *Primaspis* and *Anacaenaspis* as separate genera.

Genus ANACAENASPIS Bruton, 1967

Type species. Emended here; *Acidaspis pectinata* Angelin, 1854, from the uppermost Llandovery and Wenlock of Gotland (Lower Visby to Halla Beds), the Upper Llandovery of Scotland, and the Wenlock of Estonia.

Diagnosis. Occipital ring long (exsag.). Longitudinal furrow distinct. Antennal notch marked. Eye ridges curved, eye set close to posterior border furrow, level with L1. Genal spines very long, reaching behind thorax, base not raised markedly above lateral border. Ten to twelve long and stout cephalic border spines, the posteriormost the largest and at right angles to genal spine. Fulcral swellings large. Pygidium with major border spines much longer and stouter than, separated from, and set above the plane of, secondary border spines.

Remarks. *Anacaenaspis* is a clearly defined genus, although Bruton's (1967) concept of it was partly different from mine, because of the restricted amount of material available to him. Apart from the holotype of *A. gotlandensis*, all specimens assigned by Bruton to that species are referred here to *Dudleyaspis (Snoderaspis) krausi* sp. nov. The second species originally included, *A. emarginata* (Schmidt, 1885), is regarded here as a junior subjective synonym of *pectinata*.

The relationship of *Anacaenaspis* to *Primaspis* is discussed above. The genus is also close to *Acidaspis* Murchison, 1839, the major difference being the large median occipital spine in the latter.

Anacaenaspis pectinata (Angelin, 1854)

Plate 26, figs. 1-13; Plate 27, figs. 1-10; text-fig. 2

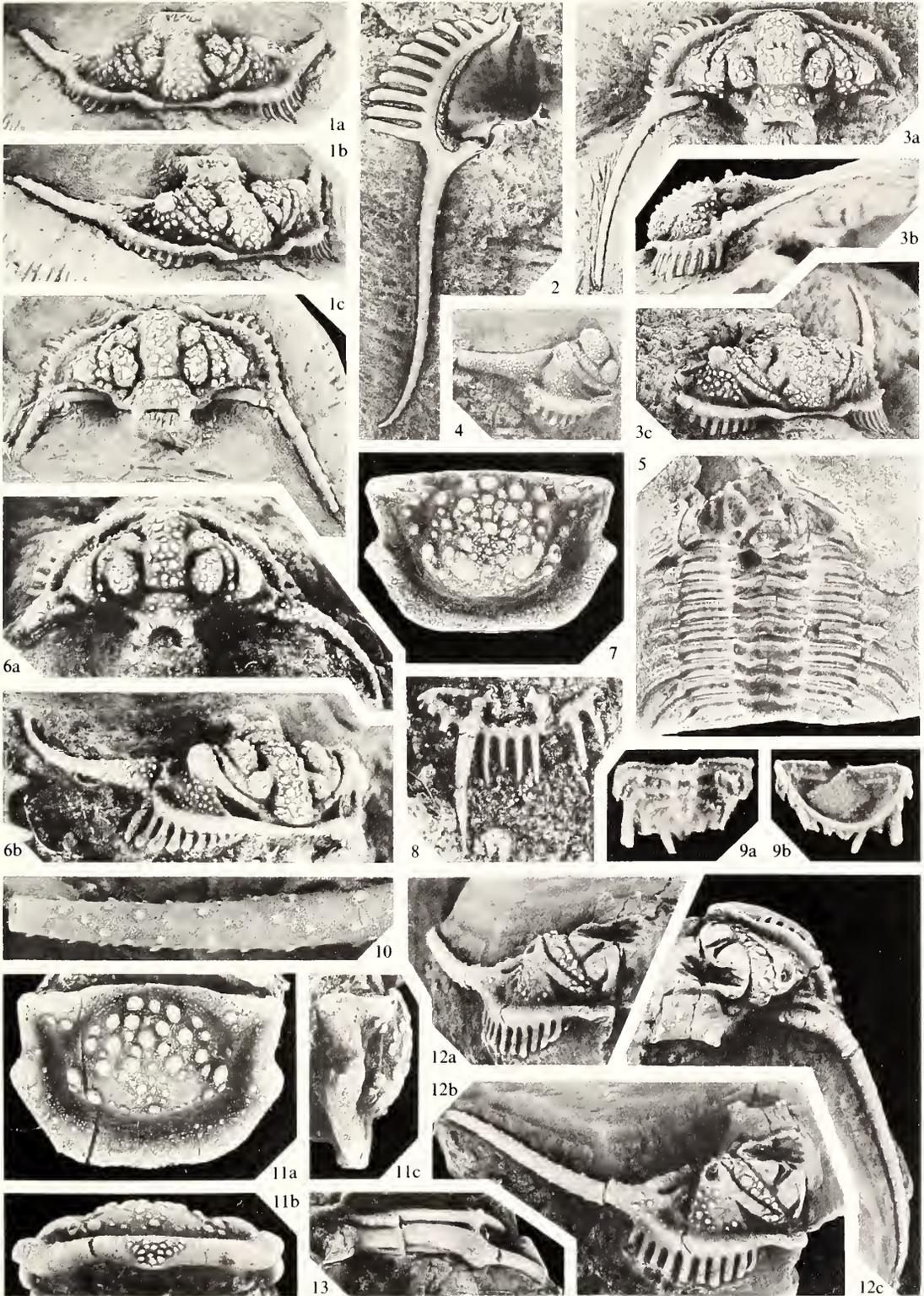
- 1851 Angelin, pl. 21, fig. 5 [illustration only, without name].
 v* 1854 *Acidaspis pectinata* Angelin, p. 33 [referring to 1851 figure].
 . 1885 *Acidaspis pectinata* Angelin; Lindström, p. 55.
 . 1885 *Acidaspis emarginata* Schmidt, p. 23, pl. 1, fig. 1.
 1889 *Acidaspis pectinata* Angelin ? = *Odontopleura ovata* Emmerich; Jaekel, p. 711 [non Emmerich, 1839].
 1896 *Acidaspis pectinata* Angelin; Lake, p. 243.
 1949 *Acanthaloma pectinata* (Angelin); Prantl and Přibyl, p. 139.
 v. 1967 *Acidaspis pectinata* Angelin; Bruton, p. 234, pl. 35, figs. 3, 5, 6.
 v. 1967 *Anacaenaspis gotlandensis* Bruton, p. 236, pl. 36, figs. 2-4, non pl. 35, fig. 10, pl. 36, fig. 5 [= *Dudleyaspis* (*Snoderaspis*) *krausi* sp. nov.].
 . 1967 *Anacaenaspis emarginata* (Schmidt, 1885); Bruton, p. 237, pl. 35, fig. 14, pl. 36, fig. 1 [with synonymy list].
 1969 *Primaspis gotlandensis* (Bruton); Schrank, p. 722 [pars].
 1973 *Primaspis* (*Meadowtownella*) *gotlandensis* (Bruton); Přibyl and Vaněk, p. 303.
 1978 *Anacaenaspis gotlandensis* Bruton; Šnajdr, p. 31 [pars].
 v. 1979 *Acidaspis pectinata* Angelin; Bruton in Jaanusson *et al.*, p. 116.
 v. 1979 *Anacaenaspis* sp.; Bruton in Jaanusson *et al.*, p. 116.
 1979 *Anacaenaspis gotlandensis* Bruton; Chatterton *et al.*, p. 828 [pars].
 1981 *Acidaspis pectinata* Angelin; Thomas, p. 81.
 1981 *Anacaenaspis gotlandensis* Bruton; Thomas, p. 85 [pars].
 . 1981 *Anacaenaspis dealgach* (Lamont, 1978); Clarkson and Howells, p. 529, pl. 81, fig. 2, pl. 82, figs. 1-4 [with synonymy list].
 . 1982 *Anacaenaspis dealgach* (Lamont, 1978); Howells, p. 58, pl. 15, figs. 10, 15.

Lectotype. Selected here; Ar30867, incomplete cephalon, Plate 26, fig. 12a-c, used for the composite figure of Angelin 1851; refigured Bruton 1967, pl. 35, fig. 6; almost certainly from Högklint Beds, Visby area.

Bruton (1967, p. 234) thought that this specimen may be one of Angelin's (1851, 1854) syntypes. The shape of the genal spine, faithfully depicted by Angelin, is due to a postdepositional fracture and secondary rotation of the spine, a deformation unlikely to be exactly similar in any other specimen. In addition, the specimen (then largely embedded in matrix) was broken at some time into three pieces. None of the fractures reveals the presence of occipital spines, but it is obvious from the pieces that the cephalon must be broken across the occipital ring, as stated by Angelin, and lacking the left half. All these factors indicate that this is the specimen used by Angelin for his reconstruction of the cephalon. Additional preparation has now revealed the shape of the occipital ring,

EXPLANATION OF PLATE 26

Figs. 1-13. *Anacaenaspis pectinata* (Angelin, 1854). Upper Visby Beds (9). Högklint Beds, unit a (2, 3), unit b? (12), unit d (5, 8). Slite Beds, Slite Marl (1, 4, 10, 11, 13). Halla Beds, unit b (6). Hörsne kanal (6), Ireviken 1 (2, 3), Rönklint (9), Valbytte 1 (1, 10, 11, 13), Vattenfallsprofilen 1 (5, 8), Visby (12), shore of Eketräsk (4), Jaani Stage, Paramaja pank, Saarema, Estonia (7). 1a-c, Ar51358, cephalon, anterior, anterolateral, and exterior views, $\times 3$. 2, Ar51629, partial cephalon with complete spine fringe and genal spine, interior view, $\times 2.5$. 3a-c, Ar51630, cephalon, exterior, lateral, and anterolateral views, $\times 2.5$. 4, SGU 1446, partial cephalon, anterolateral view, note dense tuberculation, $\times 4.5$ (coll. G. Liljevall). 5, SGU 1448, flattened exoskeleton lacking pygidium, ventral view, note displaced hypostome, $\times 4$ (coll. O. W. Wennersten 1890). 6, SGU 1447, small cephalon, exterior and anterolateral views, $\times 9$ (coll. G. Liljevall 1910). 7, Ar51750, hypostome, exterior view, $\times 8$ (coll. V. Jaanusson 1939). 8, Ar49890, small pygidium, $\times 10$. 9a, b, Ar51709, slightly distorted transitory pygidium, dorsal and ventral views, $\times 18$. 10, Ar51350, genal spine showing thorn-like tubercles with pore-openings, $\times 8$. 11a-c, Ar51354, large hypostome, exterior, posterior, and lateral views, $\times 6$. 12a-c, lectotype Ar30867, partial cephalon, figured Angelin 1851, pl. 21, fig. 5, refigured Bruton 1967, pl. 35, fig. 6, anterior, anterolateral, and exterior views, $\times 3$. 13, Ar51351, partial thoracic segment, $\times 2$.



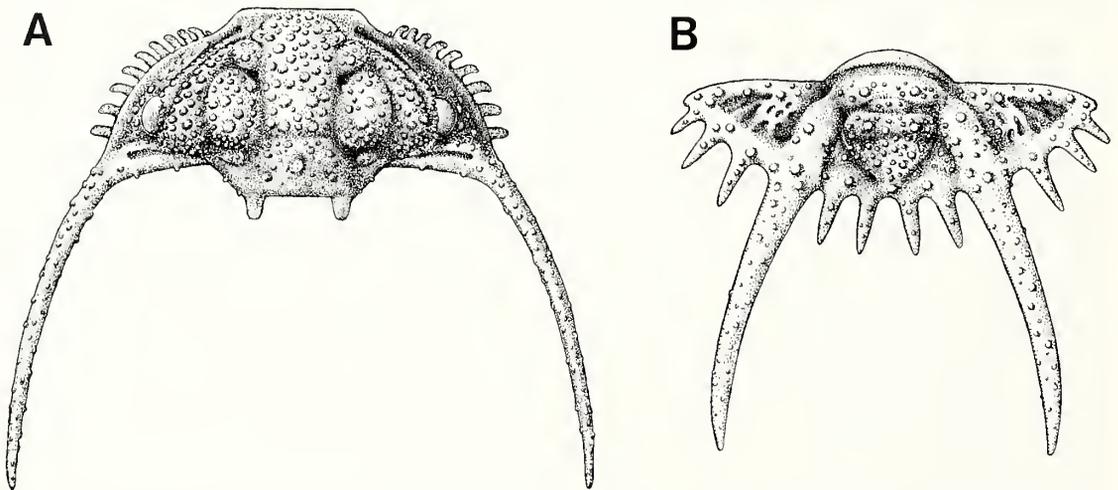
which (together with other features) necessitates a removal from *Acidaspis*. The pygidium figured by Angelin cannot be identified with certainty.

Additional material. The Scottish material from the Pentland Hills is of late Llandovery age (Clarkson and Howells 1981; see under 'Discussion' below). Estonian specimens are known from Koguva säär, Island of Muhu, and Paramaja pank, Saaremaa, both Jaani Stage (upper Wenlock; Bruton 1967). On Gotland this species ranges from the uppermost Llandovery to the upper Wenlock.

Localities. Lower and Upper Visby Beds: Lummelunda parish—Rönnklint (641181 165698). Upper Visby Beds: Västerhejde parish—Fridhem (638860 164375). Höglint Beds, unit a: Stenkyrka parish—Ireviken 1. Unit b: Visby parish—dump at Visby harbour (639275 164800), Västerhejde parish—Fridhem (638885 164425). Units b-d: Visby parish—Vattenfallsprofilen 1. Slite Beds, Slite Marl: Eskelhem parish—Valve 2, Färö parish—Haganäs 1; the southern shore of Eketräsk, Othem parish—Slite, Sanda parish—Valbytte 1. Slite Beds, unit g: Othem parish—Slite. Halla Beds, unit b: Hörsne parish—Hörsne kanal (638493 166725). The holotype of *A. gotlandensis* Bruton, 1967, is stated to be from the Hemse Marl at Petesvik, Hablingbo parish (a now overgrown locality) but this is questionable since this species is not known otherwise from Ludlow strata. One fragment from Bolarve 1, Hejdeby parish, Slite Marl, north-western part, may also belong to this species. Some cheek fragments (Ar51536–51538) from the Mulde Beds, lower part, at Djupvik, Eksta parish, are similar in most respects to *A. pectinata*, but differ slightly in having several very large tubercles on the lateral border. A definite assignment cannot be made until more complete specimens are known.

Diagnosis. Two paired, short, blunt spines posterolaterally on occipital ring. Six or seven tubercle pairs on glabella. Ten or eleven stout, nearly cylindrical, cephalic border spines. Axial rings with two paired posterolateral and one median tubercle. Very coarse cephalic tuberculation, also on hypostome. Pygidium coarsely tuberculated except on pleural field.

Description. This species has been described recently by a number of authors (see synonymy), so that only new or important features are noted here. Occipital ring with sharply defined occipital lobes (Pl. 27, fig. 9), short median spine with occipital organ, posterior margin with two paired spines. Anterior branch of facial suture indicated by a discrete ridge running from eye towards antennal notch (Pl. 26, figs. 6*b*, 12*b*), posterior branch indicated by a strong ridge running from eye to genal angle. Genal spine very long, curved downwards distally. Border spines slightly spatulate, with serrated tips (Pl. 26, fig. 2). Lateral margin (but not posterior) slightly incurved at base of genal spine. Six pairs of conspicuous tubercles (and possibly an anterior small pair) present on median lobe of



TEXT-FIG. 2. *Anacaenaspis pectinata* (Angelin, 1854). A, reconstruction of cephalon, based mainly on Ar30867, Ar51358, and Ar51630, about $\times 3$. B, reconstruction of pygidium, based on Ar51348, Ar51352, and Ar51573, about $\times 3$.

glabella. Lateral border with three conspicuous tubercles decreasing in size forwards, situated above border spines 3-4, 5-6, and 7-8 (numbered from rear forwards). Genal spine with thorn-like tubercles with a pore-opening distally at their base (Pl. 26, fig. 10).

Rostral plate unknown. Hypostome (Pl. 26, figs. 7, 11a-c, Pl. 27, fig. 7a-c) with oval, gently inflated middle body. Very faint middle furrow possibly present laterally just in front of conspicuous lateral tubercle. Maculae indicated by two smooth, oval areas. Anterior border unbroken medially, though very short, defined by wide furrow. Lateral border with blunt, subtriangular anterior wing and prominent shoulder. On the inner edge of the doublure underlying the shoulder is a small posterior wing (Pl. 27, fig. 7c). Border behind shoulder wider (tr.), confluent with equally wide (sag.) posterior border. Posterior margin has flattened, densely tuberculated subtriangular area medially (Pl. 26, fig. 11b, Pl. 27, fig. 7c). Middle body with pair of prominent tubercles laterally. Small specimens with a few additional tubercles, large specimens have middle body densely tuberculated. Ventral surface (except maculae) densely granulated.

Thorax with ten segments. Anterior and posterior pleural spines very short on first segment, progressively larger posteriorly, anterior spine blade-like to bluntly cylindrical. Axis with paired tubercles. Posterior pleural ridge with prominent tubercle at fulcrum and one at mid length.

Axial furrow in pygidium very deep except anteriorly and overhung by second axial ring and terminal piece. Pleural areas depressed, with reticulate pattern of ridges and depressions (through differentiated skeletal thickness, mostly not visible ventrally). Posteriorly are two pairs of secondary spines, laterally are three similar pairs, the anteriormost smaller and merged with articulating process (Pl. 27, fig. 2). Secondary spines situated at slightly lower level than major spines; these curve slightly inwards and upwards distally. Paired tubercles on axial rings and terminal piece. Posterior border with major tubercle above each spine-base. Tubercles on main body of pygidium and proximal part of spines elongated, with slightly bulbous tips wider than at bases.

Ontogeny. The only known transitory pygidium (Pl. 26, fig. 9a, b) is 1.20 mm wide and slightly distorted. It is similar to a late transitory pygidium of *Primaspis ascitus* described by Whittington (1956b, pl. 2, fig. 9) in having large, paired axial tubercles, a feature lost later in *ascitus* but retained in adult stages of *pectinata*. The prominent tubercle on the posterior pleural ridge, a characteristic *pectinata* feature, is also present.

In the holaspide cephalon, L1 and L2 change during growth from a more equal size to L2 being much smaller, a change accompanied by a relative widening of the median glabellar lobe, and a reduction of eye size. The paired glabellar tubercles are retained also in large specimens, although less obvious than in small ones. The hypostome becomes relatively wider during growth, and the middle body becomes more tuberculated, while the tuberculate area on the posterior margin becomes smaller. The shape of the pygidium is fairly stable, the shortening of the secondary spines being the only marked change.

Discussion. The holotype of *Anacaenaspis gotlandensis* Bruton, 1967, has been examined, and no differences between it and *A. pectinata* have been found. The occipital ring of the specimen is heavily worn, with no spines preserved, but the shape of what remains does not preclude their original presence. In addition, on the anterior axial rings of the thorax there are remains of one anteromedian and two posterolateral tubercles. Since these rings commonly have tubercles repeating the spine pattern of the occipital ring, corresponding occipital spines are to be expected (the tubercles on the axis are also preserved on a specimen from the Pentland Hills, Scotland, Pl. 27, fig. 10, and on unfigured Gotland material). The holotype has only the bases of the border spines preserved, and they cannot therefore be seen in dorsal view, a fact considered diagnostic by Bruton (but see Pl. 26, fig. 2 for length of complete spines). Other features typical of *A. pectinata* are all present, such as the strong posterior sutural ridge, the shape of the cheek border, carrying the same number of spines, and the tubercle pattern on the cheek and pleurae.

Bruton (1967) described and figured the holotype of *Acidaspis emarginata* Schmidt, 1885, from the upper Wenlock of Estonia, and listed the features distinguishing it from *A. gotlandensis* (= *A. pectinata*). The only known *emarginata* cephalon is similar to *pectinata* in all observable features, and the Estonian hypostome (Pl. 26, fig. 7) is identical to the large Gotland hypostome (Pl. 26, fig. 11a-c). *A. emarginata* is regarded here as a junior subjective synonym of *A. pectinata*. *A. dealgach* (Lamont, 1978; see Clarkson and Howells 1981, and Pl. 27, fig. 10 here), from the Upper Llandoverly of Scotland, is identical to the Gotland material and is also considered to be a junior subjective synonym of *pectinata*. *A. callipareos* (Thomson, 1857; see Howells 1982), from the Lower Llandoverly of Girvan, Scotland, is distinguished from *pectinata* mainly in lacking occipital spines and paired tubercles on the glabella, in the indented posterior margin, weak furrows and smooth surface of the

hypostome, in the granulate rather than tuberculate cephalon, and in the functional facial sutures. As so far known, these differences also apply to the Bohemian Llandovery *A. gigantea* Šnajdr, 1978, which is also distinguished by having seventeen to nineteen marginal spines in the pygidium. *A. kruegeri* (Schränk, 1969), from a late Wenlock erratic from Neu Nieköhr, DDR, differs from *pectinata* mainly in lacking occipital spines and in having eighteen rather than twelve pygidial border spines. The differences listed by Schränk (1969, p. 722) refer largely to the specimens included here in *Dudleyaspis* (*Snoderaspis*) *krausi* sp. nov. The British Wenlock *A. phasganis* Thomas, 1981, is closer to *pectinata* than recorded by Thomas (1981, p. 85), differing mainly in lacking occipital spines and in having a more adaxially placed eye.

As with the transitory pygidium (see above), the hypostomes assigned here to *A. pectinata* bear some resemblance to that of the American Middle Ordovician *Primaspis ascitus* Whittington, 1956b (pl. 1, figs. 18–21; note the tuberculate, flat area on the posterior margin) and indicates the close relationship between these genera. It also shows similarities to the hypostome of *A. cincinattiensis* Meek, 1873, also from the Middle Ordovician of North America (see Whittington 1956a, pl. 59, figs. 3, 6).

Genus DUDLEYASPIS Prantl and Přibyl, 1949

Discussion. Two subgenera are recognized here (see discussion under Odontopleurinae and respective subgenus). They both have the occipital ring at least five times as broad as long; occipital lobes present; eye lobe set at a level below L1, not in contact with posterior border furrow, transverse width between palpebral lobes at least one and one-third the length of glabella; anterior and posterior branches of (nonfunctional) facial suture run on sutural ridges; genal spine slim, not exceeding length of glabella; posterior border incurved at base of genal spine; thorax with ten segments, axis wide, fulcral swelling small; pygidium with two pairs of spines between major spines, all spines evenly spaced, at about the same level. *A. harborti* Richter and Richter, 1926, may belong to *Dudleyaspis*, but is not known well enough to be definitely assigned.

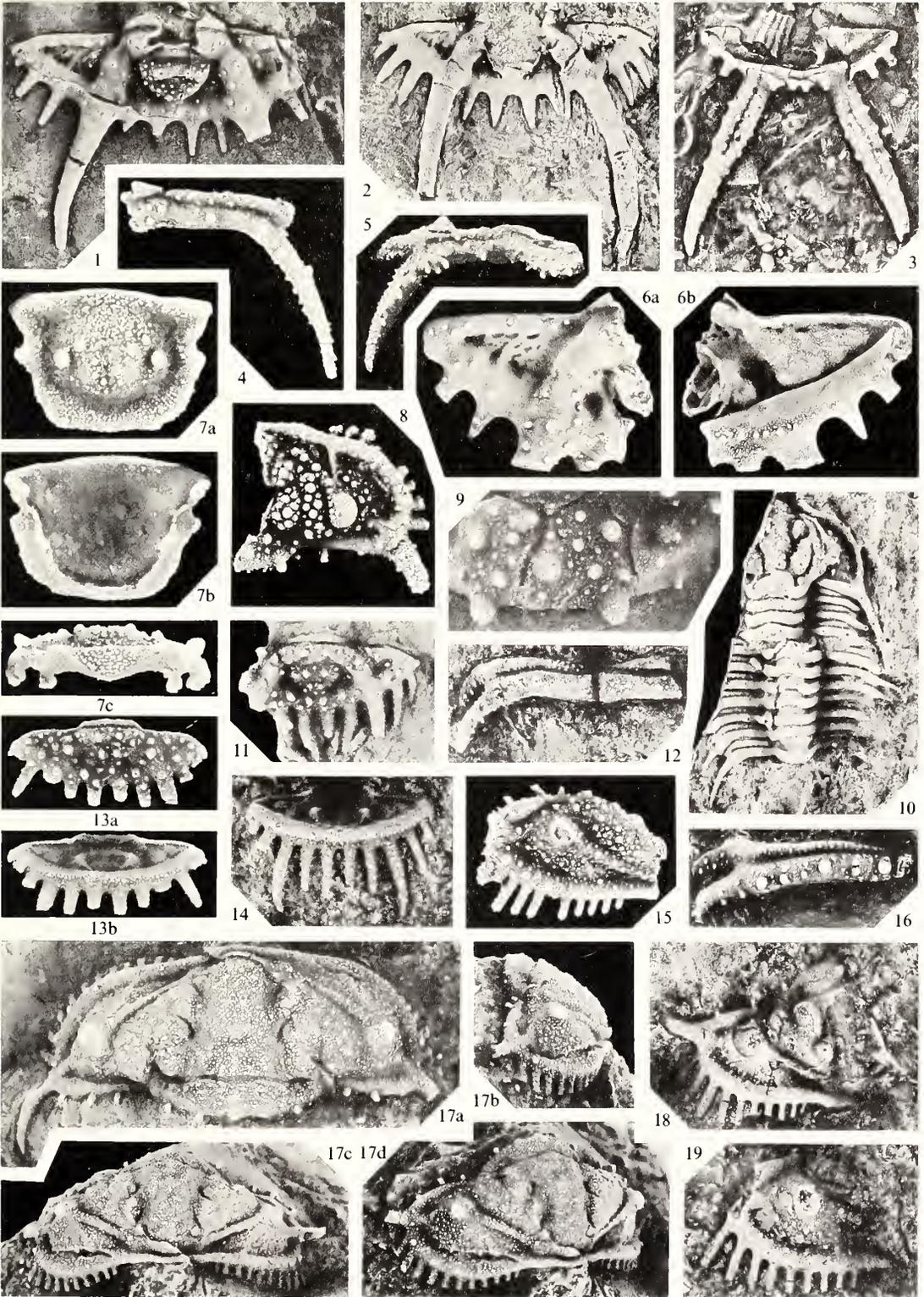
EXPLANATION OF PLATE 27

Figs. 1–10. *Anacaenaspis pectinata* (Angelin, 1854). Upper Visby Beds (4, 7–9), Höglint Beds, unit b (1, 3), Slite Beds, Slite Marl (2, 6), Halla Beds, unit b (5), Fridhem (3), Hörsne kanal (5), Rönnklint (4, 7–9), Valbytte 1 (6), Valve 2 (2), dump at Visby harbour (1), Wether Law Linn Formation (Upper Llandovery), Pentland Hills, Scotland (10). 1, Ar51348, pygidium, major spine deformed distally, $\times 3$. 2, Ar51573, pygidium, $\times 3$. 3, SGU 1449, pygidium, ventral view, $\times 4$ (coll. J. G. Andersson). 4, Ar51647, partial thoracic segment, $\times 6$. 5, SGU 1450, partial thoracic segment, $\times 10$ (coll. G. Holm). 6a, b, Ar51352, partial large pygidium, dorsal and ventral views, $\times 3$. 7a–c, Ar51645, small hypostome, exterior, interior, and posterior views, $\times 12$. 8, Ar51644, partial small cephalon, exterior view, $\times 12$. 9, Ar51643, occipital ring with complete spines and median organ, $\times 12$. 10, RSM GY 1983.18.1, latex cast of external mould of exoskeleton lacking pygidium, $\times 4$.

Figs. 11–18. *Dudleyaspis* (*Dudleyaspis*) *hamrensis* sp. nov. Hamra Beds, unit a (11–17), unit b (18). Gisle 2 (11, 12, 14, 16), Kättelviken 1 (13, 15, 17), Majstre 1 (18). 11, Ar51550,* pygidium, $\times 6$. 12, Ar51545,* partial thoracic segment, $\times 4$. 13a, b, Ar51618,* pygidium, dorsal and ventral views, $\times 6$. 14, Ar51549,* small pygidium, ventral view, $\times 9$. 15, Ar51616,* partial cephalon, anterolateral view, $\times 5$. 16, Ar51544,* partial thoracic segment, $\times 4$. 17a–d, holotype Ar51568, cephalon, exterior, lateral, anterior, and antero-lateral views, a $\times 4$, b–d $\times 3$. 18, Ar51637,* partial cephalon, anterolateral view, $\times 6$.

Fig. 19. *Dudleyaspis* (*Dudleyaspis*) *hamrensis* sp. nov.? Ar51638, partial cephalon, anterolateral view, Gannor 1, Eke Beds, lower part, $\times 6$.

* Paratypes.



RAMSKÖLD, *Anacaenaspis*, *Dudleyaspis*

Subgenus DUDLEYASPIS (DUDLEYASPIS) Prantl and Přibyl, 1949

Subjective synonym: *Primaspis* (*Taemasaspis*) Chatterton, 1971

Type species. *Acidaspis quinquespinosa* Lake, 1896, from the Much Wenlock Limestone Formation, Dudley, West Midlands, and Sedgley, Staffordshire, Great Britain.

Diagnosis. Cephalon wide and short; width to length 2·3: 1–3·2: 1. Eye set closer to axial furrow than to lateral border furrow. Facial suture with posterior branches diverging backwards at 120–180°. Genal spine directed obliquely outwards.

Dudleyaspis (*Dudleyaspis*) *hamrensis* sp. nov.

Plate 27, figs. 11–18

Name. From the type stratigraphical unit.

Holotype. Ar51568, cephalon, Pl. 27, figs. 17a–d, from Kättelvikén 1, Vamlingbo parish, Hamra Beds, unit a.

Paratypes. From the type locality, Ar51588, Ar51615–51619. From Gisle 2, Öja parish (Hamra Beds, unit a), Ar51541–51550. From Hamra Beds, unit b, Sundre parish: Majstre 1, Ar51637; north of Hoburgen, Ar51551. In total seven partial cephalata, seven thoracic segments, and six pygidia. A partial cephalon, Ar51638, from the lower Eke Beds at Gannor 1, Lau parish, may also belong to this species.

Diagnosis. Posterior cephalic margin with five very small spine pairs plus equally small median spine. Eyes set wide apart opposite anterior half of L1. Pygidium with six pairs of spines.

Description. Cephalon subtrapezoidal, highly vaulted in anterior view (Pl. 27, fig. 17c). Occipital ring occupying half of cephalic width (excluding spines). Occipital lobes very weakly defined. L3 elongate, directed at about 45° to sagittal line, with slightly bulbous tip. Longitudinal furrow wide, shallow. Axial furrow very weak. Eye ridge merging anteriorly with lateral extension of frontal lobe. Eye set exactly mid-way between axial and lateral border furrow. Cheek area between eye ridge/palpebral lobe and axial furrow large. Anterior branch of facial suture indicated by indistinct ridge, posterior branch not visible close to eye; a fairly strong sutural ridge appears near genal angle. Lateral border with eleven almost vertical spines (a twelfth knob-like anteriormost spine may be present), cylindrical, straight, blunt, the posteriormost slightly less than normal to genal spine. Three stout, elongated tubercles present on border, above border spines 1–2, 3–4, and 5–6 (counted from rear forwards), increasing in size backwards. Entire cephalon except deepest parts of furrows with a fine, spiny tuberculation. Six or seven pairs of slightly larger tubercles are barely discernible on median lobe of glabella.

Rostral plate and hypostome unknown. Thoracic segments (Pl. 27, figs. 12, 16) with axis over one-third of width between fulcra. Anterior pleural ridge widening (exsag.) distal to fulcrum into large, blade-like anterior spine. Posterior ridge produced into proximally downward-flexed, laterally more horizontal spine. On a presumed anterior segment the spine is transverse or curved slightly anteriorly, on probable posterior segments it curves backwards through 90°. Axial ring and posterior pleural ridge with three to four large, elongated tubercles each.

Pygidium (Pl. 27, figs. 11, 13, 14) with second axial ring bounded by wide (sag.) anterior and distinct posterior furrows. Terminal piece merging with border posteriorly. Pleural areas strongly depressed. Posterior to articulating process and a diminutive spine are two secondary border spines, followed by major spine and two further secondary spines. Axial rings and terminal piece each with a pair of spinose tubercles; conspicuous tubercles also at bases of all border spines.

Discussion. This species has a pygidium almost identical to that of *D. (D.) quinquespinosa*, but differs in its more vaulted cephalon, the number and size of spines on the posterior cephalic margin, the more anterolaterally situated eyes, and the only partly developed sutural ridges. It is more similar to the American upper Wenlock or lower Ludlow *D. (D.) desolator* Campbell, 1967, but is distinguished by the number and size of the posterior cephalic spines, and the slightly more abaxially set eyes. The American *D. (D.) vanhornei* (Weller, 1907), from the Niagaran dolomites, is clearly related to the above species, but is not sufficiently well known to permit a detailed comparison. These four species form a fairly tight group within *D. (Dudleyaspis)*. The remaining species referred here to the

subgenus; *Primaspis* (*Taemasaspis*) *campbelli* Chatterton, 1971 (Australian Emsian or Eifelian), *Odontopleura bowningensis* Etheridge and Mitchell, 1896 (Australian Ludlow), *Odontopleura Portlockii* Hawle and Corda, 1847 (Bohemian and British Wenlock), and *D. (D.) uncifera* sp. nov. (see below), all differ from *D. (D.) liamrensis* (and its allies) by having a non-spinose occipital ring, genal spine projecting sublaterally, base level with lateral border anterior to strong anteriorward flexure of posterior margin, weak sutural ridges, and major spines on pygidium considerably larger than secondary spines. *Taemasaspis llandoveriana* Šnajdr, 1975 (see Šnajdr 1978 for complete description), from the Bohemian Llandovery, does not show close similarities to the above species, and cannot be included in *Dudleyaspis*, but seems to be morphologically (and stratigraphically) intermediate between *Primaspis* and *Odontopleura*.

Dudleyaspis (*Dudleyaspis*) *uncifera* sp. nov.

Plate 28, figs. 1–11; Plate 30, fig. 17

v. 1979 *Dudleyaspis?* sp. indet; Bruton in Jaanusson *et al.*, p. 116.

Name. The name *uncifera* (Latin for ‘hook-bearing’) was used on a label written by G. Lindström, but it has never been published.

Holotype. Ar51652, cephalon with four articulated thoracic segments, Plate 28, fig. 1a–d, from the small point south of Kopparsvik, Visby, Upper Visby Beds.

Paratypes. ?Lower Visby Beds: Stenkyrka parish—south-west of Balsklint, 0–2 m a.s.l. (SGU 1453), Visby parish—Norderstrand (Ar5074). Upper Visby Beds: Lummelunda parish—Rönklint (641181 165698) (Ar51640a–k; parts of cephalon, thorax and pygidium from one individual, Ar51641–51642). Västerhejde parish—Högklint (SGU 1451). Visby parish—Vattenfallsprofilen 1, 1.7–1.9 m a.s.l. (SGU 1452). Several fragments from the Lower Visby Beds at Rönklint may also belong to this species.

Diagnosis. Cephalon very wide and short; width to length 3.2:1.0. Axial furrow almost effaced along glabella. Lateral glabellar furrows shallow, with an additional furrow on L1. L2 and L3 ridge-shaped. Posteriormost border spine straight and blunt, subparallel to short genal spine. Cephalon with fine granulation of low relief. Posterior pleural spines on thorax very stout, short, barbed. Pygidium with shallow axial and inter-ring furrows, seven pairs of spines, major spine stout, blunt.

Description. Cephalon subtrapezoidal. Occipital ring with occipital organ (Pl. 28, fig. 1d). Occipital lobes large. L1 twice as long (exsag.) as wide, divided into two parts by shallow furrow starting at inner end of S1 and curving laterally and posteriorly to join axial furrow. L2 small, elongated, defined faintly laterally. L3 similar in shape to L2 but smaller and almost transverse. Longitudinal furrow barely visible. Eye ridges straight, diverging at about 110°. Eyes set wide apart opposite posterior half of L1. Facial suture fused, anterior branch indicated by a faint ridge, posterior branch indicated by a short, weak ridge near genal angle. Field of cheek with reticulate pattern (of genal caecae?). Ventrally on lateral border are ten (and possibly a small eleventh) pointed, strongly curved spines, except the posteriormost which is cylindrical with an abrupt, blunt end. Genal spine small, proximally directed transversely (in dorsal view) and downwards. Median lobe of glabella carries seven obvious pairs of tubercles (Pl. 28, figs. 1b, 11), major tubercles on fixed cheek and eye ridge arranged symmetrically. Field of cheek smooth or with very sparse, fine granulation, cephalon otherwise very finely and densely granulated. Rostral plate and hypostome not known.

Thoracic segments with pleural ridges of low relief. Anterior pleural spine straight to curved backwards, cylindrical to slightly flattened, pointed, with barbed anterior and posterior edges. Posterior spine stout, barbed, almost transverse on anterior segments, posterior to this curved backwards, flexed strongly down at fulcrum. Pleurae with a few very small tubercles, spines densely and coarsely granulated.

Pygidium with ankylated articulating half ring in anterior inter-ring furrow, second ring indistinctly separated from subtriangular terminal piece. Seven pairs of border spines, the fourth the major, anteriormost spine very small (Pl. 28, figs. 2, 8). Major spine thickest at about mid length, gently curved upwards and inwards distally. Secondary spines pointed, less than half the length of major spines. Tuberculation fairly sparse, no obvious paired tubercles on axis. Secondary spines with two rows of small tubercles. Spines densely granulated, surface between tubercles otherwise almost smooth.

Discussion. This species is easily distinguished from all other *Dudleyaspis* by the almost effaced axial and lateral glabellar furrows, and the shape of the posterior pleural spines in the thorax. A unique feature is the furrow dividing L1. The closest species appears to be *D. (D.) hamrensis* sp. nov. (cf. Pl. 27, fig. 17a with Pl. 28, fig. 1c), although that species belongs to the closely knit group around the type species (see p. 248).

Subgenus DUDLEYASPIS (SNODERASPIS) subgen. nov.

Name. From the type locality of the type species, and Greek *aspis*, shield.

Type species. *Dudleyaspis (Snoderaspis) krausi* sp. nov., from the Hemse and Eke Beds (lower-middle Ludlow), Gotland.

Diagnosis. Cephalon very close to semicircular, width to length 2:1. Eye set very anterolaterally, opposite anterior half of L1, three-quarters way from axial to lateral border furrow. Eye ridges diverging at 110–120°. Facial suture with posterior branches diverging at close to 90°. Genal spine curved backwards in horizontal plane. Anterior pleural spine on thoracic segments needle-like, posterior spine long, slender, barbed.

Discussion. This subgenus is similar to previously known *Dudleyaspis* in having a straight eye ridge and a lateral eye position, in the incurvation of the posterior border at the base of the fairly small genal spine, the shape, size, and number of both cephalic and pygidial border spines, and the fine surface tuberculation. However, the course of the (non-functional) facial suture and the extreme eye position in the semicircular cephalon are features sufficiently different to warrant a new, as yet monotypic, subgenus.

Dudleyaspis (Snoderaspis) krausi sp. nov.

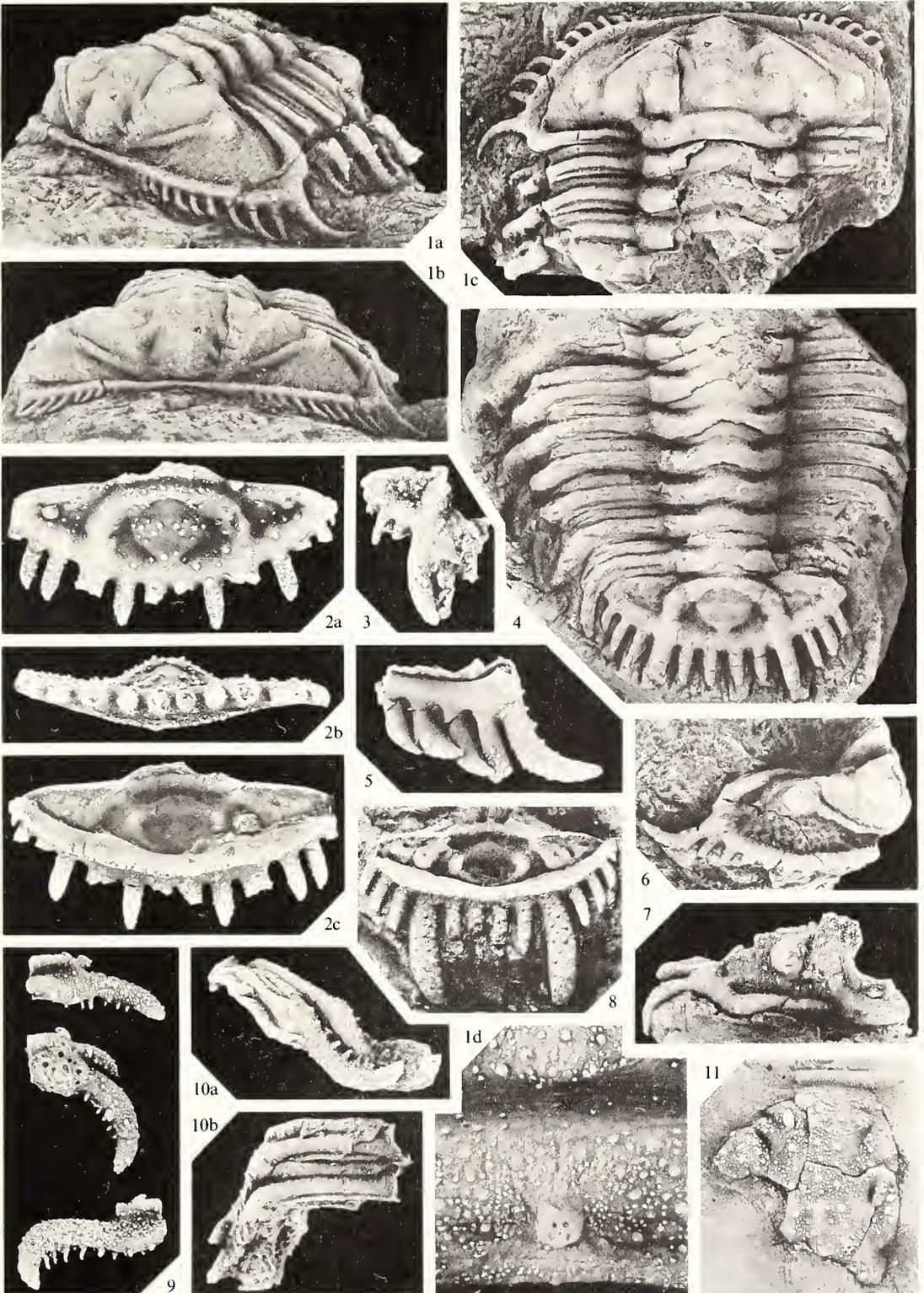
Plate 29, figs. 1, 2, 4, 8–10, 12, text-fig. 3

- . 1895 *Acidaspis* n. sp. Lindström, p. 11.
- v. 1967 *Anacaenaspis gotlandensis* Bruton, p. 236 [*pars*], pl. 35, fig. 10, pl. 36, fig. 5, *non* figs. 1–4 [= *Anacaenaspis pectinata* (Angelín, 1854)].
- v. 1967 *Anacaenaspis* aff. *gotlandensis* Bruton, p. 237 [*pars*], pl. 35, figs. 7–9.
- 1969 *Primaspis gotlandensis* (Bruton, 1967); Schrank, p. 722 [*pars*].
- 1978 *Anacaenaspis gotlandensis* Bruton; Šnajdr, p. 31 [*pars*].
- 1981 *Anacaenaspis gotlandensis* Bruton, 1967; Thomas, p. 85 [*pars*].
- 1982 *Anacaenaspis gotlandensis* Bruton, 1967; Howells, p. 58 [*pars*].

EXPLANATION OF PLATE 28

Figs. 1–11. *Dudleyaspis (Dudleyaspis) uncifera* sp. nov. ?Lower Visby Beds (8), Upper Visby Beds (1–7, 9–11). Point south of Kopparsvik, Visby (1), Högklint (4), Rönklint (2, 3, 5, 7, 9–11), Vattenfallsprofilen 1 (6), coast south west of Balsklint (8). 1a–d, holotype Ar51652, cephalon with four thoracic segments, anterolateral, anterior, and exterior views, and enlargement showing granulation and median occipital organ, a–c × 2, d × 13 (coll. G. Lindström 1897). 2a–c, Ar51640k,* pygidium, dorsal, posterior, and ventral views, × 5. 3, Ar51641,* partial small pygidium, × 9 (coll. V. Jaanusson 1981). 4, SGU 1451,* eight (seven articulated) thoracic segments and pygidium, × 2.5 (coll. H. Hedström 1921). 5, Ar51640c,* cheek fragment with genal spine and part of spine fringe, all spines complete, interior view, × 5. 6, SGU 1452,* partial distorted cephalon, anterolateral view, × 3 (coll. G. Liljevall 1908). 7, Ar51640b,* partial cephalon, exterior view, × 4. 8, SGU 1453,* small pygidium, ventral view, × 9 (coll. G. Liljevall 1911). 9, Ar51640f–h,* partial thoracic segments, anterior pleural spine intact on middle specimen, × 5. 10a, b, Ar51640e,* three (one displaced) thoracic segments, anterolateral and dorsal views, × 5. 11, Ar51640a,* cephalic fragment showing paired tubercles on glabella, × 5.

* Paratypes.



RAMSKÖLD, *Dudleyaspis*

Name. After Mr Werner Kraus, who collected the holotype.

Holotype. Ar51757, cephalon, Plate 29, fig. 4a-d, from Snoder 2, Silte parish, Hemse Marl, north-western part, Hemse Beds (lower Ludlow).

Paratypes. From the Hemse Marl, north-western part: Silte parish—Snoder 1 (Ar51566), Snoder 2 (Ar51349, Ar51611). Hablingo parish—Hemmungs 1 (Ar51796), Petesvik (Ar30871, figured Bruton 1967, pl. 36, fig. 5, correct magnification $\times 4$). Hemse Marl, top: Lau parish—Lau kanal (= Gannor; Ar30806a-b, figured Bruton 1967, pl. 35, fig. 10). Unknown locality, probably Hemse Beds (Ar30811, Ar30817—figured Bruton 1967, pl. 35, figs. 7-9, correct magnification figs. 7, 8 $\times 2$). Eke Beds, upper part: Lau parish—Lau Backar 1 (Ar51598, Ar51599, Ar51611-51614). In total four complete and seven partial cephalons, one hypostome, some thoracic segments, and three pygidia.

Diagnosis. As for subgenus.

Description. Occipital ring with faint occipital lobes, posterior margin slightly concave medially. Median occipital organ present (Pl. 29, fig. 4d). Median lobe of glabella parallel-sided, rather convex (tr., sag.). Longitudinal furrow deep. L3 small, distinct. Eye ridge running from just in front of L3 to small palpebral lobe. Area bounded by eye ridge/palpebral lobe and axial furrow very large, S-shaped in transverse profile, convex (exsag.). Eye situated at a level much below L1 (Pl. 29, fig. 4c). No palpebral furrow. Anterior branch of facial suture indicated by indistinct ridge on cheek, then curves across lateral border to antennal notch, posterior branch indicated by narrow ridge running straight from eye towards genal angle. Genal spine as long as glabella. Lateral border bearing row of twelve to thirteen gently curved, pointed spines ventrally (the number can vary even in the same individual, see Pl. 29, fig. 4c), the posteriormost at an angle of about 60° to border and genal spine. Posterior margin strongly incurved at base of genal spine. Antennal notch distinct. Entire cephalon except doublure with dense, fine, and even tuberculation.

Rostral plate unknown. The available hypostome (Pl. 29, fig. 1c) is distorted, slightly wider than long. Middle body as long as wide, inflated, extremely weak middle furrow possibly present at about mid length, maculae indicated by lack of tuberculation and darker colour. Anterior wing fairly large, lateral border narrow (tr.), with weak shoulder. Lateral border furrow narrow, distinct. Posterior border not preserved. Entire hypostome except anterior wing and maculae with dense, spiny tuberculation.

Thoracic segments with pleural ridges inflated, fulcral swellings faint. Posterior spine close to transverse proximally, curving gently backwards distally. Anterior spine straight, subparallel to posterior spine. Spines on first segment shortened (Pl. 29, fig. 1b), reaching full size on third segment. Pleural ridges with approximately two rows of spinose tubercles, tuberculation also on axis, posterior flange, spines, and in pleural furrow.

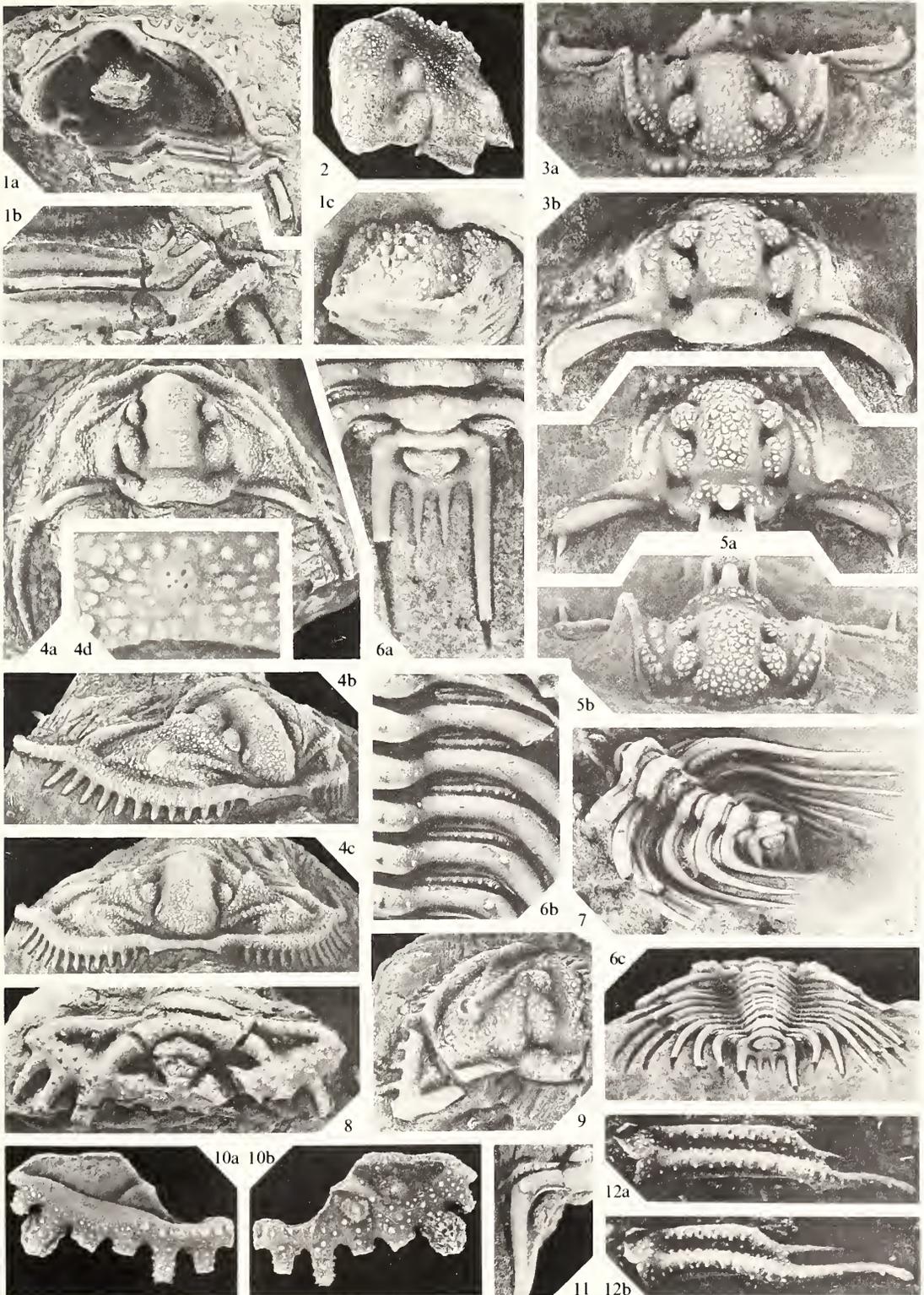
EXPLANATION OF PLATE 29

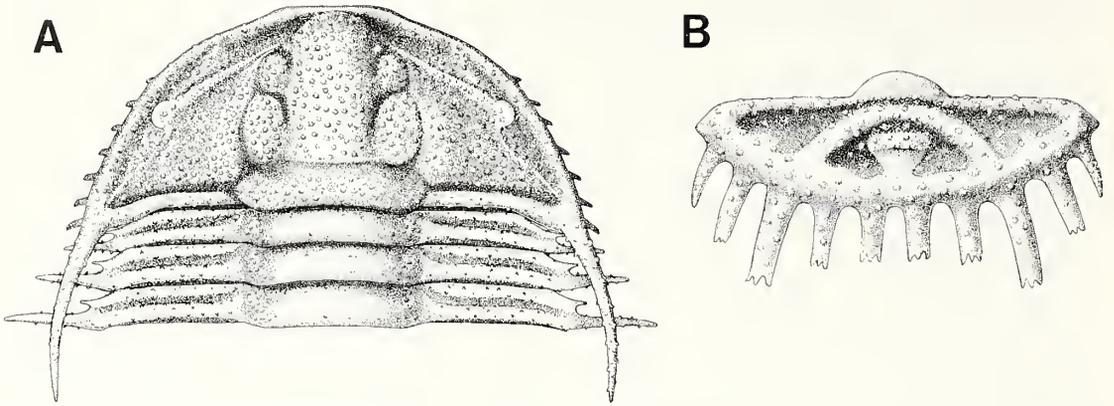
Figs. 1, 2, 4, 8-10, 12. *Dudleyaspis* (*Snoderaspis*) *krausi* sp. nov. Hemse Marl, north-western part, Hemse Beds

(1, 4, 8, 9, 12), Eke Beds, upper part (2, 10). Petesvik (8), Snoder 1 (1), Snoder 2 (4, 9, 12), Lau Backar 1 (2, 10). 1a-c, Ar51566,* partial cephalon with displaced hypostome and two articulated thoracic segments, ventral view, enlargement of pleural spines (tips lost), and oblique view of hypostome lacking posterior border, $a \times 2$, $b \times 5$, $c \times 5.5$. 2, Ar51611,* partial cephalon, exterior view, $\times 3$. 4a-d, holotype Ar51757, cephalon, dorsal, anterolateral, and anterior views, and enlargement of median occipital organ, $a-c \times 2$, $d \times 10$ (coll. W. Kraus 1981). 8, Ar30871,* pygidium, figured Bruton 1967, pl. 36, fig. 5, $\times 4$ (coll. G. Lindström). 9, partial cephalon belonging to Mr W. Kraus, Niedernhausen, dorsolateral view, $\times 2$. 10a, b, Ar51614,* partial pygidium, ventral and dorsal views, $\times 4$. 12a, b, Ar51349,* partial thoracic segment, dorsal and dorsolateral views, $\times 5$.

Figs. 3, 5-7, 11. *Leonaspis crenata* (Emmrich, 1844) *angelini* (Prantl and Přibyl, 1949). ?Halla Beds (6), Mulde Beds, lower part (11), undifferentiated (3, 5, 7). Blåhäll 1 (11), Djupviksvägen 1 (3), Lilla Karlsö (6), Nordervik (5, 7). 3a, b, Ar51368b, cranium, anterior and exterior views, $\times 6.5$. 5a, b, Ar51653, cranium, exterior and anterior views, $\times 5$. 6a-c, holotype Ar30859, complete specimen, figured Angelin 1854, pl. 22, fig. 14, refigured Bruton 1967, pl. 34, figs. 4-6, enlargement of pygidium, enlargement of pleurae, and posterior view, $a, b \times 6$, $c \times 3$. 7, Ar51654, partly disarticulated thorax and pygidium, oblique dorsolateral view, $\times 3$. 11, Ar51369b, partial thoracic segment, note granulation on anterior pleural ridge, $\times 7$.

* Paratypes.





TEXT-FIG. 3. *Dudleyaspis* (*Snoderaspis*) *krausi* subgen. and sp. nov. A, reconstruction of cephalon and part of thorax, based on Ar30817, Ar51566, and Ar51757, $\times 3$. B, reconstruction of pygidium, based on Ar30817 and Ar30871, $\times 3$.

Pygidium (Pl. 29, figs. 8, 10) with anterior axial ring continuous with pleural ridges and together with these forming a semicircle. Second ring half as wide (tr.), indistinctly separated from subtriangular terminal piece. Axial furrow very deep alongside terminal piece and second ring, indistinct anteriorly. Pleural areas strongly depressed. Two slender secondary spines on each side of only slightly stouter major border spines, which are of unknown length. Doublure (Pl. 29, fig. 10a) raised medially into spinose, transverse ridge. Entire pygidium with rather fine, sparse tuberculation, densest on axis, anterior border, and spines. No paired tubercles on axis or major tubercles at bases of spines.

Genus LEONASPIS Richter and Richter, 1917

Type species. *Odontopleura Leonhardi* Barrande, 1846; from the Kopanina Formation (Ludlow), Kolednik, Beroun, Czechoslovakia.

Discussion. The diagnosis of Whittington (1956b, p. 206) is followed here. Bruton (1967) described and discussed four *Leonaspis* species from Gotland, all from the Mulde Beds or from probable corresponding beds on the Karlsö islands. These species present difficulties in interpretation because all four type specimens either lack important structures, or come from localities that are either known imprecisely or are inaccessible for re-collecting. Most of the described material consists of water-worn specimens, although often complete individuals, from the harbour at Djupvik, Eksta parish, where collecting is no longer possible. New material from slightly higher horizons in the Mulde Beds have supplied additional information on these species, and they are in part reinterpreted here.

Leonaspis crenata crenata (Emmrich, 1844)

Plate 30, figs. 5, 7; text-fig. 4

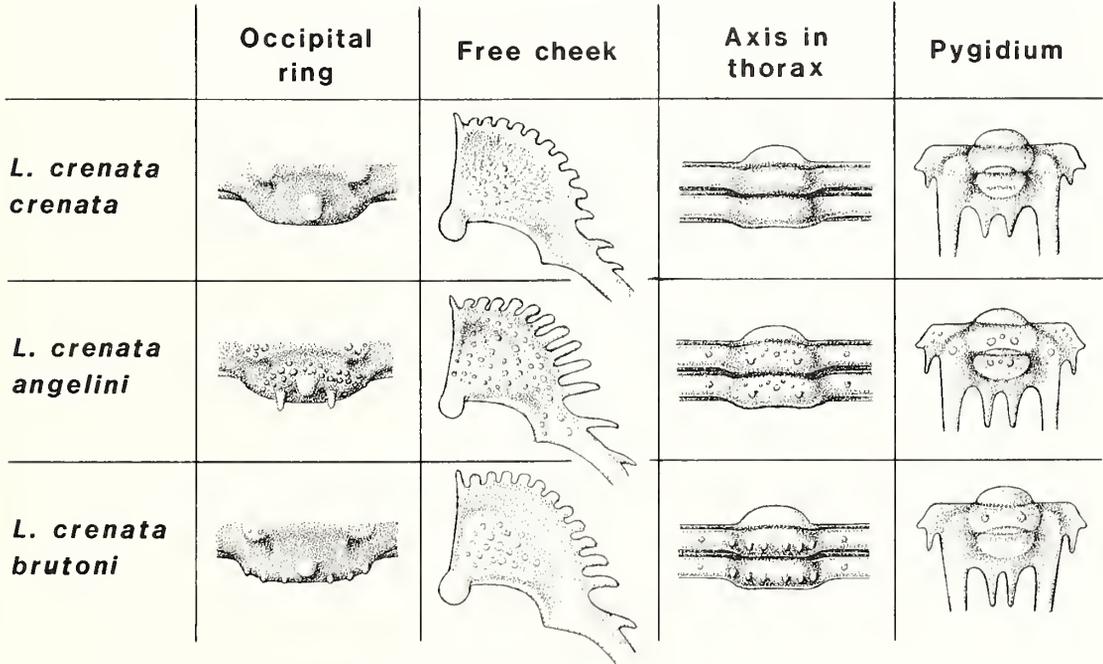
- * 1844 *Odontopleura crenata* Emmrich, p. 17.
- v. 1967 *Leonaspis crenata* (Emmrich, 1844); Bruton, p. 224, pl. 32, figs. 3–8, pl. 33, figs. 1, 2, 5, pl. 34, figs. 1, 2 [with synonymy list].
- . 1969 *Leonaspis crenata* (Emmrich, 1844); Schrank, p. 710.
- . 1977 *L. crenata* (Emmrich); Campbell, p. 113.
- . 1978 *L. crenata* (Emmrich); Šnajdr, p. 35.
- . 1981 *L. crenata crenata* (Emmrich, 1844); Thomas, p. 92.

Lectotype. Selected Bruton, 1967, p. 224; specimen in the Geological-Paleontological Museum, Humboldt University, East Berlin, HU MB 1963/29/1, incomplete cephalon with part of thorax, one of two syntypes from the Emmrich Collection, figured Bruton 1967, pl. 32, fig. 3, from Djupvik, Eksta parish, Mulde Beds, lower part.

Other material. Over a hundred more-or-less complete, enrolled specimens, plus some disarticulated material, are known from the harbour at Djupvik. The only other known locality is Mulde Tegelbruk 1, Eksta parish (Mulde Beds, undifferentiated). Washed marls from that locality have yielded several fragments, mainly of cheeks and pygidia.

Diagnosis. Occipital ring smooth except for short, stout, blunt median spine. Anterior border with row of about fourteen to sixteen tubercles. Free cheek with indistinct, shallow border furrow and weakly convex to flat border. Twelve border spines, the ten anterior short, rectangular. Genal spine long, slender, without secondary spines on dorsal surface. Cephalon finely tuberculated. Thoracic axis and anterior pleural ridges smooth. Pygidium with short secondary spines. Second axial ring well defined posteriorly. Pleural ridges with pair of small tubercles, pygidium otherwise smooth, major spines granulated.

Discussion. This taxon was described comprehensively and figured by Bruton (1967). The term 'bifid spine' should not be applied to the anterolateral corner of the pygidium since there is no spine, but merely a process carrying the articulating facet. I have prepared unworn cranidia, and there is no trace of occipital spines besides the median one; this is the main feature distinguishing the subspecies. A comparison between the three subspecies of *L. crenata* is given in text-fig. 4.



TEXT-FIG. 4. Comparison of some morphological features in the three subspecies of *Leonaspis crenata* (Emmrich, 1844). The different elements are not drawn at the same scale. The distal part of the genal spine and major pygidial spines are omitted.

Leonaspis crenata angelini (Prantl and Přibyl, 1949)

Plate 29, figs. 3, 5-7, 11, Plate 30, figs. 1-4, 8-13, text-fig. 4

- v. 1851 Angelin, pl. 22, fig. 14 [illustration only, without name].
 . 1854 *Acidaspis barrandei* Angelin, p. 38 [referring to 1851 figure].
 . 1885 *Odontopleura Barrandei* Angelin; Roemer, p. 219 (376), pl. 10, fig. 9 [*fide* Schrank 1969].
 . 1885 *Acidaspis barrandei* Angelin; Lindström, p. 53.
 . 1896 *Acidaspis Barrandei* Ang.; Lake, p. 240.
 v* 1949 *Acanthaloma angelini* Prantl and Přibyl, p. 159, pl. 10, figs. 11, 12.
 v. 1967 *Leonaspis angelini* (Prantl and Přibyl, 1949); Bruton, p. 228, pl. 34, figs. 3-6.
 . 1969 *Leonaspis angelini* (Prantl and Přibyl, 1949) (?); Schrank, p. 717, pl. 6, fig. 9, pl. 7, figs. 1-8, pl. 8, figs. 1, 2.
 . 1975 *L. angelini* (Prantl et Přibyl); Šnajdr, p. 315.
 . 1978 *L. angelini* Prantl and Přibyl; Šnajdr, p. 35.
 v. non 1979 *Leonaspis angelini* (Prantl and Přibyl); Bruton in Jaanusson *et al.*, p. 116 [= *L. sp. A* of this paper].
 . 1981 *L. angelini* (Prantl and Přibyl); Clarkson and Howells, p. 529.
 . 1981 *L. crenata angelini* (Prantl and Přibyl, 1949); Thomas, p. 88.
 . non 1982 *Leonaspis cf. L. crenata angelini* (Prantl and Přibyl, 1949); Howells, p. 54, pl. 14, figs. 22, 23 [*non L. crenata angelini* (Prantl and Přibyl, 1949)].

Holotype. By monotypy; Ar30859, almost complete specimen, figured Angelin 1851, pl. 22, fig. 14; refigured Prantl and Přibyl 1949, pl. 10, figs. 11, 12; refigured Bruton 1967, pl. 34, figs. 4-6; refigured here Plate 29, figs. 6a-c; from Lilla Karlsö, possible Halla Beds equivalents.

Other material. Apart from the holotype, only a fragmentary free cheek (Ar47407, figured Bruton 1967, pl. 34, fig. 3) has previously been known from Gotland. I have collected abundant new material at Djupviksvägen 1 and Nordervik (635350 163845), both Eksta parish, Mulde Beds, undifferentiated but higher than the horizon yielding *L. crenata crenata*. *L. crenata angelini* is also known from 'Graptolithengestein' erratics of a slightly younger age (see Schrank 1969).

Diagnosis. Occipital ring with stout, short, blunt, vertical median spine bearing occipital organ, flanked by pair of slender, pointed spines. Anterior border with row of about fourteen to eighteen tubercles. Free cheek with deep border furrow and convex (tr.) border. All twelve border spines round in section, the anterior four or five with swollen tips, the posterior pointed. Cephalon densely tuberculate. Thoracic axial rings with pair of pointed spines, decreasing in size backwards, anteromedian tubercle, and several symmetrically arranged smaller tubercles. Pygidium with long secondary spines. Second axial ring poorly defined posteriorly. Paired tubercles on axial rings, large tubercle on each pleural ridge, and additional tubercles on axis and anterolateral pleural areas.

Discussion. There are slight differences in coarseness and density of tuberculation between specimens from the three localities in the Mulde Beds: Blåhäll 1, Djupviksvägen 1, and Nordervik. The stratigraphically lowest material, from Blåhäll 1 (Pl. 30, fig. 3a), is very similar to the holotype. Specimens from Djupviksvägen 1 (Pl. 29, fig. 3b) have a more sparse, coarser tuberculation; specimens from Nordervik (Pl. 29, fig. 5a) are even coarser and slightly more densely tuberculated. These differences are small but consistent, but are not regarded here as being of taxonomic importance above the population level.

Thomas (1981, p. 92) regarded the differences between *crenata crenata* and *angelini* to be of subspecific rank only, an approach followed here. Practically all differences between these are due to the strong ornamentation of *angelini*, and from an evolutionary point of view, only a very minor genetic change would be required to produce that effect. Present data suggest that *angelini* is very slightly younger than *crenata crenata*, and so is likely to be its descendant. The material described by Schrank (1969) as *L. angelini* (?) is indistinguishable from Gotland specimens. Thomas (1981) erected *L. crenata brutoni* for British Wenlock specimens differing slightly both from *crenata crenata* and *crenata angelini*. Differences between *brutoni* and the Gotland subspecies were listed by Thomas, all

of which are valid except the notion of *angelini* and *brutoni* lacking an anterolateral 'bifid' spine in the pygidium; this structure is similar in all three subspecies. A comparison between these subspecies is made in text-fig. 4.

Howells (1982, p. 54, pl. 14, figs. 22, 23) figured and described Scottish Llandoverly material as 'cf.' (in description) or 'aff.' (in plate explanation) *L. crenata angelini*. The figured pygidium is very wide relative to its length, and has a very small second axial ring, and is on the whole more similar to *L. deflexa* (Lake, 1896). The figured thorax differs from *crenata crenata* in the extremely long pleural spines.

Leonaspis coronata bufo subsp. nov.

Plate 30, figs. 6, 14–16; Plate 31, figs. 1–6

. 1969 *Leonaspis marklini* (Angelin, 1854); Schrank, p. 714, pl. 4, figs. 9, 10, pl. 5, figs. 1–6, pl. 6, figs. 1, 2, 4–7.

Name. Latin *bufo*, toad; referring to the wart-like appearance of the surface sculpture.

Holotype. Ar51664, incomplete cephalon with nine thoracic segments, Plate 30, fig. 14a–d, from Djupviksvägen 1, Eksta parish, Mulde Beds, undifferentiated.

Paratypes. All from Eksta parish. From the type locality (Ar51363–51365, Ar51665–51684). From Blåhäll 1, Mulde Beds, lower part (Ar51685, free cheek). From Nordervik (635350 163845), Mulde Beds, undifferentiated (Ar51686–51708). In total about twelve cranidia, sixteen free cheeks, three hypostomes, some thoracic segments, and seventeen pygidia.

Diagnosis. Genal spines very long, reaching about seventh thoracic segment. Thoracic segments with slender, pointed posterior pleural spines, longest on sixth segment, short on anterior three segments, but markedly shortened on anteriormost segment only. Pygidium with major pair of spines directed exsagittally or slightly divergent backwards, secondary spines slender, pointed. Cranidium, base of genal spine, axis, and pygidium coarsely tuberculate.

Discussion. British *coronata* material (see Thomas 1981) and Gotland specimens are of approximately the same age, and are regarded here as geographical subspecies of *L. coronata*. The material from German 'Graptolithengestein' erratics described by Schrank (1969) as *L. marklini* is similar in all features to *bufo*, except possibly a greater range of variation.

None of the previously described or figured Gotland specimens referred to *L. marklini* (Angelin, 1854) are included in *L. coronata bufo*. *L. marklini* is regarded here as a *nomen dubium*. The holotype (see Bruton 1967, pl. 30, fig. 7), a worn external mould of an incomplete exoskeleton, is not identifiable since it lacks important morphological features. The shape and length of the genal spines, the lateral border and border furrow, and the main part of the cranidium, are unknown. No topotype material is known, and the type locality is inaccessible for recollecting. The free cheeks referred by Bruton (1967, pl. 30, fig. 8, pl. 31, figs. 1, 2) to *marklini* are assigned here questionably to *L. muldensis* (see below). Of the other *marklini* material described by Bruton (1967), the pygidia (*ibid.*, pl. 30, figs. 3, 5) may belong to *L. coronata bufo*, or perhaps to *L. muldensis*, the pygidium of which is poorly known, but seems to be similar to that of *bufo*. The cranidia from Lilla and Stora Karlsö (Bruton 1967, pl. 30, fig. 4, pl. 31, fig. 3) have a very narrow median glabellar lobe, especially between the basal lobes, and seem not to belong either to *bufo* or *muldensis*; they cannot be compared with the holotype of *marklini*, which lacks most of the cranidium. The fairly complete specimen figured by Lindström (1885, pl. 13, fig. 15, refigured Bruton 1967, pl. 30, fig. 6) lacks free cheeks and has a median glabellar lobe similar to *bufo* and *muldensis*, but has coarsely tuberculate spines on the thorax and pygidium, and cannot be referred with certainty to either taxon, at least until *muldensis* is better known. The material discussed above cannot be determined specifically; with regard to *Leonaspis* species, the availability of either well-preserved articulated specimens or a complete 'set' of exoskeletal parts from a single locality is a necessity for specific determination.

Two aberrant specimens of *L. coronata bufo* are known. One pygidium (Pl. 31, fig. 5) has an extra, median border spine, probably a genetically determined feature. The pygidium is slightly asymmetrical. One cranium (Pl. 31, fig. 1) shows a pathological left L2, with the entire cranium in front of L1 bent sideways. The defect is probably a result of damage during the preceding moult stage.

Leonaspis muldensis Bruton, 1967

v* 1967 *Leonaspis muldensis* Bruton, p. 227, pl. 33, figs. 3, 4, 6, 7.

v? 1967 *Leonaspis marklini* (Angelin, 1854); Bruton, p. 219, pl. 30, fig. 8, pl. 31, figs. 1, 2 [free cheeks only].

. 1978 *L. muldensis* Bruton; Šnajdr, p. 35.

Holotype. Ar30826, enrolled specimen lacking pygidium, figured Bruton 1967, pl. 33, figs. 3, 4, from the harbour at Djupvik (635602 164128), Eksta parish, Mulde Beds, lower part.

Other material, diagnosis, and description. See Bruton 1967, p. 227.

Discussion. Only the three specimens already described by Bruton are known. They are all severely water-worn, lack genal spines and surface sculpture, and only one has the pygidium attached, which is badly worn. From the locality yielding these specimens are also several isolated free cheeks. These were assigned by Bruton (1967) to *L. marklini*, but it seems more likely that they are conspecific with the enrolled specimens from the same beds. This view is neither contradicted nor supported by the morphology of the specimens, since the free cheeks of the enrolled specimens are poorly preserved. On the assumption that *L. muldensis* should be retained as a valid taxon it can easily be distinguished from other *Leonaspis* by the shape of the free cheeks, if these belong to *muldensis*, but is otherwise very similar to *L. coronata* and *L. mutica* (Emmrich, 1844).

L. muldensis occurs together with, and is strongly outnumbered by, *L. crenata crenata*. Similarly, *L. coronata bufo* is always accompanied by, and outnumbered by, *L. crenata angelini*. This occurrence of two *Leonaspis* forms together is common, and has been discussed by several authors (see Campbell 1977, p. 113), and the forms are sometimes referred to as morphs of the same species. In the Gotland examples the forms are assigned to separate species, since the differences are so profound.

EXPLANATION OF PLATE 30

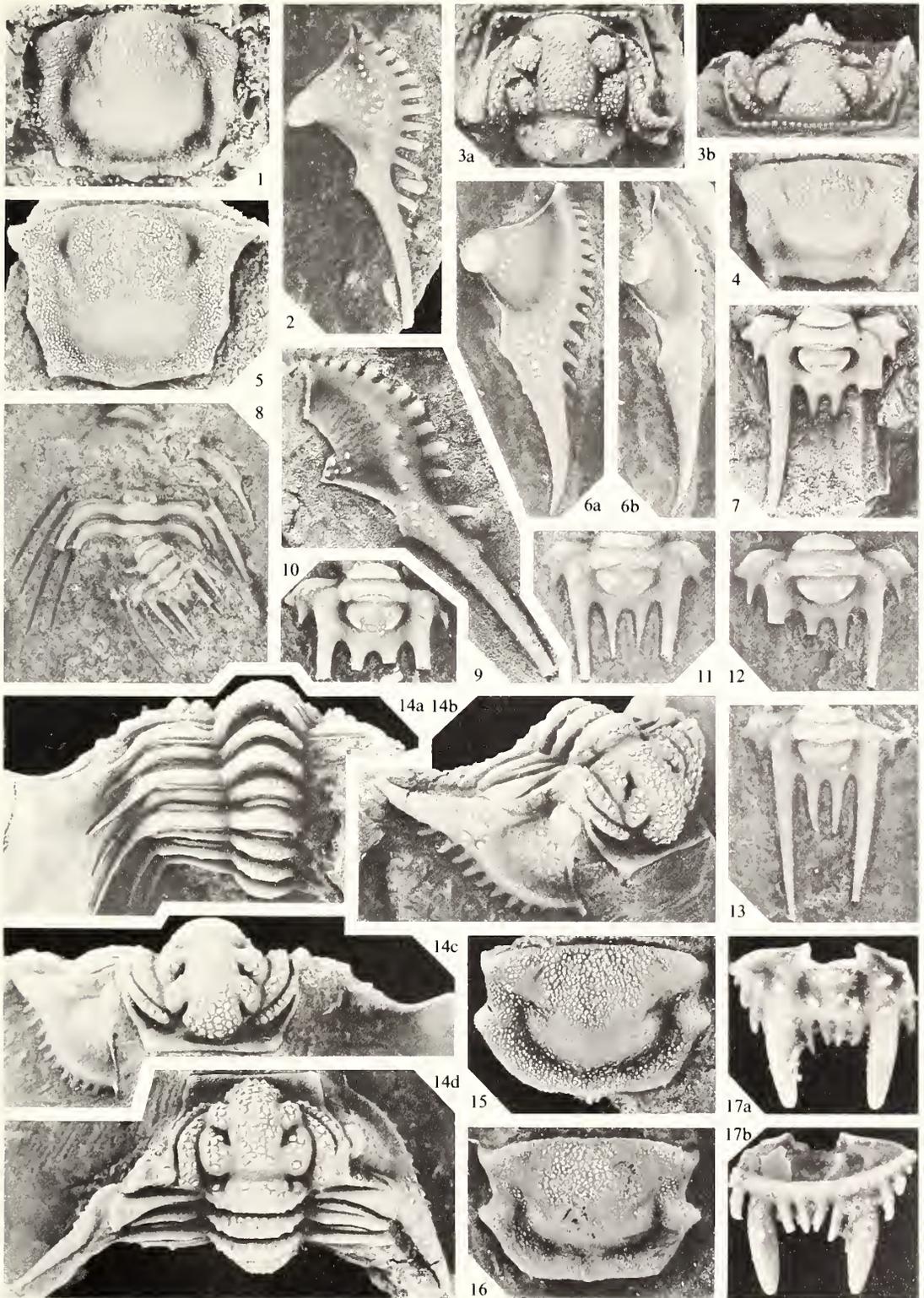
Figs. 1-4, 8-13. *Leonaspis crenata* (Emmrich, 1844) *angelini* (Prantl and Přibyl, 1949). Mulde Beds, lower part (3), Mulde Beds, undifferentiated (1, 2, 4, 8-13). Blåhäll 1 (3), Djupviksvägen 1 (9), Nordervik (2, 4, 8, 10-13), shore south of Djupvik (1). 1, displaced hypostome of complete specimen belonging to K. and W. Amelang, Aachen, exterior view, $\times 10$. 2, Ar51655, free cheek, dorsolateral view, $\times 5$. 3a, b, Ar51369a, cranium with dense tuberculation, exterior and anterior views, $\times 5$. 4, Ar51656, small hypostome, exterior view, $\times 20$. 8, Ar51657, disarticulated thorax and pygidium of small holaspis, $\times 8$. 9, Ar51367, free cheek with sparse tuberculation, dorsolateral view, $\times 6$. 10, Ar51658, pygidium, $\times 6$. 11, Ar51659, pygidium, $\times 6.5$. 12, Ar51660, pygidium, $\times 5$. 13, Ar51661, pygidium, $\times 8$.

Figs. 5, 7. *Leonaspis crenata crenata* (Emmrich, 1844). Mulde Beds, lower part, Djupvik. 5, Ar30840, hypostome, exterior view, $\times 12$. 7, Ar30812, pygidium, $\times 7$.

Figs. 6, 14-16. *Leonaspis coronata* (Salter, 1853) *bufo* subsp. nov. Mulde Beds, undifferentiated. Djupviksvägen 1 (14-16), Nordervik (6). 6a, b, Ar51686,* free cheek, dorsolateral and dorsal views, $\times 5$. 14a-d, holotype Ar51664, partly disarticulated specimen lacking pygidium, thorax, oblique anterolateral, anterior, and exterior views, $\times 5$. 15, Ar51665,* hypostome, exterior view, $\times 9$. 16, Ar51363,* hypostome, exterior view, $\times 10$.

Fig. 17. *Dudleyaspis* (*Dudleyaspis*) *uncifera* sp. nov. Ar51710,* earliest? holaspis pygidium, dorsal and ventral views, Rönklint, Upper Visby Beds, $\times 22$.

* Paratypes.



Leonaspis sp. A

Plate 31, figs. 7-11, 13

v. 1979 *Leonaspis angelini* (Prantl and Přibyl); Bruton in Jaanusson *et al.*, p. 116, non Prantl and Přibyl, 1949.

Material. All specimens are from Visby parish. Högklint Beds, unit b: Vattenfallsprofilen 1, 20·1-20·2 m a.s.l. (SGU 1454-1456). Dump at Visby harbour (639275 164800) (Ar51347). Högklint Beds, undifferentiated: 'Visby' (Ar30878, Ar30879).

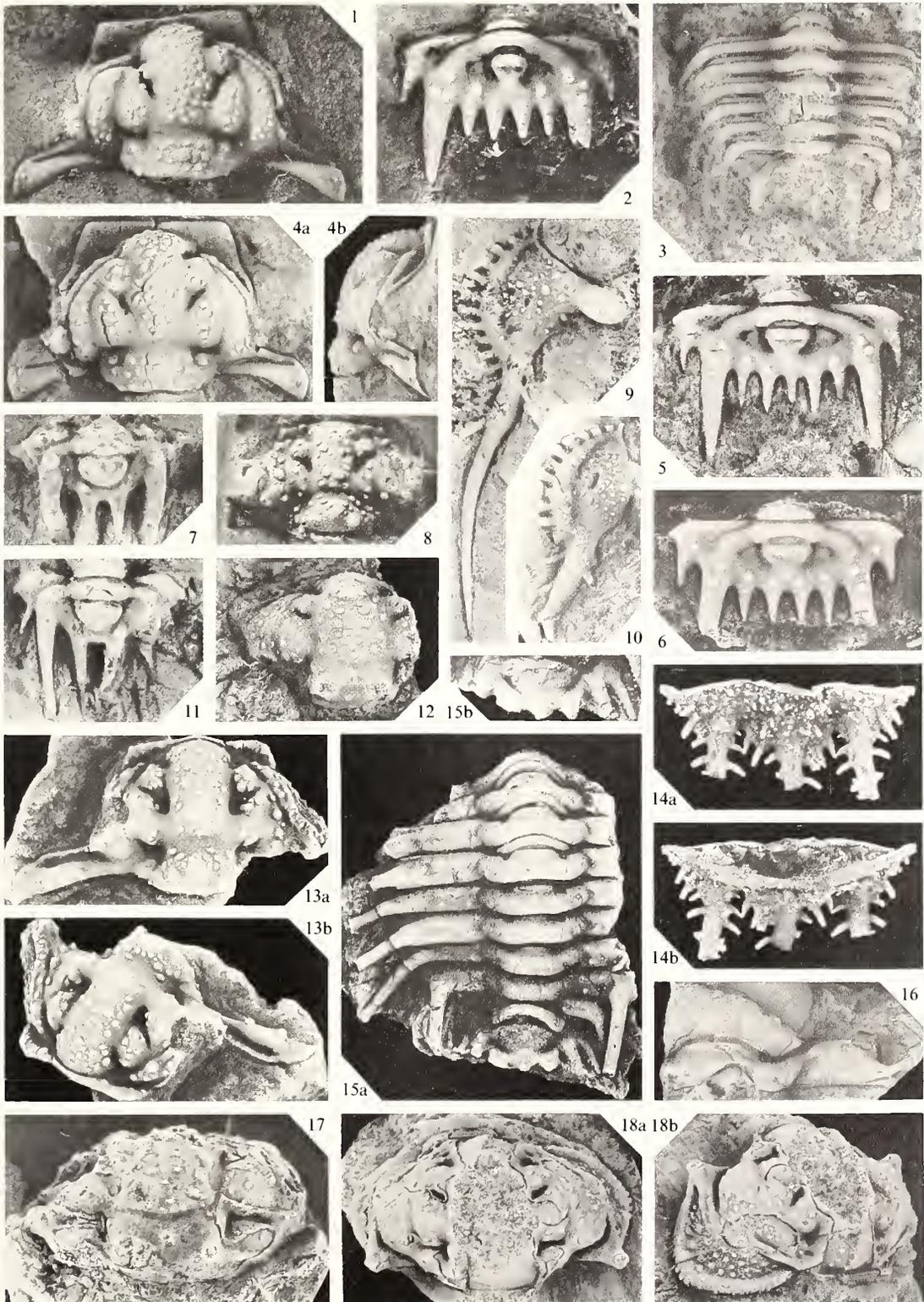
Discussion. These specimens may well represent a new species, but more and better-preserved material is needed before it can be established formally. The main distinguishing features are as follows: occipital ring with a stout median spine flanked by a pair of slender spines; median glabellar lobe narrow (tr.), parallel-sided; L1 confluent with cheek laterally due to effaced axial furrow; anterior border with a row of tubercles; anterior margin convex forwards; paired tubercles on glabella; close to facial suture is a spine dorsally on genal spine, but not on posterior margin of cranium; free cheek with thirteen border spines; genal spine very long, slender; pygidium fairly similar to that of *L. crenata angelini*, but with narrower axis, very large tubercle-pair on pleural ridges, and with a tubercle-pair above bases of posterior border spines.

L. sp. A is closest to *L. crenata angelini*, although the differences are quite marked, especially in the shape of the glabellar lobes. Bohemian Ludlow specimens assigned by Přibyl and Vaněk (1966, p. 295, pl. 2, fig. 1, pl. 3, figs. 3, 4) to *L. geinitziana* (Hawle and Corda, 1847; regarded as a synonym of *L. leonhardi* (Barrande, 1846) by Bruton 1968, p. 20), show some similarity to *L. sp. A*, both in the shape of the glabellar lobes and in the pygidium (if the associated parts of each species really belong together). It differs, however, e.g. in the shape of the occipital ring and the axial furrow, and perhaps in the number of pygidial spines. No close comparison can be made until both species are better known.

EXPLANATION OF PLATE 31

- Figs. 1-6. *Leonaspis coronata* (Salter, 1853) *bufo* subsp. nov. Mulde Beds, undifferentiated. Djupviksvägen 1 (1, 2, 4, 5), Nordervik (3, 6). 1, Ar51368a,* cranium showing pathological asymmetry, $\times 7$. 2, Ar51365,* pygidium, $\times 6$. 3, Ar51688,* latex cast of external mould of pygidium with part of thorax, $\times 4$. 4a, b, Ar51364,* cranium, exterior and lateral views, $\times 4$. 5, Ar51684,* pygidium with extra (median) spine, note slight asymmetry, $\times 7$. 6, Ar51687,* pygidium, $\times 6$.
- Figs. 7-11, 13. *Leonaspis* sp. A. Högklint Beds, unit b (7, 9-11), undifferentiated (8, 13). Dump at Visby harbour (10), Vattenfallsprofilen 1, 20·1-20·2 m a.s.l. (7, 9, 11, coll. G. Liljevall 1908), Visby (8, 13). 7, SGU 1454, worn pygidium, $\times 7$. 8, Ar30878, small cranium, exterior view, $\times 7$. 9, SGU 1455, free cheek, dorsolateral view, $\times 7$. 10, Ar51347, partial free cheek, dorsolateral view, $\times 6$. 11, SGU 1456, pygidium, $\times 7$. 13a, b, Ar30879, cranium, exterior and anterolateral views, $\times 6$.
- Figs. 12, 15-18. *Ceratocephala barrandii* (Fletcher in Salter, 1853). Högklint Beds, middle-upper part (15, 17), Halla Beds, unit b (16, 18), undifferentiated (12). Hörsne kanal (16, 18), Ireviken (17), Lilla Karlsö (12), south of Visby cement factory (15). 12, Ar30792, internal mould of partial cranium, exterior view, $\times 4$ (coll. A. Florin 1891). 15a, b, SGU 1457, partial thorax and pygidium, exterior view and dorsal view of pygidium, $a \times 2.5$, $b \times 3$ (coll. G. Liljevall). 16, SGU 1458, anteriormost? thoracic segment, $\times 2$ (coll. G. Liljevall 1909). 17, mainly internal mould of partial cranium, belonging to K. and W. Amelang, Aachen, exterior view, $\times 2$. 18a, b, SGU 1459, partly exfoliated cephalon, exterior and anterolateral views, $\times 2$ (coll. G. Liljevall 1909).
- Fig. 14. *Ceratocephala* sp. Ar51626, small pygidium, dorsal and ventral views, Rönklint + 7·5 m, Lower Visby Beds, $\times 13$ (coll. V. Jaanusson 1981).

* Paratypes.



A few pygidia of *coronata* type are also stated (on the labels) to be from the Högklint Beds, and a second species may thus be present. However, these specimens come from old collections with locality stated only as 'Visby', and a large number of Mulde Beds specimens mislabelled 'Visby' are known, so that the locality quoted must be regarded with caution.

Leonaspis sp.

Material. Ar51758–51765, small fragments of cranidia, free cheeks, thoracic segments and pygidia, from the Lower Visby Beds at Rönnklint (641181 165698), Lummelunda parish.

Discussion. The material is very fragmentary, but may represent a new species. The free cheeks have a very weak lateral border and border furrow, similar to *L. crenata crenata*, but have a secondary spine dorsally on the genal spine, similar to *L. sp.* A described above. An incomplete pygidium has two secondary spines between the major spines. The species is fairly common in the Lower Visby Beds at Rönnklint, and new material will hopefully make a specific assignment possible.

Subfamily MIRASPIDINAE Richter and Richter, 1917

Genus CERATOCEPHALA Warder, 1838

Type species. By monotypy; *Ceratocephala goniata* Warder, 1838, from the middle Silurian, Springfield, Ohio.

Ceratocephala barrandii (Fletcher in Salter, 1853)

Plate 31, figs. 12, 15–18

- v. 1851 Angelin, pl. 21, fig. 7 [illustration only, without name].
- * 1853 *Acidaspis Barrandii* Fletcher in Salter, pl. 6, p. 6.
- v. 1854 *Trapelocera bicuspis* Angelin, p. 31 [referring to 1851 figure].
- v. 1933 *Ceratocephala bicuspis* (Angelin); Warburg, p. 13.
- v. 1967 *Ceratocephala bicuspis* (Angelin, 1854); Bruton, p. 241, pl. 36, fig. 11 [with synonymy list].
- 1981 *Ceratocephala barrandii* (Fletcher in Salter, 1853); Thomas, p. 94, pl. 24, figs. 11–14, 18–23, pl. 25, figs. 1–7 [with synonymy list].

Material. From Visby, most probably Högklint Beds, units b and c; Ar2184, partial cephalon, holotype of *T. bicuspis* Angelin; Ar6152, partial thoracic segment; SGU 1457, partial thorax and pygidium. From Hörsne kanal (638493 166725), Hörsne parish, Halla Beds, unit b; SGU 1458–1459, cephalon and partial thoracic segment (the two specimens discussed by Warburg 1933, p. 13). From Lilla Karlsö, ?Halla Beds; Ar30792, partial cranidium.

Discussion. This species was described recently by Thomas (1981). The Gotland material is identical to British specimens and *T. bicuspis* Angelin, 1854 is accordingly considered to be a junior subjective synonym of *A. barrandii* Fletcher in Salter, 1853. The few Gotland specimens do not add any new information on the morphology of the species.

Ceratocephala sp.

Plate 31, fig. 14

Material. Ar51626 (small pygidium), Ar51751–51756 (fragments of thoracic segments and pygidia), all from the Lower Visby Beds at Rönnklint (641181 165698), Lummelunda parish.

Discussion. One incomplete large and one small pygidium (Pl. 31, fig. 14) both have only three marginal spines. This is a feature unique among Silurian *Ceratocephala*, and the material almost certainly represents a new species. It may be related to *C. barrandii* since one fragment is probably a free distal part of the tenth thoracic segment, indicating the presence of a structure similar to that described by Thomas (1981, p. 94) for *barrandii*. Several Ordovician species also have three-spined pygidia and sutures on the tenth thoracic segment, but the Gotland specimens seem distinct from each of these, although a comparison is not meaningful without more material.

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RHYNIOPHYTINA AND TRIMEROPHYTINA FROM THE EARLY LAND FLORA OF VICTORIA, AUSTRALIA

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ABSTRACT. New records of northern hemisphere plant genera are described from the Lower Plant Assemblage (Late Silurian, Ludlovian) and the Wilson Creek Shale (Early Devonian, Pragian/Siegenian) of Victoria, Australia. The genera, the rhyniophyte *Salopella* of which there are two new species *S. australis* and *S. caespitosa*, and *Dawsonites*, represented by *D. subarcuatus* sp. nov., which is the first recording of a trimerophyte in Victoria and probably in the Southern Hemisphere, were found associated with *Baragwanathia* and are new additions to the *Baragwanathia* flora.

SINCE the work of Lang and Cookson (1930, 1935) and Cookson (1935, 1949) no formal studies have been made on the *Baragwanathia* flora of the Lower Devonian of Victoria, Australia. For many years this flora was regarded as Silurian, the oldest vascular land plant flora in the world. Elles (in Lang and Cookson 1935) had identified the associated graptolite as *Monograptus uncinatus* Tullberg (an Early Ludlow species), which often occurred on the same bedding plane as specimens of *B. longifolia* Lang and Cookson. Investigations by Jaeger commencing in 1959 (see Jaeger 1966) led to the description of this as a new species, *M. thomasi* Jaeger. Associated with *M. thomasi* and slightly higher is *M. aequabilis notoaequabilis* Jaeger and Stein. The range of this latter species in other parts of the world is Pragian. *M. thomasi* has since been identified from Malaya (Jaeger 1970) and as *M. aff. thomasi* in Russia (Koren' 1971) in rocks believed to be Pragian. Jaeger considers that the evidence suggests the *Baragwanathia* flora as described by Lang and Cookson (1930, 1935) is Pragian, a view with which Koren' concurs. However, the precise age range of *M. thomasi* is still uncertain. The range of *Baragwanathia* itself extends above that of *M. aequabilis notoaequabilis* and, in Victoria, below that of *M. thomasi*.

Garratt (1978) reported two distinct *Baragwanathia* floras from the Yea district: the Upper and Lower Plant Assemblages. The Upper Plant Assemblage is equivalent in age to the flora described by Lang and Cookson. The 1929 collecting party (Harris and Thomas 1941) obtained plant fossil material from the Upper and Lower Plant Assemblages in the Yea district. The Lower Plant Assemblage material was collected from a road cutting about 30 m from the Limestone Road locality described here. None of this material had been included in Lang and Cookson's papers on the *Baragwanathia* flora. The Upper Plant Assemblage material illustrated by Lang and Cookson (1935) was collected from Killingworth Road, Yea.

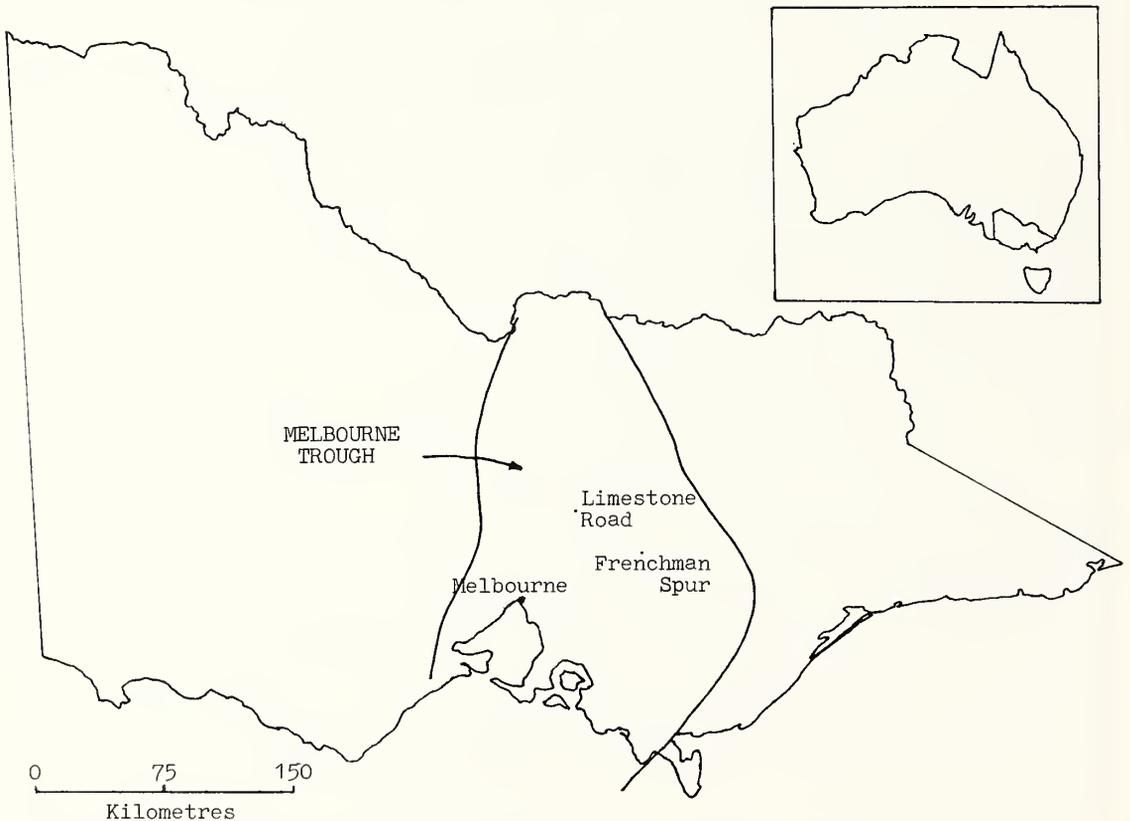
Separating the two assemblages is 1,700 m of virtually unfossiliferous sandstone. The Lower Plant Assemblage contains the oldest known *Baragwanathia* and is regarded, somewhat controversially, as being of Ludlovian age (Edwards *et al.* 1979; Garratt 1981). The dating, based initially on field evidence, is now on the basis of associated graptolites (Rickards 1982, pers. comm.). While no new species have been added to the *Baragwanathia* flora in the intervening years since the 1930s, when the late Dr. Isabel Cookson did her pioneering work, it is clear from the new records reported here, together with others still under investigation, that the *Baragwanathia* floras are more diverse than have been recognized.

LOCALITIES AND MATERIALS

LOCALITY 1. Frenchman Spur: roadside exposure on the fire access track known as Frenchman Spur Road about 10 km west of Matlock (Grid reference 077-656. Matlock: Australia Sheet 8122—IV, 1 : 50,000) (text-fig. 1).

The exposed strata are near the top of the 150 m thick Wilson Creek Shale which outcrops in the area at a number of localities that have yielded *Baragwanathia*. The unit comprises a fossiliferous shale interbedded with thick siltstones. Sediments at Frenchman Spur when fresh are hard and grey-black; they are almost impossible to split along bedding planes. The weathered material, which is buff coloured, splits easily and was the source of most of the specimens. Preservation of the plant fossils varies from compressions with considerable amounts of fragmentary mineral to pink-stained impressions. The Wilson Creek Shale has been subjected to at least one generation of folding which appears to have fragmented the mineral remains of the plant into microscopically small pieces, often arranged in two diagonal rows with the space in between filled with secondary silica. Most of the plant detail and cellular structure has been lost. Maceration with Schulze's solution yielded no fragments or spores; cellulose acetate film pulls failed to show any structure or *in situ* spores in either fresh or weathered rock.

Age and correlation. Early Pragian (= Siegenian); *M. thomasi* is sometimes found on the same bedding plane as plants, but more frequently in dense clusters on different planes. *M. aequabilis notoaequabilis* is not present, but has been recorded at nearby localities in the Wilson Creek Shale.



TEXT-FIG. 1. Locality map showing location of the Melbourne Trough and the two collection sites.

The only other animal fossils are eurypterid fragments. The flora, therefore, is at the same stratigraphic level as the Upper Plant Graptolite Horizon (Couper 1965; Garratt 1978; Jaeger 1966) and is of Early Devonian age.

Flora. Rhyniophytina: *Salopella australis* sp. nov., *S. caespitosa* sp. nov., *Yarravia oblouga* Lang and Cookson, *Hedeia* spp. Zosterophyllophytina: *Zosterophyllum* sp., other undescribed zosterophylls. Lycophytina: *B. longifolia* Lang and Cookson, *B. sp.*, other lycopods, fragmentary but not *Baragwanathia*. Trimerophytina: *Dawsonites subarcuatus* sp. nov.

The site has been mentioned as a *Pachytheca* locality (Moore 1965) but this identification has not been substantiated.

LOCALITY 2. Limestone Road, Yea: a recently widened road cutting 2 km south-east of Yea. (Grid reference 466-088. Yea: Australia Sheet 7923—I, 1 : 50,000.) This locality was cited by Harris and Thomas (1941) as Brackley's Cutting, Geological Survey locality 4, by Couper (1965) as locality 62, and by Garratt (1978) as locality 4 (text-fig. 1).

The plant-bearing strata are thin brown to grey claystones near the top of the Yea Formation (see stratigraphic section in Garratt 1978), and occur immediately below the Rice Hill Sandstone member. The horizon is some 1,700 m stratigraphically below that of the main *Baragwanathia* floras (Upper Plant Graptolite Horizon). Preservation is very poor; often only a depression in the plane of the rock to indicate the outline (e.g. Pl. 32, fig. 5). Some remains are of a white mineral and others of a brown deposit, occasionally occurring together (Pl. 32, fig. 6). No cellular structure or spores have been found.

Age and correlation. Ludlow Series; Garratt (1978, 1981) considers the assemblage to be of Late Silurian (Ludlow) age. He bases this on detailed geological mapping in this region, together with evidence from the associated fauna and lithological affinities and especially on the presence of several graptolite species known only from Ludlow strata elsewhere. These are *Pristiograptus dubius* and *Bohemograptus* sp. *M. aff. uncinatus uncinatus* has not been recorded at Yea, but occurs together with these two species and *Baragwanathia*, some 3 km to the north (Garratt 1978, locality 1). The Limestone Road assemblage also contains undescribed gastropods, orthocerids, *Hyolithes* spp., *Necklania* (bivalve), and *Maoristrophia banksi* (brachiopod).

The relatively large size of the axes, up to 400 mm, suggests either that they have not been transported far or had been transported gently. Garratt (pers. comm.) believes that the plants came from the south.

Flora. Rhyniophytina: *Salopella australis* sp. nov., *Hedeia* sp. Zosterophyllophytina: At least one zosterophyll (report in preparation), two other probable zosterophylls. Lycophytina: *Baragwanathia longifolia*, at least one other lycophyte.

SYSTEMATIC PALAEOLOGY

Three new species have been erected. All material (except that on Pl. 32, figs. 5, 6) housed at the National Museum of Victoria.

Subdivision RHYNIOPHYTINA Banks 1968
Family RHYNIACEAE Kidston and Lang 1920
Genus SALOPELLA Edwards and Richardson 1974

Type species. *S. allenii*.

Salopella australis sp. nov.

Plate 32, figs. 1-6; Plate 34, figs. 4, 5; text-fig. 2A-C

Diagnosis. Axes with at least two dichotomies, 0.9-2.4 mm wide with central line. Plant at least 145 mm high. No obvious branching at the base of the sporangia. Sporangia 6.5-14.0 mm long and

1.3–2.0 mm wide, with parallel sides in the lower two-thirds of the presumed fertile portion. Sterile sporangial apex tapering to a point in the upper third. Spore characters unknown.

Range. Late Silurian (Ludlovian)–Early Devonian (Pragian).

Type locality. Frenchman Spur.

Horizon. Wilson Creek Shale (Pragian).

Holotype. NMV part and counterpart, P50,008. Plate 32, figs. 1, 2.

Derivation of specific name. 'australis'—southern.

Description. More than twenty specimens have been collected from two sites, Limestone Road (Ludlovian) and Frenchman Spur (Pragian). Most are compressions (*sensu* Schopf 1975) but some are so weathered that they have been reduced to impressions. Preservation varies from a pink stain on a buff-coloured matrix to a finely divided material of coaly appearance, as seen in specimens from Frenchman Spur, and red-brown and white minerals on similar coloured background from Limestone Road. One Limestone Road specimen (Pl. 32, fig. 3) is white on a blue-grey matrix, with its ultimate branches on different planes in the rock. The majority of specimens have had some covering matrix removed.

The specimens show the remains of a possible vascular trace, 0.22 mm wide, in some cases as a faint dark line in the centre of the stem (Pl. 32, fig. 1) and in others, a central ridge (Pl. 32, fig. 3). The ridge branches with the axis.

The maximum total length of axes is 145 mm. Eleven of the specimens are dichotomously branched (another possibly so) and of these, four have two dichotomies. Of the remaining six specimens, one is an isolated axis apex and the others are of axis lengths up to 40 mm. Axis width decreases with successive branching but remains constant between nodes. Maximum width is 2.4 mm and the minimum 0.9 mm. Average widths for the lowest branch are 2.1 mm (range 1.8–2.4 mm), the intermediate 1.8 mm (1.0–2.2 mm) and the ultimate branch 1.4 (0.9–1.7 mm).

Each axis terminates in a single presumed sporangium. In the better-preserved specimens an oval-shaped area of dark mineral is present a few millimetres below the apex. These areas are presumed to be sporogenous, although no spores could be isolated from them. The junction between axis and sporangium could not be clearly defined, as many axes show an increase in diameter 2–3 mm below the presumed spore mass. Measurement of the sporangia was taken from the base of the dark area or the remaining outline. Where there was no increase in the axis diameter below the sporangium the sporangial width was the same as that of its axis. Average length of twenty-six sporangia is 10.2 mm (range 6.5–14.0 mm). The average width of the sporangia is 1.8 mm (1.3–2.9 mm). The presumed spore-containing area where visible averaged 5.7 mm in length (4.4–7.5 mm). The sporangia are of acute convex shape in the presumed sterile upper portion. In half the specimens there is evidence of a slight indentation where the sterile tips connect with the fertile area (e.g. Pl. 32, fig. 5). The maximum widths of the sporangia coincide with those of the presumed fertile areas. The sporangia are parallel-sided for at least half their length.

EXPLANATION OF PLATE 32

Figs. 1–6. *Salopella australis* sp. nov. 1, 2, NMV P50,008 part and counterpart; holotype showing the sterile apex of the sporangium, the dark presumed sporogenous region and dichotomous branching; Frenchman Spur; fig. 1, $\times 3.8$, fig. 2, $\times 2.2$. 3, NMV P50,011; plant remains preserved as a white mineral on a steel-blue coloured matrix; the two branches with eight sporangia are most likely from the one plant (see reconstruction, text-fig. 2c); central ridge on the lower part of the plant is the probable remains of the vascular trace; Limestone Road, $\times 1.8$. 4, NMV P50,014; an axis with a dichotomy just below the sporangia; this specimen has the longest sporangia and is unusual in branching just below the dark spore masses; Frenchman Spur, $\times 1.1$. 5, one of the longest specimens (123 mm) from Limestone Road; although it cannot be seen from this illustration using a unilateral light source, the two sporangia on the left both have a dark area, the remains of a presumed spore mass; remains of the vascular trace are visible in the lower part of the axis (arrow); $\times 1$ (this specimen is from Dr. J. Douglas's private collection). 6, the extreme left-hand sporangium of fig. 5, showing the large dark presumed spore mass; photograph was taken using overhead light and high contrast film and paper; remainder of the specimen is not visible using this technique; $\times 1.5$.



Angles of the ultimate branches average 38° ($25\text{--}60^\circ$), while the lower branching angle is wider at 60° ($48\text{--}70^\circ$). The specimen illustrated on Plate 32, fig. 5 and text-fig. 2B has at first glance a much broader angle. If the angle is examined 1 mm from the dichotomy, it can be seen that the angle is 70° and the further spreading of the branches may be an artefact of deposition. In most examples, the branch axes curve in together until they become almost parallel.

As may be seen in Plate 32, fig. 1, naked axes of similar widths often occur on the same bedding planes as the specimens referred to as *Salopella*. Some of these naked axes are up to 200 mm long and often curved. There is little direct evidence of the habit of *Salopella*, but if the long axes are portions of this species, it is possible that the plant was partially prostrate. It is unlikely that such slender axes would exceed this height, although this would depend to some extent on stem anatomy.

In conclusion, the Victorian specimens are part of a small, open-branched plant, at least 145 mm high with slender naked axes terminating in elongate sporangia. Axes dichotomize at least twice, with successive planes of dichotomy, probably at 90° . The specimen illustrated in Plate 32, fig. 3 and text-fig. 2C demonstrates this and has different orders of branches on different planes in the rock. No spores could be isolated from the sporangia and no cell detail was present in any of the remains. The basal parts of the plant are unknown.

Discussion. Edwards and Richardson (1974) erected the form genus *Salopella* to distinguish compression fossils having *Rhynia*-like sporangial shape and naked dichotomizing axes from the much better-preserved plants from the Rhynie Chert. It is clear that this new species belongs in the form genus, but there are differences from the type species *S. allenii*, and from *Rhynia*. There are other characters which are common to both the new *Salopella* and other members of the Rhyniaceae.

There are seven genera in the family Rhyniaceae (*sensu* Banks 1975). Of these, five have sporangia with height exceeding the width. *Rhynia* and *Salopella* are in this group, as are *Horneophyton lignieri* (Kidston and Lang) Barghoorn and Darrah, *Steganotheca striata* Edwards, and *Eogaspesia gracilis* Daber.

Eogaspesia from the Gaspé Peninsula, Quebec is a gregarious plant with small oval sporangia (Daber 1960). The narrow axes rarely branch and its bushy habit readily distinguishes it from *Salopella australis*. *Horneophyton lignieri* has small cylindrical sporangia with a distinct columella. There is no indication of such tissue preserved in *Salopella*. *Steganotheca striata* Edwards (1970) has truncated fusiform sporangia and a branching habit whereby the tips of the branches are parallel, a branching pattern (see Edwards 1970, Pl. 84, fig. 1.2) closely resembling the branching illustrated for *Salopella australis* in Plate 32, figs. 1–5. *Steganotheca striata* also has axes which gently taper to increase in diameter below the sporangia so that the sporangial bases are not clearly defined; the sporangia are small (1.8 mm) and cup shaped.

The dimensions of the sporangia and axis width of the new *Salopella* are almost exactly the same as those of *Rhynia major*. *R. gwynne-vaughani* has smaller sporangia which abscise, protuberances on the axes and an adventitious branching system. From the descriptions of Kidston and Lang (1917 and 1920), it appears that *R. major* not only does not branch as frequently as *Salopella*, but also has axes tapered from 6 mm at their bases to 1.5 mm below the sporangia. Both *Rhynia* species have clearly defined sporangial bases and although *R. major* has some sterile tissue at the apex of the sporangium (Kidston and Lang 1917, Pl. 9, fig. 62), it is not extensive. Although it is difficult to compare impression fossils with petrifications, *R. major* appears to have the broadest part of its sporangium about one-third its length from the base, the upper two-thirds tapering slightly to a rounded apex.

The sporangia of *S. allenii* also differ from those of the new species. Although the dimensions of the sporangia are the same, *S. allenii* has true fusiform sporangia, compared to the parallel-sided ones of the new *Salopella*. *S. allenii* sporangia lack the defined spore area as seen on most specimens of *S. australis*; the sporangial bases of *S. allenii* are more clearly defined and their axes dichotomize directly below the sporangia. This character was observed only once (Pl. 32, fig. 4) in the Victorian specimens.

The new *Salopella* is a larger plant in terms of axis length and does not dichotomize as frequently as *S. allenii*, although it is important to note that *S. allenii* is known from only one specimen.

Another genus with terminal oval sporangia which is known in Victoria is *Sporogonites*. Halle (1916), in his diagnosis of *Sporogonites*, described the sporangium as 'a capsule obovoid or clavate' with a slender rigid stalk. The stem broadens to form the basal region of the capsule. *Sporogonites* has a possible central horizontal line of dehiscence, longitudinal ridges, and is not regarded as being a

vascular plant (Andrews 1960). A Victorian species, *S. chapmani*, is known from the late Early Devonian (Emsian) Walhalla Group (Lang and Cookson 1930). Cookson (1949) reported *S. sp.* from the Ruddock Siltstone which may be equivalent to, or slightly younger than the Wilson Creek Shale. *Sporogonites* has not been reported from the Wilson Creek Shale, and *S. chapmani* is quite distinct when compared with *Salopella australis* in terms of axis width and sporangial shape and size.

Edwards and Richardson (1974) comment on the similarity of *S. allenii* sporangial shape to that of another Victorian genus, *Hedeia corymbosa* (Cookson 1935). They point out that *H. corymbosa* has a more compact fructification, with up to four orders of branching in a comparatively short length of axis.

A period of at least 20 million years probably separates the two deposits in which *S. australis* is found, but there is no evidence at present to suggest that changes have occurred in the species over this interval. Specimens collected from the older beds at Limestone Road tend to have longer axes. Although the plant remains at Frenchman Spur have been further fragmented by the close jointing pattern at the site, they were probably of shorter lengths than those at Limestone Road at the time of deposition.

While no anatomy is preserved in the new *Salopella*, from the gross morphology it would appear that the fertile portion of *S. australis* may be little more than a zone of the shoot apex in which spores develop, and it therefore lacks an organ that could be clearly defined as sporangium. If this proves to be so, it may represent the most primitive sporangial condition known amongst the early land plants. The small indentation noted in some specimens may indicate a position where the apex breaks off to release the spores. From the faint lines and ridges in two specimens it is presumed that this plant was vascularized.

Because of the small differences in branching and sporangial shape, and the geographical separation between this species and *S. allenii*, it seems advisable to erect a new species with the specific name '*australis*' for the southern hemisphere plant.

Salopella caespitosa sp. nov.

Plate 33, figs. 1-4; Plate 34, fig. 3; text-fig. 2D

Diagnosis. Tufted plant at least 85 mm high of slender naked axes 1.2 mm wide, bearing ovate to fusiform sporangia averaging 4.5 mm long and 1.7 mm wide. There are up to three orders of branching, the ultimate dichotomy normally at least 25 mm below the sporangia, but occasionally at the sporangial base.

Range. Pragian.

Type locality. Frenchman Spur.

Horizon. Wilson Creek Shale.

Holotype. NMV P50,016. Plate 33, figs. 1-4; Plate 34, fig. 3.

Derivation of specific name. 'caespitosa'—tufted.

Description. The diagnosis is based on one specimen, part and counterpart. Preservation is poor, with little mineral remaining except on some sporangia and an occasional fine line along the centre of the axis. A brittle film of almost transparent mineral is all that remains of most of the axes and the exterior part of the sporangia.

The plant consists of a number of axes, in excess of 20. The axes do not taper but after each dichotomy decrease in diameter. They cross each other and disappear into the matrix, making it impossible to follow fertile axes to the bottom of the specimen, and axes from the lower parts to their apices. The broadest axis on the specimen measures 1.9 mm, while the lowest portion of axis known to terminate in sporangia (sporangia 1-3, see Pl. 33, figs. 1, 2) has a width of 1.7 mm. After three orders of branching, this width decreases to 1.1 mm. When axes can be traced to termination, all appear to be fertile. Many axes show a fine central line 0.2 mm wide, presumably the remains of the vascular trace. The angles of branching are narrow (10-45°), although the extremes of this range may be an artefact of preservation.

There are twenty-six sporangia visible in the part and counterpart (see Pl. 33, fig. 1), although some of these are

incomplete. The sporangia range from ovate to fusiform in shape, the larger being more fusiform and the smaller ovate. The size ranges from 3.2–6.0 mm (average 4.5 mm) in length and 1.3–2.0 mm (average 1.7 mm) at the widest point. The longest sporangia are not always the broadest. Three axes probably have more than one sporangium at their apices (Pl. 33, figs. 3, 4). Sporangium 13, illustrated in Plate 33, fig. 3, appears to have two sporangia, partially superimposed. The tops of them have been broken away but Plate 33, fig. 4, illustrating the counterpart, has the apices visible. Sporangium 14 is also broader than other single sporangia. The presumed vascular trace of the axis of sporangium 15 appears to divide at the base of the sporangium. The preservation is not good enough to determine whether the trace actually goes to two presumed spore bodies, or even three. Sporangia 13, 14, and 15 are all in close proximity, although their axes do not appear connected. These are the only axes which appear to divide so close to the base of their sporangia.

Of the intact axes, none was seen to terminate in a sterile tip. Variation in sporangial shape could be due to the stage of maturity of the sporangia, the longer and more fusiform (e.g. sporangia 6–9) possibly being less mature. It is recognized also that sporangia 13–15 could be the result of the manner of preservation, either in compression to give a broader appearance to a single sporangium, or by superimposition, as shown by the axes of sporangia 5 and 6. However, the axes of sporangia 13 and 14 remain as one for their entire length, so it appears unlikely that superimposition has occurred. Similarly, it seems unlikely that squashing and spreading should only happen to these sporangia. It is also possible that they are at a stage of dehiscence, with the sporangial wall breaking away (see especially sporangium 14; Pl. 33, fig. 1). As the axes of these sporangia are broader (1.6, 1.5, and 1.5 mm respectively) just below the sporangial base than any other axis at the same point, it appears that each axis supports two sporangia.

Surrounding most of the dark spore bodies is a deposit of the semi-transparent mineral (e.g. sporangia 1–3, 7, 8, and 10). No spores could be isolated from the presumed spore bodies, nor could any line of dehiscence be seen. Basal parts of this plant are unknown and the tufted habit is assumed on the basis of the orientation of the axes as preserved.

Discussion. It may be inferred from this specimen of semi-aligned axes that they are all from the one plant, arising perhaps from a rhizome or gametophyte. Fragments of axes of comparable diameter from the Wilson Creek Shale are rare. It appears that this species was either more delicate and hence unable to survive a long period of immersion, or that the plant was less abundant than other Victorian rhyniophytes.

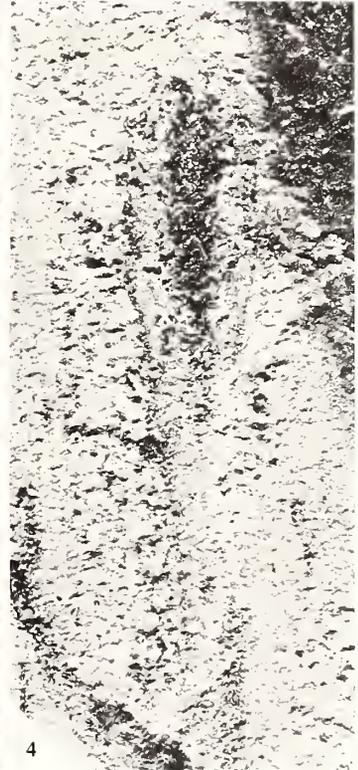
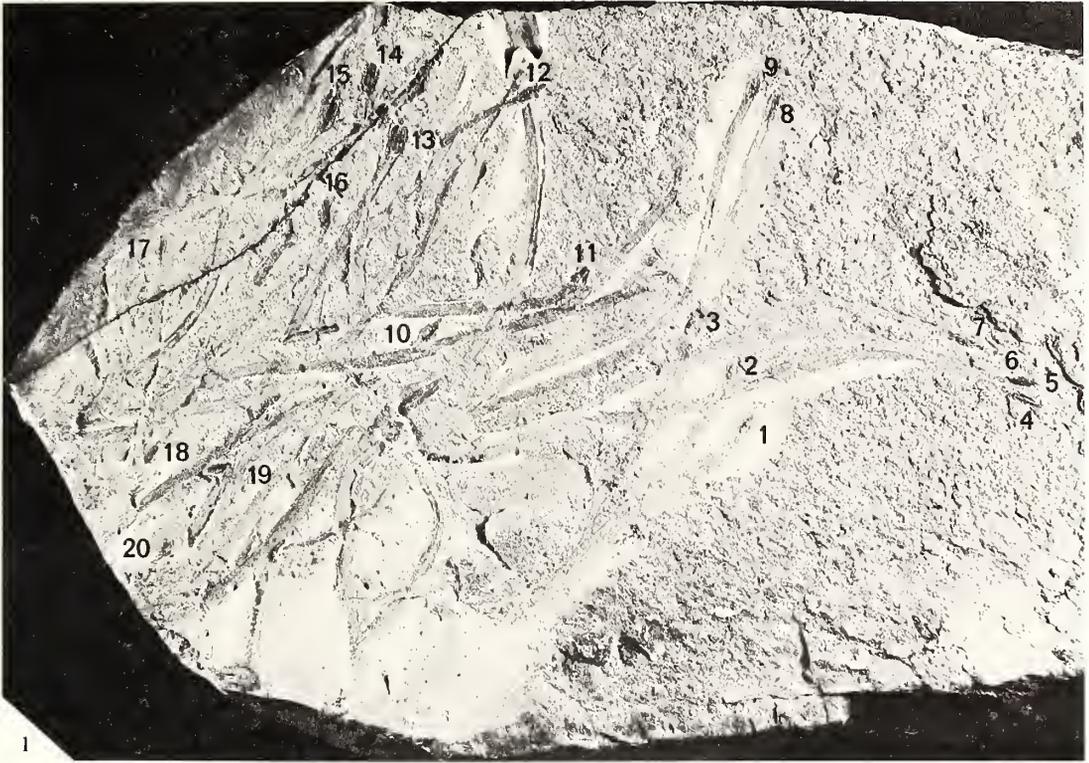
The points made in the discussion on *Salopella australis* are also relevant here. In habit the plant resembles several northern hemisphere Early Devonian plants—*Steganotheca striata*, *Renalia lueberi* Gensel, and *Eogaspesia gracilis*. *Hicklingia edwardii* Kidston and Lang from the Middle Devonian is also similar in appearance. *Hicklingia* is considered a zosterophyll on the basis of its sporangial arrangement (Edwards 1976). Gensel (1976) considers *Renalia* to be intermediate between the Rhyniophytina and the Zosterophyllophytina. *Eogaspesia* has few fertile axes and the sporangia are elliptical rather than ovate; the axes rarely dichotomize and the genus is thought by Höeg (1967) and Gensel (1976) to be non-vascular.

Rhynia gwynne-vaughani has sporangia only slightly smaller and of similar shape to the tufted plant we have described as *Salopella caespitosa*. The habit of *R. gwynne-vaughani* (see Edwards 1980) is distinct, with adventitious branching. As is the case with *S. australis*, *S. caespitosa* cannot be compared adequately with the well-described genus *Rhynia*, and is more appropriately placed in the form genus *Salopella*.

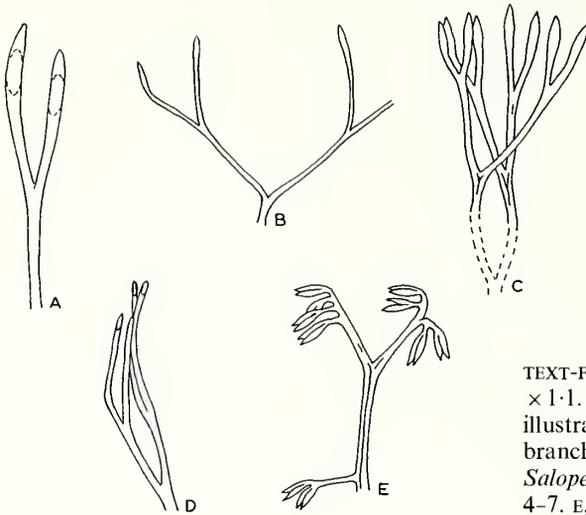
More is known of the habit of *S. caespitosa* than of the type species *S. allenii*. They both differ from *S. australis* in sporangial size and in having a definite base to the sporangium. *S. australis* axes are

EXPLANATION OF PLATE 33

Figs. 1–4. *Salopella caespitosa* sp. nov.; holotype; NMV P50,016. 1, complete specimen (part) showing numbered sporangia (refer to text); Frenchman Spur; $\times 1$. 2, branching in *S. caespitosa*; stems bearing sporangia nos. 4–7 (part); see also text-fig. 2D; $\times 1.1$. 3 and 4, part and counterpart of sporangium 13; fig. 3 shows the stem with the remains of the presumed vascular trace; this sporangium gives the appearance of being double; however, the counterpart (fig. 4) does not show this nearly as well; $\times 10$.



TIMS and CHAMBERS, *Salopella*



TEXT-FIG. 2. A, *Salopella australis*, diagram of holotype, $\times 1.1$. B, *S. australis*, diagram of large branched specimen illustrated in Pl. 32, fig. 5, $\times 0.5$. C, *S. australis*, possible branch structure of specimen illustrated in Pl. 32, fig. 3. D, *Salopella caespitosa*, branching of axis bearing sporangia 4-7. E, *Dawsonites subarcuatus*, reconstruction.

broader, have wider branch angles, and the fragmentary nature of the remains suggests that it may not have been a gregarious plant.

The possible development of two sporangia terminating the one axis as in *S. caespitosa* may indicate a higher level of organization towards more complex Rhyniophytina with multisporegiate terminal fructifications, such as *Yarravia* and *Hedeia*. *Y. oblonga* is found with both species of Australian *Salopella* at Frenchman Spur. However, an as yet undescribed *Hedeia* is present in the Ludlovian Lower Plant Assemblage. If the organization seen in *Hedeia* evolved from the simpler organization of *Salopella*, this must have occurred earlier than the Ludlovian.

Subdivision TRIMEROPHYTINA Banks 1968

Genus DAWSONITES Halle 1916

Type species. *D. arcuatus*.

Dawsonites subarcuatus sp. nov.

Plate 34, figs. 1, 2; text-fig. 2E

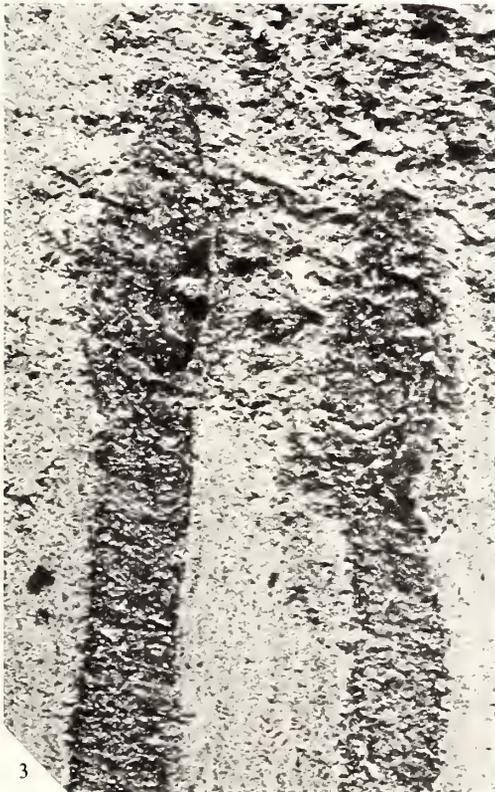
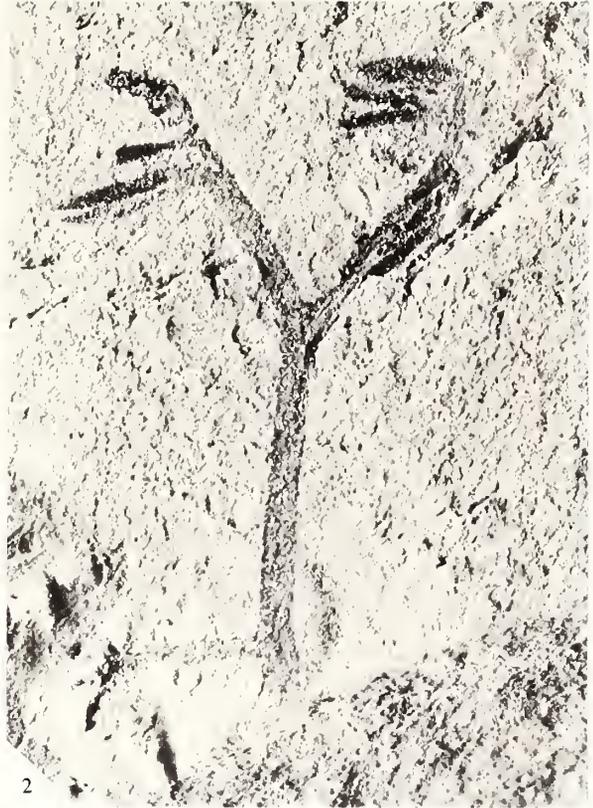
Diagnosis. Dichotomizing branch system with sympodially formed main axis due to dominance of the leading branch. Ultimate branches tapering, and bearing at the apex of each dichotomy narrow, straight, lanceolate sporangia, 3-4 mm long.

EXPLANATION OF PLATE 34

Figs. 1, 2. *Dawsonites subarcuatus*; NMV P33,215; part and counterpart. Specimen with one pseudomonopodial branch near the base and ultimate dichotomous branching; at least four sporangia are present on the left branch (fig. 2) and six on the right; counterpart shows the central line down the axis, the presumed vascular trace (arrow); Frenchman Spur; $\times 4.5$.

Fig. 3. *Salopella caespitosa*; NMV P50,016; sporangia 8 (right) and 9; sporangium 9 shows the clear delineation of the sporangial wall; $\times 15$.

Figs. 4, 5. NMV P50,013; *Salopella australis*; counterpart and part; part shows the dark presumed sporogenous area, whilst the counterpart has no such dark area; Frenchman Spur; $\times 1.7$.



Range. Early Devonian (Pragian).

Type locality. Frenchman Spur.

Horizon. Wilson Creek Shale.

Holotype. NMV P33,215a and b. Plate 34, figs. 1, 2.

Derivation of specific name. 'subarcuatus': 'sub'—somewhat or almost, 'arcuatus'—curved like a bow.

Description. This is based on a single specimen from Frenchman Spur, part and counterpart of a plant of a form not previously recorded from Australia but closely resembling *D. arcuatus* Halle. Overall the specimen measures 18 mm in length. The naked axis branches at four levels, the first unequally 1.5 mm from the base of the specimen, at an angle of almost 90°. A further 9 mm up the axis is a dichotomy with a 70° angle between the forks. The axis itself is 1 mm broad at the base and narrows to 0.7 mm at the dichotomous branching. A further branching occurs on one fork of the dichotomy (the right fork of P33,215a, shown in Pl. 34, fig. 1, shows this best), to give two groups of sporangia (see also text-fig. 2E). Because of the manner of preservation the actual point of branching cannot be seen. The fourth level of branching takes place 0.7 mm below the sporangia. The stem has a central strand, about 0.2 mm wide, visible as a ridge of thicker carbon in P33,215a and a corresponding depression in the counterpart. The ridge branches with the axis and is the presumed remains of the vascular trace.

All the branches terminate in elongate fusiform sporangia which point to the left of the axis (right in the counterpart). This is probably a depositional effect and in life the sporangia may have been semi-pendent. Each branch divides to carry at least three sporangia on separate stalks, except for one which bears two sporangia on the one stalk. Whole sporangia are 3–4 mm long and 0.4–0.7 mm broad. Sporangia of the first branch are absent from the counterpart. No obvious lines of sporangial dehiscence are shown. Cellulose acetate film pulls of the sporangia yielded no spores.

Discussion. When Halle (1916) erected the genus *Dawsonites* for fragments of branched axes with terminal recurved pairs or groups of sporangia, he was aware of their close similarity to sporangia assigned to *Psilophyton princeps* by Dawson (1859, 1871). However, because of the lack of physical connection between the spiny axes and the terminal sporangia of the northern hemisphere species, *P. princeps*, Halle considered a new genus was justified for the specimens he found in Norway. The two taxa, *D. arcuatus* and *P. princeps*, have been proved by Hueber and Banks (1967) to be conspecific. However, in the intervening period *Dawsonites* has become a form genus for fragmentary axes bearing terminal sporangia. Banks *et al.* (1975) state that *Dawsonites* should be used in Halle's restricted sense rather than that of Höeg (1967), who cited eight species and widened the concept of the genus. The Wilson Creek Shale specimen fits into the original description of the genus.

The resemblance of specimen P33,215 to Halle's original *D. arcuatus* is quite apparent. There are, however, a number of minor differences. The sporangia of P33,215 do not droop from recurved branches but hang, probably semi-pendently, from straight branches which dichotomize at a wider angle than those of *D. arcuatus*. Also, the sporangial shape differs slightly, most sporangia being more elongate in the Victorian specimen. There are no ridges on the stem, although this feature may have been lost in preservation. Spines, which are a characteristic of *P. princeps* and also of the lower portions of some of the specimens identified as *D. arcuatus* in the Northern Hemisphere, are absent from the Victorian specimen. This may be because the specimen is such a small fragment and spines could have been present further down the axis. Spiny axes are rare in the Victorian Lower Devonian. Cookson (1935) recorded some non-fertile spiny axes from the Mt. Pleasant Sandstone and we have collected some recently from the Frenchman Spur locality.

Psilophyton axes also have pseudomonopodial branching, and a few specimens of naked axes from other Early Devonian strata of Victoria have been found with branching of this type. At present, however, there is no evidence that the fertile specimen and the axes are related.

It is recognized that if more material comes to hand this specimen may be reassigned to another genus. The specimen resembles *D. arcuatus* in size and overall form extremely closely. It fits well into Halle's diagnosis for *Dawsonites*, 'sporangium bearing branch systems, dividing dichotomously, or differentiated into a sympodially formed main axis and bifurcating lateral branches. Ultimate

branches slender and curved, bearing terminal capsules of a narrowly obovoid or short fusiform shape and usually 3–5 mm long.' It is the only representative of the subdivision Trimerophytina yet found in the Victorian early land flora. This record of a trimerophyte in the Victorian Siegenian is contemporaneous with the first appearance of the group in the Northern Hemisphere.

The geographic separation of Halle's species from Norway and those in south-eastern Australia, together with their minor differences mentioned above, have led to the designation of this specimen as a new species, *D. subarcuatus*.

GENERAL CONCLUSIONS

The Lower Plant Assemblage

The Lower Plant Assemblage contains, in addition to *Salopella australis*, *Baragwanathia longifolia*, a new species of *Hedeia*, a new genus from the Zosterophyllophytina, and other unidentified fragmentary remains. Only three species, *S. australis*, *B. longifolia*, and the new *Hedeia* are common to both the Lower Plant Assemblage and the Wilson Creek Shale. The Wilson Creek Shale contains other species as mentioned previously. In other words, the floras are quite distinct, having a minority of species in common. Even in *B. longifolia*, there are some small differences in form—this will be discussed fully elsewhere.

We recognize that the dating of the Lower Plant Assemblage as Ludlovian is controversial, and has already been questioned (Edwards *et al.* 1979; Hueber 1983). We also acknowledge our own caution as to the age. The two pre-Devonian floras of Wales (Edwards 1979; Edwards and Rogerson 1979) and Podolia (Obrhel 1962) from the Northern Hemisphere consist of simple, tiny plants in comparison. There is, however, mounting evidence on the associated graptolites that the Lower Plant Assemblage is indeed Ludlovian. Recent studies (Rickards and Garratt, pers. comm.) have shown there are two Ludlovian genera of graptolites.

Palaeogeographic maps of the Early Devonian (Smith *et al.* 1973; Heckel and Witzke 1979) show Europe and Australia in equatorial regions on opposite sides of the globe. Is it possible that the flora could have developed in isolation 20,000 km from the *Cooksonia* floras of Wales and Podolia? *Cooksonia*-type plants were present in the Wenlockian in Ireland (Edwards and Feehan 1980) but little development in vascular plant form seems to have occurred in Europe until the beginning of the Devonian. Did a period of rapid evolution occur in the flora of the Melbourne Trough, and was it contained there until the Early Devonian? The only possible vascular plants older than the Lower Plant Assemblage currently known in Victoria are found as *Hostinella*-type chaff about 180 m stratigraphically below the Lower Plant Assemblage and in the same district. There is no sign of *Baragwanathia* in the chaff, despite the fact that *Baragwanathia* is easily recognized even in small fragments.

The Early Devonian

The three new species described here are from genera previously recorded only from the Northern Hemisphere. Edwards (1973) considers that there were two contrasting floras in the Early Devonian, one being that of the Northern Hemisphere and Australia, and the other restricted to the southern hemisphere continents: South America, southern Africa, and Antarctica. While it must be remembered that *Salopella* and *Dawsonites* are form genera only and may not be genetically related to their northern hemisphere counterparts, they come, with *Zosterophyllum*, from three separate subdivisions. The presumed non-vascular *Sporogonites* and *Pachytheca* are common to both the Northern Hemisphere and Australia. *Baragwanathia* is very similar to the northern hemisphere genus *Drepanophycus* and, indeed, a new species of *Baragwanathia* from Canada has been described by Hueber (1983). These records must be considered as strong evidence to support the link between the floras of Australia and the Northern Hemisphere during Early Devonian times. This evidence also suggests that some mixing of the floras had occurred before the Pragian.

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THE CRETACEOUS AMMONITE *AMMONITES REQUIENIANUS* D'ORBIGNY, 1841

by W. J. KENNEDY and C. W. WRIGHT

ABSTRACT. *Coilopoceras requienianum* (d'Orbigny, 1841) is revised on the basis of the types and other material. It shows wide intraspecific variation and dimorphism of the type demonstrated in North American species of the genus. Similar dimorphism is shown in other Old World species, especially Nigerian forms, with *Glebosoceras* Reyment, 1954, a strongly ornamented genus which is treated as a synonym of *Coilopoceras* Hyatt, 1903. The *Coilopoceras* from Algeria described by Pervinquier (1910) and said to be of Cenomanian age are confirmed as members of the genus, but they are shown to be upper Turonian; so this occurrence does not contradict previous views that the genus arose during the Turonian via *Hoplitoides* von Koenen, 1898.

AMERICAN species of the late Cretaceous ammonite genus *Coilopoceras* Hyatt, 1903, as well as the genus and family, have recently been reviewed by Cobban and Hook (1980), but *Ammonites requienianus* d'Orbigny, 1841, the first described species of the genus and its chief Old World representative, is poorly known. Restudy of d'Orbigny's types and other material in early collections allows us to give a reasonably full description of the ontogenetic development, variation, and dimorphism in the species. These accord with that shown by American species, and lead to an examination of other problematic Old World forms.

SYSTEMATIC PALAEOLOGY

Repositories of specimens. BM(NH), British Museum (Natural History), London; EMP, École des Mines, Paris, Collections now housed in the Université Claude-Bernard, Lyon; FSL, Faculté des Sciences, Université Claude-Bernard, Lyon; MNHP, Muséum National d'Histoire Naturelle, Paris; SP, Collections of the Sorbonne, now housed in the Université Pierre et Marie Curie, Paris.

Dimensions. Dimensions are given in millimetres, in the following order; diameter (D), whorl breadth (Wb), whorl height (Wh), and breadth of umbilicus (U); c = costal, ic = intercostal. Figures in parentheses refer to dimensions as a percentage of diameter.

Suture terminology. The suture terminology of Wedekind (1916; see Kullman and Wiedmann 1970) is followed here; I = Internal lobe, U = Umbilical lobe, L = Lateral lobe, E = External lobe.

Superfamily ACANTHOCERATAEAE de Grossouvre, 1894
Family COILOPOCERATIDAE Hyatt, 1903

[= Hoplitoidinae Wright, 1952, *nom. correct. ex* Hoplitoidinés H. Douvillé, 1912]

Genus COILOPOCERAS Hyatt, 1903, p. 91

Synonyms. *Namadoceras* Vredenberg, 1907; *Glebosoceras* Reyment, 1954.

Type species. *Coilopoceras colleti* Hyatt, 1903, p. 91, pl. 10, figs. 5-21; pl. 11, fig. 1.

Diagnosis. Large, up to 800 mm in diameter; involute, compressed to inflated, lanceolate to cordate in section, with more or less sharp venter; variable broad low ribs may or may not persist; in inflated forms (*Glebosoceras*) they are raised into large bulges on the inner part of the flank on outer whorls;

in some such forms ribs may strengthen into ventrolateral nodes. Suture variable; accessory saddle may exceed in size the second lateral saddle, with auxiliary saddles tending to become entire in outline. Dimorphic: one member of pair compressed and feebly ornamented, the other more inflated and ribbed.

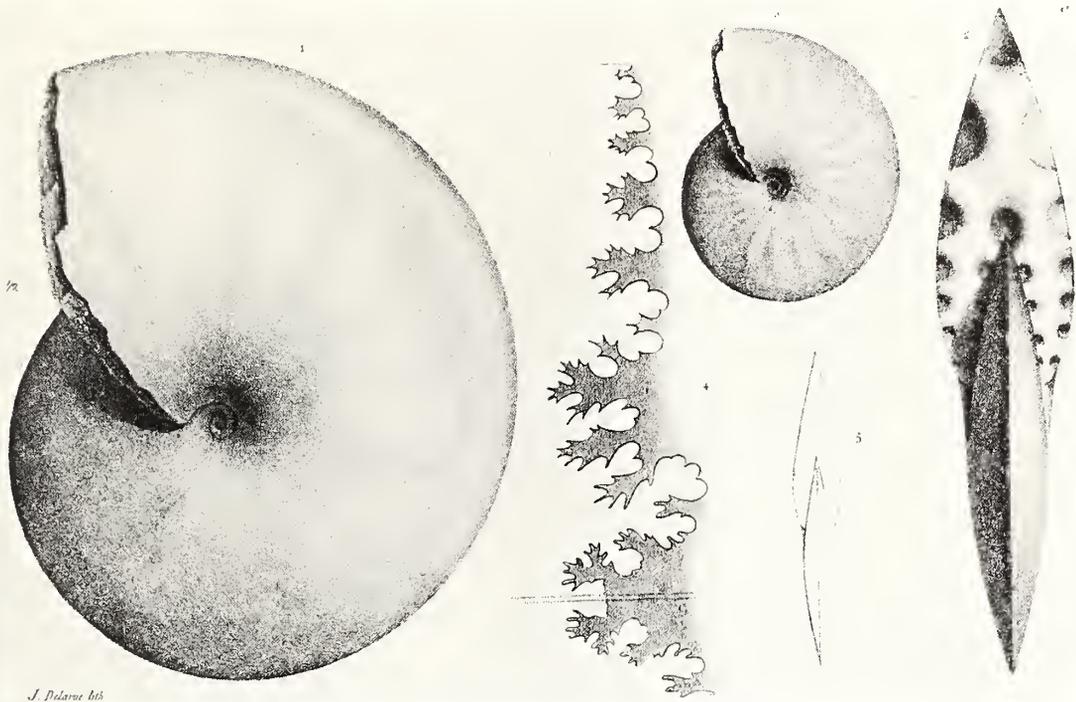
Discussion. Cobban and Hook (1980) provided a detailed account of the type species and other North American *Coilopoceras*. They demonstrated convincingly the succession from *Hoplitoides sandovalensis* Cobban and Hook, 1980, in the lower part of the upper Turonian *Prionocyclus hyatti* Zone, to *C. springeri* Hyatt, 1903 in the upper part of the same Zone. *C. springeri* and *H. sandovalensis* are indistinguishable when adult, and only the acute venter of the early stages of the former and the tabulate venter of the early stages of the latter serve to distinguish them. *C. springeri* gave rise to *C. colleti* Hyatt, 1903, of the succeeding *P. macombi* Zone. This species develops distinctive ventrolateral tubercles when adult (see Cobban and Hook 1980, text-fig. 9). Juveniles have only incipient tubercles, with the ends of the ribs projecting and accentuated. They also differ in sutural characteristics: in *C. colleti* L/U₂ is asymmetrically bifid; in *C. springeri* the three divisions of the ventral half of this lobe enlarge so that there are five large lobules rather than two. The youngest American species is *C. inflatum* Cobban and Hook, 1980. This is very inflated indeed and also develops tubercles (see Cobban and Hook 1980, text-fig. 14). In all these species Cobban and Hook demonstrated the presence of both slender, feebly ornamented and stout, strongly ribbed forms which they regard as dimorphs, a view followed here. They were unable to show a size difference between adults of the two forms, so that the two morphs cannot yet be identified as microconch and macroconch. As is shown below under the systematic description of *C. requienianum*, the same variation and dimorphism can be demonstrated in this Old World member of the genus.

Occurrence. Upper Turonian of France, Germany, North and West Africa, Madagascar, Israel, Lebanon, Baluchistan, Colorado, Wyoming, Texas, New Mexico, Mexico, Trinidad, Ecuador, Colombia, and Peru.

Coilopoceras requienianum (d'Orbigny, 1841)

Plates 35, 36; text-figs. 1-5

- 1841 *Ammonites Requienianus* d'Orbigny, p. 315, pl. 93, figs. 1-4.
 1894 *Sphenodiscus Requieni* d'Orbigny sp.; de Grossouvre, p. 140, text-fig. 59.
 ?1896-1897 *Sphenodiscus Requieni* (d'Orbigny); Peron, p. 34, pl. 17(4), figs. 2, 3; pl. 11(17), fig. 4.
 1903 *Coilopoceras requienianum* (d'Orbigny); Hyatt, p. 99.
 1903 *Coilopoceras? grossouvrei* n. sp. Hyatt, p. 100, pl. 12, fig. 7.
 1904 *Sphenodiscus Requieni* d'Orb; Solger, text-fig. 74 (*pars*) (after de Grossouvre).
 1907 *Sphenodiscus Requieni* d'Orbigny; Pervinqui re, p. 221, text-fig. 90.
 1907 *Sphenodiscus Requienianus* (d'Orbigny); Boule, Lemoine and Th venin, text-fig. 27B (copy of de Grossouvre).
 ?1912 *Coilopoceras Requieni* d'Orbigny; Douvill , p. 308, text-figs. 36-38, 68.
 1913 *Coilopoceras Requienianum* d'Orbigny; Roman and Mazeran, p. 28, pl. 3, fig. 5; text-figs. 5, 6.
 1938 *Coilopoceras* (sic) *Requieni* (d'Orbigny); Roman, p. 499, pl. 51, figs. 477, 477a (copy of d'Orbigny).
 ?1941 *Coilopoceras* (sic) *requieni* (d'Orbigny); Chiplonkar, p. 274, text-fig. 6 (indeterminate).
 1952 *Coilopoceras requienianum* (d'Orbigny); Basse, p. 665, fig. 30 (copy of d'Orbigny).
 1958 *Coilopoceras requienianum* (d'Orbigny); Luppov and Drushchits, p. 130, text-fig. 103d (copy of Roman 1938).
 ?1965 *Coilopoceras requieni* d'Orb.; Collignon, p. 24, pl. 385, fig. 1658 (indeterminate from figure).
 ?1975 *Coilopoceras* cf. *requieni* (d'Orbigny); Dassarma and Sinha, p. 70, pl. 9, fig. 6; pl. 12, fig. 5 (indeterminate).
 1976 *Coilopoceras requienianum* (d'Orbigny); Lommerzheim, p. 231, pl. 2, fig. 4; text-fig. 10a-c.
 non 1977 *Coilopoceras requieni* (d'Orbigny); Gonzalez-Arreola, p. 170, fig. 2d, e.
 ?1981 *Coilopoceras requieni* d'Orbigny; Obata, Kanie, Ranaivoson and Ratsimba, pl. 1 (indeterminate from figures).



TEXT-FIG. 1. *Ammonites requienianus* d'Orbigny, 1841 (pl. 93). Copy of d'Orbigny's original figures.

Types. D'Orbigny must have had a series of specimens before him when erecting this species, for in his explanation of the plate (1841, p. 317), which is reproduced here in text-fig. 1, he states as follows: 'Pl. 93, fig. 1, Individu réduite de moitié, vu de côté. De la collection de M. Requier et de la mienne. Fig. 2. Le même, vue de côté de la bouche, montrant le dessus d'une cloisone. Fig. 3. Un jeune de la variété ondulée. Fig. 4. Une cloisone de grandeur naturelle, calquée par moi sur la nature.' The larger specimen in the Requier Collection was re-illustrated by Roman and Mazeran (1913, text-fig. 5) and referred to as the 'type'; this is not, however, a valid lectotype designation. The posthumous catalogue of the d'Orbigny Collection lists thirteen specimens from Uchaux, Vaucluse, and fourteen are in the collections under the number 6775. All of these specimens rank as syntypes; the Requier specimen refigured by Roman and Mazeran is here designated lectotype; the paralectotypes are all rather poorly preserved and none demonstrably agree with d'Orbigny's pl. 93, fig. 3. A selection of the better specimens are refigured in text-fig. 2.

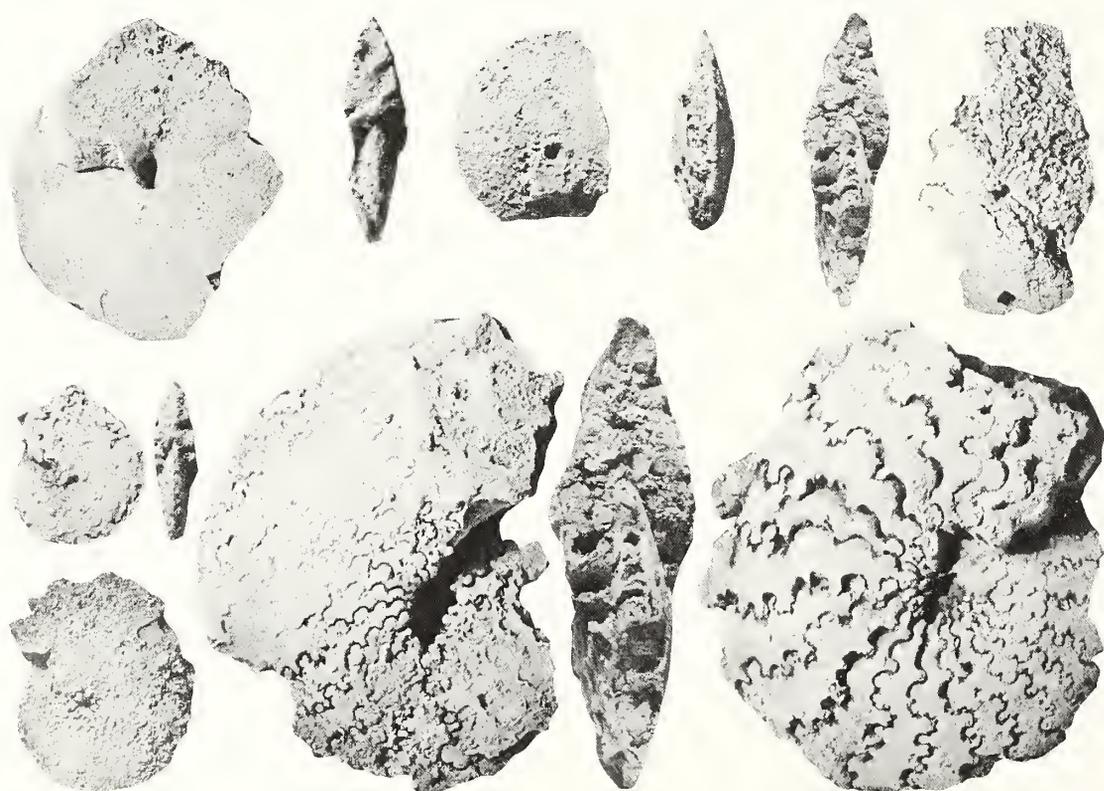
Material. We have studied nearly fifty specimens in the EMP, FSL, MNHP, SP, Université de Marseilles, and other French collections, all from localities in the Uchaux Massif, and variously labelled 'Colline de Boncavail', 'Uchaux', or 'Mondragon'. One specimen in the SP collections is from the Tuffeau Jaune de Touraine of Courtinot, Touraine (Hébert Collection); Oxford University Museum no. KZ15177 and specimens in J. M. Hancock's Collection are from the Tuffeau Jaune at Vreigne, near Francueil, Indre-et-Loire.

Description. The material occurs either as silicified nuclei, some of which retain the silicified dorsal shell layer and traces of the internal suture, or as sandstone moulds. The largest specimen we have seen is 200 mm in diameter.

Two forms of the species occur. At one extreme are smooth oxycones with a lanceolate whorl section and sharp venter (text-figs. 3, 4A). At the other are ribbed individuals which are generally stouter and a little more evolute (text-fig. 4B). Juveniles of the latter show pairs of low broad rounded primary ribs that are best developed on the inner flank but may also be accentuated on the ventrolateral shoulder before declining, while shorter intercalated ribs are also present. The largest ribbed variant is shown in Plate 36, fig. 12. There are six strong

umbilical bulges per whorl, which give rise to pairs of coarse broad primary ribs, and single shorter intercalated ribs. These strengthen before terminating abruptly, and there is a smooth zone on either side of the venter, which is acutely fastigiate. The siphuncle is very large. The suture line is shown by relatively few specimens (text-fig. 5). E is broad and shallow; L very broad, open, and symmetrically bifid. The saddle E/L is squat, with broad rounded frills, as is L/U_2 and the minor saddles on the umbilical lobe.

Dimensions	D	Wb	Wh	Wb:Wh	U
FSL 14.200d	23.9(100)	6.4(26.8)	13.3(55.6)	0.48	— (—)
FSL 14.200c	26.5(100)	8.0(30.1)	15.2(51.4)	0.53	1.0(3.7)
FSL 14.200a	64.0(100)	14.6(22.8)	36.3(56.7)	0.42	2.3(3.6)
FSL 14.201	51.0(100)	16.0(31.4)	27.6(54.1)	0.58	2.8(5.5)
FSL 14.200e	79.0(100)	19.8(25.0)	44.6(56.5)	0.45	2.1(2.7)
FSL 14.202	94.4(100)	22.1(23.4)	50.5(53.5)	0.44	— (—)
SP Pervinquière Coll.	93.7(100)	24.0(25.6)	52.4(55.9)	0.46	2.8(3.0)
SP Toucas Coll.	136.0(100)	31.8(23.4)	72.1(53.0)	0.44	— (—)
SP 'Mondragon' c	165.0(100)	38.0(23.0)	74.5(45.1)	0.51	18.0(10.9)
ic	165.0(100)	42.0(25.5)	74.5(45.1)	0.56	18.0(10.9)
FSL 14.210	170.0(100)	40.0(23.5)	94.5(55.6)	0.42	8.5(5.0)



TEXT-FIG. 2. *Ammonites requienianus* d'Orbigny, 1841. MNHP 6775 (d'Orbigny Collection), seven of the better preserved paralectotypes, all of which are silicified and from Uchaux (Vaucluse). All $\times 1$.

Discussion. *C. requienianum* is best known from the Uchaux region, but has been recorded from Touraine by several authors. The specimens we have seen include both ribbed and smooth individuals and have similar sutures. Hyatt (1903, p. 100) renamed the specimen from Usseau (Vienne), of which de Grossouvre (1894, text-fig. 59) illustrated the suture line, *C.? grossouvrei* because of differences in detail from the suture figured by d'Orbigny. Comparison of d'Orbigny's figure with the lectotype and other Uchaux specimens shows d'Orbigny's figure to be highly misleading with its very long narrow elements.

The presence of ribbed and smooth forms within *Coilopoceras* species has already been described in both the type species, *C. colleti* Hyatt, 1903, and the slightly later *C. springeri* Hyatt, 1903 and *C. inflatum* Cobban and Hook, 1980 (see Cobban and Hook 1980 for a full review of these species), and treated as dimorphism; the proportions of the two morphs are variable. As yet it is not known whether this difference in ornament is accompanied by a size difference. *C. requienianum* can be distinguished from these American species chiefly on the basis of the suture line (text-fig. 5); in *C. colleti* E/L is narrower and much more deeply incised, with elongate rather than squat frills, as well as asymmetrically bifid, while the inner lobes and saddles are also more incised. In *C. springeri* the saddles are even more incised with narrow stems, while E/L is very broad and asymmetrically trifid. *C. inflatum* Cobban and Hook, 1980 (p. 19, pl. 1, figs. 9–11; pl. 11, fig. 2; pls. 12–17; pl. 18, figs. 1–3, 11–13; pls. 20, 21; text-figs. 14, 15) has similarly distinctive sutures, is far more inflated than any known *C. requienianum*, and develops ventrolateral tubercles.

The above species and *C. requienianum* are the only ones in which a reasonable number of specimens has been described. As Cobban and Hook (1980) noted, at least twenty-seven species in addition to the American forms have been described. We agree with them that the groups of species described from single horizons and localities and separated on details of suture and ornament probably represent no more than single variable species. Particularly relevant to this issue is *C. requienianum altesellata* Collignon, 1965 (p. 62, pl. 403, figs. 1688, 1689; p. 64, pls. 404, 405) from the upper Turonian of Madagascar. Collignon referred a series of smooth forms to this 'variety', which he differentiated from the nominate form on the basis of the saddle E/L; this is narrow, deeply incised, and like that of the American forms noted above. It appears to be a distinct species and, interestingly, occurs with stouter ribbed specimens identified as *Glebosoceras glebosum* Reyment, 1954 (Collignon 1965, p. 60, pl. 402, figs. 1686, 1687). These have the same sutural peculiarity, and we again take them to be a dimorphic pair. *G. glebosum* Reyment, 1954 (p. 161, pl. 2, fig. 3; pl. 4, fig. 1; text-fig. 5; Reyment 1955, p. 75, text-fig. 35) from Nigeria has a similar suture line to *C. discoideum* Barber, 1957 (p. 55, pl. 2, fig. 1; pl. 3, figs. 1, 2; pl. 25, figs. 1–4) according to Barber, and they may be a further pair. Certainly, *Glebosoceras* is no more than an inflated *Coilopoceras*.

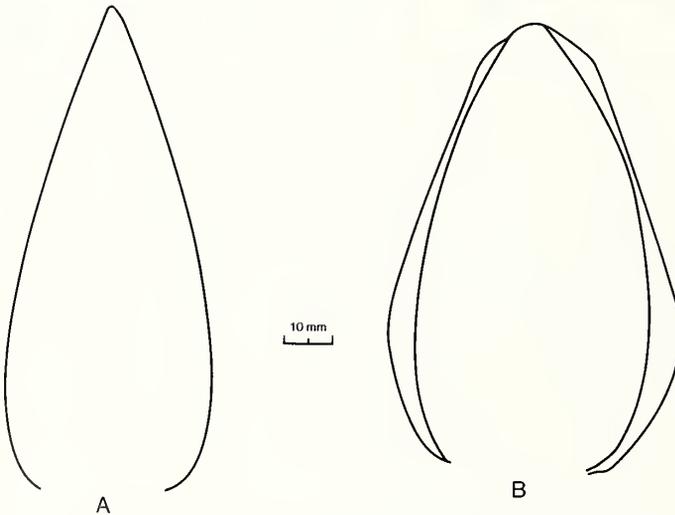
Occurrence. The type material is from the Uchaux Massif, where it is an upper Turonian *Subprionocyclus neptuni* Zone species. It is also known from scattered localities in the upper Turonian Tuffeau Jaune of Touraine, occurring at Usseau (Vienne) (de Grossouvre 1894), Courtinot (Touraine), and Vreigne, near Francueil (Indre-et-Loire). Lommerzheim (1976) has recorded a fragment from the condensed Turonian of Mulheim (Westphalia) that may belong here. The North African material whose sutures were illustrated by Douvillé (1912) are only doubtfully referable to the species.

DISCUSSION

Observations on *C. requienianum* show that compressed feebly ornamented and more inflated ribbed forms occur side by side, as in the North American type species and wherever *Coilopoceras* occurs. Cobban and Hook (1980, p. 5) accepted *Glebosoceras* as a distinct genus on the grounds that the ribs bend sharply forward on the outer part of the flank. A re-examination of the holotype, BM(NH) C47336, shows that this is a pathological condition. The forward projection is shown only by the third and fourth ribs of the figured side of the specimen (Reyment 1954, pl. 4, fig. 1) and is not a criterion for separation from *Coilopoceras*.



TEXT-FIG. 3. *Coilopoceras requienianum* (d'Orbigny, 1841). FSL 14.210, large specimen of compressed form from Uchaux, Vaucluse; 175 mm in diameter.



TEXT-FIG. 4. *Coilopoceras requienianum* (d'Orbigny, 1841). Whorl sections. A, compressed form, based on FSL 14.210 from Uchaux, Vaucluse. B, inflated form, based on an unregistered Sorbonne specimen from Mondragon, Vaucluse.

EXPLANATION OF PLATE 35

Figs. 1-6. *Coilopoceras requienianum* (d'Orbigny, 1841). 1-3, FSL 14.202, ribbed juvenile from the environs of Bollène (Vaucluse) (Sayn Collection). 4-6, a more compressed, feebly ribbed juvenile, Sorbonne Collections, labelled 'Mondragon?' (Pervinière Collection). All $\times 1$.



1



2



3



4

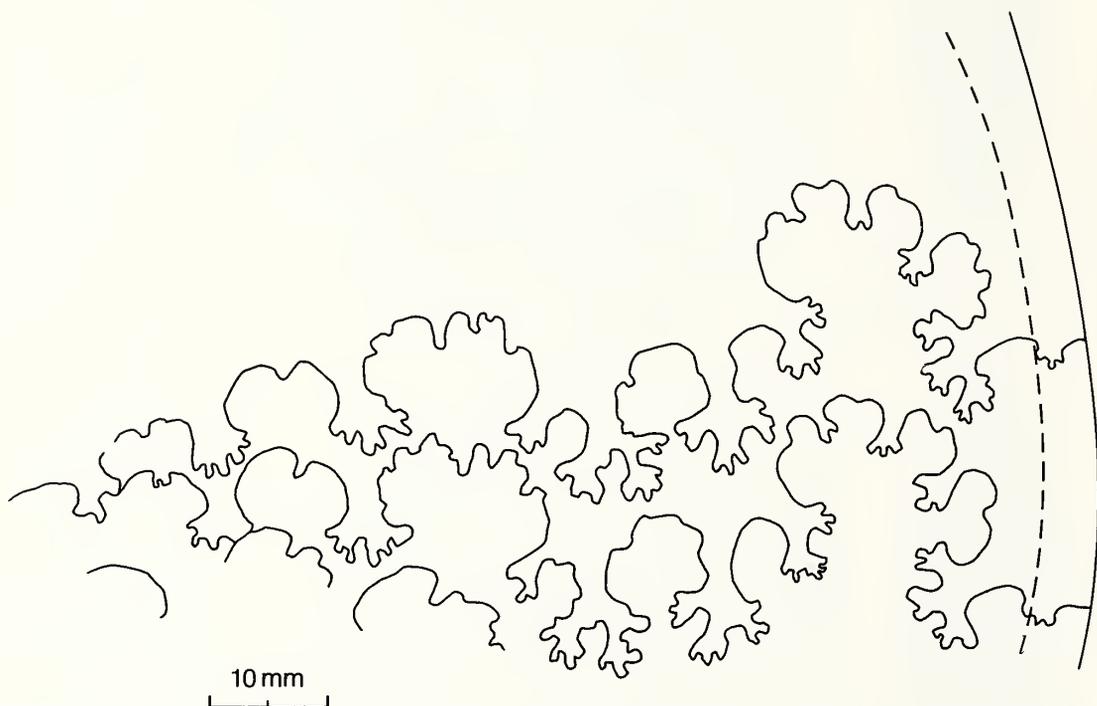


5



6

Cobban and Hook (1980) made it quite clear that *Hoplitoides* occurs in New Mexico in association with *Collignonicerus woollgari* (Mantell, 1822), that the earliest *Coilopoceras* in that area occurs with *Prionocyclus lyatti* (Stanton, 1894), and that later forms of *Coilopoceras* occur with *P. macombi* Meek, 1876 and *P. wyomingensis* Meek, 1876. This dating does not agree with the general recording of *Hoplitoides* as lower Turonian, and in particular Reyment's (1954, 1955) and Barber's (1957) records from Nigeria of *Hoplitoides* as 'lower Turonian' and *Coilopoceras* as 'lower Turonian (*Paravascoceras* horizon)' or even earlier (Barber 1957, p. 59). Careful reading of these papers, however, shows remarkably few cases of actual associations of specimens of either genus with other genera; neither appears in the only measured section, at Pindiga (Barber 1957, p. 60). The only definite reference appears to be to the occurrence in 'the limestone near Makurdi' of various *Hoplitoides* and *C.*(?) sp. with *Mammites mutabilis* Reyment, 1955, *Benueites*, and *Kamerunoceras jacobsoni* Reyment, 1955. None of these are yet known to entail any definite horizon within the Turonian. Otherwise, all the records of *Hoplitoides*, *Gleboscoceras*, and *Coilopoceras* in Nigeria are from imprecise horizons which may cover several zones.



TEXT-FIG. 5. *Coilopoceras requienianum* (d'Orbigny, 1841). External sutures from an unregistered specimen, Sorbonne Collections (ex Pervinière Collection).

EXPLANATION OF PLATE 36

Figs. 1-12. *Coilopoceras requienianum* (d'Orbigny, 1841). 1-3, FSL 14.200b, almost smooth juvenile. 4-6, FSL 14.201, a more inflated, ribbed juvenile, the original of Roman and Mazeran (1913, pl. 3, fig. 5). 7, 8, FSL 14.200c. 9-11, FSL 14.200d, smooth nuclei. 12, the most strongly ornamented specimen seen, Sorbonne Collections. 1-11 are labelled 'Uchaux', 12 'Mondragon', both in Vaucluse. All $\times 1$.



KENNEDY and WRIGHT, *Coilopoceras*

In Peru (Benavides-Cáceres 1956), *Coilopoceras* is recorded as common. One new species, *C. jenkinsi*, is said to be the commonest species in the Coñor Formation (ibid., p. 473), though is not listed among the fossils of that formation on p. 384. However, the Coñor Formation may be up to 200 m thick and, despite a statement (ibid., p. 473) that *C. jenkinsi* 'is usually associated with *Hoplitoides inca*, *Mammites nodosoides afer*, *Pseudaspidoceras reesei*, *Thomasites fischeri*, *Broggioceras olssoni*, and *B. humboldti*', we cannot see here any hard evidence for its relative dating; the 'associated' species cover *Parvasoceras* and *M. nodosoides* zones and, since they comprise all the ammonites listed from the whole Conñor Formation (ibid., p. 384), the biostratigraphic information is weak. Etayo-Serna (1979) included in his zonation of central Colombia a 'Mammites nodosoides appellatus-Franciscoites suarezi Assemblage Zone' in which *Hoplitoides* occurs, but this Zone could in fact cover the whole Turonian. Abundant *Coilopoceras*, including *Glebosoceras*-like forms, in collections before us from Colombia (University of California Collection), are never associated with species of other genera.

A similar situation is found on close investigation of the many references to the occurrence of *Hoplitoides* or *Coilopoceras* in the lower Turonian or earlier. In the case of the *Coilopoceras* described from the Cenomanian of North Africa by Pervinquièrre (1910), Reyment (1955, p. 75) suggested that they were schloenbachiids. However, Cobban and Hook (1980, p. 12) pointed out that the sutures of the Algerian species resemble those of true *Coilopoceras* in the general appearance of the first lateral lobe, but that the rest of the suture has only two or three lateral lobes. Part of the type material of both *C. africanum* Pervinquièrre, 1910, and *C. haugi* Pervinquièrre, 1910 is refigured here (Pl. 37, figs. 1-12); they are not schloenbachiids. *C. africanum* has a broadly bifid first lateral lobe (but with a third subsidiary lobule) and *C. haugi* a trifid one, but in our view they belong to a single variable species. The more strongly ornamented specimens compare well with small specimens of *C. inflatum* (e.g. Cobban and Hook 1980, pl. 18, figs. 1, 2, 8) and we believe them to be true *Coilopoceras*, showing the same range in ornament and whorl section as other species. We doubt, however, the dating of this material. *C. africanum* is based on eight specimens and fragments said to be from the middle Cenomanian of Djebel Guessa and Berrouaghia, collected by Thomas and Peron; *C. haugi* on three complete specimens and a dozen fragments also said to be from the middle Cenomanian of Berrouaghia, also collected by Thomas and Peron. The '*Acanthoceras* cf. *Ac. Newboldi* Kossmat' of Pervinquièrre (1910, p. 45, pl. 13, fig. 37) was also collected by Thomas and is in the Peron Collection; it was said to be from the '2^e zone, moyenne' of Berrouaghia, but is a juvenile *Romaniceras* (*Romaniceras*) *deverianum* (d'Orbigny, 1841) (Kennedy *et al.* 1980, p. 330, pl. 39, figs. 7-10), a high Turonian species commonly associated with *Coilopoceras*. This suggests that the *Coilopoceras* too are misdated, while we have independent unpublished evidence that limonitic Turonian ammonites occur in the Berrouaghia-Aumale area of Algeria.

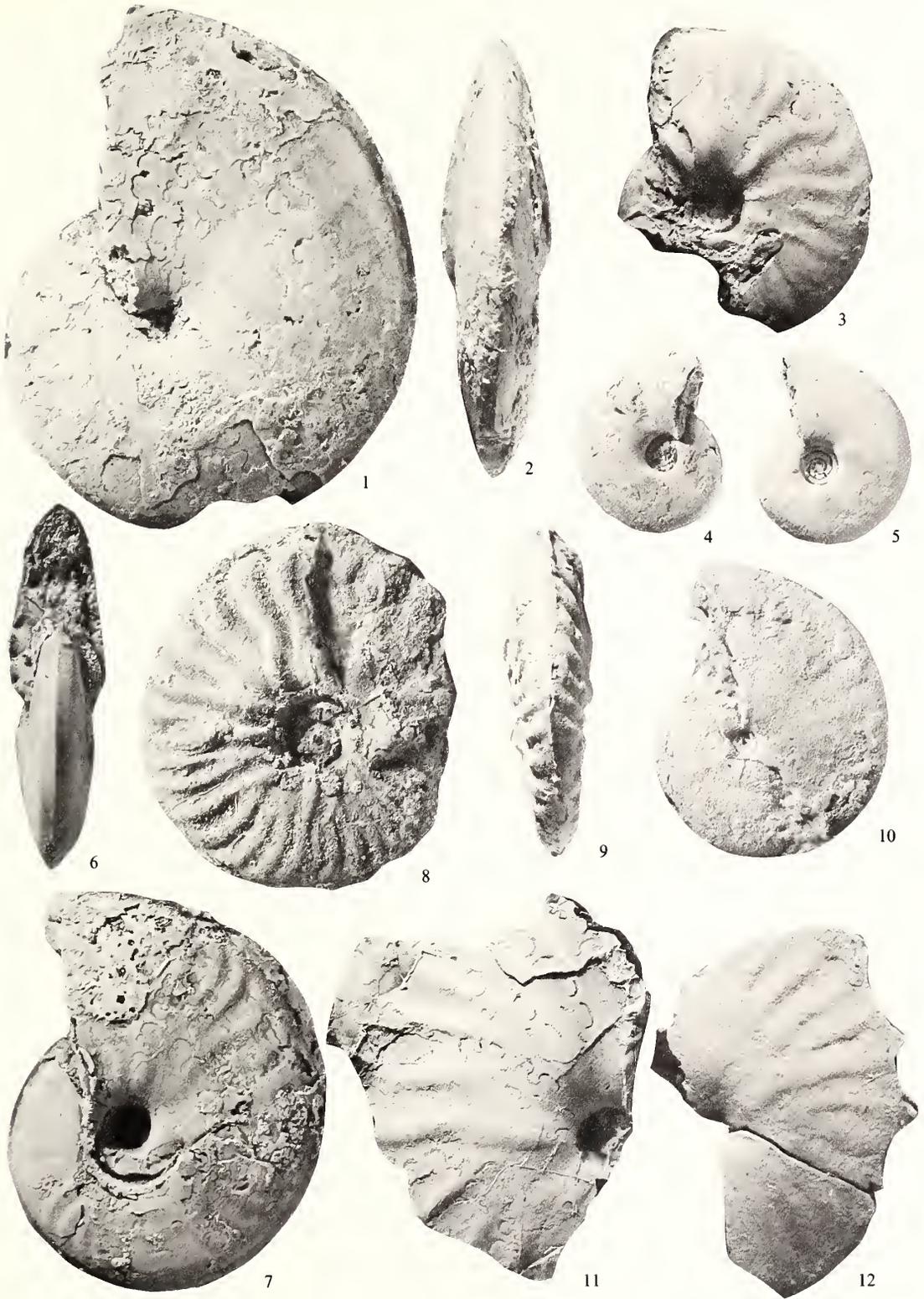
We are thus led to conclude that there is no strong evidence for the occurrence of *Hoplitoides* or *Coilopoceras* before the middle Turonian, although it is possible that the former's occurrences in West Africa are in rocks that are datable, at least in part, to the upper part of the lower Turonian. On this basis there is no longer any difficulty in accepting the evolution of *Coilopoceras* from *Hoplitoides* (Wright 1957, p. L425; Cobban and Hook 1980, p. 13).

EXPLANATION OF PLATE 37

Figs. 1, 2, 8-12. *Coilopoceras africanum* Pervinquièrre, 1910. 'Cotypes' from Djebel Guessa, Algeria, Sorbonne Collections.

Figs. 3-7. *Coilopoceras haugi* Pervinquièrre, 1910. 'Cotypes' from Berrouaghia, Algeria, Sorbonne Collections.

All $\times 2$.



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NEW POROCHARACEAE FROM THE BATHONIAN OF EUROPE: PHYLOGENY AND PALAEOECOLOGY

by MONIQUE FEIST *and* NICOLE GRAMBAST-FESSARD

ABSTRACT. The anatomical characters of some European Bathonian charophyte gyrogonites have been studied. The presence of a multipartite basal plate in representatives of the Porocharaceae/Porocharoideae justifies the creation of a new genus, *Musacchiella* gen. nov., represented by three new species: *M. douzensis*, *M. palmeri*, *M. sp. A*. No clear relationship has been demonstrated with extant and fossil Characeae/Nitelloideae in which a multipartite basal plate is also to be found. On the other hand, the outline of the apical pore suggests relationships with the family Raskyellaceae. A possible link is suggested between the unusual 'Y calcification' in the spiral wall cells of these species and a brackish water habitat.

IN the long history of the charophytes, the Middle Jurassic represents one of the intervals that is still practically uninvestigated. Thus, from the Bajocian to the Oxfordian, the only known species are the three described by Peck (1957) from Montana and Wyoming, U.S.A., and the seven studied by Bhatia and Mannikeri (1977) from the Callovian of Western India. Other than in these two publications, only undetermined forms or unattributed species of genus *Porochara* Mädlar have been cited. The present study is part of a comprehensive work on the charophyte flora from the Middle Jurassic. It is based mainly on our own collecting in the Bathonian of the 'Causses' (Southern France) and also on material from contemporaneous deposits of other regions: those from the English Midlands were found by Dr. T. Palmer, University of Wales, and those from Eastern Sardinia by Dr. I. Dieni, University of Padua. Amongst these Bathonian floras we have restricted ourselves in the present study to those representatives of the family Porocharaceae Grambast which possess a gyrogonite with a segmented basal plate (genus *Musacchiella* gen. nov.). This is because of the great phylogenetic importance of this structure and its relative rarity amongst fossil forms.

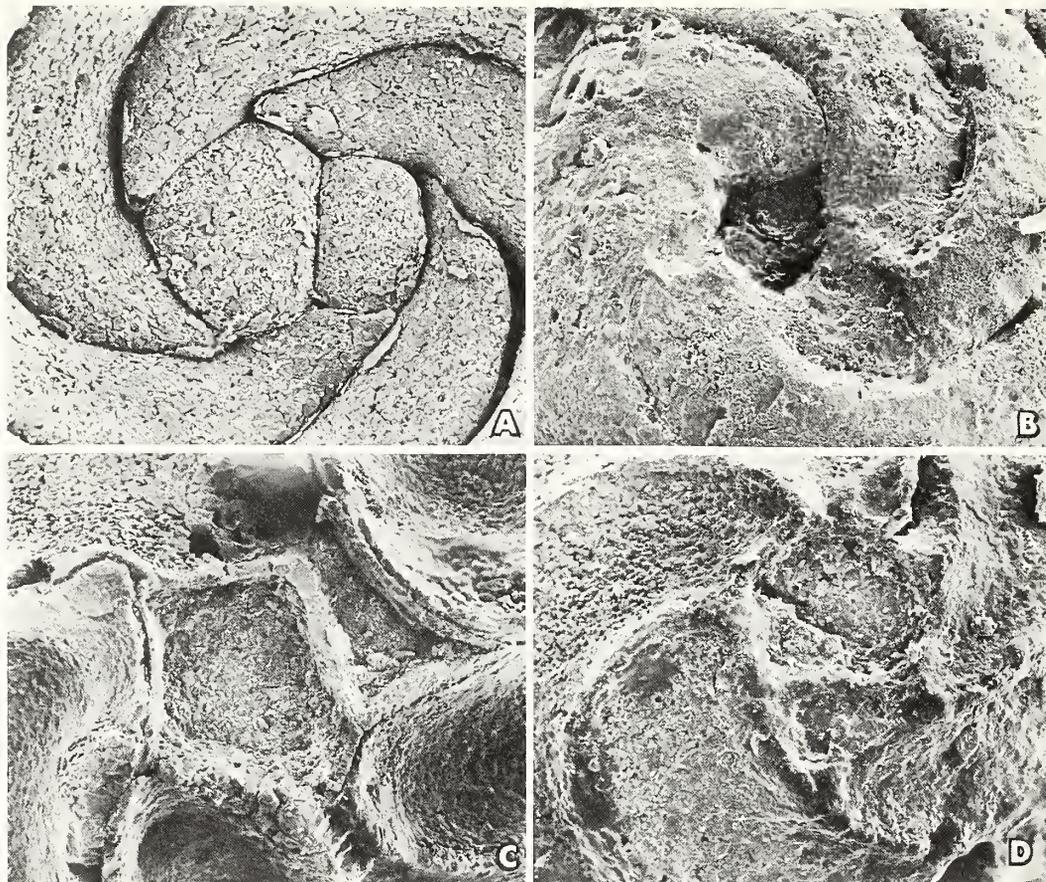
The abundance and the excellent state of preservation of these fossils has permitted new observations on the apical opening of the gyrogonite, suggesting a direct relationship with a family first known in the Upper Cretaceous. The presence of a special structure in the calcified gyrogonite wall of the three described species is also noted and discussed with relation to the original environmental conditions.

THE SEGMENTED BASAL PLATE

Occurrence of a divided basal plate amongst the Charophyta

Grambast (1956*b*) first pointed out that, amongst the fossil Charophyta, there existed representatives with a divided basal plate, and he assigned these to the genus *Tolypella* (Characeae Nitelloideae). This structure corresponds to the assemblage of calcified sister cells of the oosphere = sterile oogonial cells. These true *Tolypella* (with a multipartite plate) were first noted from the Lutetian (Grambast 1958; C120, Pont Bernard, unpublished material). Only one pre-Tertiary example is known: *T. grambasti* Musacchio (Uliana and Musacchio 1978) from the late Cretaceous of Argentina.

Amongst the extant forms, those which possess several sterile oogonial cells all belong to the non-calcified Nitelloideae: genus *Nitella* and genus *Tolypella* section *Tolypella*. Daily (1969) and Sawa and Frame (1974) have in fact pointed out that the calcified *Tolypella* (section *Rothia* R. D. Wood) possess an undivided plate, resulting from the calcification of a single sterile cell.



TEXT-FIG. 1. Multipartite basal plates. A, *Musacchiella palmeri* sp. nov., inside view of the gyrogonite, $\times 455$. B, *M. palmeri* sp. nov., external view, $\times 273$. C, *M. douzensis* sp. nov., external view, $\times 455$. D, *M. douzensis* sp. nov., external view.

With regard to the representatives of the three subfamilies of the Porocharaceae, all of which are fossil, often no mention has been made of the existence of a basal plug. When it does exist the illustration does not always allow its presence to be seen (e.g. Mädler 1952, pl. B, fig. 28). In other cases, only a single plate has been described or illustrated, e.g. some species from the Upper Jurassic of Mongolia (Kyansep-Romashkina 1975, pl. I, fig. 3) and the Upper Cretaceous of China (Wang 1978, pl. 3, figs. 9–14 and 31–34). In the case of *Porochara gildemeisteri* Koch and Blissenbach from the Upper Cretaceous of Peru, the section given by Grambast (*in* Grambast *et al.* 1967, pl. I, fig. 14) appears to show a vertical wall crossing the middle of the plate. However, in sections at this level it is generally extremely difficult to distinguish true cell walls from fractures or crystal faces. On the other hand, Grambast (1964, p. 72) mentions, without giving any information on the age or origin of the material, the existence of Porocharaceae with a segmented plate. It is on the basis of this reference alone that Soulié-Märsche (1979a) formulated her hypothesis concerning the origin of extant forms with three sterile oogonial cells.

The observations described herein provide the first unequivocal evidence for the coexistence, within the family Porocharaceae, of two types of basal plate.

The divided basal plate in the Bathonian Porocharaceae

In the specimens studied the different parts of the basal plate are especially conspicuous in internal views of hollow unrecrystallized gyrogonites. In such cases, the number of parts observed is always two. They are small sized, and one is pentagonal, the other smaller, triangular or nearly rectangular (text-fig. 1A). From the exterior, observation is generally more difficult, because the partition wall is often hidden by the ends of the spiral cells or reduced by wear or by the presence of sedimentary particles. This is the aspect shown by the basal view of *Musacchiella palmeri* sp. nov. (text-fig. 1B). In certain cases, however, the partition may appear rather more clearly, as in *M. douzensis* sp. nov. (text-fig. 1C) or as in an internal pyritized mould of *M. sp. A* from Sardinia (text-fig. 1D).

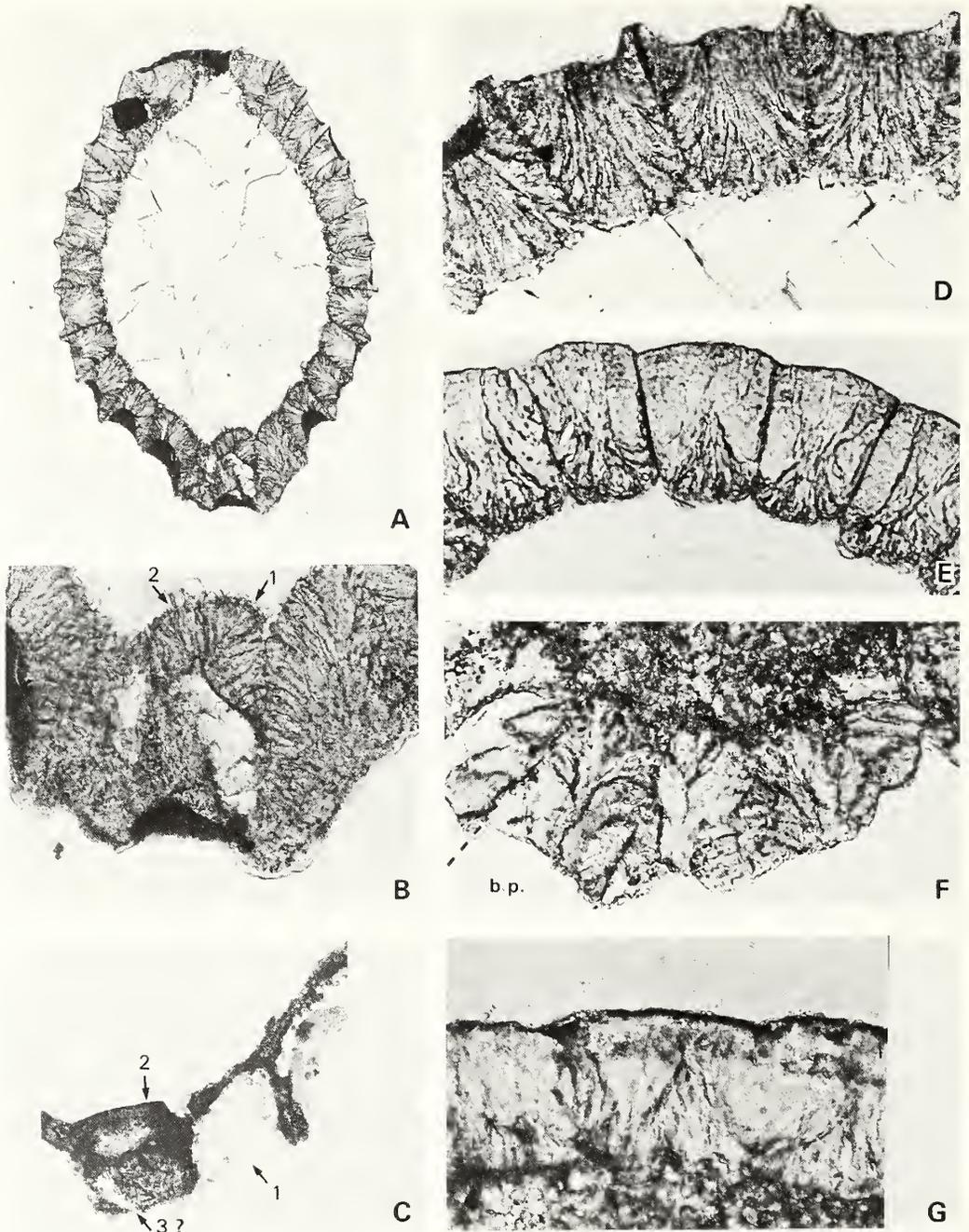
The presence of two components at the basal plate level is also conspicuous in longitudinal axial sections of *M. douzensis* sp. nov. (text-fig. 2A, B) and of *M. palmeri* sp. nov. In a section of a pyritized internal mould of *M. sp. A* (text-fig. 2C) the presence of three cavities is visible at the gyrogonite base and these cavities might represent the location of the three sterile oogonial cells. The three corresponding calcified pieces appear to be present again in the section of *M. sp. A* where the calcite shell is preserved (text-fig. 2F).

Comparison with the other known occurrences of multipartite basal plates

The only variation in all known cases is in the number of components observed. There are generally two in the Bathonian *Musacchiella* described here, as well as in *T. grambasti* Musacchio from the Maastrichtian and in a *Tolypella* species from the Upper Eocene of the Paris Basin illustrated by Soulié-Märsche (1979b, pl. 45, fig. 7). In *T. pumila* Grambast from the Lower Oligocene of Belgium, two components are also seen in a basal exterior view (Grambast *in* Stockmans 1960, fig. 39a). However, the same species from the Paris Basin shows a tripartite basal plate *in situ* in an inner side view of the gyrogonite and Grambast (1956b, 1958) mentions that the number and arrangement of the plate elements are here variable. In the Bathonian *Musacchiella*, a bipartite basal plate seems to be the norm, but in *M. sp. A* this seems to vary according to the angle of observation, and the elements may appear to be two (text-fig. 2F) or three (text-fig. 2c). It must be noted that amongst the extant species possessing several sterile oogonial cells, the number of these cells is controversial. According to Sawa and Frame (1974), and contrary to the views of other authors like Maier (1973), the third cell ought always to be present and, if it is not observed, it is probably due to its small development. In the present state of knowledge of extant as well as fossil forms, no particular significance is attached here to the biological (reproductive cycle) or phyletic nature of the number of components (2 or 3), but only to the fact that the basal plate is multipartite.

Multipartite basal plate and phylogeny

Other than in the Bathonian Porocharaceae, multipartite plates are known only amongst the Characeae/Nitelloideae and naturally it is with this group that affinities are to be sought. Although we now have evidence that forms with a divided plate have existed since the Middle Jurassic, it is only at the end of the Cretaceous that another species with this character (*T. grambasti* Musacchio) is to be found. These represent two widely spaced steps which do not for the moment allow the reconstruction of a direct lineage exhibiting no anatomical particularity other than the basal plate. The genera *Musacchiella* and *Tolypella* clearly belong, on account of their apical structure, to two markedly distinct groups. We shall see later on that in *M. douzensis* sp. nov. the other anatomical characters of the gyrogonite (apical opening, wall of spiral cells) suggest multiple relationships, without apparent connections with the demonstrated affinities of the Nitelloideae. We consider for this reason that the Bathonian Porocharaceae with a segmented basal plate may belong to the ancestral stock of the Nitelloideae, but we cannot state that they represent their direct ancestor. It is, therefore, difficult to agree with the phylogenetic diagram drawn by Soulié-Märsche (1979a) in which the origin of the extant genera of Characeae goes back to the Jurassic or even, for some, to the basal Trias. Indeed, as a result of the successive allocations of all the Triassic species to the family Porocharaceae (Grambast 1962; Saïdakovsky 1971), it appears that no true representative of the Characeae is to be found before



TEXT-FIG. 2. Longitudinal sections of the gyrogonite. A, *Musacchiella douzensis* sp. nov., $\times 70$. B, Same, detail of the basal pole, $\times 200$; 1, 2, the two parts of the basal plate. C, *M. sp. A*, $\times 250$; 1, 2, 3, location of the three basal cells. D, *M. douzensis* sp. nov., $\times 300$, detail of the wall of the spiral cells. E, *M. palmeri* sp. nov., $\times 300$, detail of the wall of the spiral cells. F, *M. sp. A*, $\times 370$, detail of the basal pole; b.p., site of the multipartite basal plate. G, *Lamprothamnium priscum* Castel and Grambast (topotype), $\times 300$, detail of the wall of the spiral cells.

the Middle or even the Upper Jurassic. Moreover, the basal plate morphology in the Jurassic species is in no case typical of the Nitelloideae genera: *Sphaerochara* (plate undivided, thick, visible at outer surface level), *Tolypella* and *Nitella* (segmented plate).

Taxonomic implications of the presence of a segmented plate

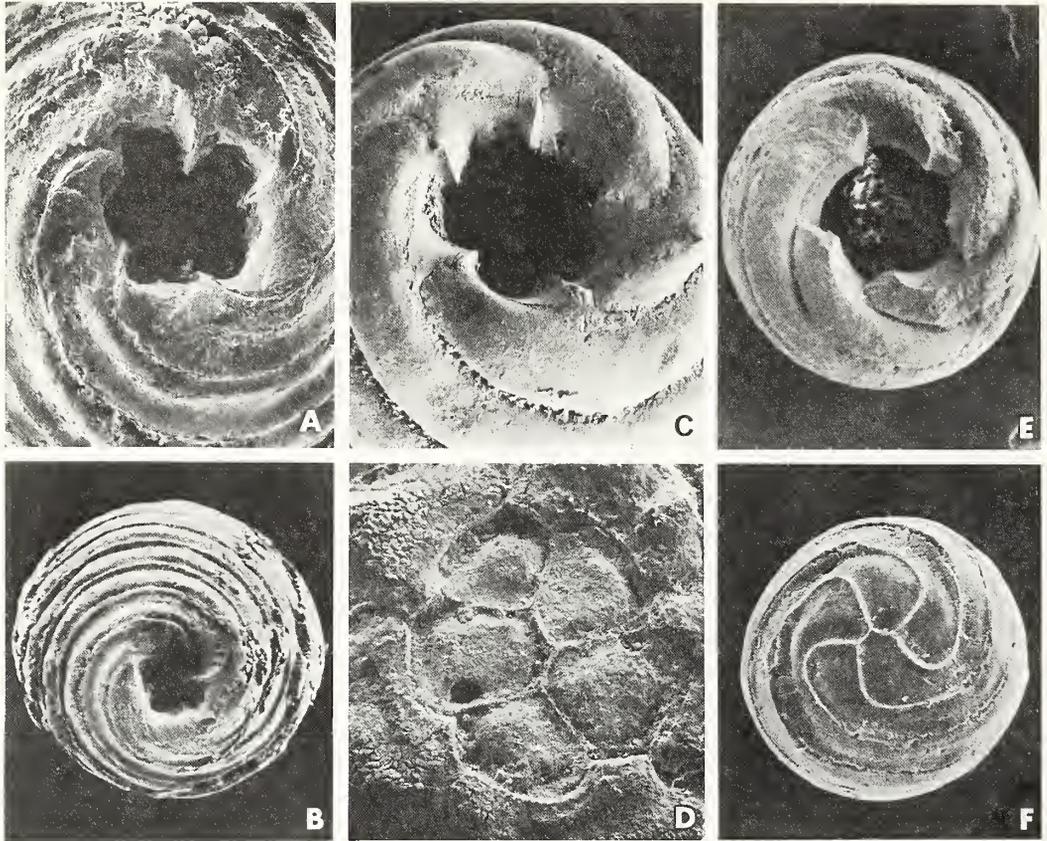
In the classification of fossil Charophyta (Grambast 1962, 1974) and more particularly of the order Charales to which all the post-Palaeozoic species belong, the apical structure of the gyrogonite is considered to be of primary importance. The species studied here, in which the apical pore is always open, but not lying at the top of a neck, belong, without any doubt, to the Porocharaceae/Porocharoideae. Within this subfamily, there coexist species with a single basal plate and others, first described here, with a divided one. The systematic value of this character can be argued. Grambast (1956*b*) has shown that, in the Tertiary Characeae, the basal plate constitutes an important diagnostic character and the presence of a segmented basal plate justifies the inclusion of a species in a special subfamily. In the present case, the described species are quite closely related to each other, both on account of their morphology and chronological isolation in the Middle Jurassic. So it seems to us that they naturally fall into a single new genus. It is possible, however, that in the future a higher rank division may have to be considered, particularly if other ancient forms with a segmented plate are discovered.

THE APICAL OPENING OF THE GYROGONITE

In the Porocharaceae/Porocharoideae the apical pore of the gyrogonite is always open and is often somewhat sunken, with a small diameter and with a more or less rounded pentagonal shape. Some specimens of *Musacchiella* gen. nov. show a somewhat different form. In *M. douzensis* sp. nov. for example (text-fig. 3A, B) the shape and arrangement of the spiral cell ends are seen very distinctly: the central part of these cells outlines a rounded recess limited by the forwardly tapering intercellular sutures which form tooth-shaped projections. The whole shape is that of a rose and looks like the opening left by the loss of the calcified operculum in the family Raskyellaceae, as seen for example in *Rantzieniella nitida* Grambast (text-fig. 3C). Such a form differs fundamentally from the cog-wheel shape ('roue dentée' in Grambast 1956*a*) evident in a dehiscent gyrogonite of the family Characeae, shown here in *Gyrogona lamarcki* Grambast (text-fig. 3E). In this case, dehiscence takes place through the breakage of the spiral cell ends and not through the loss of special opercular cells (text-fig. 3D) such as occurs in the Raskyellaceae (Grambast 1957; Feist *in* Anadón and Feist 1981).

From a biological point of view the shape of the apical opening in *Musacchiella* suggests the possibility in the Porocharoideae of closure by means of an operculum made of five apical cells which, in the Middle Jurassic, would not have been calcified. Moreover, the Porocharoideae and Raskyellaceae exhibit other similar features in the fructifications. They are often ovoidal in shape, with a thick lime-shell and basal plate, and a small apical pore compared to the general diameter of the gyrogonite. As for *Musacchiella* this combination of characters implies even more affinities with the Raskyellaceae than with the Nitelloideae which, however, have in common with the Jurassic forms the peculiarities of the basal plate as discussed above. The evolution of the Porocharoideae to the Raskyellaceae may have taken place by the calcification of the operculum, most probably amongst forms with an undivided basal plate, in the Upper Cretaceous, i.e. not long before the extinction of the Porocharaceae, near the Cretaceous-Tertiary boundary (Feist 1979).

The apical structure of *Musacchiella* also shows an inclination of the ends of the cells into the centre of the somewhat sunken apex. This bending is commonly observed within the genus *Porochara*, for example in *P. globosa* Grambast and Gutiérrez (1977, pl. I, fig. 8). The distinction of the genus *Euaclistochara* Wang, Huang and Wang, 1976, which depends upon this feature alone, is thereby questionable. As no segmented plate has been described in the species attributed to *Euaclistochara*, we consider all of them as belonging to the genus *Porochara* Mädlar. In fact, the four species of Peck (1957) attributed by Wang *et al.* (1976) to *Euaclistochara* were previously ascribed to this genus.



TEXT-FIG. 3. Apical structures of the gyrogonite. A, *Musacchiella douzensis* sp. nov. (Porocharaceae), $\times 155$. B, Same, paratype, CF2098-4, apical view, $\times 60$. C, *Rantzieniella nitida* Gramb. (Raskyellaceae), (topotype—Aquitainian), dehiscent summit, $\times 95$. D, *Raskyella vadaszi* Gramb. (Raskyellaceae), (Laguarrés, prov. Huesca, Spain; Upper Eocene; from Anadón and Feist 1981, pl. 2, fig. 2), entire summit, $\times 110$. E, *Gyrogona lamarcki* Gramb. (Characeae), (Nogent l'Artaud, Aisne, France; Upper Eocene; from Grambast and Grambast-Fessard 1981, pl. 1, fig. 7), dehiscent summit, $\times 30$. F, *Psilochara* aff. *repanda* Gramb. (Characeae), (La Débruge, Vaucluse, France; Upper Eocene; from Feist-Castel 1977, pl. 5, fig. 6), entire summit, $\times 50$.

THE CELL WALL STRUCTURE

Description. The Bathonian *Musacchiella* species studied here exhibit in longitudinal sections (text-fig. 2A, D, E, F) a peculiar aspect of the calcified wall of the spiral cells, that is quite different from that generally observed. A system of radial convergent lines is found here in addition to the usual parallel lamination first described by Migula (1897, p. 49). These lines depart from the suture and from the adaxial wall, going towards the median part of the spiral cell. At a low magnification, the limit of these radial stripes outlines, in the middle of the cell, a letter 'Y', the fork of which is directed towards the centre of the gyrogonite.

This structure strongly recalls that described by Soulié-Märsche (1979b, pl. 9; 1982) in the extant species of the genus *Lamprothamnium*, under the name of 'structure en éventail' (fan-shaped). However, in this case, the laminae depart only from the intercellular sutures and form divergent

bunches, the junction of which again delimits a Y at the cell centre. The same aspect can be seen, less distinctly, in the fossil species *Lamprothamnium priscum* Castel and Grambast from the Eocene (text-fig. 2G). A similar structure is also present in one species of Porocharaceae/Stellatocharoideae: *Stellatochara sellingsii* (Horn af Rantzien 1954, pl. 2, figs. 4, 5) from the Trias of Sweden.

Phylogenetic relationships. It is tempting to search for relationships between the forms with the 'Y' calcification wall structure, but it seems that this character alone cannot be used to demonstrate natural affinities. On the one hand, the genera *Stellatochara* and *Musacchiella* belong to distinct subfamilies, Stellatocharoideae and Porocharoideae, which, separate since the Permian, apparently correspond to distinct phyla (Saidakovsky and Shajkin 1976). On the other hand, we have shown above, on the grounds of the anatomical characters of the base and apex of the gyrogonite, that the likely affinities of *Musacchiella* lie with the Nitelloideae and Raskyellaceae, and not with the Charoideae, to which *Lamprothamnium* belongs. Thus, although this peculiar 'Y' calcification appears to be characteristic of some genera, these are not necessarily linked through a direct line. The most we can say is that they may have possessed a remote common ancestor.

Ecological relationships. The question also arises as to whether the presence of the 'Y' calcification of the spiral cells is related to the life conditions of the studied *Musacchiella*. The extant representatives of the genus *Lamprothamnium* live in lagoons and may tolerate high salinity (Burne *et al.* 1980). Likewise, *L. priscum* from the Eocene comes from a brackish facies (Castel and Grambast 1969). However, other Characeae species found in the same outcrop that yields *L. priscum*, such as *Nitellopsis (Tectochara) thaleri* Feist-Castel, do not have the same wall structure. Horn af Rantzien (1954, p. 20) does not provide any precise information on the habitat of *Stellatochara sellingsii*.

With regard to the outcrops yielding *Musacchiella*, some information on the primary environmental conditions, especially the salinity, is provided by the ostracod faunas. According to Palmer (1979, p. 194), at Wood Eaton 'the ostracod fauna is predominantly brackish' and 'the abundance of charophytes also suggests the influence of fresh water'. Furthermore, he states that the absence of vegetative fragments implies that the fructifications were transported from lakes upstream. It may be noted, however, that several living and fossil species have been reported, herein and elsewhere, from brackish lagoons. Moreover, not all charophytes possess a calcified thallus. It is thus quite likely that *M. palmeri* shared the same environment as the ostracods. Dr. Palmer (pers. comm. 1982) acknowledges this as being quite compatible with his own palaeoecological analysis of the basal part of the Hampen Marly Formation at Wood Eaton.

The ostracods associated with *M. douzensis* at the southern France locality (F. Dépêche, pers. comm.) are mainly freshwater species, but may have been transported as suggested by the poor state of preservation of the shells. In addition, there is one euryhaline species, *Kliciana levis* Oertli. As communicated by Dr. I. Dieni (pers. comm.), this latter species is predominant at the Sardinian locality and indicates there a brackish environment. Thus it seems to be true that the forms showing a 'Y' calcification are found preferentially in somewhat saline environments, but it cannot be said that there is a causal relationship between these two facts.

SYSTEMATIC PALAEOONTOLOGY

Division CHAROPHYTA

Order CHARALES

Family POROCHARACEAE Grambast 1962

Subfamily POROCHARAOIDEAE

Genus MUSACCHIELLA nov.

Type species. *Musacchiella douzensis* sp. nov.

Derivation of name. The genus is named in honour of Dr. E. Musacchio, Buenos Aires, for his work on fossil charophytes.

Occurrence. Middle Jurassic (Bathonian) of Oxfordshire, England; Causses, southern France; eastern Sardinia.

Diagnosis. Gyrogonite of Porocharoideae with a small apical pore, ovoidal shape, and segmented basal plate.

Affinities. The new genus bears most resemblance to *Porochara* Mädlér amongst the Porocharoideae (characterized by an apical opening not lying at the top of a neck), in its general ovoidal to ellipsoidal shape and in the morphology of the somewhat sunken apical opening which may occasionally possess a 'rose' outline. It differs in the particular character of a divided basal plate. We limit, therefore, the genus *Porochara* to forms with an undivided, or unknown, basal plate. In practice, of course, it will not always be possible to recognize the new genus, since the basal plate structure will not always be visible.

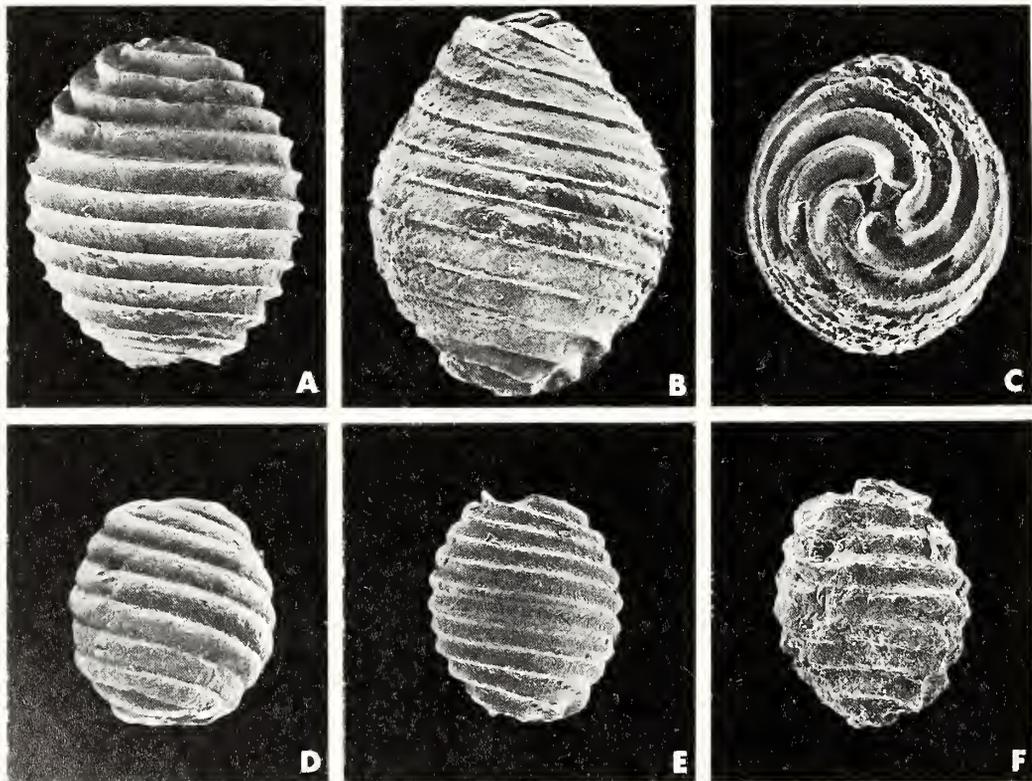
Musacchiella douzensis sp. nov.

Types. Holotype (text-fig. 4A), CF2038-1. Paratypes (text-figs. 4B, C; 3B), CF2038-2 to 5. Coll. M. Feist, Université des Sciences et Techniques du Languedoc, Montpellier, France.

Type horizon and locality. Lignitic marls from the Bathonian, Middle Jurassic; Les Douzes, commune of Mures-la-Parade, Lozère, France.

Material. About 300 specimens.

Derivation of name. From the name of the type locality.



TEXT-FIG. 4a-c, *Musacchiella douzensis* sp. nov., $\times 60$. A, holotype, CF2098-1, profile. B, paratype CF2098-2, profile. C, paratype, CF2098-3, base. D, E, *M. palmeri* sp. nov., $\times 60$. D, holotype, C 1094-1, profile. E, paratype C1094-2, profile. F, *M.* sp. A, specimen CF1598-1, profile, $\times 60$.

Diagnosis. Gyrogonite of *Musacchiella*, the largest diameter being at mid height. Segmented basal plate, visible from the outer side at the bottom of a shallow pit bordered by the truncation of the spiral cells. Dimensions: 625–975 μm long, 500–550 μm wide; 10–13 convolutions; L/W ratio varying from 1.1 to 1.4.

Remark. The spiral cells are frequently concave, but even when they are plane or slightly convex in the middle part of the gyrogonite, they become more hollow at its base where the sutures are always prominent.

Affinities. Other than in plate characters, *M. douzensis* differs from the *Porochara* present in the same bed in its distinctly larger dimensions and its widened outline at the equator of the gyrogonite. In this latter character the new species is reminiscent of *Porochara rotunda* (Peck) Shajkin from the Middle Jurassic of U.S.A., the basal plate of which is unknown; however the dimensions and the number of convolutions are distinctly smaller in the latter species (Peck 1957). Similarly, (*S.*) *raoi* Bhatia and Mannikeri 1977, from the Callovian of India, is rather enlarged at the equator of the gyrogonite but is smaller overall and apparently has an undivided basal plate. According to the divisions established by Grambast (1962), the features of the apex, which is open and not drawn into a neck, lead us to ascribe this species to the Porocharoideae, and more precisely to the genus *Porochara* Mädlar, with regard to its general shape and apical morphology.

Musacchiella palmeri sp. nov.

Types. Holotype (text-fig. 4D), C1094-1. Paratypes (text-fig. 4E), C1094-2 to 5. Coll. Grambast, Université des Sciences et Techniques du Languedoc, Montpellier, France.

Type horizon and locality. Lignitic marls of the Bathonian, Middle Jurassic; Wood Eaton, 5 miles north-east of Oxford, Oxfordshire, England (Palmer 1973).

Material. About 250 specimens.

Derivation of name. The species is named after Dr. T. J. Palmer, who collected the material at Wood Eaton and sent it for study to the late Dr. L. Grambast in 1970.

Diagnosis. Gyrogonite of *Musacchiella*, most often ellipsoidal, tapering near the apical and basal ends. Segmented basal plate nearly on a level with the basal pore. Dimensions: 275–650 μm long, 250–500 μm wide, 7–9 (exceptionally 6–10) convolutions; L/W ratio varying from 1.08 to 1.36.

Remarks. In the Wood Eaton outcrop, only representatives of the genus *Musacchiella* are found, as confirmed by the examination of basal plates. In histograms of the dimensions, the specimens are divided in two sets with bimodal peaks interfering for lengths 400–450 μm and widths 350 μm . As the characters, other than the convexity or concavity of the spiral cells, do not vary significantly, we assign the whole population to a single species.

Affinities. *M. palmeri* differs from *M. douzensis* by its more dumpy shape, its smaller dimensions, and the conformation of the basal region. However, the two species have in common two characters: the variability of the cell relief (concave to convex) as well as the salient features of the lime-shell, these peculiarities being also found in *M.* sp. A from Sardinia. On the other hand, the largest specimens with concave cells look somewhat like *P. sublaevis* (Peck) Grambast in Saïdakovsky (1966, p. 132) from the Middle Jurassic of Montana, U.S.A., of which the basal plate has not been described. The specimens with large dimensions may also be compared with '*S.*' *sahnii* and '*S.*' *jaisalmerensis* both described by Bhatia and Mannikeri (1977). Their number of convolutions is however higher and there is no mention of the basal plate. These two taxa seem to us to belong to only one species with various degrees of calcification. Their apical morphology leads us to conclude that they must be ascribed, together with '*S.*' *raoi*, to the genus *Porochara*.

Musacchiella sp. A

Text-fig. 4F

Occurrence. Funtana sa Mela, near Siniscola, Nuoro province, Sardinia; Bathonian, Middle Jurassic (specimens collected by Dr. I. Dieni).

Description. Gyrogonite ellipsoidal, with concave spiral cells; basal plate apparently made of three pieces, which have been observed in longitudinal section (text-fig. 2C). Basal plate not visible from the outer side of the gyrogonite.

Remark. The small number of specimens and the often rather poor state of preservation do not allow the creation of a new species, so we are leaving the described form in open nomenclature. However, it would appear that, on the basis of their morphology and in spite of the deformations observed, the specimens from Sardinia cannot be assigned to either of the two former species of *Musacchiella*.

CONCLUSIONS

Within the present work on Bathonian charophytes, we have described a new genus, *Musacchiella*, which includes Porocharaceae/Porocharoideae species combining an unusual assemblage of characters in the gyrogonite: the apical opening recalling the family Raskyellaceae (Upper Cretaceous–Lower Miocene), the divided basal plate of the Characeae/Nitelloideae type (Upper Cretaceous–Recent), and the ‘Y’ calcification of the wall resembling that in *Lamprothamnium* (Characeae/Charoideae, Upper Cretaceous–Recent). Furthermore, this particular calcification appears to be related to a brackish habitat. Thus a great diversity of valuable characters is present amongst forms which are rather unspectacular at first sight: small-sized gyrogonites without any ornamentation. One may see in this contrast the expression of an evolutionary potential amongst these Porocharaceae from the Middle Jurassic. It has been previously suggested (Grambast 1962, 1974) that the Porocharaceae constitute the common stock from which the families Raskyellaceae and Characeae, which comprise nearly all the Tertiary forms, are derived. The example of *Musacchiella* lends support to this point of view. In addition, the genus *Musacchiella* has a wide geographical distribution in Western Europe: England, France, Sardinia. Also associated with this genus are species now ascribed to *Porochara* which are currently being investigated.

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ADAPTIVE SIGNIFICANCE OF SHELL TORSION IN MYTILID BIVALVES

by ENRICO SAVAZZI

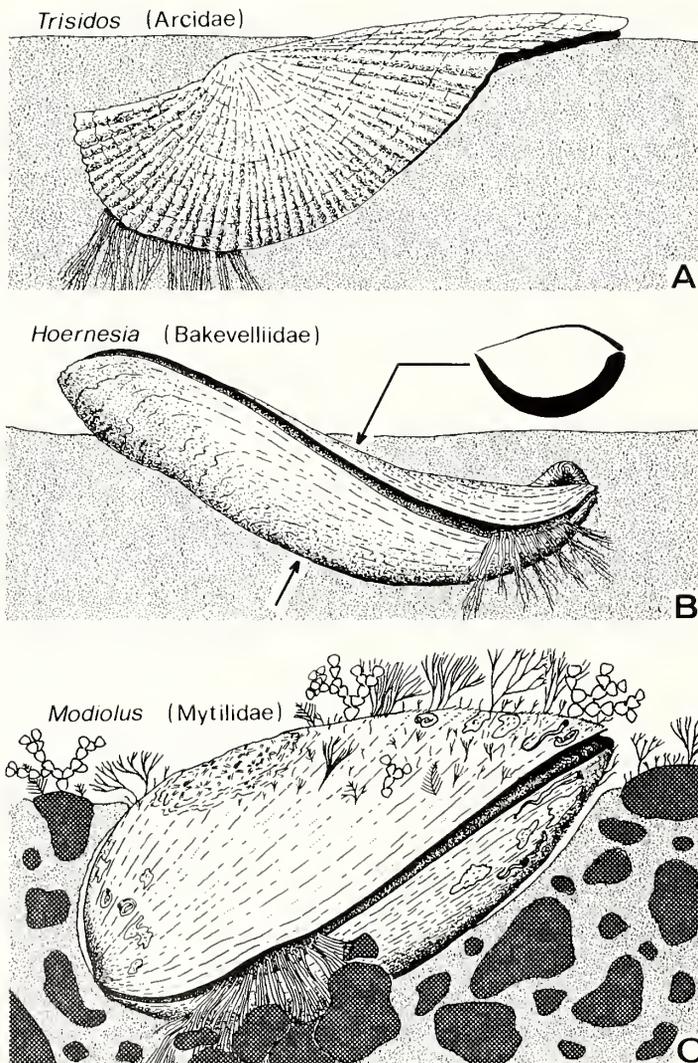
ABSTRACT. A twisted commissure plane is a common feature in several species of the mytilid genus *Modiolus*. Observations on a semi-infaunal population of *M. americanus* in Bermuda suggests that the twisted shell morphology maximizes the length of posterior commissure raised above the sediment surface while keeping its profile low, with minimum risk of accidental damage. Thus, the shell morphology in the twisted Mytilidae represents adaptive convergence with the twisted Arcidae and Bakevelliidae. In these two families, however, the torsional direction is genetically fixed, while in the Mytilidae both the direction and the amount of torsion seem to develop as a phenotypic response to the shell orientation relative to the substrate.

SEVERAL infaunal or semi-infaunal representatives of the bivalve families Arcidae and Bakevelliidae possess a twisted commissure plane (McGhee 1978; Savazzi 1981). The twisted Arcidae (*Trisidos* and at least one species of *Barbatia*) are typically endobyssate soft-bottom dwellers, although some of the less-twisted species can live facultatively as epibyssate dwellers on solid substrates (McGhee 1978; Savazzi 1981). *Trisidos* is a sluggish burrower (Tevesz and Carter 1979). The twisted commissure lifts the posterior region of the shell above the surface of the sediment and aligns it roughly horizontally (text-fig. 1A). This allows the inhalant and exhalant mantle regions to be widely spaced (McGhee 1978). The twisted Bakevelliidae (*Hoernesia*, *Gervillia*) were similarly soft-bottom dwellers. They are not likely to have been active burrowers, and lived partly buried in the sediment resting on one valve. The anchoring function of the byssus was supplemented by selective thickening of the lowermost valve (with the possible exception of the Cretaceous *Pseudoptera*). This adaptation facilitated passive re-orientation of the organism by waves or water currents after accidental disturbance of the life position (text-fig. 1B). Shell torsion offers the additional advantage that the posterior commissure, emerging from the sediment roughly horizontally, offers less resistance to water currents and is less likely to be accidentally damaged by objects rolling on the bottom (McGhee 1978; Savazzi 1981).

The torsional direction is defined as the direction of twisting of the proximal part of the shell with respect to the distal one, orienting the shell with the hinge parallel to the line of sight. Both clockwise and counter-clockwise torsion is known to occur in the Arcidae and Bakevelliidae (McGhee 1978; Savazzi 1981 and unpublished data). In all instances, however, the torsional direction is constant at the generic or specific level, and therefore appears to be genetically fixed. Evidence suggests that the twisted shell morphology evolved repeatedly within both families. It is therefore reasonable to expect that shell torsion also evolved convergently in other similarly pre-adapted bivalve groups. Further examples of shell torsion in different taxonomic groups would provide an opportunity for indirectly checking the ideas on the adaptive value and evolution of the twisted-shell morphology in the Arcidae and Bakevelliidae (cf. Savazzi 1983).

Infaunal representatives of the Mytilidae are the most likely candidates for this search, since they have life habits comparable with those of the twisted Arcidae and Bakevelliidae and, lacking siphons, they similarly need to leave a consistent length of the posterior commissure exposed above the surface of the sediment, in order to avoid fouling by sediment particles and mixing of the inhalant and exhalant currents. In addition, since the Mytilidae belong to the superfamily Pteriomorphia together with the Arcidae and Bakevelliidae, they possess relatively close anatomical affinities. In fact, a survey of Recent mytilids showed that several species of *Modiolus* are often noticeably twisted about the hinge axis in a manner closely comparable with the twisted Arcidae. Singularly enough, no

mention of shell torsion was found in the literature on these species. A number of other mytilid species often display a wavy or otherwise irregular commissure. Although these irregularities do result in a non-planar commissure, they do not conform to the definition of shell torsion (McGhee 1978) and are therefore excluded from the present discussion. Since the twisting in *Modiolus* is always greatest between the antero-ventral and the posterior shell regions, as in the twisted Arcidae and Bakevelliidae, it seemed possible that the shell torsion could be similarly adaptive. However, the degree of twisting turns out to be extremely variable within a single species, and only some of the individuals display torsion at all. Furthermore, it was found that both clockwise and counter-clockwise torsion normally occur side by side within the same species. It was therefore felt that the functional interpretation of the twisted-shell morphology would remain questionable in this specific case, unless direct observations could be carried out on twisted mytilids in their natural environment.



TEXT-FIG. 1. Schematic illustration of twisted bivalves in life position. A, *Trisidos yongei* Iredale, Recent, East Indies. B, *Hoernesia socialis* (Schlotheim), Middle Triassic, southern West Germany. The transverse section shows the characteristic thickening of the lowermost valve. C, *Modiolus americanus* Leach, Recent, Bermuda.

MATERIAL AND METHODS

Modiolus americanus Leach, one of the mytilids exhibiting shell torsion, is a large species living in the West Indies. Stanley (1970) described it as occurring in clear sand or in subtidal grass flats, mostly or totally buried in the sediment and byssally attached to the roots of seaweeds or to coarse sediment particles. The writer located a population of this species living at a depth of 1–2 m along the southeastern coast of Harrington Sound, Bermuda, in August 1982. The bivalves were living in coarse, muddy sand mixed with sandstone pebbles deriving from a nearby overhanging rocky cliff. The thick byssus was always found to be anchored to a fairly large amount of coarse sediment particles, requiring considerable physical effort to dislodge the shell. Roughly one-third of the shell surface was exposed and heavily overgrown by algae and encrusting organisms. The life position was initially recorded by marking the exposed parts before dislodging the shell, but it was subsequently found that the distribution of epibionts is a fairly reliable indicator of the exposed shell regions. Only thirty-one individuals could be located, since their distribution was patchy, and the sediment type rapidly changed to barren muddy sand, unsuitable for *M. americanus*, a few metres away. Dead shells and isolated live individuals were collected elsewhere in Bermuda, but no other population was found. A total of forty-one individuals was observed in the living position.

The angle of shell torsion was measured by projection on to a plane perpendicular to the hinge axis. The inclination of the posterior commissure relative to the surface of the sediment could not be reliably measured because of irregularities in the substrate. For most individuals, it was estimated at 30° to 60°. Only two individuals were found lying with the commissure plane approximately vertical.

RESULTS

The data relative to live *M. americanus* (text-fig. 2A) show an almost perfect association between the direction of shell torsion and the lateral inclination of the commissure plane in the living position. With a single exception, possibly due to a previous disturbance, the direction of shell torsion is such as to maximize the length of posterior commissure raised above the surface of the sediment, as found in other twisted bivalves (text-fig. 1C). Lateral asymmetries (other than twisting about the hinge axis) were not noticed in the anatomy of the soft parts, nor in the distribution of the periostracal hairs on the outer surface of the shell. The two specimens with a vertically oriented commissure showed negligible torsion. Otherwise, the lack of information on inclination of the commissure relative to the substrate precludes detection of any correlation between torsional angle and obliquity of shell insertion in the sediment.

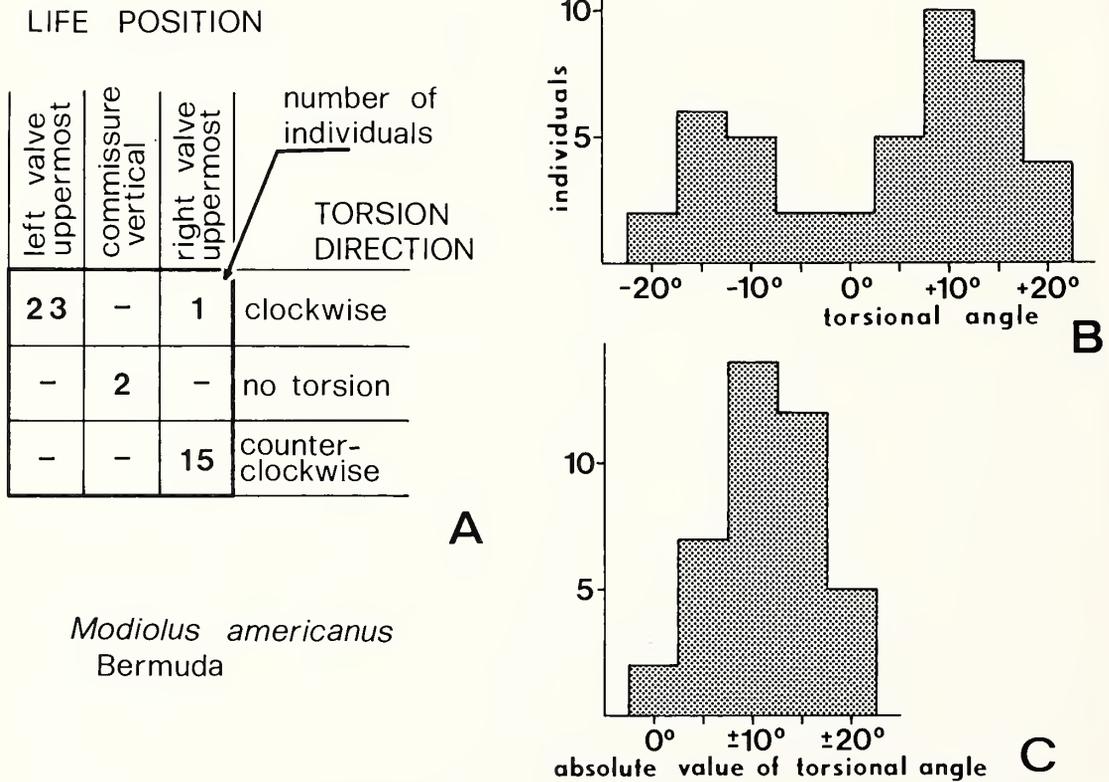
The histogram in text-fig. 2B shows the degree of twisting of the commissure plane for the living individuals of *M. americanus* collected for this study. The torsional angle of counter-clockwise twisted individuals is arbitrarily given a negative sign. When the absolute value of the torsional angle is displayed, the distribution becomes unimodal (text-fig. 2C). Together with the comparable number of clockwise and counter-clockwise twisted individuals, this suggests that the direction of shell torsion is determined by a stochastic process.

The bimodal distribution in text-fig. 2B contrasts with those obtained from dead shells of *M. americanus* and other Recent species from museum collections (text-fig. 3). This discrepancy can be explained by the fact that species in museum collections are usually represented by several shell-lots from different localities and environments. According to the functional interpretation of shell torsion as a facultative adaptation to life in soft sediments, the twisted-shell morphology should be expected to occur only in populations living infaunally or semi-infaunally. *M. americanus*, for instance, occurs as an epibyssate dweller on rocky bottoms in North Carolina (Van Dover and Kirby-Smith 1979). In such a case, shell torsion would not be expected. Environmental data are usually absent in museum material, so that the above hypothesis cannot be tested. None the less, it is interesting to note that the percentage of twisted individuals in museum collections was found to be extremely variable among shell-lots of the same species but from different localities.

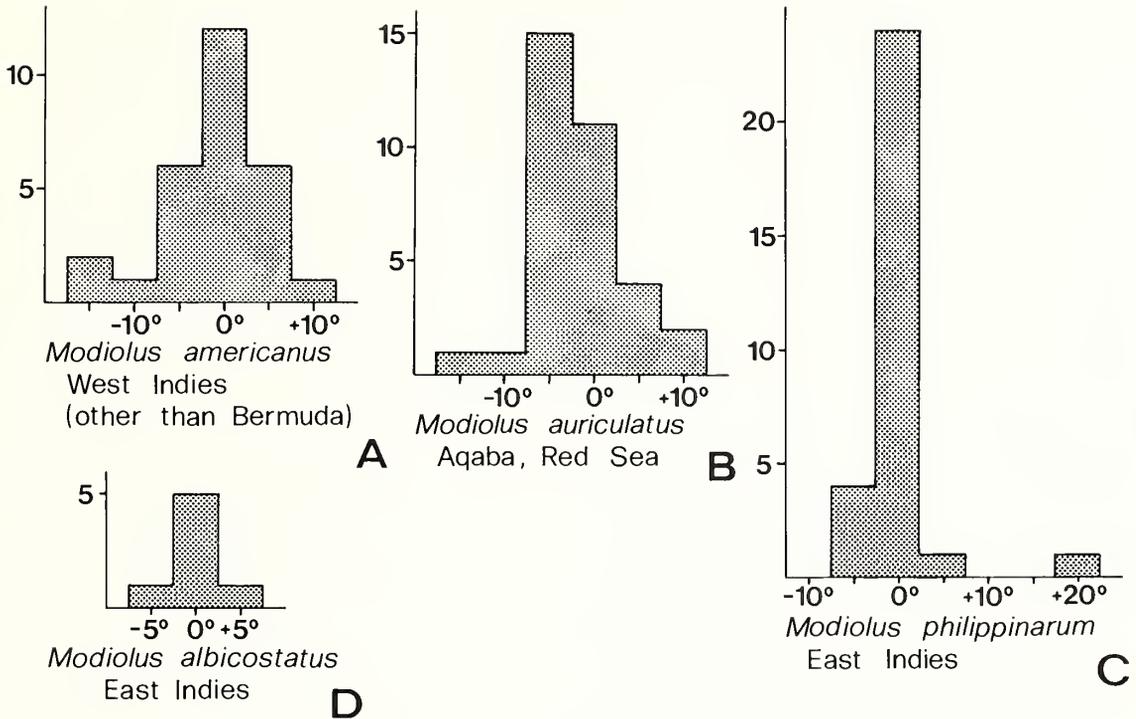
DISCUSSION

The relatively small number of individuals of *M. americanus* and the other twisted mytilids available for this study does not allow an effective statistical treatment. However, the approximately equal number of clockwise and counter-clockwise twisted individuals (with the exception of *M. auriculatus*, which is represented by a beach collecting and could therefore be biased by sorting) suggests that the direction of shell torsion in *Modiolus* is not genetically determined, but rather develops as a phenotypic response to the shell orientation relative to the substrate. The twisted Arcidae and Bakevelliidae are usually found in loose, essentially homogeneous sediments. The correct life orientation can be assumed by the settling veliger and/or be subsequently established by active or passive means. Therefore, a genetically fixed direction of torsion does not decrease the adaptiveness of the organism. A fixed torsional direction probably simplifies the introduction of other coadaptive inequivalve characters (differential valve weighting in the Bakevelliidae, different valve overlap in the Arcidae, functional inequivalve shell sculpture in representatives of both families: McGhee 1978; Savazzi 1981) in the morphogenetic programme of the shell.

M. americanus as observed during the present study, on the other hand, is better described as a byssally anchored semi-infaunal nestler among sediment-covered pebbles, rather than as a true soft-sediment dweller. The local topography of the substrate, rather than a preference of the veliger, seems



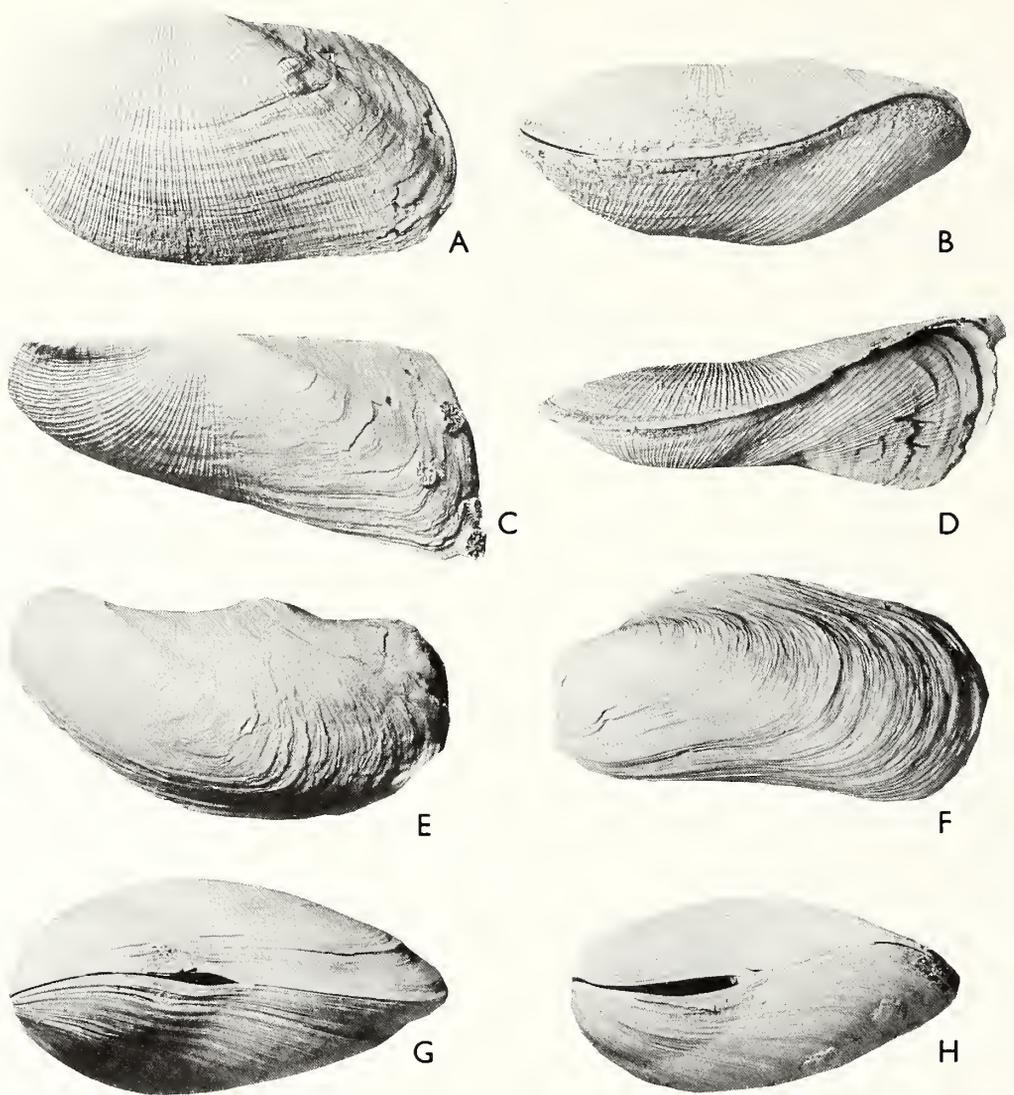
TEXT-FIG. 2. Occurrence of shell torsion in *Modiolus americanus* from Bermuda. A, relationship between life position and direction of shell torsion. B, distribution of the amount of shell torsion. Counter-clockwise and clockwise torsion are given negative and positive values, respectively. C, distribution of the absolute value of the amount of shell torsion.



TEXT-FIG. 3. Occurrence of shell torsion in Recent mytilid species. See preceding figure for explanation.

to be the most likely factor determining which valve will happen to lie uppermost. The possibility of developing either direction of torsion would therefore considerably increase the adaptiveness of the organism and, since apparently not associated with other inequivalve characters, it would not require a particularly complex morphogenetic programme. The alternative hypothesis, i.e. that the direction of torsion is genetically fixed and that the organisms assume a life position compatible with the anticipated torsion direction, would require a considerably more complex morphogenetic and behavioural programme. Since the possible shell orientation is highly constrained by the substrate morphology, only a proportion of the settling veligers would be in the condition of taking advantage of the shell twisting.

Other characters indicate that the adaptive strategy of *M. americanus* is rather different from that of both twisted Bakevelliidae and Arcidae. In these two families, the torsional angle reaches its maximum value between the posterior commissure line and the byssal gape. In *M. americanus* and in other twisted mytilids, on the other hand, the maximum torsional angle, relative to the posterior commissure, is often found slightly anterior to the byssal gape. When *M. americanus* is feeding normally, the shell gapes all around, and the long and slender pedal retractor muscles are contracted, pulling the byssus anteriorly. As a result, the shell is pushed backwards and upwards about half a centimetre, thus elevating the posterior commissure clear of the sediment surface and the surrounding algae. The torsion in the shell region anterior to the byssal gape causes the shell to rotate slightly as it is pushed backwards, further elevating the posterior commissure. When the mollusc adopts the feeding position, a cavity forms between the buried shell surfaces and the surrounding sediment, allowing the growth of interstitial cemented epibionts on the shell (text-fig. 1c). Since the shell surfaces exposed above the substratum are heavily overgrown by algae, the encrusting red algae



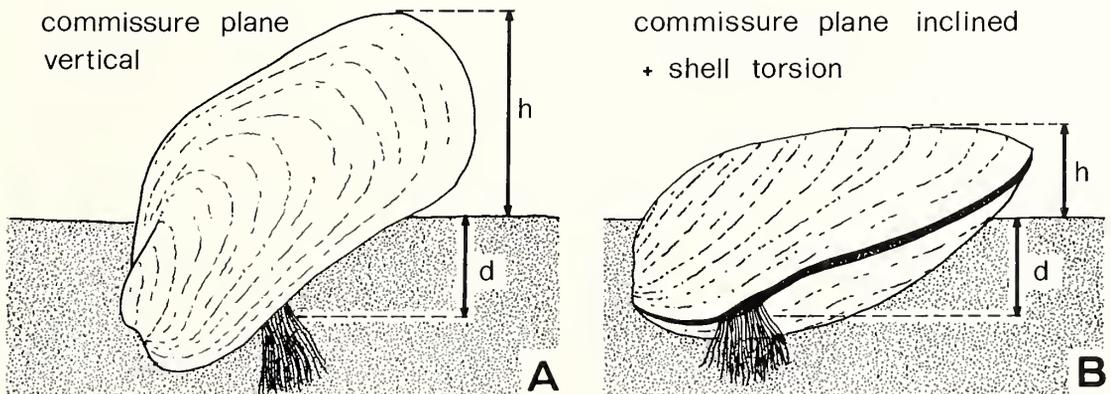
TEXT-FIG. 4. Twisted bivalves. A-B, *Trisidos semitorta* (Lamarck), Recent, Philippines; left lateral and ventral views, $\times 0.75$, NRS (NRS = Naturhistoriska Riksmuseet Stockholm). C-D, *Tr. tortuosa* (Linnaeus), Recent Philippines; left lateral and ventral views, $\times 0.75$, NRS. Note the corals attached to the posterior region of the left valve, which is exposed in life position (compare with text-fig. 1A). E, *Hoernesia socialis* (Schlotheim), Middle Triassic, Württemberg (West Germany); left lateral view, $\times 1.5$, Paleontologiska Institutionen Uppsala. F-G, *Modiolus americanus* Leach, Recent, Bermuda; left lateral and ventral views, $\times 0.75$. H, *M. philippinarum*, Recent, Bali; ventral view, $\times 2$, NRS. Note that the specimens in G and H are counter-clockwise and clockwise twisted, respectively.

and worm tubes are often more frequently found on the buried shell regions, where they face little spatial competition. In other twisted mytilids, in contrast, the exposed parts are more heavily overgrown by calcareous algae than the buried parts. Therefore, the distribution of cemented epibionts would be of little use as an indicator of the life habits of fossil mytilids.

Repaired minor damage to the posterior commissure is a common feature in the twisted Arcidae and Bakevelliidae and in most twisted *Modiolus* (text-fig. 4). Such damage is probably the result of the impact of objects rolled on the sea floor by waves or water currents. Traces clearly referable to the attack by shell-chipping predators are uncommon. In the twisted Arcidae and Bakevelliidae, the anterior and ventral commissure is generally immune from damage, since these parts are buried. In *M. americanus*, on the other hand, repaired damage to the shell margin is often also observed in the byssal region (text-fig. 4F). This is explained by the fact that *Modiolus*, unlike the other twisted bivalves, is byssally attached to, and surrounded by, buried rock fragments. When the posterior end of the shell is moved, the shell surface exerts a leverage against these solid bodies, the byssus acting as a fulcrum. A closely similar breakage pattern is often observed in epibyssate bivalves (e.g. *Mytilus*, *Arca*). Thus, it may be difficult to infer the life habits of fossil *Modiolus* from either the distribution of epibionts or the patterns of repaired marginal fractures. Shell torsion, on the other hand, is an easily recognizable feature and therefore a useful tool in autecological analysis, since it should be expected to occur only in those individuals living semi-infaunally and lying on one valve. As shown by the records in the literature, the life habits of single species can vary in different localities, resulting in a variable percentage of twisted individuals.

It was not possible to assess the frequency of occurrence of shell torsion in fossil mytilids. However, a late Caenozoic mould of a *Modiolus* species from the West Indies, closely related to *M. americanus* (Paleontologiska Institutionen Uppsala Nr. 1b 6007) shows pronounced shell twisting.

The principal adaptive advantages of shell torsion in the Arcidae and Bakevelliidae, i.e. leaving a suitable length of the posterior commissure clear of the sediment, to facilitate the respiratory and feeding current exchanges, and aligning it approximately horizontally, so that it would be less likely to be accidentally damaged (McGhee 1978; Savazzi 1981), apply to the twisted Mytilidae as well. The frequency of repaired damage to the posterior commissure in all twisted bivalves attests to the vulnerability of this exposed shell region. Other bivalves living in similar environments with part or all of the commissure exposed rely on several protective mechanisms. The shell margins are very thick



TEXT-FIG. 5. An idealized comparison of life positions with the commissure plane vertical (A) and inclined (B) shows that the latter reduces the height of the portion of the shell projecting above the surface of the substratum (h). The length of exposed posterior commissure is the same in both cases. Shell torsion coupled with a reclining position on one side (B) allows the byssus to be buried at a suitable depth within the substratum (d) to provide firm anchorage.

(e.g. epibyssate arks; some oysters), or the mollusc relies on extensive repair capabilities (e.g. *Pinna*; Yonge 1953). Alternatively, thick periostracal bristles or flexible and frilled shell margins may act as elastic shock absorbers (*Pteria*, *Isognomon*, some mytilids). Text-fig. 5 shows how shell torsion in *Modiolus* significantly reduces the height and vulnerability of the parts of the shell projecting above the surface of the sediment, while at the same time it allows the byssus to be buried at a suitable depth to ensure a reliable anchorage. A nearly horizontal posterior commissure, moreover, allows feeding on the particle-rich bottom layer of water.

According to McGhee (1978), evolution of the twisted morphology in the Arcidae and Bakevelliidae was rendered possible when a morphogenetic programme supplemented or substituted the interference of the byssus with the mantle margins in determining the shape of the byssal gape. The byssal gape is a weakly controlled region of the shell also in the Mytilidae, as shown by its greatly variable shape and extension. Therefore, McGhee's explanation can be applied to this family as well.

CONCLUSIONS

The twisted-shell morphology in *Modiolus* represents an adaptation to a semi-infaunal life habit with the commissure plane lying on one side, and constitutes therefore a functional convergence with the twisted Arcidae and Bakevelliidae. While the potential for shell torsion is present in several species of *Modiolus*, its expression is dependent upon life habits and environmental conditions. It is significant that shell torsion in *Modiolus* was observed solely in species possessing a relatively unspecialized shell shape. Very streamlined and elongated species, adapted to burrowing at a high angle to the sediment surface, and *Mytilus*-like species with a broad flat ventral region, suitable for epibyssate attachment, were never found to be twisted. Similarly, shell torsion was not found in the mytilinid genus *Brachidontes*, whose infaunal representatives burrow at a high angle to the sediment surface (Stanley 1970).

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EARLY ORDOVICIAN TRILOBITES NORA FORMATION, CENTRAL AUSTRALIA

by RICHARD A. FORTEY and JOHN H. SHERGOLD

ABSTRACT. This is the first detailed account of the trilobites from the platformal carbonate/clastic Nora Formation of central Australia. The fauna records a remarkable, endemic radiation of the Family Asaphidae, producing forms with inflated, tuberculate frontal glabellar lobes unlike any other asaphids, but with a general resemblance to certain unrelated trilobites which lived in former epeiric habitats. The fauna is probably of mid-late Arenig age. The generic composition indicates that Australia lay in equatorial latitudes during the early Ordovician, attached or close to the Gondwanaland of the time and well-removed from other continents spanning the palaeoequator. The fauna includes eighteen species, of which four are left under open nomenclature. The concept of the Leioptegidae is reviewed to include *Aunamitella*, formerly regarded as a bathyurid. The classification of trinucleine trilobites is briefly reviewed. The peculiar blind trilobite *Prosopiscus*, hitherto considered an aberrant cheiruracean, is reclassified in the Phacopina, and for its reception a separate family, Prosopiscidae nov., is proposed. The following new taxa are described: *Aunamitella strigifrons*, *A. brachyops*; *Norasaphus*, *N. (Norasaphus) skalis*, *Norasaphites*, *Norasaphus (Norasaphites) monroecae*, *N. (N.) vesiculosus*; *Lycophron*, *L. rex*; *Fitzroyaspis irritans*, *Hungioides acutinasus*, *Nambeetella embolion*, *Gogoella brevis*, and *Prosopiscus praecox*. On the basis of the trilobite fauna two assemblage zones are defined in the Nora Formation.

THE trilobites described here were collected from the Nora Formation during 1976. Although the formation has a wide geographic distribution (text-fig. 1) extending over at least a 300 km east-west belt, we have restricted our present investigations to the faunas of the Toko and Toomba Ranges, respectively the eastern and western limbs of the Toko Syncline. This area has been more thoroughly documented by members of the Australian Bureau of Mineral Resources Georgina Basin Project than the sequences of either the Tarlton or Dulcie Ranges to the west; the formation is thought to be most completely developed in the Toko Syncline where its stratigraphic relationships are better known, and the trilobite faunas are more prolific.

During the Arenig the continental interior of Australia was immersed beneath a shallow, tropical sea, which supported a rich fauna of trilobites, brachiopods, and molluscs. Outcrops of rocks of this age are widely distributed in the Georgina and Amadeus Basins, but their inaccessibility has meant that the faunas have only recently been studied in any detail. Platform faunas of this kind are relevant to the assessment of the paleogeographic position of Australia during the early Ordovician. This paper describes the trilobite fauna of the Nora Formation, which crops out along the southern margin of the Georgina Basin, central Australia. The fauna is of particular interest because it records endemic morphologies arising within what was evidently a short time; probably no better example exists of the adaptability of the trilobite exoskeleton in the epeiric habitat.

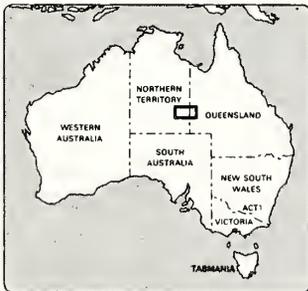
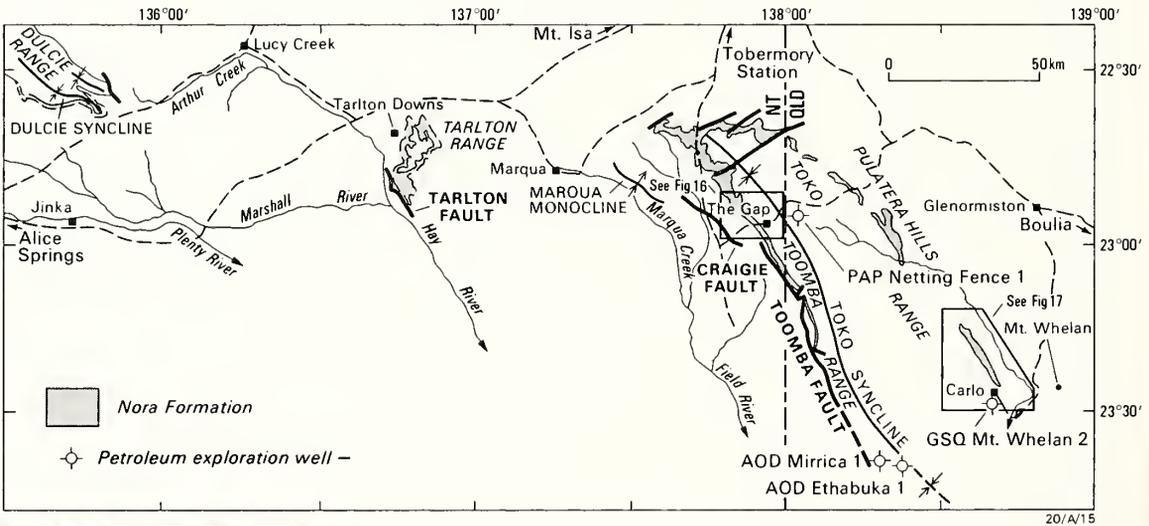
Type material described here is prefixed CPC, and is deposited in the Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra, Australia. A representative non-type suite of material is deposited in the British Museum (Natural History), London, and is prefixed BM It. R. A. F. contributed pp. 318-360, although joint responsibility is accepted for the scientific content of the paper.

STRATIGRAPHIC SYNOPSIS

The Nora Formation was named by Casey (*in* Smith 1963a, p. 10, table 1) for the informally designated rock unit 01-8 of Pritchard (1960, pp. 112-113). Originally referred to the Toko Series (Whitehouse 1936) or Toko Beds (Casey 1959; Pritchard 1960), the Nora Formation is now

recognized as the basal formation of the Toko Group, as revised by Draper (1980, pp. 473-474) who also illustrates the historical development of nomenclature for these rocks. Stratigraphic relationships are illustrated in text-fig. 2. The type area of the Nora Formation is in the northern continuation of the Toomba Range, in the vicinity of Halfway Dam (text-fig. 16), 71 km south of Tobermory. A type section has never been defined. In its type area the formation consists of brown ferruginized coquinite at the base, succeeded by quartz sandstone and siltstone (Smith 1965). Elsewhere a basal clastic interval of varying thickness occurs, sometimes containing pelletal or pebble skeletal grainstone. The clastic to carbonate ratio increases as the formation is followed from north to south.

Three petroleum exploration wells and a Geological Survey of Queensland stratigraphic corehole have penetrated the Nora Formation (text-fig. 1) which, together with surface outcrop measurements, give some idea of the thickness and lithological variation within the formation in the Toko Syncline. Drilling in the Netting Fence Anticline in the northern part of the Toko Syncline (unpublished well completion report, Papuan Apinaipi Petroleum Co. Ltd., 1965), penetrated 114 m of Nora Formation which consisted of 41 m of sandstone, shale, and coquinite, overlain by 73 m of fine sandstone and shale. This total correlates well with a similar sequence, 119 m thick, in the Pulatera Hills in the central portion of the Toko Range, and the approximate 100 m measured in the type area. At the southern end of the Toomba Range, the Nora Formation is 250 m thick in AOD Ethabuka No. 1 (unpublished well completion report, Alliance Oil Development, Australia N.L. 1975) where it is reportedly composed mainly of shale with minor amounts of dolomitic sandstone and coquinite. Similarly, at the extreme southern end of the Toko Range, GSQ (Geological Survey of Queensland) Mount Whelan No. 2 stratigraphic hole penetrated 235 m of Nora Formation, again mainly composed of silty shale and sandstone with minor limestone (Green and Balfe 1980, p. 173).

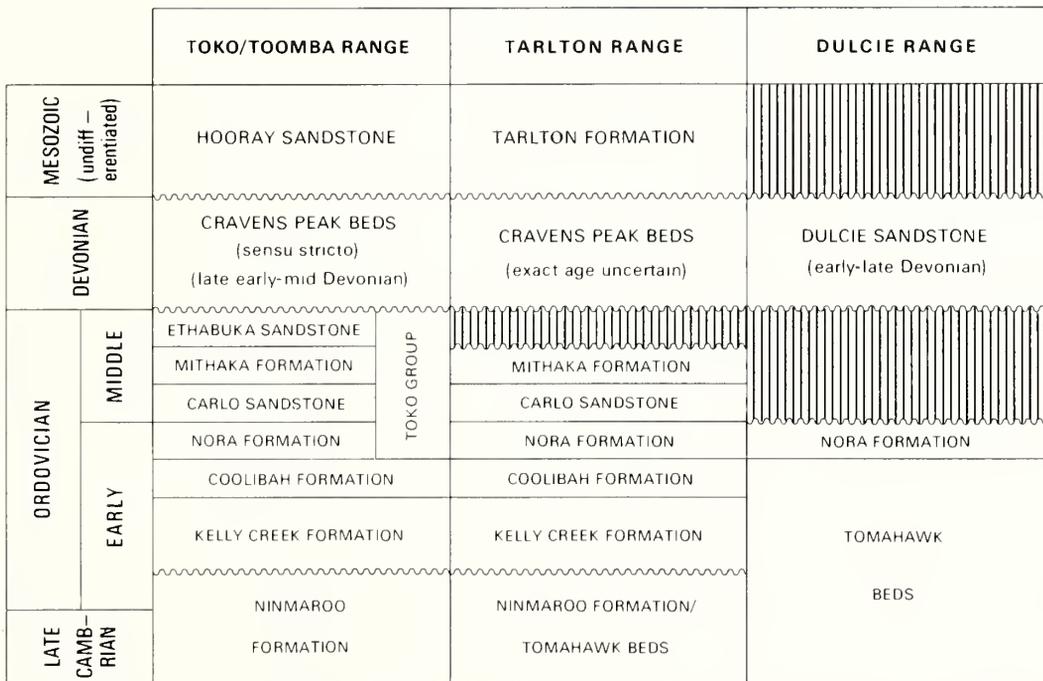


McDONALD DOWNS 5953	ARAPUNGA 6053	LUCY 6153	ALGAMBA 6253	ALKEA 6353	TOBERMORY 6453			
ONEIPER 5952	JINKA 6052	JERVOIS 6152	TARLTON 6252	MARQUA 6352	TOKO 6452	NEEYAMBA HILL 6552	GLENORM- ISTON 6652	
Index of 1:100 000 scale geological series sheets covered by this map						AOAM 6451	ABUDDA LAKES 6551	MOUNT WHELAN 6651

TEXT-FIG. 1. Location and geographic distribution of the Nora Formation in central Australia.

Elsewhere, the Nora Formation is 70–100 m thick in the Tarlton Range (Smith 1965, 1972), where it conformably overlies sandy carbonates and dolomites ascribed to the Kelly Creek Formation, the Coolibah Formation not being recognized (Smith 1972, p. 128). The internal lithostratigraphy of the Nora Formation in the Tarlton Range is similar to that in the northern Toko Range. At the eastern end of the Dulcie Syncline, in the Huckitta district some 120 km further west, Smith (1963*b*) has recorded a predominantly dolomitic, coquinitic, ferruginized sequence (including oolitic ironstone) up to 125 m thick, and conformably overlying Tomahawk Beds of late Cambrian and early Ordovician age.

Webby (1978, 1981) has correlated the Nora Formation of the Georgina Basin with the Horn Valley Siltstone of the Amadeus Basin, and the Willara and Gap Creek Formations of the Canning Basin in Western Australia. On the basis of these correlations, Webby (1978, fig. 6*B*) has reconstructed a palaeogeography for late early Ordovician time wherein the Nora Formation is deposited under the influence of a warm equatorial current in a narrow, basically east–west orientated, Larapintine Sea. Within this seaway, Draper (1977) considers the Nora Formation to represent below wave base sediments, in part contemporaneous with sand bars (Carlo Sandstone on his fig. 2) and lagoon bay sediments (Mithaka Formation on his fig. 2), but there is no palaeontological evidence to confirm this relationship. As far as regional correlation of stratigraphic units within this seaway go, the conodonts of the Horn Valley Siltstone suggest a mid-Arenig age, within the *Oepikodus evae* and *Baltoniodus navis*/*B. triangularis* Biozones of the Baltic region, according to Cooper (1981). Based on this information, and as yet unpublished conodonts from the Georgina Basin, Cooper (*op. cit.*) concluded that the Horn Valley Siltstone is equivalent to the Coolibah and basal Nora Formations of Toko Syncline, thus supporting our contention (below) of a mid-late Arenig age for the Nora Formation. While this information does not alter the palaeogeographic picture, it may suggest a certain diachroneity of the stratigraphic units correlated by Webby.



20/A/16

TEXT-FIG. 2. Stratigraphic relationships of the Nora Formation to adjacent Formations in central Australia.

AGE OF THE NORA FORMATION

The Nora Formation is in places extremely fossiliferous and, collectively, a large biota has been recorded: bivalves, nautiloids, gastropods, rostroconchs, brachiopods, ostracodes, bryozoans, pelmatozoa, sponges, corals, conodonts, trilobites, ichnolites, and questionable foraminifera (see Shergold and Druce 1980, p. 163). Of these groups, some actinoceratoid nautiloids have been described by Beard (*in Hill et al.* 1969) and Wade (1977*a, b*), and these are considered to have an early middle Ordovician age. Similarly, the conodonts illustrated by Nieper (*in Hill et al.* 1969) are ascribed an early middle Ordovician age, by virtue mainly of the presence of *Histiodela*. This is disputed by Druce (*in Shergold and Druce* 1980, p. 163) who regards the Nora conodonts as indicating an age late in the early Ordovician (late Arenig), based on the presence of non-fibrous Scandinavian forms. The Nora Formation has also yielded ten species of bivalves which include an ambonychiid form, a family not known elsewhere earlier than the beginning of the middle Ordovician. Together with the other bivalve evidence, Pojeta and Gilbert-Tomlinson (1977, pp. 4–5) suggest an age near the early/middle Ordovician boundary. The rostroconch species *Technophorus* sp. and *Euchasma skwarkoi* described by Pojeta *et al.* (1977) are not age diagnostic. The orthoid and plectambonitid brachiopods, a variety of gastropods (?*Lophospira*, ?*Clathrospira*, ?*Helicotoma*, a bellerophonitid), a monoplacophoran, and the ichnolites, are yet to be described in detail, although some are illustrated by various authors *in Hill et al.* (1969).

The definition of lower and middle Ordovician in the preceding discussion is that customarily adopted by North American workers; the base of the middle Ordovician is taken at the base of the Whiterock Stage of the North American platform sequence at a horizon approximately equivalent to the base of the Llanvirn. Part of the apparent conflict between lower and middle Ordovician determinations in the Nora Formation may be a reflection of the correlation problems involved with the Whiterock Stage. Fortey (1980*d*) has suggested that the Whiterock is diachronous and often underlain by an interval in which shelly fossils are rare, or a disconformity, equivalent at the least to the upper part of the Arenig Series. Faunas of 'Whiterock aspect' (e.g. Wade 1977*a*) may appear within this interval if the appropriate facies is developed. To give one example, Hill *et al.* (1969, pl. O-IV, fig. 3) figure *Cacheoceras trifidum* Flower, 1968 from the Nora Formation. Flower's original description cites the horizon as 'certainly within Zone K of Ross (1951)' (Flower 1968, p. 32). If the base of the Whiterock is taken as the base of the succeeding Zone L, as is usual, then this occurrence indicates lower, not middle, Ordovician. Correlation of Zone K with the late Arenig was suggested by Fortey (1980*a*); so the cephalopod and trilobite evidence below are not greatly at odds.

The trilobite fauna described here is mostly endemic to Australia. Of the endemic genera, *Fitzroyaspis*, *Gogoella*, and *Nambeetella* are all present in the Canning Basin in Arenig rocks (Legg 1976), but we have determined all our forms as new species so they cannot be used for precise correlation. *Presbynileus* cf. *utahensis* is compared with a species from zone J of Utah (Hintze 1953) which correlates with the middle part of the Arenig Series (Fortey 1976). Among the pelagic forms, *Carolinites genacinaca* occurs in the earliest part of the Nora Formation only, the upper part having *C.* cf. *ekphymosus*. *Carolinites* spp. with narrow fixed cheeks like the latter are not known outside Australia before the late Arenig (*Isograptus* Zone and equivalents), while *C. genacinaca* is widespread in mid-Arenig faunas over a great area (Fortey 1975). So, on the evidence of these species comparisons, the Nora Formation is assuredly Arenig and probably belongs within the middle and upper part of the Series (for informal definitions of lower, middle, and upper Arenig see Cooper and Fortey 1982). If this assessment is correct, it means that several of the trilobite genera in the Nora Formation are making their first appearances. *Hungioides* is elsewhere Llanvirn; *Prosopiscus* and *Phorocephala* have previously recorded ranges from Llanvirn to Caradoc; *Annamitella* is widely distributed in rocks of late Arenig and Llanvirn age. For correlation purposes we place more emphasis on the few, close species-level comparisons than on the generic composition as a whole.

Zonal subdivision

The Nora faunas divide broadly into two; since the facies is similar throughout we can recognize two assemblage zones, with the bulk of the Formation lying in the upper Zone. The readiest zonal guides are the extraordinary endemic asaphids of the genus *Norasaphus* which are also common in most localities. The lower Zone of *N. (N.) skalis* is dominated by the eponymous species but also includes: *Lycophron* sp. A., *C. genaciuaca*, *Annamitella strigifrons*, *Phorocephala* cf. *P. genalata* Lu. The upper Zone of *N. (Norasaphites) monroae* includes also: *N. (N.) vesiculosus* (common), *Lycophron rex*, *A. glabra*, *Presbynileus* cf. *P. utahensis* (Hintze), *C.* cf. *C. ekphymosus* Fortey, *Naubeetella enibolion*, *Hungioides acutinasus*, *G. brevis*, and *F. irritans*. *Prosopiscus* spp. span both zones (text-fig. 3). The few trilobites in common with the faunas of the Canning Basin indicate a broad correlation with Fauna 3 of Legg (1978). Because trilobites become rare at the top of the Nora Formation it is not possible to pick up overlap between the Nora faunas and those of the overlying Carlo Sandstone, although sedimentation appears to have been continuous.

PRESERVATION OF THE TRILOBITES

Most of the trilobites are preserved as moulds in fine sandstones. All are fragmentary and some of the larger pieces are broken. Some beds are full of fine trilobitic hash. The detail preserved on external moulds varies from locality to locality, but at its best the preservation is good enough to show sculptural details. All specimens are in full relief. A few beds in the lower part of the Nora Formation are carbonate-rich, and in these the trilobites are preserved with their exoskeleton intact. The fragmentary nature of the fossils makes association of the different parts especially difficult, and we have stated the reasons for making particular associations where these are not obvious. It seems there has been post-mortem sorting of the trilobites, and it is not possible to identify 'communities' in the fauna. Yet the endemic character of most of the fauna indicates that the trilobites all lived in an inshore, cratonic environment.

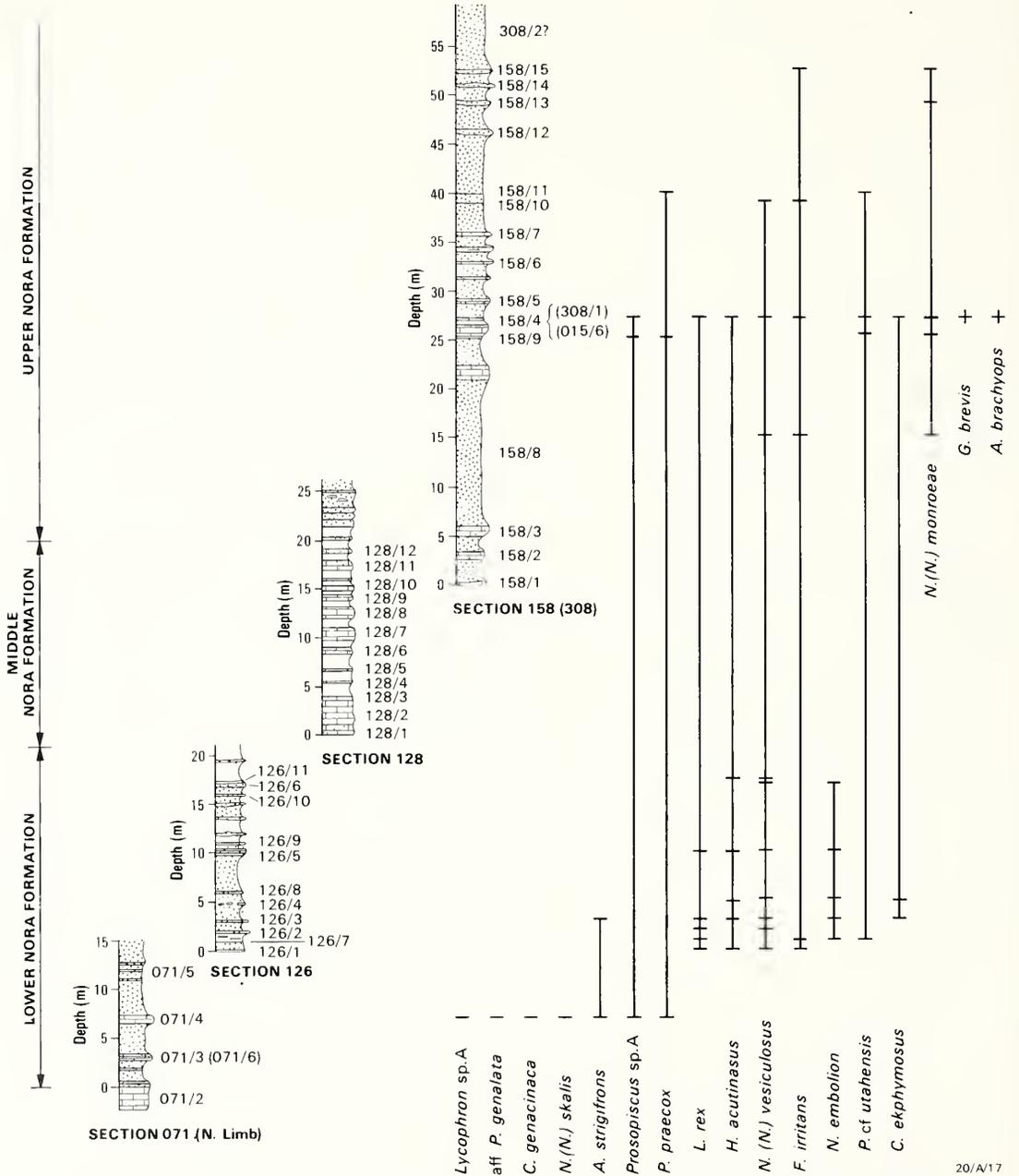
BIOGEOGRAPHIC ASSESSMENT OF THE NORA FORMATION FAUNA

Shallow-water cratonic faunas like that from the Nora Formation are the most sensitive indicators of provincial affinities (Cocks and Fortey 1982), being specifically adapted to ambient temperature and substrate conditions. It is appropriate to consider what the Nora trilobite faunas tell us about the early Ordovician palaeogeography of Australia. Sedimentology of earlier Ordovician formations (Radke 1981) indicates limestone deposition under tropical conditions; the occurrence in Australia of early Ordovician cephalopods (Gilbert-Tomlinson, *in* Hill *et al.* 1969), molluscs and conodonts (Druce and Jones 1971) known elsewhere from areas lying near the palaeoequator, as well as typical 'Pacific' province graptolites in Victoria, all leave no reason to doubt that Australia straddled low latitudes in the earlier part of the Ordovician. Larval dispersal doubtless varied considerably from one group to another, and the trilobites tend towards endemicity more than, say, conodonts. This means that the trilobites are a better guide to former continent separation than many other groups, although concomitantly less useful in inter-regional correlation. Comparisons are considered at generic and specific level.

In the first place there are a few elements in the Nora trilobite fauna which are familiar from North America at a considerable distance around the equatorial great circle. These are *Caroliuites* spp., a species intermediate between *Goniophrys* and *Phorocephala* (= *Carrickia*), and a *Presbynileus* species close to, if not identical with, one from Utah and Nevada. The first two named belong to the pelagic family Telephinidae; their independence from facies type and continent distribution, and their circum-equatorial distribution, has been familiar for some time (Fortey 1975). The last named is so far unrecorded outside North America. These aside, there is little in common between faunas from North America, or north-eastern Siberia, and that from the Nora Formation, and when apparently similar forms appear (e.g. *Lycophron* gen. nov. compared with *Isotelus*) this is because of convergence rather than phylogenetic continuity.

The most common trilobites in the Nora Formation, comprising about 85 per cent of the benthic

elements, are a group of curious endemic asaphids (*Lycophron*, *Fitzroyaspis*, *Norasaphus*), especially the unique tuberculate genus *Norasaphus* which frequently covers entire bedding planes. Two other genera, *Gogoella* and *Nambeetella*, were described by Legg (1976) from the Canning Basin, north-western Australia (but for taxonomic problems see systematic section). Well over half the benthic forms are unknown outside Australia and include the dominant elements in the fauna.



TEXT-FIG. 3. Composite stratigraphic section through the Nora Formation with ranges of trilobites.

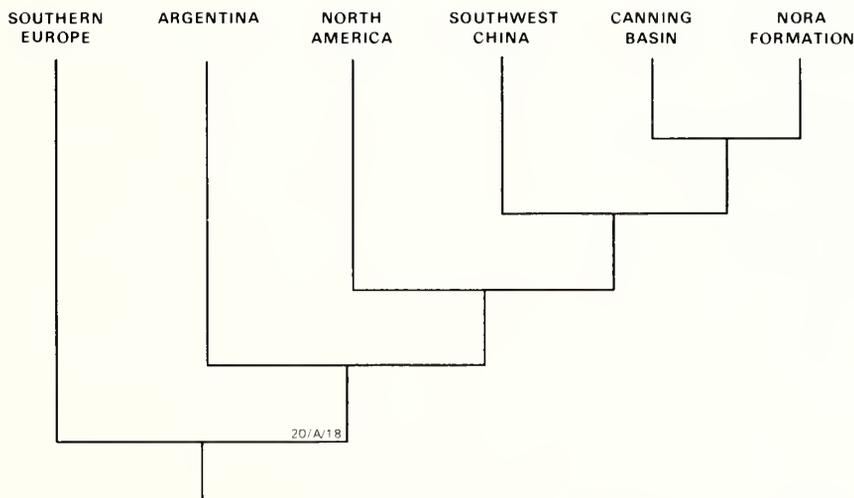
There remain a few genera which are 'Gondwanan' in distribution, notably *Hungioides* and *Prosopiscus*. Both occur in southern China. *Hungioides* has a wide distribution through South America (= *Argentinops* Přibyl and Vaněk 1980) to Bohemia and Thuringia. *Prosopiscus* occurs also in the Himalaya (Salter 1865). Finally, the genus *Annamitella* is very widely distributed through China, Kazakhstan, Vietnam, and with various occurrences off volcanic islands in Maine, Newfoundland, and Anglesey, Wales. Although such a spread might suggest planktonic habits like the Telephinidae there is nothing in the morphology of *Annamitella* to suggest that this was the case.

Only one explanation seems to us to explain the different elements combined in the Nora trilobite faunas. An equatorial position explains the pelagic elements, the dispersal of which is not inhibited by distance. Yet the dominance of peculiar endemics implies that platformal Australia was separated from other cratonic areas near the Ordovician palaeoequator sufficiently to induce speciation among available families—especially Asaphidae. A few forms (*Annamitella*, *Presbynileus*) were more widely distributed, probably because of efficient larval dispersal. Finally, the presence of otherwise Gondwanan elements suggests that Australia may have been attached to, or at least close to, the rest of Ordovician Gondwanaland (as in the reconstruction of Scotese *et al.* 1979), sufficient for the penetration of a few more eurytopic genera. Text-fig. 4 summarizes the relationships of the Nora Formation trilobites to those of other areas.

It is interesting to note that the fauna from the Canning Basin described by Legg (1976) is the closest to that from the Nora Formation (six genera in common), but it also includes a number of very widely distributed benthic genera such as *Triarthrus*, *Ampyx*, *Shumardia*, and *Ogygiocaris*. Both the lithologies and associated graptolites and conodonts (North Atlantic community type) indicate that deeper water, peripheral-cratonic facies are represented in this area. These include biofacies deep enough not to be restricted geographically in the same way as the on-craton faunas of Queensland and the Northern Territory.

SYSTEMATIC DESCRIPTIONS

Terminology follows that of the *Treatise on Invertebrate Paleontology, Part O, Artthropoda 1* (Harrington, Moore, and Stubblefield, *in* Moore 1959), with the addition of certain terms from Őpik (1967) and Fortey (1975). Glabella is usually understood to include the occipital ring. Systematic order is by family as they appear in the *Treatise*.



TEXT-FIG. 4. Diagram to show relative resemblances at generic level of the trilobite faunas from the Nora Formation to those of other areas. The scale ranges from six genera in common in the Canning Basin to one only in southern Europe.

Family LEIOSTEGIIDAE Bradley, 1925

Discussion. We extend the concept of the Leiostegiidae to include a number of Ordovician genera which have hitherto been referred to other families. In particular, we regard *Annamitella* (and its three possible synonyms *Bathyriscops*, *Monella*, and *Proetiella*) as belonging to a late radiation of the leiostegiids in which the dorsal furrows are fully expressed. Species of this type have been regarded as bathyurids (Whittington 1963). Recent revision of Canadian bathyurid genera (Fortey 1979) shows that any resemblances to that family are misleading, and that *Annamitella* and related forms are not closely comparable to either Bathyrinae or Bathyrellinae. In particular the long, anteriorly truncate glabella (concave-sided in some species) and the straight, inward- and backward-directed IP glabellar furrow are not bathyurid features; in the latter the IP furrows, when developed, are broadly arched or hooked backwards. The pygidium is possibly most similar to that of *Bathyurina* among bathyurids, but again the resemblance is misleading as there are twice as many axial segments in most species of *Annamitella*, and the broad, convex pleural fields surrounded by a narrow, 'rolled' border are leiostegiid features. It also seems likely that *Agerina* Tjernvik, 1956, which shares glabellar characters with *Annamitella*, should be removed from the Bathyridae. The pygidium in this genus is much smaller than in *Annamitella*, however. *Leiostegium* itself and its close relative *Lloydia* are highly effaced genera, but since effacement is of all trilobite characters the one most susceptible to polyphyletic derivation, it is apparent that subdued furrows cannot be used in the definition of the superfamily, as in the *Treatise* (Lockman-Balk in Moore 1959, p. 313). Of *Lloydia* species with an elongate glabella like that of *Annamitella* we may cite *L. oblonga* (Billings) from the Lévis Conglomerate. There is also a tendency in *Lloydia* for the border to become reclined against the glabella, a process carried to completion in *Annamitella*. Note also that there are strong apodemal pits at the anterolateral corners of the glabella in *L. bituberculata* (Billings), pits which occur in exaggerated form in the homologous site in *Annamitella*. It is also possible to see muscle insertion areas on the glabella of *L. spp.*, comparable in form (though more anteriorly placed) to those in *Annamitella*.

Transitional forms between conventional Leiostegiidae and *Annamitella* occur in Tremadoc rocks. In particular the genus *Szechuanella* Lu, 1959 (type species *S. szechuanensis*—see Lu 1975, p. 3, figs. 3–9) has a pygidium almost indistinguishable from that of *Annamitella*, while the cranidium, although relatively effaced, clearly shows the backward-directed IP glabellar furrow, and the border is tipped back against the front of the glabella. Co-apertive structures like those described below in *Annamitella* have been described on *Pagodia* (*Wittekindtia*) *variabilis* by Wolfart (1970, pl. 8, fig. 5b). Lu (1975, p. 458) also erected a new family Eucalymenidae for some Arenig–Llanvirn trilobites from central China. Lu included two genera in the family: *Eucalymene* Lu, 1975 (itself a probable synonym of *Pseudocalymene* Pillet, 1973) and *Bathyriscops* Lisogor, in Keller and Lisogor, 1954. As discussed below, the latter is a subjective synonym of *Annamitella*. The former resembles *Szechuanella* and differs from *Annamitella* in its relatively small palpebral lobes being somewhat removed from the glabella, and in the characters of the cranidial border. *Eucalymene* has strong glabellar furrows of *Annamitella* type; its pygidium has interpleural furrows, and the pygidial border is almost obsolete. These characters are scarcely of familial significance. Hence, we regard the Eucalymenidae as synonymous with the Leiostegiidae.

Once the Leiostegiidae is extended to include forms *en grande tenue*, we can speculate on the inclusion of other candidates within at least the same superfamily. When three glabellar furrows are developed on *Annamitella*, they have a distinctive form, with 1P steeply backward-inclined, 2P only gently so, and 3P anteriorly directed close to 2P. The same kind of furrow arrangement is seen on the diminutive earliest Canadian genus *Missisquoia* (particularly the type species *M. typa*, e.g. Stitt 1971, pl. 8, fig. 2). The systematic position of *Missisquoia* has long been problematic; the family Missisquoidae Hupé, 1953, is generally regarded as of uncertain ordinal affinities, although Shergold (1975, 1980, 1982) has consistently referred the family to the Leiostegiacea. We propose that *Missisquoia* is a neotenous derivative from a leiostegiacean. Additional features suggestive of a neotenous origin include especially the pygidium, in which the numerous segments are arranged as

if 'ready for release', and the extremely long, narrow glabella (which is like smaller *Annamitella*). Curiously, we have never seen leiostragiids in the same beds as *Missisquoia*, and so it does not seem probable that the small trilobite is simply a growth stage of a larger, more conventional leiostragiid.

Genus *Annamitella* Mansuy, 1920

Type species. Annamitella asiatica by original designation.

Revised diagnosis. Leiostragiid genus with dorsal furrows strongly expressed. Glabella long, subparallel-sided to slightly tapering forwards, with a tendency towards a slight expansion of the frontal lobe in some species. Two or three pairs of glabellar furrows, 1P straight and strongly backward-directed, 2P more transverse. Frontal border incorporated into glabella medially. Eyes large, close to glabella; width of preocular cheeks correspondingly reduced. Genal spines long to reduced. Pygidium strongly furrowed, four to nine axial rings, five or six pleural ribs. Axis extends to near posterior margin. Pygidial border variable, usually narrow and convex, but may be almost absent, to moderately broad and flattened.

Discussion. Dean (1973) and Whittington (1963) have noted that *Bathyuriscops* Lisogor, in Keller and Lisogor 1954, *Proetiella* Harrington and Leanza, 1957, and *Monella* Bates, 1968 could all prove to be synonyms of *Annamitella*. Our well-preserved material of *Annamitella* enables some clarification of the problems involved.

The material of the type species *A. asiatica* Mansuy (1920, pl. 2, figs. 7a-k) is not entirely satisfactory, being somewhat distorted internal moulds. Nevertheless, they do show the long glabella, two pairs of glabellar furrows, and, most important, what Mansuy interpreted as a third pair of glabellar furrows—in fact the trace on the internal mould of the lateral edge of the anterior border (cf. Pl. 38, fig. 4). The pygidium is like that of our Australian species, but with one less pleural rib posteriorly, a narrower border, and one or two less axial rings. But these differences are scarcely of generic standing, and we regard our assignment of the species from the Nora Formation as well-founded. The type species of the other genera named above are also poorly preserved. *Bathyuriscops*, type species *B. granulatus* (Weber 1948, pl. 1, figs. 22–24; also Keller and Lisogor 1954, pl. 1, figs. 1–7; Chugaeva 1958, pl. 1, figs. 1–3) from the Llandeilo of Kazakhstan, is also apparently known from exfoliated material but, except for deeper glabellar furrows (and in some of the figured specimens a greater median contraction of the glabella), the resemblance to our species is overwhelming; *Bathyuriscops* is accordingly regarded as a subjective synonym of *Annamitella*. *Proetiella* from the Llanvirn of Argentina is also closely similar in all major features, but one specimen of a cranidium of the type species (*P. tellecheai*, see Harrington and Leanza 1957, fig. 59, 3) shows what is probably a 3P glabellar furrow immediately in front of 2P. The type species of *Monella* (*M. perplexa* Bates, 1968, from the Arenig rocks of Anglesey) is very badly preserved but also shows evidence of the 3P glabellar furrow (e.g. Bates 1968, pl. 11, fig. 18), so there may be a case for regarding the presence of the 3P furrow as a generic discriminant. Unlike the type species of the other genera, *M. perplexa* has a broad and probably flattened pygidial border. The Australian species have a broader anterior cranial border (vertically) than any of the species discussed so far, also well-developed co-apertative devices; no other species have been described fully enough to be sure whether structures similar to the latter were present or not. In any case we do not regard the presence of such structures as of generic significance because they are found in several leiostragiids.

In summary, we incline to the view that *Annamitella* is the senior synonym of *Bathyuriscops*, *Proetiella*, and *Monella*. Further information on *P. tellecheai* may possibly allow for the discrimination of a second genus (of which *Monella* will be a junior synonym), but the presence of a 3P glabellar furrow alone seems inadequate grounds for so doing at the moment. Taking the broad view of *Annamitella* advocated here the following described species may be assigned to the genus: *A. asiatica* Mansuy, 1920; *B. granulatus* (Weber, 1948); *P. tellecheai* (Rusconi, 1951); *B. kantsingensis* Chang and Fan, 1960; *A.? borealis* Whittington, 1963; *M. perplexa* Bates, 1968; *A.? insulana* Dean,

1973; and *A? guizhouensis* Yin, 1978. North American and European occurrences seem to be confined to Ordovician volcanic islands, but the Asiatic and southern hemisphere occurrences are apparently in normal platform facies.

Annamitella strigifrons sp. nov.

Plate 38; text-fig. 5

Diagnosis. *Annamitella* species with granulate surface sculpture. Anterior border, incorporated into glabella, forming a wide anterior wall on cranidium, carrying raised lines. Palpebral lobes very long, anterior limit at or in front of 2P glabellar furrow. Pygidium with seven or eight axial rings, and distinct, narrow convex border. Genal spines reduced to stub on large free cheeks.

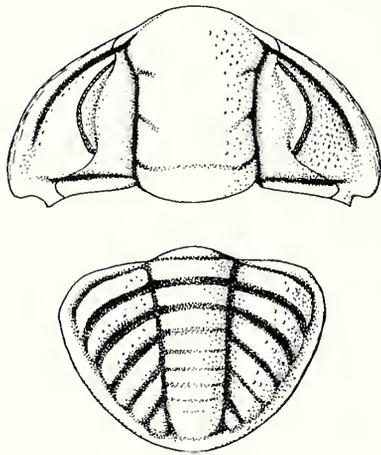
Derivation of name. Latin *strigifrons*, 'ridged-front'.

Holotype. Largely exfoliated cranidium, CPC 22642, from loc 071/4.

Other material. Cranidia, CPC 22643–22645, 22775, 22776; librigenae, CPC 22646–22648, 22777; pygidia, CPC 22649–22652, 22778–22782.

Occurrence. Lower part of Nora Formation, locs. 071/4, 126/3.

Description. Most of the material is stripped of exoskeleton, but enough remains to describe the dorsal surface of this species. The cuticle is very thick and the internal mould retains little trace of the surface details. Since most other species of *Annamitella* have been described from exfoliated material it is evident that many of the salient details are not known from these. All furrows internally are deeper and wider.



TEXT-FIG. 5. *Annamitella strigifrons* sp. nov. Reconstruction of cephalon and pygidium, about $\times 2$.

EXPLANATION OF PLATE 38

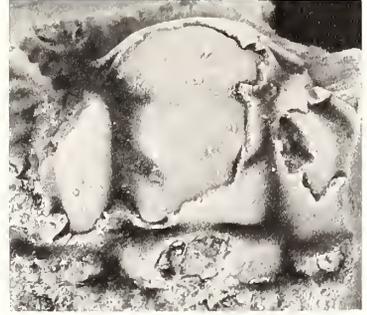
Figs. 1–15. *Annamitella strigifrons* sp. nov. Loc. 071/4 (1–13) and loc. 126/3 (14, 15). 1, 2, CPC 22643, cranidium retaining cuticle but damaged posteriorly; dorsal (1) and anterior (2) views to show incorporation of border into frontal lobe of glabella, $\times 6$. 3, 5, CPC 22642, holotype, well-preserved, but largely exfoliated cranidium in dorsal (3) and anterior (5) views, $\times 6$. 4, CPC 22644, typically preserved internal mould of cranidium, $\times 5$. 6, CPC 22646, testate free cheek with ridges as well as tubercles, tilted forwards to show posterior margin, $\times 6$. 7, CPC 22645, small cranidium, internal mould, $\times 7$. 8, CPC 22647, small free cheek, internal mould showing genal spine, $\times 7$. 9, 10, CPC 22648, well-preserved free cheek in dorsal (9) and anterior (10) views, the latter showing notch in border, $\times 7$. 11, CPC 22649, lateral view of internal mould of pygidium, $\times 6$. 12, CPC 22650, small pygidium, $\times 8$. 13, CPC 22651, pygidium largely retaining cuticle, $\times 6$. 14, 15, CPC 22652, typical internal mould preservation of pygidium; dorsal view (14), and latex cast (15) from second specimen on same rock piece photographed from anterior end to show doublure and pair of prominent prongs proving relationship with pagodiids, $\times 6$.



1



2



3



4



5



6



7



8



9



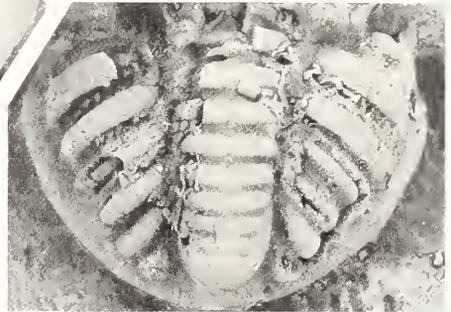
11



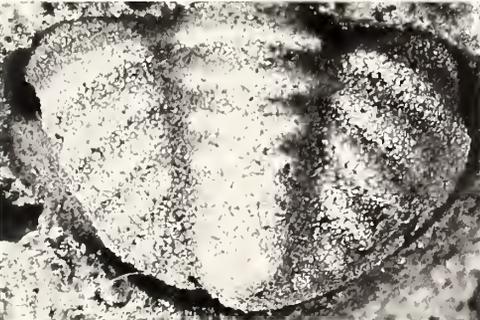
10



12



13



14



15

Cranidium of sagittal length about three-quarters maximum width across posterior margin. Glabella of relatively low transverse convexity, not projecting above level of intraocular cheeks, sloping downwards steeply over anterior half, width at mid-length a little over half maximum sagittal length (dorsal view). Glabella tapers forwards gently, to minimum width at 2P glabellar furrows, with frontal lobe expanding in width more rapidly towards anterolateral corners; front margin broadly rounded about mid-line. Deep occipital furrow, deepest laterally and gently forward-arched medially, so that the occipital ring correspondingly widens medially. Two pairs of glabellar furrows, both deep, short, and straight to very gently curved; 1P opposite mid-length of palpebral lobes, steeply inward-backward inclined, 2P about halfway between 1P and anterior border (exsag.), transverse to slightly backward inclined. No trace of 3P furrow on larger crania, but a small cranidium (Pl. 38, fig. 7) shows a faint pair of dimples which may be the vestiges of 3P. The small cranidium also has a narrower glabella with less taper posteriorly. Axial furrows are hugely deepened at the anterolateral corners of the glabella to form a pair of stout, ventrally-directed apodemes which presumably articulated with the wings of the hypostoma. The anterior cranial border is defined immediately in front of these pits, where it is narrow (exsag.) and ridge-like. Adaxially the border merges with the front of the glabella, and the furrow defining it becomes obsolete quite rapidly. The course of the border is, however, revealed by the ridges that cover its outward-facing surface (Pl. 38, fig. 2); one specimen shows a slight median dip in the height of the border.

Preocular cheeks steeply downward sloping, narrow (tr.) and convex. Gently arcuate palpebral lobe extremely large, forward end closest to glabella, opposite or slightly in advance of outer end of glabellar furrow 2P, posterior end at occipital furrow. Palpebral furrow deep, broadly outward-bowed, outlining a convex, relatively narrow palpebral rim. Cheeks inside palpebral lobes are somewhat inflated. Postocular cheek triangular, width (tr.) about two-thirds that of occipital ring, with deep transverse border furrow, and narrow, convex posterior border which widens laterally. Sutures diverge at a high angle behind palpebral lobes; anterior divergence slight, subparallel with anterior expansion of frontal glabellar lobe; they then appear to converge across downward slope of border before running across edge of border to meet at mid-line. Dean (1973, pl. 7, fig. 8) seems to have incorrectly interpreted the steep border as a rostral plate.

Surface sculpture on glabella and occipital ring of dense and posteriorly somewhat flat-topped tubercles, stopping abruptly at fine elevated ridges on vertical part of border. Free cheek with outline in dorsal view almost a quarter circle, genal fields broadly convex. Genal spine reduced to small stub, but still present on small cheeks (Pl. 38, fig. 8). Lateral border furrow exceedingly deep and narrow anteriorly, but shallowing abruptly and dying out near genal angle. Major part of lateral border a steep, outward-facing 'wall' continuous with that on cranidium, excavated by a deep notch at about mid-length. This notch received a prong on the pygidial doublure during enrolment, a co-adaptive device for this species. Exterior to the notch the border is less steep. Posterior border carries a broad, backward-directed projection of about the same dimensions as the genal spine remnant; presumably this was connected with the anterolateral articulation of the first thoracic segment. Eyes not preserved; beneath the eye there is a deep, smooth groove. Sculpture on genal fields tuberculate like glabella. One specimen has some of the tubercles carried on low ridges (Pl. 38, fig. 6); we incline to the view that this is an intraspecific variant, particularly as there is a tendency on the other cuticulate specimen for the tubercles to form lines, and the cheeks agree in all other respects.

Pygidium with maximum width near anterior margin, 1.3-1.4 times sagittal length including half-ring. Width of axis at anterior margin equal to, or slightly exceeding, that of adjacent pleural field plus border. Axis tapers initially very gently, becoming parallel-sided at fourth or fifth axial ring. Up to eight axial rings are present, which become only slightly narrower (sag.) backwards, of which the first four or five are clearly defined, the seventh and particularly the eighth (which is not discernible on some internal moulds) poorly so. Small rounded terminal piece. Axis extends to border to which it slopes down almost vertically. Pleural fields broadly convex (tr.). Pleural ribs flat-topped on exterior surface, separated by deep furrows of about half their width; on internal moulds the dimensions are reversed, with furrows exceeding width of more rounded ribs. Six pairs of such ribs, the last developed as triangular nodes adjacent to the terminal piece of axis. Border of same width as axial rings, continuous around posterior perimeter, gently convex. Steeply downsloping triangular facets less than half width of anterior margin. Pygidial doublure (Pl. 38, fig. 15) steeply reflexed inside border and narrowing a little medially. Anterolateral edges carry a pair of prominent, ventrally projecting prongs, visible as pits in the external mould, which obviously served to engage with the notches in the cephalic border during enrolment. Exterior to the prong there is a slight groove which probably received the lateral edge of the median part of cephalic border. Small pygidium (Pl. 38, fig. 13) is slightly longer, and shows only seven axial rings, with a longer terminal piece on the axis.

Discussion. No other species of *Annamitella* is preserved as well as *A. strigifrons*, and comparisons are generally difficult, although Dean (1973) showed that the exterior surface of *A. insulana* (Arenig-

Llanvirn, Newfoundland) was tuberculate, and with a comparable cranial border ('rostral plate' of Dean 1973, pl. 7, fig. 8). *A. insulana* is otherwise difficult to compare, being greatly distorted. However, the palpebral lobe is assuredly shorter, and there is a genal spine in the adult of this species. The type species (Mansuy 1920, pl. 2, figs. 7a-k) has a longer frontal glabellar lobe (more like our immature specimen), the pygidial border appears to be much reduced, and there are apparently no more than six axial rings. *A. borealis* Whittington, 1963 apparently lacks tubercles externally, has the 2P glabellar furrow effaced, a narrower cephalic border, genal spines, and fewer pygidial segments defined. *A? guizhouensis* Yin, 1978 also has large eyes, but has a distinct 3P glabellar furrow, and the pygidium has only four pairs of ribs. *A. kantsingensis* (Chang and Fan 1960, pl. 5, figs. 9-12) includes granulate cranidia, but with the glabella expanding uniformly forwards, the one pygidium (ibid., fig. 11) with a much broader, flattened border than in *A. strigifrons*. The latter character also distinguishes *A. monensis* Bates, 1968 which additionally has a much narrower cranial border, defined faintly across the mid-part of the glabella. The pygidial proportions of *A. tellecheai* (Harrington and Leanza, 1957) are closely similar to the Australian species; cranial differences include the probable presence of a 3P glabellar furrow, a (?) narrow cranial border (ibid., fig. 59, 7), and smaller palpebral lobes that fall short of the 2P glabellar furrow. The closest species to *A. strigifrons* is *A. granulata* from the Karakansk Formation of Kazakhstan (Keller and Lisogor 1954, pl. 1, figs. 1-7; Chugaeva 1958, pl. 1, figs. 1-3). This species has eyes as large as *A. strigifrons*, and seems to lack genal spines. Posterior forward taper of the glabella (adjacent to the IP lobe) is very strong on the Kazakhstan species, however, and there are only four fully developed pleural ribs on the pygidium, the fifth pair being represented by triangular remnants, as is the sixth pair on *A. strigifrons*.

The very wide dispersal of a whole suite of closely similar species may lead one to wonder whether this genus had pelagic habits. Curiously, *Annamitella* does not seem to have penetrated into the platform carbonates of either North America or north-east Siberia. It seems to be associated particularly with clastic facies, as it is in Australia, and if this is the case then it must have spent much of its life feeding near the bottom; but its dispersal remains wider than that of any other genus in the Nora Formation apart from the truly pelagic *Carolinites*.

Annamitella brachyops sp. nov.

Plate 45, figs. 15-17

Diagnosis. *Annamitella* with short (exsag.) and highly curved palpebral lobes; glabella parallel-sided and broadly rounded in front; IP glabella furrows gently curved. Sculpture of granules.

Derivation of name. Greek *brachyops*, 'short-eyed'.

Holotype. Cranidium, CPC 22772, from loc. 308/1.

Material. Cranidia, CPC 22773, 22783-22785; pygidia, CPC 22774, 22786-22788; small librigena, CPC 22789.

Occurrence. Upper part of Nora Formation, locs. 158/4, 308/1.

Discussion. This second species of *Annamitella* differs in several features from *A. strigifrons*: (1) the glabella is parallel-sided, rather than expanding at the frontal glabellar lobe which has a nearly semicircular outline in *A. brachyops*; (2) glabellar furrows, especially IP, are more transverse and gently curved in *A. brachyops*; (3) palpebral lobes are less than one-third (exsag.) length of whole cranidium in dorsal view, compared with one-half or more in *A. strigifrons*; (4) surface sculpture (but only seen on one external) apparently of rather discrete, fine granules. The palpebral lobes are nearly semicircular in *A. brachyops*. This difference makes the cranidium of *A. brachyops* relatively wide compared with that of *A. strigifrons*, width across palpebral lobes 1.4 to 1.5 times sagittal length, compared with 1.1 to 1.3 times in the latter. Pygidia of the two species are closely similar; posterior border on *A. brachyops* may be slightly wider laterally, and only five pleural ribs are clearly developed.

Of the species of *Annamitella* listed above only two have short palpebral lobes like *A. brachyops*:

these are *A. (Proetiella) tellecheai* Harrington and Leanza, 1957, and the material of *A. ('Bathyriscops') granulata* illustrated by Weber (1948) and Chugaeva (1958). The type material in Weber (1948) of the latter has a long, narrow glabella with a strongly curved front margin, and the 1P glabellar furrow is certainly more oblique. The cranidium illustrated by Chugaeva (1958) from the Kopalin Formation in Kazakhstan, of late Arenig to Llanvirn age (Fortey 1975, p. 31), is extremely close to the Australian specimens, particularly with regard to the curved palpebral lobe symmetrically disposed about 1P, and may be conspecific. The Argentine species *A. macrophthalma* is also similar, and apparently granulate (Harrington and Leanza 1957, fig. 59, 7 bottom right), and really differs only in the distinctly truncate forward margin of the glabella, and the straight course of the 1P glabellar furrow.

Family ASAPHIDAE Burmeister, 1843
Subfamily ASAPHINAE Burmeister, 1843
Genus *Norasaphus* gen. nov.

Diagnosis. Asaphine trilobites with tuberculate or smooth dorsal surfaces. 1P glabellar furrows excavated as deep pits, or uniting across glabella to cut off basal glabellar lobe. Frontal glabellar lobe may become greatly inflated. Cephalic borders narrow but distinct. Long and narrow genal spines. Eyes small, far back. Cephalic doublure broad under cheeks, greatly narrowing medially, with very deep lateral marginal vincular furrow. Hypostoma with U-shaped notch, and maculae. Pygidium relatively small, with or without narrow border, with two to five axial rings defined. Pygidial pleural (and in some species interpleural) furrows exceptionally deeply incised.

Derivation of name. Combination of Nora (Formation) with *Asaphus*, to which genus the new one is related.

Discussion. This new genus includes the most extraordinary trilobites of the Nora Formation. Looking at the most advanced species (Pl. 40, fig. 1) it is difficult to imagine that such a *Phacops*-like trilobite could be an asaphid at all. In particular, dorsal tuberculation is otherwise unknown (and unlikely) in other asaphids, and its absence was used by Jaanusson (*in* Moore 1959, p. 334) as one of the defining characters of the family. However, we are certain that we have good grounds for assigning the closely related set of species from the Nora Formation to the Asaphidae. The stratigraphically earliest species, *N. (N.) skalis*, is also the most primitive, and, if we are able to ignore the dorsal tuberculation, is in most respects a typical asaphine, with its deep 1P apodemal furrows, well-defined occipital ring, and immediately pre-occipital glabellar tubercle. It may be compared with a genus like *Basiliella* Kobayashi, for example. The hypostoma is conventionally asaphine, as is the lateral vincular furrow on the free cheek. Subsequent evolution of the *Norasaphus* group produces exaggeration of the aberrant features. The 1P glabellar furrows become united across the glabella, producing a transverse furrow which chops off a basal median glabellar lobe. The posterior lobes adjacent to the glabella are discretely defined to become baculae. These advanced characters are the basis of the subgenus *Norasaphus (Norasaphites)*.

Within *Norasaphus (Norasaphites)* one species (*N. monroae*) loses cephalic tuberculation, acquires stalked eyes, and a tendency towards posterior effacement, while *N. (Norasaphites) vesiculosus* takes the peculiarities of *N. (Norasaphus) skalis* further, with very dense tuberculation and exceptional inflation of the frontal glabellar lobe, which in many specimens overhangs the anterior border, and highly incised furrows in all parts. This species is furthest removed from conventional asaphids, and yet we presume that all these profound anatomical modifications took place within the span of deposition of the Nora Formation, only a part of the Arenig Series (say about 5 million years). It is an indication of the flexibility of the external skeletal structure of the trilobites that such modifications can occur even in a generally conservative group like the Asaphidae when circumstances permit, and shows that caution is necessary to determine familial affinities in the face of homeomorphic resemblance.

We considered the possibility that the new forms merited subfamilial status. Since *N. (N.) skalis* is clearly an asaphine (*sensu* Fortey 1980a), and the new species taken together are more closely related

to other Asaphinae than to Niobinae or Isotelinae, in a phylogenetic classification they are to be included in the first-named subfamily, of which they are an extraordinary and probably short-lived branch.

What circumstances may be invoked to explain their unique modifications? Most inshore asaphids are the most highly effaced of the group, and their cuticle is not exceptionally thick (see, for example, *Isotelooides* in Fortey 1979). By contrast *Norasaphus* has a very thick cuticle (Pl. 39, fig. 1), but occurs with isotelines which are not unusual in this regard. In other shallow-water faunas of about the same age, for example the St. George (Catoche Formation) fauna of western Newfoundland, smooth isotelines occur with other trilobites with tumid glabellar frontal lobes, elevated eyes far back, thick cuticles, and strong tuberculate sculpture. In the St. George, the closest trilobite is *Petigurus* (re-described by Fortey 1979), an anomalous bathyurid. *Petigurus* also has a pygidium with strong interpleural furrows, and a narrow border, superficially like that of *Norasaphus*. It is unlikely to be coincidence that both *Norasaphus* and *Petigurus* are convergent with *Phacops*, which was also adapted to carbonate facies of epeiric seas, in the Devonian. Phacopid convergence with *Norasaphus* extends even to pygidial details: the pygidium of *N. monrocae* is strikingly like that of *Eophacops*. We term this repeated morphological type the *phacomorph* design. Tubercles may have been partly concerned with strengthening the cuticle, but those of some of the phacopids have sophisticated internal structures ('pseudo-tubercles' of Miller 1976) which might argue for a more specific function. Eldredge (1971) has suggested that phacopids 'relied more heavily on labral secretion than appendage manipulation for ingestion' of food, which he associated with an oesophageal expansion housed beneath the inflated frontal glabellar lobe, like that so conspicuous on *N. (Norasaphites) vesiculosus*. The basal transglabellar furrow in phacopids and *Norasaphus (Norasaphites)* was presumably connected with the insertion of muscles for a powerful posterior appendage pair.

Whatever the functional explanation of phacomorph design, it was obviously one which could arise from different phylogenetic sources at different times, and was associated with inshore, or at least shallow-water carbonate habitats. In the case of midcontinent faunas, and both the St. George in Newfoundland and the Nora Formation in central Australia are typical examples, there seem to have been a limited number of potential stocks from which phacomorphs could be derived. We assume that the opportunity to occupy the phacomorph niche (or niches) was taken by the asaphids in Australia and the bathyurids in Newfoundland; in both cases their tenure of the niche was short-lived. The morphological distance travelled in a comparatively short time was considerable in both cases, which may relate to theories that the rates of evolution of inshore trilobites in warm climates were relatively rapid (Eldredge 1974; Fortey 1980*b*).

Subgenus *Norasaphus* subgen. nov.

Type species. N. (N.) skalis sp. nov.

Diagnosis. Subgenus of *Norasaphus* with tuberculate sculpture: glabellar furrows of normal asaphine type. Narrow pygidial border.

Norasaphus (Norasaphus) skalis sp. nov.

Plate 39; text-fig. 6

Diagnosis. *Norasaphus (Norasaphus)* is monotypic; diagnosis follows that of subgenus.

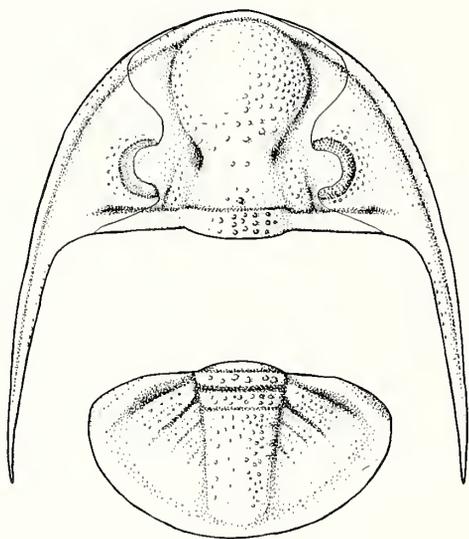
Derivation of name. Greek *skalis*, a hoe or mattock, referring to the shape of the anterior border.

Holotype. Cranidium, CPC 22653, from red limestones near base of Nora Formation, loc. 071/4.

Other material. Cranidia, CPC 22654-22660, 22790-22793; librigenae, CPC 22664, 22665, 22801, 22802; hypostomata, CPC 22666, 22667, 22803; pygidia, CPC 22661-22663, 22794-22800.

Occurrence. Numerous in lower Nora Formation at locs. 071/4, 127/2, 127/4, 127/12, 127/15.

Description. This species is known from well-preserved material in limestone, preserving details of the external cuticular surface. Cranidia have maximum width at posterior margin, only slightly greater than width across palpebral lobes, and about one and a half times maximum glabellar width at frontal lobe. Sagittal cranial length about equal to maximum width. Glabella with maximum convexity across frontal lobe, minimum convexity at median constriction. Frontal lobe broadly pear-shaped, well-defined all round, posterior part enclosed by axial furrows which diverge forwards to enclose an angle of 50–70 degrees. These axial furrows continue backwards to form powerful, broad, deepened 1P apodemes. Axial furrows again shallow posteriorly to continue as depressions between basal glabellar lobe and inflated genal lobes to meet lateral end of occipital furrow. Basal genal lobes fusiform, inclined inwards-forwards, and greatly inflated, extending forwards to a point near anterior edge of palpebral lobes. These basal lobes are mostly outside the area subtended by the occipital ring, and they are of extraglabellar origin, being produced by an adaxial inflation of the genal region. Occipital furrow transverse, and especially deep at either side; occipital ring of uniform width (sag., exsag.) deeply downcurved laterally to meet posterior border. Presumed axial furrows passing on outside of basal lateral glabellar lobes, diverging backwards, very shallow anteriorly and deepening to border furrow. Strong glabellar tubercle in front of occipital furrow. Palpebral lobes elevated to about the level of frontal glabellar lobe, small (about one-sixth glabellar length) and close to axial furrows, strongly curved to slightly more than a semicircle. Apparently narrow palpebral rims. Postocular cheeks acutely triangular, transverse width about half that of occipital ring, posterior border narrow (exsag.) and highly convex, as defined by a deep border furrow. Preocular sutural divergence somewhat exceeds that of anterior section of axial furrows so that the downward-sloping preocular cheeks, which are very narrow (tr.) in front of eyes, increase gradually in transverse width forwards. Sutures converge across anterior border, presumably running marginally to meet at mid-line. Border abruptly breaks downward slope of preocular cheeks, being flat to slightly concave with rounded rim. Anterior edges of border converge towards mid-line at a large obtuse angle, but rounded medially. Border furrow broad and diffuse; preglabellar field lacking.



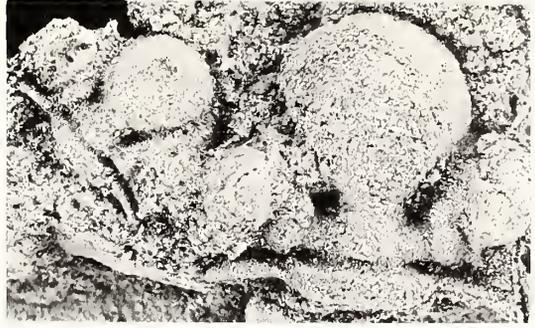
TEXT-FIG. 6. *Norasaphus (Norasaphus) skalis* gen. et sp. nov. Reconstruction of cephalon and pygidium, $\times 1$.

EXPLANATION OF PLATE 39

Figs. 1–8. *Norasaphus (Norasaphus) skalis* gen. et sp. nov. Lower part of Nora Formation, loc. 071/4 (1, 3–8) and loc. 127/12 (2). 1, CPC 22653, holotype, well-preserved but slightly incomplete cranium, $\times 6$. 2, CPC 22654, 22655, latex cast taken from external mould of two crania, $\times 4$. 3, CPC 22664 free cheek, plan view partly exfoliated, $\times 4$. 4, CPC 22656, latex cast from small cranium from same bed as holotype, $\times 6$. 5, CPC 22661, incomplete large pygidium, showing surface sculpture, $\times 4$. 6, CPC 22662, small pygidium, excavated to doublure on right, $\times 6$. 7, CPC 22666, hypostoma, exfoliated, $\times 6$. 8, CPC 22663, large, exfoliated pygidium; dorsal surface sculpture is not reflected on the internal surface, and more axial rings are visible, $\times 3$.



1



2



3



4



5



6



7



8

Surface sculpture of tubercles and granules on glabella, occipital ring, and anterior rim. Tubercles sparse but large on posterior median lobe of glabella and occipital ring; these large tubercles reflected also on internal moulds, but pre-occipital glabellar tubercle exceeds all in prominence. Finer tubercles on frontal glabellar lobe, basal lobes, and fine granules on forward part of anterior border; these not reflected on internal moulds.

Free cheeks with long, slightly curved genal spine. Genal field convex (exsag.) with zone of tubercles surrounding base of eye but not extending anteriorly or laterally. Deep posterior border furrow narrows abruptly abaxially over region corresponding to inner margin of doublure. Lateral border continues from cranidium narrowing round periphery of cheek and passing on to genal spine, which thereby carries a groove down its exterior surface. Eye strip-like, slightly elevated from cheek on smooth socle. Doublure broad beneath genal fields, recurved beneath cheek well beyond border but narrowing as the suture is approached to form a comparatively narrow band extending anteriorly beneath cranial border to median suture. Deep vincular furrow about one-third length of lateral border on cheek, bounded by ridges on doublure. Terrace lines on ventral doublural surface not reflected on its dorsal surface.

Hypostomata of type consistently found with *Norasaphus*, and therefore associated with some confidence. Conventional asaphine type, similar to that of *Basilicus*, for example, with subcircular middle body, ill-defined, carrying pair of forward-inclined, smooth maculae. Lateral borders wide, with maximum width at about half hypostomal notch with shape like inverted U. Terrace lines relatively fine and transverse on middle body, parallel to margins of borders.

Pygidium with sagittal length about twice maximum width, pleural fields convex, with steep downward slope to border. Axis occupying less than one-third pygidial width at anterior margin, and extending to posterior border, with rounded tip; gentle axial taper encloses angle of no more than 20 degrees. On specimens preserving cuticle two axial rings are clearly defined, separated by deep ring furrow. Ring furrows become faint after that defining second axial ring, definition of third and fourth rings poor, principally on flanks of axis. Internal moulds show up to seven faint rings. Articulating half-ring of similar (sag.) length as first axial ring. Dorsal surface shows four pairs of pleural furrows, the first of which extends to the border, the posterior three progressively shorter and further removed from border. Interpleural furrows divide the first three ribs just anterior to centre line, much shallower than pleural furrows, and not reflected on internal mould. Broad, triangular facet about twice transverse width of border. Border gently downsloping laterally, becoming progressively narrower and more steeply sloping posteriorly. Definition of border sharper on small specimens. Sculpture, mostly on axis and faint on pleural ribs, tubercles like those on glabella; few faint scalloped terrace lines on border.

Discussion. This is the only species attributed to *Norasaphus* (*Norasaphus*). Small cranidia show that the 'basal glabellar lobes' originate from an extra-glabellar position adjacent to the base of the glabella (Pl. 39, fig. 2). With increase in size they tend to migrate adaxially. In many Asaphinae the posterior part of the glabella tends to effacement, and in these circumstances it can be difficult to distinguish the 'glabellar' from the genal areas. The distinguishing asaphine feature appears to be the deepening of the axial furrows at what we have termed the IP position at the rear end of the frontal lobe, a feature which remains constant whatever the degree of effacement on the rest of the cranidium.

Subgenus *Norasaphites* subgen. nov.

Type species. *N. (Norasaphites) monroae* sp. nov.

Diagnosis. *Norasaphus* species with smooth or tuberculate exoskeleton. IP united across glabella to form definite transglabellar furrow. Pygidial border absent.

Derivation of name. Diminutive of *Norasaphus*.

Species included. *N. (Norasaphites) monroae* sp. nov., *N. (N.) vesiculosus* sp. nov.

Norasaphus (Norasaphites) monroae sp. nov.

Plate 40, figs. 1-4, 6-10; text-fig. 7

1980 Asaphid gen. nov.; Fortey, p. 256, fig. 2.

Diagnosis. *Norasaphus (Norasaphites)* species lacking surface sculpture; frontal glabellar lobe not greatly inflated; eyes strongly stalked. Pygidium tending to effacement on posterior part of axis and pleural lobes, with only three pairs of pleural furrows.

Derivation of name. Dedicated to Marilyn Monroe.

Holotype. Cranidium, CPC 22668, from loc. 158/9.

Other material. Cranidia, CPC 22669, 22804–22822; pygidia, CPC 22670–22672, 22833–22839; librigenae, CPC 22673, 22674; hypostomata, CPC 22675, 22676, 22843.

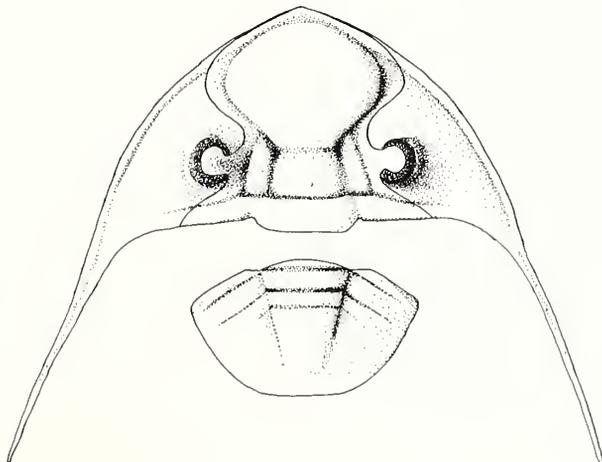
Occurrence. Upper part of Nora Formation, locs. 015/6, 122/1?, 158/4, 158/8, 158/9, 158/13, 158/15, 308/1.

Description. Cranidium of relatively low transverse convexity compared with other species of *Norasaphus*. Glabella well-defined, hardly inflated, width at narrow 'neck' slightly less than half maximum width at anterolateral corners. The narrowest part of glabella lies at about one-quarter length of pre-occipital glabella. Deep axial furrows converge forward gently to this point, in front of which they diverge markedly around forward lobe of glabella, enclosing an angle of 75–80 degrees. Front margin of glabella broadly rounded about mid-line. Transglabellar furrow straight, less deep than occipital furrow. Occipital ring not as wide (tr.) as widest part of glabella, and of length (sag.) only slightly less than that of posterior glabellar lobe. Axial furrows are shallower where defining lateral ends of occipital ring. Occipital furrow narrow, deep, and straight transverse. Inflated bacculae three times longer than wide, inclined gently inwards until cut off by forward expansion of glabella at a point a little in front of the transglabellar furrow. Palpebral lobes greatly elevated above level of rest of cranidium, such that the intraocular cheek is nearly vertical, and sited at about mid-cranidial length. Narrow (tr.) preocular cheeks also inward-inclined, with outline closely following that of forward glabella lobe. Anterior border of cranidium acuminate, almost flat, wider medially, and at lateral edges. Posterior cranidial border convex, pointed, extending laterally to a point just beyond that of anterior cranidial border. External surface of cranidium lacking tubercles. Small cranidia (sag. length 0.5 cm or less) differ from the larger ones in having less marked expansion of the frontal glabellar lobe, and the pre- and postocular sutures are also less divergent.

Free cheek generally like that of *N. (N.) skalis*, but lateral border furrow shallower, and the genal spine is much shorter, pointed, not curved. The posterior border furrow becomes completely effaced as it approaches the doublure. The eye is borne on a distinct stalk (Pl. 40, fig. 6), such that it must have projected above the level of the rest of the trilobite.

Hypostoma rather flat, anterior width (tr.) of middle body about two-thirds maximum width across broad wings. Lateral margins of wings converge backwards to almost pointed tips separated by wide, shallow fork. Middle body not well-defined posteriorly, tapering to forward edge of fork, with pairs of shallow maculae.

Pygidium about two-thirds as long as wide, convex. Axis occupies more than one-third of total pygidial width anteriorly, tapering posteriorly such that the axial furrows enclose an angle of 25–30 degrees, at the same time becoming less convex so that its tip is not clearly defined from the postaxial field. Only two narrow axial rings are defined across the mid-part of the axis, and the second of these is faint. Third and fourth rings faintly indicated laterally. Half-ring of about same width (sag.) as first axial ring. Pleural furrows relatively narrow, first two pairs almost reaching margin, third usually extending no more than half-way across pleural fields (very faint fourth pair suggested on some specimens). Broad facets extend close to axis. Small pygidia relatively more transverse, with axis better defined.



TEXT-FIG. 7. *Norasaphus (Norasaphites) monroecae* gen. et sp. nov. Reconstruction of cephalon and pygidium, $\times 1.5$.

Discussion. This species is distinguished from *N. (Norasaphites) vesiculosus* below. The relatively low convexity, strongly stalked eyes and lack of surface sculpture are features which contrast with *N. (N.) skalis* stratigraphically below it; if we are correct in proposing a derivation of *N. (Norasaphites) monroae* from this more generalized form, there should be a functional explanation for the changes. One suggestion is that *N. monroae* was adapted to shallow infaunal life. The relative smoothness, and loss of convexity on the frontal glabellar lobe would have reduced sediment resistance during burial, and the high-perched eyes would have protruded above the sediment surface even when the rest of the animal was completely concealed. By contrast, *N. (Norasaphites) vesiculosus* carries the morphological peculiarities (tuberculation, glabellar inflation) of *N. (Norasaphus) skalis* even further and it was presumably a surface dweller. So in this case the speciation events producing *monroae* on the one hand and *vesiculosus* on the other were by niche partitioning, presumably operating sympatrically or parapatrically.

Norasaphus (Norasaphites) vesiculosus sp. nov.

Plate 40, fig. 5; Plate 41; text-fig. 8

1969 *Proetus?* sp.; Gilbert-Tomlinson in Hill *et al.*, pl. O-V, figs. 5, 6.

Diagnosis. *Norasaphus (Norasaphites)* species with tuberculate surface sculpture, frontal glabellar lobe greatly inflated, often overhanging border; eyes not so elevated as *N. (Norasaphites) monroae*. Pygidium with three or four strong pleural ribs.

Derivation of name. Latin *vesiculosus*, 'covered in blisters'.

Holotype. Cranidium CPC 22677, from loc. 158/8-9.

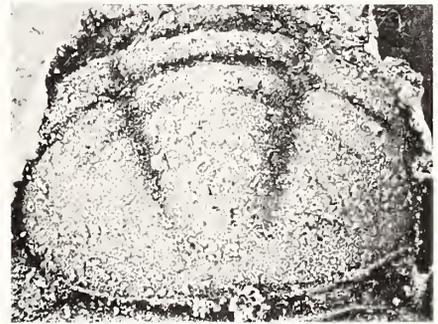
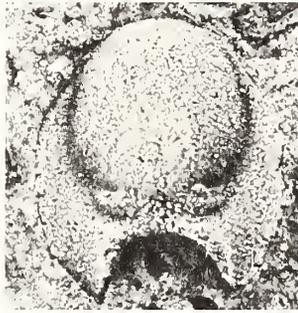
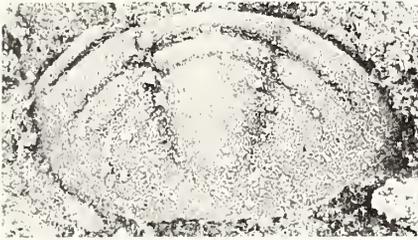
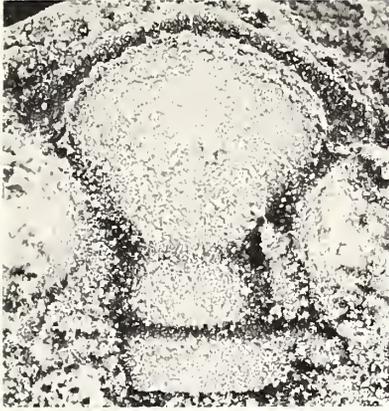
Other material. Cranidia, CPC 22678-22685, 22844-22857; pygidia, CPC 22686, 22687, 22858-22862; librigenae, CPC 22688, 22689, 22863-22865; hypostomata, CPC 22690, 22866.

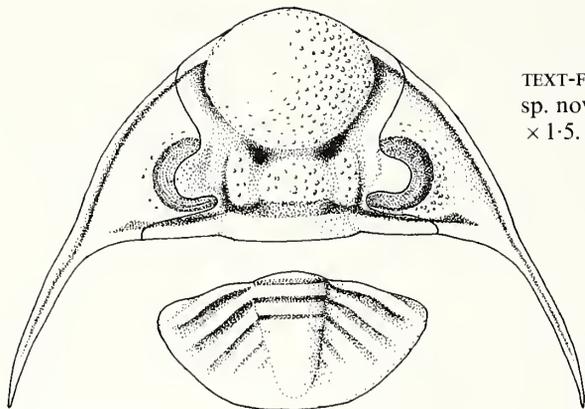
Occurrence. Higher parts of Nora Formation, locs. 015/6, 122/1, 122/4, 126/1-7, 126/11, 139/4, 156/1, 158/4, 158/8, 158/9, 158/10, 308/1.

Discussion. This species is best discussed briefly in relation to *N. (N.) monroae*, from which it differs in the following features: (1) The frontal lobe of the glabella is subspherical rather than wedge-shaped. Especially in stratigraphically later examples this lobe becomes enormously inflated, often becoming extended into an almost conical protuberance. The frontal lobe overhangs the cranial border, which becomes very narrow medially, forming a convex rim. (2) The anterior divergence of the facial sutures is lower. (3) The glabella (and adocular part of the free cheek) carries a sculpture of tubercles, which are quite coarse on some specimens; internal moulds are smooth. (4) The bacculae do not slope inwards. (5) The palpebral lobes, although elevated, are not higher than the frontal glabellar lobe; the eye is not stalked. (6) The free cheek is acutely triangular, with a distinct, narrow lateral border, the border furrow continuing on to the genal spine as a groove. (7) The pygidium is similar to that of *N. (N.) monroae* in lacking a border, and only two axial rings are clearly defined, the posterior part of the axis being smooth except for faint lateral indications of two or three segments.

EXPLANATION OF PLATE 40

Figs. 1-4, 6-10. *Norasaphus (Norasaphites) monroae* subgen. et sp. nov. Loc. 158/9 (1, 2, 4, 6, 7, 9, 10), loc. 308/1 (3), and loc. 015/6 (8). 1, 2, 10, CPC 22668, latex cast from holotype, external mould of cranidium in dorsal (1), anterior (2), and oblique (10) views, $\times 6$. 3, CPC 22669, internal mould of cranidium, $\times 4$. 4, CPC 22670, latex cast from pygidium, external mould, $\times 6$. 6, CPC 22674, latex cast from fragmentary free cheek, to show stalked eye, $\times 6$. 7, CPC 22675, internal mould of hypostoma probably belonging to this species, $\times 6$. 8, CPC 22673, internal mould of free cheek, $\times 2$. 9, CPC 22671, latex cast of external mould of pygidium, $\times 6$. Fig. 5. *N. (N.) vesiculosus* subgen. et sp. nov. CPC 22690, loc. 158, internal mould of hypostoma, $\times 6$. Fig. 11. Asaphid gen. et sp. indet. CPC 22770, lowest Nora Formation, loc. 071/4, pygidium, $\times 6$.





TEXT-FIG. 8. *Norasaphus (Norasaphites) vesiculosus* gen. et sp. nov. Reconstruction of cephalon and pygidium, about $\times 1.5$.

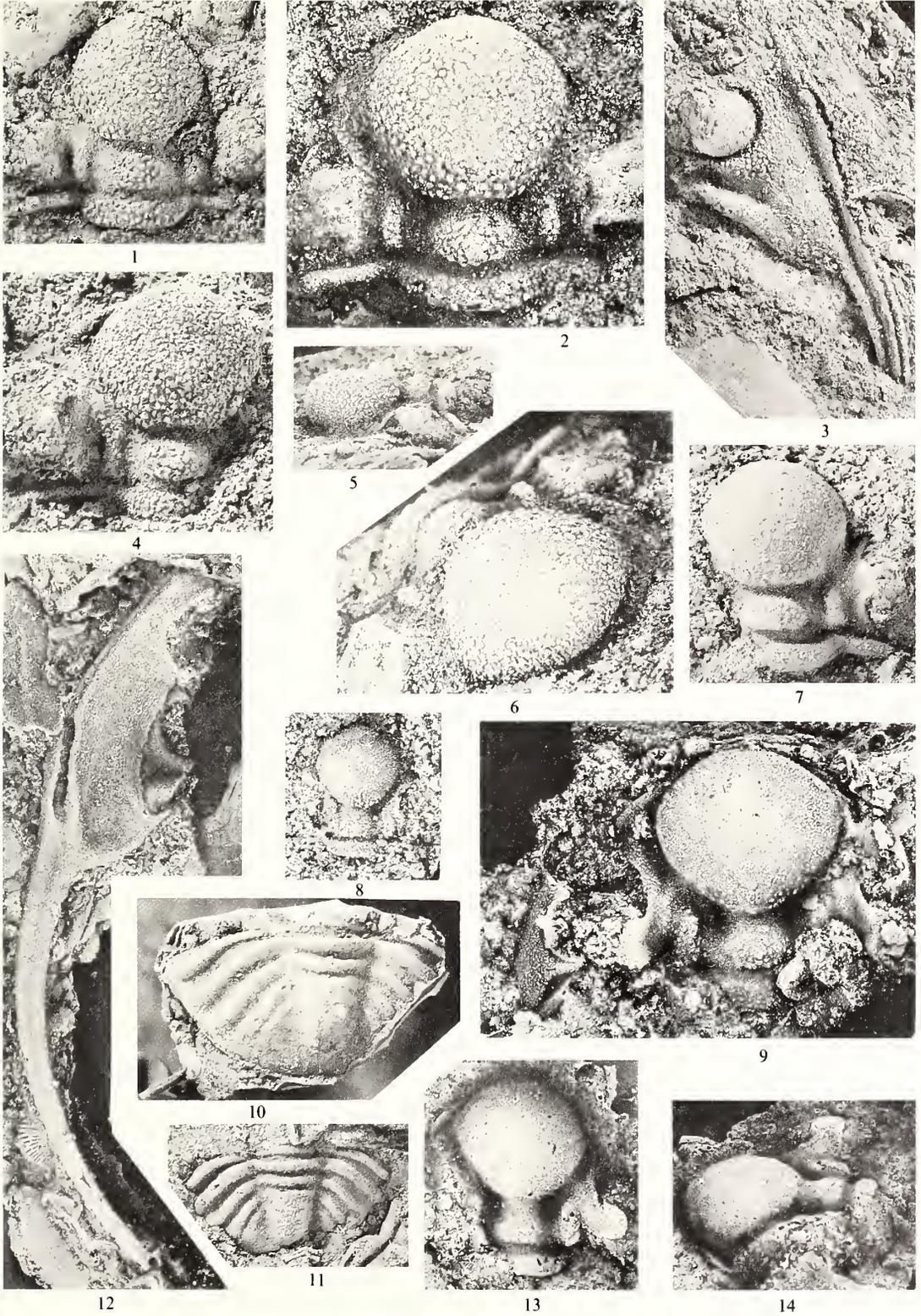
However, the tip of the axis is defined close to the posterior margin, and the pleural furrows are broad and deep, with the first three pairs running close to the margin and the fourth to about two-thirds the extent of the anterior pairs. There remains only a small, smooth triangular area adjacent to the posterior part of the axis. The areas between the pleural furrows, and between the first pair of furrows and the facets, are elevated into distinct ribs, which die out shortly before the pygidial margin. We have not, however, detected coarse granulation on the pygidial axis.

We admit a great deal of intraspecific variation in our concept of *N. (N.) vesiculosus*. This particularly relates to the development and sculpture of the anterior glabellar lobe. In some specimens this lobe is only about one and a half times the width (tr.) of the posterior glabellar lobe, in others fully twice as wide (Pl. 40, fig. 2); the inflation of the lobe varies also, some specimens becoming almost pointed. The coarseness of the tuberculation is variable: some specimens are coarsely tuberculate all over the glabellar lobes, others grade into fine granulation over the mid-part of the anterior lobe (Pl. 41, fig. 9). The more finely tuberculate form is associated with a free cheek which carries a longer, more curved genal spine than the typical form, which is that shown on the reconstruction in text-fig. 8.

The more inflated form seems to come from higher in the Nora Formation than the granulose form. However, there appears to be every transition between these various morphs and, for this reason, we take a taxonomically conservative view and incorporate them within a single species. The great variability is presumably another indication of the processes of endemic speciation at work, and would repay study with larger populations than we have available.

EXPLANATION OF PLATE 41

Figs. 1-14. *Norasaphus (Norasaphites) vesiculosus* subgen. et sp. nov. All latex casts from external moulds. 1, CPC 22678, loc. 308/1, cranidium of morph with pointed frontal glabellar lobe, $\times 4$. 2, 5, 6, CPC 22677, loc. 158/8-9, holotype in dorsal (2), anterior (5) ($\times 6$), and lateral (6) ($\times 3$) views. 3, CPC 22688, loc. 308/1, free cheek; note sculpture around base of eye, $\times 4$. 4, CPC 22679, loc. 308/1, cranidium of morph with especially expanded (tr.) frontal glabellar lobe, $\times 6$. 7, CPC 22680, loc. 122/4, cranidium of morph with relatively subdued tuberculation, but glabellar proportions like holotype, $\times 3$. 8, CPC 22681, loc. 126/3, small cranidium, $\times 3$. 9, CPC 22682, loc. 126/7, cranidium, with incomplete free cheek on left; this is the morph with expanded frontal lobe (as fig. 4), but with frontal lobe granulate rather than tuberculate, and somewhat elevated palpebral lobes, $\times 3$. 10, CPC 22686, loc. 308/1, pygidium, $\times 2$. 11, CPC 22687, loc. 015/6, incomplete pygidium, showing granulation on terminal piece of axis, $\times 2$. 12, CPC 22689, loc. 126/7, free cheek associated with the sparsely tuberculate morph, same locality; cast taken to show ventral surface with double and vincular notch, $\times 3$. 13, 14, CPC 22683, loc. 126/7, cranidium of sparsely tuberculate morph, dorsal (13) and lateral (14) views, $\times 3$.



FORTEY and SHERGOLD, *Norasaphus* (*Norasaphites*)

Subfamily ISOTELINAE Angelin, 1854

Genus *Fitzroyaspis* Legg, 1976

Type species. Priceaspis (Fitzroyaspis) guppyi Legg, 1976.

Discussion. Effaced asaphids are always a problem to classify, and the new species from the Nora Formation, described below, is no exception. Its few distinctive characters include a well-defined cephalic border, rounded genal angles, large medially placed eyes, and low sutural divergence behind the eyes. The pygidium is characteristically asaphid, but with no particularly distinctive features. Few asaphids have facial sutures that are not highly divergent behind the eyes, and of those with weakly divergent sutures (e.g. *Asaphellus*) most have small eyes and long genal spines. *Isotelus* itself has generally smaller eyes, the cephalic border is ill-defined, and the pygidium is characteristically triangular in outline; any resemblance between this typically North American genus and the Australian form is because of convergence. The same probably applies to such genera as *Anataphrus* and *Homotelus* in which effacement has gone even further; these genera lack defined cranial borders altogether, although the general cranial outline of certain species of *Anataphrus* is like that of our material. Legg (1976) described the type species of *Priceaspis (Fitzroyaspis)* from the early Arenig of the Canning Basin. The general cephalic structure is like our species, especially with regard to the well-defined, but narrow cephalic border. The pygidial border is comparatively poorly defined, a difference we do not consider of generic importance. The major point of difference lies in the more posterior extension of the eyes in *F. guppyi*, with a concomitant high angle of postocular suture divergence, and the presence in that species of distinct posterior border furrows. The cranidium of our species is also somewhat broader in proportion to its length. We regard these differences as of specific significance only, effectively produced by an anterior migration of the eyes compared with *F. guppyi*. A similar 'trend' happens also in *Isotelus* comparing the position of the eyes and sutural form in *I. copenhagenensis* Ross and Shaw (1972, pl. 2, fig. 8) with *I. gigas* Dekay. Legg separated *Fitzroyaspis* as a subgenus of his relatively uneffaced genus *Priceaspis*; with the inclusion of a second species in *Fitzroyaspis* we prefer to accord it full generic status until the phylogenetic relationships of these asaphids can be fully worked out.

Fitzroyaspis irritans sp. nov.

Plate 42, figs. 1-4, 7; text-fig. 9

Diagnosis. Highly effaced *Fitzroyaspis* lacking cephalic posterior border furrows; eyes smaller than in *F. guppyi*; postocular sutures divergent at a low angle; pygidium with border expressed laterally.

Derivation of name. Latin *irritans*, 'irritating', referring to the problem of its generic assignment.

Holotype. Cranidium, CPC 22691, from loc. 158/10.

Other material. Cranidia, CPC 22692, 22867-22878; hypostomata, CPC 22697, 22888; librigenae, CPC 22693, 22694, 22879-22881; pygidia, CPC 22695, 22696, 22882-22887.

Occurrence. Through most of higher Nora Formation, locs. 122/4, 126/7, 158/4, 158/10, 158/15.

EXPLANATION OF PLATE 42

Figs. 1-4, 7. *Fitzroyaspis irritans* sp. nov. Middle to upper Nora Formation. 1, CPC 22697, loc. 158/4, latex cast of hypostoma most probably belonging to this species, $\times 3.5$. 2, CPC 22691, loc. 158/10, latex cast taken from holotype, external mould of cranidium, $\times 2$. 3, CPC 22693, latex cast taken from external mould of free cheek, $\times 2$. 4, CPC 22694, loc. 158/15, free cheek, prepared to show doublure and vincular furrow, $\times 3$. 7, CPC 22695, loc. 126/7, latex cast from external mould of pygidium, $\times 4$.

Figs. 5, 6. *Presbynileus* cf. *P. utahensis* Hintze, 1953. Upper Nora Formation. 5, CPC 22710, loc. 308/1, internal mould of cranidium, $\times 3$. 6, CPC 22712, loc. 158/11, internal mould of pygidium, $\times 3$.



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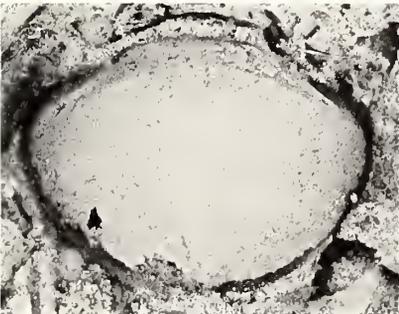
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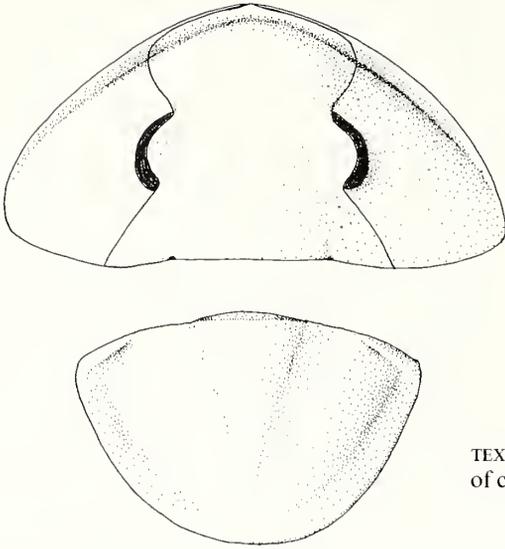
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TEXT-FIG. 9. *Fitzroyaspis irritans* sp. nov. Reconstruction of cephalon and pygidium, $\times 1$.

Description. Cranidium with width across palpebral lobes 0.85 of sagittal length on large cranidia; small cranidia tend to be more elongate. Very low convexity across the axial region suggesting glabella forward-tapering from prominent articulating notches at posterior margin, opposite hind ends of palpebral lobes. Steep downturn around frontal glabellar lobe and in front of palpebral lobes on to virtually flat cranial border, which does not exceed one-eighth (and may be as little as one-tenth) of the total glabellar length at mid-line. Palpebral lobes medially placed, tilted only slightly upwards, and with length (exsag.) one-third glabellar length. Facial sutures distinctly isoteliform, diverging at a low angle (20–40 degrees) in front of the eyes, and at a scarcely higher angle behind the eyes. The gently downsloping, triangular postocular cheeks so defined terminate acutely. Internal moulds show prominent glabellar tubercle (not visible externally) placed at about one-quarter glabellar length. Also some internal moulds show what are probably prominent 1P muscle impressions constricting the glabella shortly in front of the tubercle. Small cranidia of sagittal length 1 cm or less have more divergent sutures in front of and behind the eyes, but the fixed cheeks do not become extended (tr.) in the manner of *F. guppyi*. We tentatively associate a hypostoma (Pl. 42, fig. 1) of typical isoteline type, which does not belong to *Norasaphus*, and is from the same bed in which *F. irritans* is common.

Free cheek somewhat longer (exsag.) than wide in plan view, showing border becoming narrower and feebler towards the broadly rounded genal angle. On doublure vincular furrow runs parallel to border.

Pygidium two-thirds as long as wide, with gently convex pleural fields sloping down to ill-defined, still sloping border, which peters out around tip of axis. Pleural fields unfurrowed. Axis extends to more than two-thirds pygidial length; on the external moulds no ring furrows are visible, but on internal moulds four (?five) rings may be visible, of which only the first two are defined across the mid-part of the axis. Doublure broad, and concave towards outer edge, carrying at least twenty terrace lines which are approximately parallel to the posterior margin peripherally but slope backwards at a much more acute angle to the sagittal line near inner edge of doublure. Lateral tip of doublure sharply downward-flexed.

Discussion. *F. irritans* is distinguished from *F. guppyi* by its smaller eyes and wider cranidium, and by the low angle of divergence of the facial sutures behind the eyes; the pygidial border of the new species is better defined. In addition to the genera discussed above there is a certain resemblance between the cranidium of *F. irritans* and that of *Ptyocephalus*, especially *P. accliva* (Hintze 1953, pl. 15, fig. 2). However, the important features of *Ptyocephalus* are outside the axial region—a compression of the lateral pleural area resulting in laterally truncate free cheeks and pygidium.

Genus *Lycophron* gen. nov.

Type species. *Lycophron rex* sp. nov.

Diagnosis. Large, effaced isotelines with elongate, triangular cephalon and pygidium. Cephalon with

extremely narrow, acute lateral borders. Pygidium usually lacking border altogether. Hypostoma narrow (tr.) anteriorly, with very long fork with pointed tips.

Derivation of name. After the third-century Greek philosopher Lycophron.

Discussion. This genus resembles *Megistaspidella* and *Isotelus*. It is convergent upon both, but we believe that there is no phylogenetic connection. *Megistaspidella* is confined to the Baltic continent in the early middle Ordovician, and is related to the *Megistaspis* plexus of species. Its pointed, unforked hypostoma lies at the opposite morphological extreme among asaphids to that of *Lycophron*, and is sufficient evidence of their separate origins. *Isotelus* includes some species, such as *I. gigas*, which are like *L. rex*. These *Isotelus* species are much younger than the Australian genus. Early representatives of *Isotelus*, such as *I. harrisi* (see Shaw 1968, pl. 22), are quite different, with relatively broad cephalic and pygidial borders, and wide lateral borders on the hypostoma. These in turn are related to the early middle and early Ordovician genera *Stegnopsis* and *Isoteloides* which are unlike *Lycophron* in almost every particular, although they are its North American contemporaries. So in our view *Isotelus* species resembling *Lycophron* were independently derived later in the Ordovician (see also *Lycophron* sp. A below). The hypostoma of the *Isotelus-Isoteloides* group remains generally conservative, with broader borders than in *Lycophron*, and flared tips to the fork. The pygidial border is visible in *Isotelus*. The similarities between *Lycophron*, *Isotelus*, and *Megistaspidella* probably indicate similar life habits in response to a comparable environment: all are found in calcareous, epicratonic sediments.

Species included. *L. rex* sp. nov., *Asaplus howchini* Etheridge, 1894, *L.* sp. A (below).

Lycophron rex sp. nov.

Plate 43, figs. 1–10; text-fig. 10

Diagnosis. As for genus.

Derivation of name. Latin *rex*, 'king', for the largest of the Nora trilobites.

Holotype. Pygidium, CPC 22698, from loc. 126/5.

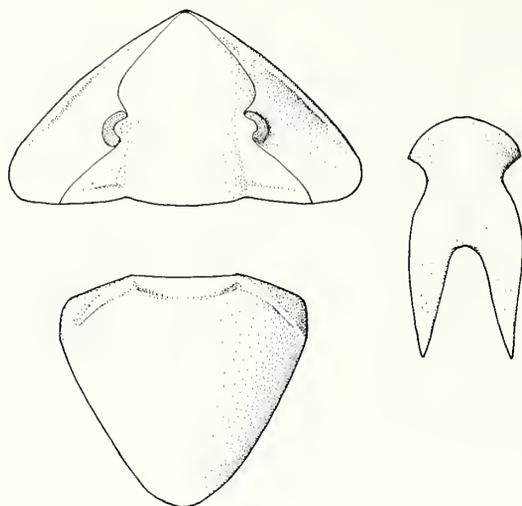
Other material. Cranidium, CPC 22699; librigenae, CPC 22700, 22701, 22889–22891; hypostomata, CPC 22706, 22707, 22897, 22898; pygidia, CPC 22702–22705, 22892–22896.

Occurrence. Ranges throughout the Nora Formation except the basal part: at locs. 118/7, 122/1, 122/3, 126/1, 126/2, 126/3, 126/5, 127/7, 127/12, 152/9, 308/1.

Description. One or two large hypostomata, and pygidial fragments, indicate that this species grew to a considerable size. Most pygidia are 1–2 cm long, and the description is based on material of this size. Pygidia are abundant in the Nora Formation; cranidia are distinctly rare. There does not seem any reason to doubt that the association is correctly made. Disparity between the numbers of pygidia and cranidia preserved is rather common among asaphids; possibly the irregularly shaped cranidium was susceptible to fracture during post-mortem current sorting compared with the compact pygidium.

Cranidium with outline generally like isosceles triangle; relatively long and pointed anterior 'nose' distinctly convex transversely, while there is a gentle downward slope on the posterior fixigenae. Glabella defined by shallow furrows converging forwards to pass well inside palpebral lobes; anterior course of axial furrows not well-marked, but they appear to swing out towards the posterior margin of the frontal cranial lobe. There was probably a faintly defined occipital ring, incompletely preserved on our material. Small palpebral lobes slightly elevated, and in relatively forward position for an asaphid at about mid-cranial length. Acute triangular postocular cheeks defined by sutures which run in a nearly straight course to the posterior margin. Border furrow relatively deep, especially near glabella. Slight tendency towards flattening of anterior, pointed part of cranidium.

Long and acutely triangular free cheeks are assigned to this species, having the eye in the appropriate advanced position, and lacking genal spines. There is a narrow border, having a narrow and steep exterior face, and topped by an acute rim; border furrow at its mid-length, but fading out before the genal angle, and also anteriorly. A sharp vincular notch truncates the outside face of the border near the genal angle, where the border furrow fades out.



TEXT-FIG. 10. *Lycophron rex* gen. et sp. nov.
Reconstruction, $\times 1$.

Hypostoma remarkably long and narrow, looking like a tuning fork. Anterior margin bowed forwards. Front part of hypostoma narrower (tr.) than width at front end of fork. The fork itself is so deep that the prolongations on either side are more than twice, or even three times, as long as wide. Middle body does not seem to be defined on our specimens, the whole of the posterior part of the hypostoma forming an almost flat plane. The large examples, which almost certainly belong to this species, have a broader, less acute fork, and a pair of faint depressions represent the maculae.

Deeply convex (tr.) pygidia are typically triangular, with an acute tip slightly rounded, and with width equal to, or slightly exceeding, the sagittal length. There is no sign of axis or border, although the width of the former at the front margin is indicated by a distinctly defined, fusiform half-ring occupying 0.4 of maximum pygidial width. The broad (tr.) articulating facets are backed by convex half-ribs, and a single pair of deep but narrow pleural furrows which do not extend to the pygidial margin. Doublure narrow for an asaphid, gutter-like. The combination of long, triangular shape, high effacement, yet deep furrows on the anterior segment only makes these pygidia distinctive compared with most asaphids. Some specimens (Pl. 43, fig. 8), from stratigraphically high in the range of the species, are relatively even more elongate and tend towards flattening of the posterior tip of the pygidium. We do not have enough specimens to know whether this is a consistent difference deserving taxonomic recognition. There is no indication of surface sculpture in this species, apart from terrace lines on doublure and hypostoma.

Discussion. Etheridge (1894) described *Asaphus (Megalaspis) howchini* from the MacDonnell Ranges, figuring a large pygidium with attached thoracic segments, very similar to *L. rex* and undoubtedly congeneric. A similar pygidium from the Nora Formation was figured by Gilbert-Tomlinson (*in Hill et al.* 1969, pl. O-V, fig. 4). Etheridge's original specimen is refigured here as text-fig. 11. The pygidial axis is defined, whereas all specimens of *L. rex* are completely effaced. Even small (3 mm long) pygidia

EXPLANATION OF PLATE 43

Figs. 1-10. *Lycophron rex* gen. et sp. nov. Middle to upper Nora Formation. 1, CPC 22700, loc. 118/7, latex cast from free cheek, $\times 3$. 2, 3, CPC 22699, loc. 158/4, cranium in dorsal (2) and lateral (3) views, $\times 2$. 4, CPC 22702, 22703, loc. 126/2, latex cast showing two pygidia, $\times 2$. 5, CPC 22706, latex cast of hypostoma, same bed as holotype, $\times 6$. 6, 10, CPC 22698, loc. 126/5, holotype, latex cast of large pygidium in dorsal (6) and oblique lateral (10) views, $\times 5$. 7, CPC 22704, loc. 127/7, pygidium, relatively short compared with other examples, $\times 10$. 8, CPC 22705, loc. 308/1, pygidium, most elongate form in which the tip shows tendency to become spatulate, $\times 3$. 9, CPC 22701, loc. 158/4, cast from free cheek, $\times 2.5$.
Figs. 11, 12. *Lycophron* sp. A. CPC 22708, lower Nora Formation, loc. 071/4. Pygidium in dorsal (11) and posterior (12) views, $\times 6$.



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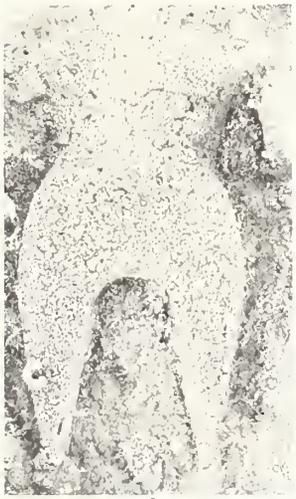
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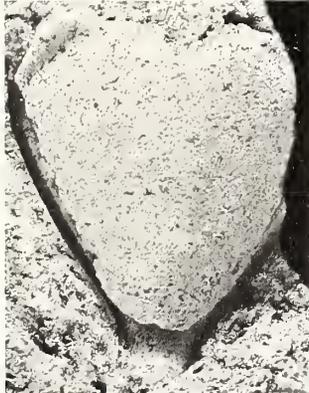
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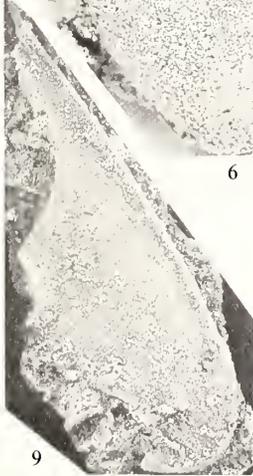
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TEXT-FIG. 11. *Lycophron howchini* (Etheridge), South Australian Museum type collection, F 7104. Lectotype thorax and pygidium, $\times 0.5$.

of *L. rex* show no indication of the pygidial axis; definition of dorsal furrows in asaphids is usually more marked in smaller specimens. So the difference between *L. rex* and *L. howchini* is real, and unlikely to be because of a difference in preservation or size. Etheridge (1894, pl. 3, fig. 2) figured an asaphid hypostoma, which is very likely that of *L. howchini*. A species which may prove to be *L. howchini* occurs commonly in the Carlo and Mithaka Formations overlying the Nora Formation in the Georgina Basin.

Lycophron sp. A

Plate 43, figs. 11, 12

Material. Pygidia, CPC 22708, 22709, from loc. 071/4.

Occurrence. Lowest part of Nora Formation, loc. 071/4.

Discussion. A second species of *Lycophron* is represented by pygidia only, occurring stratigraphically beneath *L. rex*. We cannot formally name it on the basis of this sparse material. It differs from the type species in having a well-defined pygidial axis extending almost to the posterior margin, furrowed pleural fields and a distinct border, but it shares the distinctive triangular shape. At least fifteen pairs of muscle impressions are visible on the flanks of the pygidial axis, and ten or eleven segments are expressed on the pleural fields, represented by shallow pleural and interpleural furrows which stop at the border. Like *L. rex*, only the first pair of pleural furrows are deep. The pygidium is more transverse than that of *L. rex* or *L. howchini*, and the latter also has unfurrowed pleural fields and no border. Presumably *L. sp. A* shows the primitive condition in *Lycophron*—furrowed pleural regions and pygidial borders are primitive for the Asaphidae as a whole. Note that this pygidium is unlike that of *Isoteloides* (from which *Isotelus* was probably derived) and *Megistaspis* (a close relative, if not the ancestor of *Megistaspidella*) which may be taken as evidence that any resemblance between *Lycophron* and *Isotelus* or *Megistaspidella* is a matter of convergence rather than phyletic relationship.

Genus *Presbynileus* Hintze, 1954

Type species. *Paranileus ibexensis* Hintze, 1953, by original designation.

Presbynileus cf. *P. utahensis* (Hintze, 1953)

Plate 42, figs. 5, 6

Material. Cranidia, CPC 22710, 22899–22903; pygidia, CPC 22712, 22713, 22904, 22905.*Occurrence.* Mid to upper parts of the Nora Formation, locs. 038/38, 126/7, 158/9, 158/11, 308/1.

Discussion. This highly effaced asaphid is quite frequent in the higher part of the Nora Formation; cranidia are immediately distinguishable from those of *Fitzroyaspis irritans* in lacking a border. The cranidium has medially placed palpebral lobes and very short (tr.) postocular cheeks, defined by distinctly curved sutures. The pygidium assigned here also lacks all traces of a border. *Presbynileus* includes several species from the early Ordovician of Utah which agree with the Nora material in their salient features; only one of these, *P. utahensis*, has convex postocular sutures and narrow cheeks like our species. Hintze's (1953, pl. 13, fig. 2) cranidia are only about 0.5 cm long, whereas we have specimens up to 2 cm long. We can see no points of difference between the type cranidium and that illustrated on Plate 42, fig. 6, other than slightly shorter palpebral lobes in the Nora form (which could well be accounted for by difference in growth stage). Pygidia are of similar dimensions, although the axis of the Nora form is wider. We have not recovered a hypostoma from the Nora Formation. The similarities between material from these widely separated localities are sufficient to suggest conspecificity. We retain a qualification to cover the pygidial difference, and because we have not yet recovered the distinctive hypostoma from Australia.

Asaphid gen. et sp. indet.

Plate 40, fig. 11

Material. Pygidium, CPC 22711.

Discussion. One or more asaphids additional to those described above occur in the Nora Formation; they are fragmentary and difficult to associate, and no formal nomenclature is possible. The pygidium illustrated is from the lower Nora Formation at 071/4. It is similar to that of a species described by Legg (1976) as *?Asaphellus pricensis* from the Canning Basin, except that the pygidial axis is somewhat longer in our form.

Family DIKELOKEPHALINIDAE Kobayashi, 1936

Genus *Hungioides* Kobayashi, 1936*Synonymy.* *Argentinops* Přibyl and Vaněk, 1980, p. 38, fig. 11.*Type species.* *Dikelokephalina bohémica* Perner, in Novák and Perner 1918, by original designation.

Discussion. Lu (1975, p. 357) has discussed the definition of genera in the Dikelokephalinidae. He cites the presence of two pairs of pygidial spines as diagnostic of *Hungioides*. Material from the Nora Formation should be placed in *Hungioides* on the basis of this character. However, Lu also regards a 'bell-shaped glabella with rounded frontal lobe' as typical, whereas the Australian material shows a conical forward part of the glabella, in this respect resembling certain *Asaphopsis* species, or *Asaphopsoides*. In the family as a whole there appears to be a good deal of variation in glabellar shape between species, as there is in incision of glabellar furrows, and we regard the pygidial structure as the better generic discriminant in this case. Přibyl and Vaněk (1980) distinguished the genus *Argentinops* (based on *Asaphopsis intermedia* Harrington and Leanza) on the basis of its more slender exterior pair of pygidial spines. This is scarcely adequate for generic discrimination, and may be subject to ontogenetic variation as well; hence we regard *Argentinops* as a subjective synonym of *Hungioides*.

Hungioides acutinasus sp. nov.

Plate 44

Diagnosis. *Hungioides* with conical glabellar front; highly divergent preocular facial sutures;

palpebral lobes half glabellar length (including occipital ring). Pygidial spines relatively slender compared with other species.

Derivation of name. Latin *acutinasus*, 'sharp-nose', referring to the shape of the glabella.

Holotype. Cranidium, CPC 22714, from loc. 126/3.

Other material. Cranidia, CPC 22715, 22716, 22906–22908; pygidia, CPC 22717–22720, 22909–22915; probable librigenal fragment, CPC 22721.

Occurrence. Lower to upper Nora Formation, locs. 071/4, 122/1, 126/1, 126/3, 126/4, 126/5, 126/11, 152/9, 158/4, 308/1.

Description. This species must have attained a large size. Cranidia probably attained a length of about 4 cm and a width of at least 6 cm; pygidia were over 4.5 cm long (including spines); complete specimens probably exceeded 12 cm in length. The well-preserved cranidia are all small, 2 cm long or less, and the description is mostly based on these. The general convexity of this species is remarkably low: the highest parts of the cranidium are the glabellar mid-line and the palpebral lobes, the latter being quite elevated, which would result in the visual surfaces on the free cheeks being higher than most of the rest of the exoskeleton. Glabella with maximum width at occipital ring, being 0.7 sag. length. Gentle forward taper increases greatly at level of 3P glabellar furrows, such that the front part is broadly conical, although rounded medially. Occipital ring well-defined, furrow shallower medially, deepened slightly on line with inner ends of glabellar furrows. Three pairs of glabellar furrows, isolated as pits within glabella: 1P forked at inner end, the posterior branch of fork especially strong; 2P and 3P close together, broadly oval (tr.), 3P placed opposite forward end of palpebral lobe. Distance between 2P and 3P approximately half that between 2P and 1P and between 1P and the occipital furrow. Furrow circumscribing glabella uniformly narrow and shallow. Prominent 'alae' are here semicircular, depressed areas about half as long as the palpebral lobes and with hind ends adjacent to the occipital furrow. Palpebral lobes large (measured exsag. about half total glabellar length), and posteriorly placed such that the posterior ends are behind the occipital furrow; hence the postocular cheeks are reduced to very narrow strips. Divergent anterior sections of the facial sutures are broadly sigmoidal, mid-section making an angle of 45–60 degrees with sag. line on smaller cranidia; on a large, fragmentary specimen this angle has increased to more than 80 degrees, resulting in an extremely wide (tr.) preglabellar area. Paradoublural line meets the preocular suture at about its mid-length. This line serves to divide posterior depressed area from the very gently convex preglabellar/anterolateral field, which widens towards the exsagittal part of glabella. Broad, depressed border furrow separates this convex area from narrow, distinctly upturned brim.

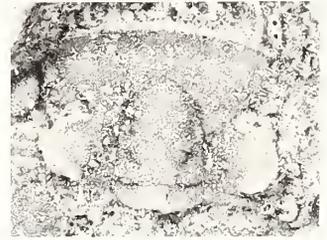
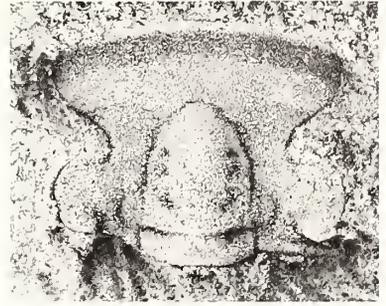
As far as preserved, the cuticle on this large species was very thin. The biggest specimen preserves traces of some terrace lines running approximately parallel with the anterior margin across the preglabellar field and border.

Pygidia are mostly fragmentary, but several prove the existence of two pairs of marginal spines. The narrow axis tapers uniformly backwards to more than half pygidial length, and is continued into a postaxial ridge which does not extend on to the border (the exact tip of the axis is thus hard to discern). Up to seven axial rings are present, of which the first four are well-defined. Ribs number six, adaxial parts sloping progressively backwards posteriorly; they fade out on inner part of concave border, which had terrace lines like those on the cephalic border. On large pygidia the marginal spines are slender, and the exterior pair are about as long as the pygidial axis. A well-preserved, small pygidium (Pl. 44, fig. 6), which is probably referable to *H. acutinasus*, shows a relatively broad (tr.) outer pair of spines, and it seems likely that these became more slender during later ontogeny.

Discussion. The type species (Novák and Perner 1918, pl. 1, figs. 4, 6; Marek, *in* Horný and Bastl 1970, pl. 5, fig. 7) from the Llanvirn Šarka Formation of Bohemia, has a pygidium with at least eleven axial

EXPLANATION OF PLATE 44

Figs. 1–7. *Hungiooides acutinasus* sp. nov. 1, CPC 22715, loc. 126/3, fragment of large exfoliated cranidium, $\times 2$. 2, CPC 22714, loc. 126/3, holotype cranidium, internal mould, $\times 3$. 3, CPC 22716, latex cast of small cranidium, same bed as holotype, $\times 3$. 4, CPC 22721, locality as holotype, incomplete free cheek probably belonging here, internal mould, $\times 3$. 5, CPC 22717, loc. 126/5, latex cast from incomplete, large pygidium, $\times 2$. 6, 7, CPC 22718, loc. 071/4, latex cast from well-preserved smaller pygidium (6), $\times 6$; and sculptural detail (7), $\times 12$.



rings, and a more prominent, stubbier interior pair of marginal spines. If the cranium of *H. bohemicus* (Novák and Perner 1918, pl. 1, fig. 6) is correctly assigned, it has a more uniformly parabolic glabella and eyes further forward than in *H. acutinasus*. *H. graphicus* Richter and Richter, 1954, is generally similar to *H. bohemicus*, and differs from our species in the same pygidial features. Kobayashi (1936) separated the original pygidium of Novák and Perner (1918, pl. 18, fig. 5) as *H. novaki*; the marginal spines of this species are subequal in length, short and wide, and conjoined at their bases. The same kind of pygidial structure is shown by *H. mirus* Lu (1975, pl. 29, figs. 8–15). Both differ from *H. acutinasus* in the prominent development of the interior pair of spines, and the broad bases of the exterior ones. Cephalic characters of the Chinese species show that the eyes are in a similar posterior position to those of our species, but the anterior branches of the facial sutures are less divergent, and there is apparently no cranial border. Another species described by Lu (1975), *H. constrictus* from the Tremadoc, has a truncate glabella, smaller eyes, less divergent sutures, and an ill-defined border compared with *H. acutinasus*. '*Asaphopsis*' *intermedia* Harrington and Leanza, 1957, from the Llanvirn of Argentina also shows a small inner pair of pygidial spines, and is better referred to *Hungioides*. As in *H. acutinasus* the outer pair of spines are slender, but originate more adaxially. Apart from being more convex, the Argentine species has a pygidium with eleven axial rings and seven or eight pleural ribs. Přibyl and Vaněk (1980) erected a new genus, *Argentinops*, based on this species, which we consider to be a junior subjective synonym of *Hungioides*. The new species is thus readily distinguished from all others, but differences concerning sutural divergence and pygidial spines are not of generic significance.

Hungioides has a curious distribution. It extends from that part of Europe which was part of the *Selenopeltis* (high latitude) province through central and south-western China (also South America) to platform Australia, which as we have discussed was probably near the palaeoequator in the earlier Ordovician. Its thin cuticle, flattened form, and large size argues for benthic habits. This distribution is the only one known to us which shows independence of palaeolatitude at the generic level. The distribution does, however, appear to be peri-Gondwanan, but the genus is only at all common on the eastern part of its geographic range.

Family TELEPHINIDAE Marek, 1952

Discussion. We follow here the expanded concept of the Family Telephinidae introduced by Fortey (1975). The family includes five genera which had pelagic habits: *Carolinites* Kobayashi, *Telephina* Marek, *Goniophrys* Ross, *Oopsites* Fortey, and *Phorocephala* Lu (= *Carrickia* Tripp, 1965, see below).

Genus *Phorocephala* Lu, 1965

Type species. *Phorocephala typa* Lu, 1965, by original designation.

Discussion. The generic name *Phorocephala* has publication priority over *Carrickia* Tripp, 1965 (see Tripp 1976, p. 423). The type species of both genera are so similar that it is likely that both should be referred to the same genus, *Phorocephala*. *Phorocephala* species are distinguished from those of *Goniophrys* by their long (tr.) anterior cranial borders, and relatively gently curved palpebral lobes (Fortey 1976, fig. 11). The species from the Nora Formation is an early one, and retains a few features suggestive of derivation from *Goniophrys*.

Phorocephala sp. aff. *P. genalata* Lu, 1975

Plate 45, figs. 1–6

Material. Cranidia, CPC 22722–22724; pygidium, CPC 22725.

Occurrence. Lower part of Nora Formation, locs. 071/4, 127/3?.

Description. Glabella highly vaulted above fixed cheeks, maximum width being half that of cranium measured transversely at back end of palpebral lobes. The glabellar outline is broadly parabolic, much like that of *Oopsites* or *Goniophrys*. Muscle impressions are lacking, except for a vague indication of 1P isolated within the glabella opposite hind part of palpebral lobes. Occipital ring about one-fifth total glabellar length. Axial and preglabellar

furrows uniformly deep around perimeter of glabella, but deepened into a pit anteromedially. Preglabellar field short, hardly downward sloping, merging without a sharp break into flat or gently concave border, the two together having about the same length (sag.) as that of the occipital ring when viewed dorsally. Lateral part of the preocular fixed cheeks steeply declined, so that the front edge of the cranidium is broadly upward-arched about the mid-line. Palpebral lobes of length 0.4 that of glabella (sag.), narrow and slightly convex, forward two-thirds curving gently inward-forward, posterior third curved inward-backwards. Palpebral furrow follows change of curvature of palpebral lobe with a somewhat angulate bend. Palpebral furrow is deep but at anterior end it terminates at a poorly defined eye ridge. Intraocular cheek very slightly convex. Posterior border not clearly preserved on available material. Glabella smooth, scattered punctae on cheeks.

Small, wide pygidium is attributed to this species. Wide axis tapers posteriorly and terminal piece merges with a deep, steeply downsloping posterior border, the outline of which is transverse medially. Two axial rings are completely defined, a third faintly. Similarly, two segments are defined on the narrow (tr.) pleural fields, with pleural and interpleural furrows about equally incised, with a short, faint pleural furrow of a third segment.

Discussion. This species differs from the type species of *Phorocephala*, *P. typa* Lu, 1965 (pl. 123, fig. 14; 1975, pl. 34, fig. 13) in its parabolic glabella and punctate (rather than pustulose) surface sculpture; the palpebral lobes of *P. typa* are less curved. Our species has a glabellar form like that of *G. prima* Ross, 1951 (pl. 18, fig. 17), which is primitive for the Telephinidae. The curvature of the palpebral lobes is also reminiscent of *Goniophrys*. On the other hand, the wide, transverse cranial anterior border precludes its inclusion in that genus and clearly allies it with *Phorocephala*. The glabella and palpebral lobes are primitive characters retained from a *Goniophrys*-like ancestor, which is in accord with the early stratigraphic occurrence of our species compared with that of other described *Phorocephala* (= *Carrickia*) spp. The closest comparison is with *P. genalata* Lu, 1975 from a late Arenig occurrence in south-west China, which has a similar glabella. Unfortunately it is described from poor material: the preglabellar field appears to be longer, and the intraocular cheeks are wider than in our species. *Goniophrys* (sic.) *venustus* Ancigin, 1977 (pp. 70–71, pl. 1, figs. 14–20, 24), from the early Ordovician, Karakol–Mikailov Formation of the southern Urals, differs from our species in its very wide glabella, and broad, flattened border on the pygidium. Although ours is therefore apparently a new species, the material is insufficient to name it as such—hence our comparative reference to *P. genalata*. One Llanvirn species with punctate sculpture is that referred by Whittington (1965) to *Goniophrys breviceps*? (Billings) from the Llanvirn of Newfoundland; this species is also referable to *Phorocephala*. The very long palpebral lobes and convex cranial border immediately distinguish it from our species.

Genus *Carolinites* Kobayashi, 1940

Type species. *Carolinites bulbosus* Kobayashi, 1940, by original designation.

Discussion. The morphology of *Carolinites* is now well-known from a number of species, and the stratigraphic importance of the genus is established. It is unfortunate that the type species, *C. bulbosus*, has not been redescribed from topotype collections. As interpreted by Legg (1976) from Canning Basin material, *C. bulbosus* would be the senior synonym of the widespread species *C. genacinaca* Ross, 1951. Legg's specimens are undoubtedly conspecific with the species from North America, but it is less clear that this applies also to the type material of *C. bulbosus*. The width of the fixed cheek (Kobayashi 1940, pl. 12, fig. 6) adjacent to the baccula, for example, is less than in typical specimens of *C. g. genacinaca*, and belongs to the range of overlap between that species and *C. ekphymosus* Fortey, 1975 (text-fig. 14; pl. 39, figs. 4, 10), a species which is probably a senior synonym of *C. pardensis* Legg, 1976. However, the pygidium, possibly incorrectly assigned to *C. bulbosus* by Kobayashi, is unlike that of any other *Carolinites* species, being relatively transverse, and with a flattened border. In view of these uncertainties we prefer to compare our material with previously described species for which cranidium, pygidium and free cheek are known.

Carolinites genacinaca Ross, 1951 (s.l.)

Plate 45, figs. 7–10

Synonymy. Synonymy of this species, and its two subspecies, was given by Fortey (1975; 1980a, pp. 103, 104).

Material. Cranidia, CPC 22728, 22729; pygidia, CPC 22726, 22727.

Occurrence. Basal Nora Formation, loc. 071/4.

Discussion. The species is divided into two subspecies: *C. g. genacinaca* Ross, 1951, and *C. g. nevadensis* Hintze, 1953, both known from silicified material. Detailed comparative discussion of these subspecies was given by Fortey (1975). A crucial point of distinction is the presence of a marked subocular ridge in *C. g. nevadensis*. We do not have a free cheek from the Nora Formation which might show this feature, and so we prefer to identify the species *sensu lato*. That apart, the relative size of the bacculae adjacent to the base of the glabella, and the clear definition of the third pygidial axial ring shown by the Australian material, are features of the subspecies *C. g. genacinaca*, a mid-Arenig form.

The type specimen of *C. minor* (Sun, 1931) was re-illustrated by Lu (1975, pl. 2, fig. 20); it is very like cranidia of *C. genacinaca* of the same small size. *C. minor* may prove to be the senior synonym both of *C. genacinaca* and *C. bulbosus*, but in view of the uncertainty surrounding the identity of the type species, we employ the well-characterized species *C. genacinaca* here.

Carolinites cf. *C. ekphymosus* Fortey, 1975

Plate 45, figs. 11–14

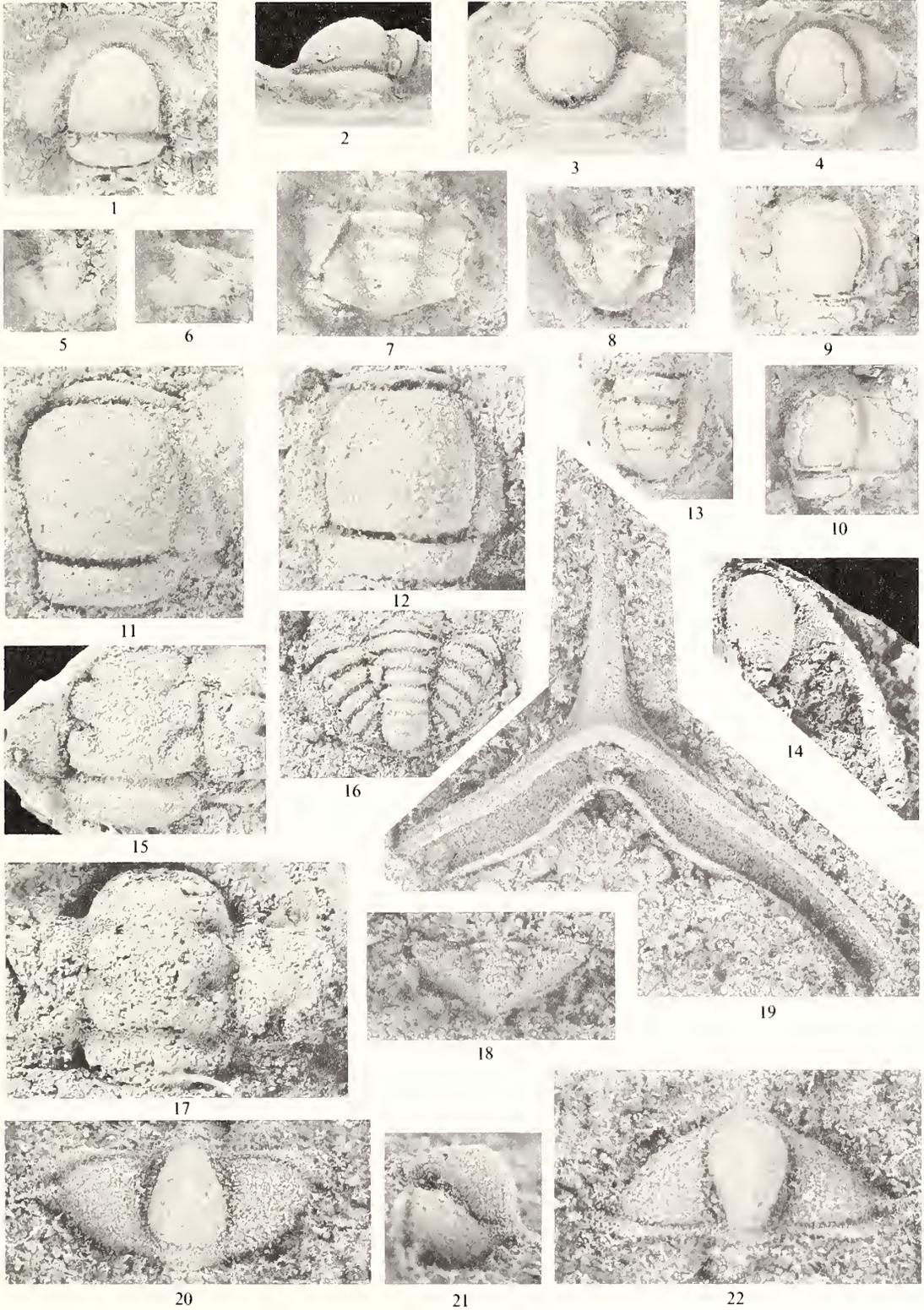
Material. Cranidia, CPC 22732–22740, 22916–22930; librigenae, CPC 22748–22750; pygidia, CPC 22741–22747, 22931–22942.

Occurrence. Ranges through much of the higher part of the Nora Formation, locs. 118/7, 122/4, 126/3, 126/4, 158/4, 308/1.

Discussion. This species of *Carolinites* with narrow fixed cheeks is mostly represented by poorly preserved external moulds, but a few good specimens allow comparison with previously described species. Narrow-cheeked *Carolinites* include *C. sibiricus* Chugaeva, 1964 (= *C. angustagena* Ross, 1967) and *C. ekphymosus* Fortey, 1975 (= *C. pardensis* Legg, 1976, see Fortey 1980a, p. 104). The former has the genal spine reduced to a small stub, whereas the Nora species has a well-developed and curved genal spine. This is like *C. ekphymosus* from the late Arenig of Spitsbergen (Fortey 1975, pl. 39, fig. 2). Well-preserved Nora cranidia are also very like those of *C. ekphymosus* (compare Pl. 45, fig. 11 with Fortey 1975, pl. 39, fig. 3). One of the characteristics of *C. ekphymosus* is a finely granulate surface sculpture, and none of the Australian material is well enough preserved to show this. The pygidia of *C. ekphymosus* from Spitsbergen show a faintly defined fourth axial ring on the pygidium,

EXPLANATION OF PLATE 45

- Figs. 1–6. *Phorocephala* sp. aff. *P. genalata* Lu, 1975. All from Nora Formation, loc. 071/4. 1–3, CPC 22722, exfoliated cranidium in dorsal (1), lateral (2), and anterior (3) views, $\times 8$. 4, CPC 22723, cranidium, $\times 8$. 5, 6, CPC 22725, pygidium, dorsal (5) and posterior (6) views, $\times 8$.
- Figs. 7–10. *Carolinites genacinaca* Ross, 1951 (s.l.). All from lowest Nora Formation, loc. 071/4. 7, CPC 22726, pygidium, $\times 6$. 8, CPC 22727, pygidium, $\times 6$. 9, CPC 22728, incomplete cranidium, $\times 6$. 10, CPC 22729, small cranidium with well-preserved cheek on right side showing relatively great width compared with *C. cf. ekphymosus*, $\times 6$.
- Figs. 11–14. *Carolinites* cf. *C. ekphymosus* Fortey, 1975. 11, CPC 22732, loc. 118/7, cast of cranidium, $\times 6$. 12, CPC 22733, loc. 308/1, cast of cranidium with narrowest cheeks, $\times 7$. 13, CPC 22741, loc. 308/1, cast of pygidium, $\times 6$. 14, CPC 22748, loc. 308/1, free cheek, latex cast, $\times 6$.
- Figs. 15–17. *Annamitella brachyops* sp. nov. 15, CPC 22773, loc. 308/1, latex cast of incomplete cranidium showing granulose sculpture, $\times 4$. 16, CPC 22774, loc. 308/1, pygidium, $\times 6$. 17, CPC 22772, loc. 308/1, holotype, internal mould of cranidium in typical preservation, $\times 6$.
- Figs. 18–22. *Nambeetella embolion* sp. nov. 18, CPC 22757, loc. 126/7, pygidium, internal mould, $\times 6$. 19, CPC 22755, loc. 126/3, cephalic doublure with median spine, same bed as holotype, $\times 6$. 20–22, CPC 22751, loc. 126/3, holotype, latex cast of external mould of cranidium, in anterior (20), lateral (21), and dorsal (22) views, $\times 6$.



FORTEY and SHERGOLD, Nora Formation trilobites

which we have not seen on Australian specimens. These small differences could be because of preservation, but it is preferable to retain a qualification in the determination. Narrowest-cheeked specimens from the Nora Formation (Pl. 45, fig. 12) are like *C. sibiricus*, but no associated free cheek that we have prepared has the genal spine reduced, and the fourth pygidial axial ring is clearly defined on *C. sibiricus*. Regardless of specific identity no *Carolinites* with large bacculae but narrow fixed cheeks is known elsewhere before the later Arenig.

Family ALSATASPIDIDAE Turner, 1940

Emended diagnosis. Trinucleine trilobites in which the median cephalic spine originates from the cephalic doublure. Eyes present primitively; later forms blind. Some forms tend to multiplication of thoracic segments (probably to as many as thirty in *Selenecece*).

Discussion. Fortey (1975, p. 92) noted the difficulties in an objective definition of this family. We now believe that the presence of a long anterior spine, originating from the cephalic doublure (rather than the glabella as in raphiophorids), is a shared, derived character unusual enough to indicate a monophyletic group. As thus recognized, the Alsataspididae would include *Selenecece*, *Falanaspis*, *Nambeetella* (below), and '*Hapalopleura*' *longicornis* Harrington and Leanza, 1957. As Fortey noted, the reconstructions of the first- and last-named given in the *Treatise* (Moore 1959) are incorrect in showing what appears to be a dorsal origin for the frontal spine. Whittard (1958) clearly observed the ventral origin of the frontal spine in *Selenecece*, while Fortey noted that specimens of '*H*' *longicornis* lacking free cheeks also lacked the frontal spine, which was present on entire specimens. This early Tremadoc species also has small eyes. The implication is that the alsataspidids became blind subsequently. Presumably all trinucleine groups were primitively sighted, and blindness could be polyphyletically derived. *Selenecece* shows another tendency widespread in raphiophorid-like trilobites—the multiplication of post-cephalic segments. We regard this as an adaptation for life in poorly oxygenated environments (Fortey 1975, p. 93; Fortey and Owens 1978, p. 239), and not of high level taxonomic significance. In support of this is the fact that such highly segmented forms are developed at different times in different groups (*Hapalopleura* in the Tremadoc; *Edmundsouia*, a middle Ordovician raphiophorid; and *Selenecece*, an alsataspidid).

If this phylogenetic view is correct, there are no grounds for separating the Hapalopleuridae from the Orometopidae (Henningsmoen 1959, p. 170) and the latter family name would take precedence. The extended Orometopidae would embrace primitively sighted genera including the ancestors of raphiophorines and endymioniines. Rushton (1982) has shown the origin of *Myiuda*-like forms from orometopids (in our sense) resembling *Araiopleura*; this shows that *Myiuda* (and *Myindella*), hitherto regarded as comprising a separate family, should be included as a subfamily of Orometopidae.

In summary, we would classify the Trinucleina into the following families: Trinucleidae; Dionididae (syn. Tongxinaspidae Zhou, 1981); Orometopidae (syn. Hapalopleuridae), including Subfamily Myindinae; Alsataspididae; Raphiophoridae (Subfamilies Raphiophorinae, Endymioniinae, and possibly Ampyxinellinae). We are inclined to regard *Eotrinucleus*, the only genus ascribed to the Eotrinucleidae Zhou and Zhang, 1978, as a harpedid.

Genus *Nambeetella* Legg, 1976

Type species. *Nambeetella fitzroyensis* Legg, 1976, by original designation.

Diagnosis. Alsataspidids with convex, flask-shaped glabella not overhanging cranidial margin. Triangular pygidium with one or two pairs of pleural furrows.

Discussion. The use here of Legg's genus *Nambeetella* requires some justification. Legg did not describe the free cheeks of the type species, and the free cheeks include the critical alsataspidid feature of the anteromedian spine. The cranidium alone is extremely like that of *Globampyx trinucleoides* Fortey (1975, pl. 29, fig. 1) from the Arenig of Spitsbergen, but this is a raphiophorine entirely lacking a frontal median spine. Legg (1976) compared *Nambeetella* with *Mendolaspis*, but again this genus appears to have an anterior tubercle on the glabella homologous with the anterior spine of

raphiophorines (Fortey 1975, pl. 30, fig. 8). On our analysis both *Globanpyx* and *Mendolaspis* are raphiophorids, and any resemblance to the alsataspidid from the Nora Formation is a matter of convergence. We have made the assumption, however, that the Nora material and that from the Canning Basin (*N. fitzroyensis*) is congeneric. In view of the other genera in common between the two areas (*Fitzroyaspis*, *Gogoella*, *Prosopiscus*, etc.), and the endemic character of the fauna as a whole, this does not seem an unreasonable assumption. But it requires the discovery of the cephalic doublure of the type species before it can be proven. If the anteromedian spine proved to be lacking on *N. fitzroyensis*, *Nambeetella* would become a junior subjective synonym of *Globanpyx*, and a new generic name would be required for the species described below.

As understood here, *Nambeetella* is distinguished from other genera of the Alsataspididae by its narrow, vaulted glabella and relatively large pygidium; it is the most raphiophorid-like of the family. We regard the presence of the median spine on the doublure as the more reliable indicator of its affinities.

Nambeetella embolion sp. nov.

Plate 45, figs. 18-22

Diagnosis. *Nambeetella* with steeply sloping and somewhat tumid preglabellar field; lateral tips of fixed cheeks extended into spine-like projections. Pygidium about twice as wide as long, with axis occupying about one-third transverse pygidial width at front margin.

Derivation of name. Greek *embolion*, 'javelin', referring to the frontal spine.

Holotype. Cranidium, CPC 22751, from loc. 126/3.

Other material. Cranidia, CPC 22752-22754, 22952, 22953; librigenae, CPC 22755, 22756; pygidium, CPC 22757.

Occurrence. Lower part of Nora Formation, locs. 126/3, 126/4, 126/5, 126/6, 126/7, 127/7.

Description. Cranidia, free cheeks, and pygidium are all from a short stratigraphic interval in which no other trinucleines occur, so their association is made with confidence. Cranidium twice as wide as long, glabella even at maximum width occupying a third cranidial width, or less. Transverse glabellar vaulting increases forwards from quite low near the occipital ring to a maximum at about two-thirds length in dorsal view, in front of which there is a decrease in convexity to the preglabellar furrow. One might expect a tubercle on the anterior high point of the glabella but none is visible—probably the preservation is too coarse to see it. For the same reason no sculptural details are preserved. Two pairs of subcircular muscle impressions on narrow, posterior part of glabella. Fixed cheeks curve downwards progressively forwards, running into the preglabellar field, which protrudes slightly forwards, slopes steeply downwards, and is gently inflated. Axial furrows are quite broad posteriorly but there is no indication of inflated 'alae' within. Short (sag., tr.) anterior cranial border weakly indicated at mid-part of preglabellar field. Well-defined posterior border becomes wider and steeply forwards inclined away from glabella. The most distinctive feature of the cranidium is the prolongation of the borders, and narrow, triangular slivers of the fixed cheeks in front, into curious spine-like projections at the posterolateral corners of the cranidium.

We have two examples of the cephalic doublure bearing the median spine; all that remains of the dorsal part of the free cheeks is a narrow strip running around the anterior margin of the cranidium. The doublure itself is divided along its length with a somewhat ventrally depressed posterior band, and its inner edge is turned upwards and embayed about the mid-line. The frontal spine tapers from a stout base to reach a length possibly exceeding that of the cranidium; the underside of the spine is flattened near its base, but the cross-section is nearly circular distally. It was probably slightly downward-declined. A curious feature of both specimens is the lack of genal spines. All trinucleines have genal spines, and it seems unlikely that they were absent in *Nambeetella*, but it is difficult to see why they should have been broken off when the anteromedian spine is preserved, particularly in so symmetrical a fashion.

Pygidium twice as wide as long, with steeply downturned posterior border which is not arched up about the mid-line. Gently convex axis occupies about one-third of the pygidial width at the front margin, tapering gently posteriorly, and extends as far as border, but preservation is not good enough to see whether it encroached on to the border in the manner of some raphiophorids. Four narrow axial rings appear to be defined. On the pleural fields only the first pair of pleural furrows are deeply defined. The pygidium is an internal mould, and it is possible that an additional pair of furrows could have been expressed dorsally.

Discussion. The reasons for assigning the species from the Nora Formation to *Nambeetella* have been discussed above. *N. fitzroyensis*, the type and only other species, has a narrower preglabellar field, and Legg (1976) does not mention the distinctive, pointed extensions of the posterolateral angles of the fixed cheeks which are a feature of *N. embolion*. The pygidium assigned to *N. fitzroyensis* is relatively much wider than that of *N. embolion*, with a proportionately narrow axis; a second pleural furrow is defined.

Family PLIOMERIDAE Raymond, 1913

Genus *Gogoella* Legg, 1976

Type species. *Gogoella wadei* Legg, 1976, by original designation.

Gogoella brevis sp. nov.

Plate 46, figs. 11–14; text-fig. 12

Diagnosis. *Gogoella* with glabella wider than long, forward-expanding; fixed cheeks narrow (tr.). Pygidial ribs broad (tr.), steeply downturned, with somewhat truncate spinose tips.

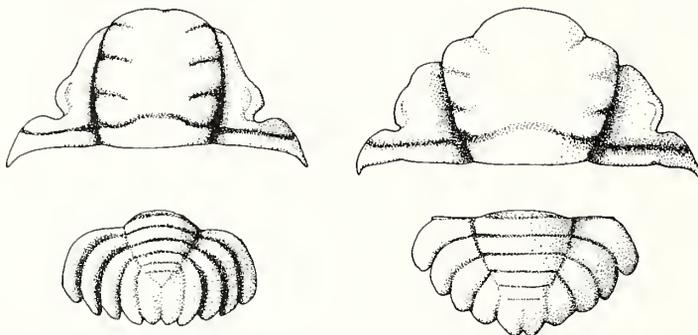
Derivation of name. Latin *brevis*, 'short'.

Holotype. Cranium, CPC 22758, from loc. 308/1.

Other material. Cranidia, CPC 22954–22956; pygidia, CPC 22759–22761, 22957–22960.

Occurrence. Upper part of Nora Formation, locs. 308/1, 158/4.

Description. A small species, cranium not exceeding 5 mm in length, but transversely convex. Cranium with postocular cheeks steeply downturned, glabella squat and flat-topped. Glabella expands forwards so that maximum width is at 3P lobes, this exceeding its sagittal length. Front glabellar margin gently rounded about



TEXT-FIG. 12. Comparative reconstructions of *Gogoella wadei* Legg (left), from the Canning Basin (reconstructed from Legg 1976), and *G. brevis* sp. nov. (right) from the Nora Formation, both about $\times 2$.

EXPLANATION OF PLATE 46

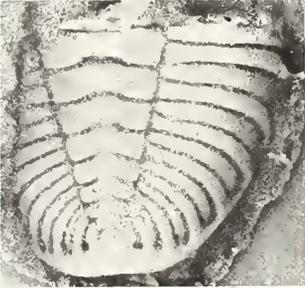
- Figs. 1–6, 9. *Prosopiscus praecox* sp. nov. 1, 2, CPC 22762, lower Nora Formation, loc. 071/4, holotype, well-preserved, but broken testate cranium in dorsal (1) and oblique anterior (2) views, $\times 4$. 3, 5, CPC 22764, loc. 158, latex cast from well-preserved pygidium, dorsal (3) and oblique posterior (5) views, $\times 3$. 4, CPC 22765, loc. 158/9, latex cast from smaller pygidium, $\times 3$. 6, CPC 22766, loc. 158/4, latex cast from pygidium, $\times 5$. 9, CPC 22763, loc. 071/4, incomplete cranium from same bed as holotype, $\times 6$.
- Figs. 7, 8, 10. *Prosopiscus* sp. A. 7, CPC 22767, loc. 071/4, cast from fragmentary, but well-preserved cranium, $\times 8$. 8, CPC 22768, loc. 308/1, small cranium, imperfect internal mould, $\times 8$. 10, CPC 22769, loc. 158/9, latex cast from the pygidium most likely to belong here, dorsal view, $\times 3$.
- Figs. 11–14. *Gogoella brevis* sp. nov. 11, CPC 22760, loc. 308/1, pygidium, latex cast, showing all five ribs, $\times 6$. 12, CPC 22758, loc. 308/1, holotype cranium, internal mould, $\times 8$. 13, 14, CPC 22759, loc. 158/4, latex cast from external mould of pygidium, shown in dorsal (13) and posterior (14) views, $\times 6$.



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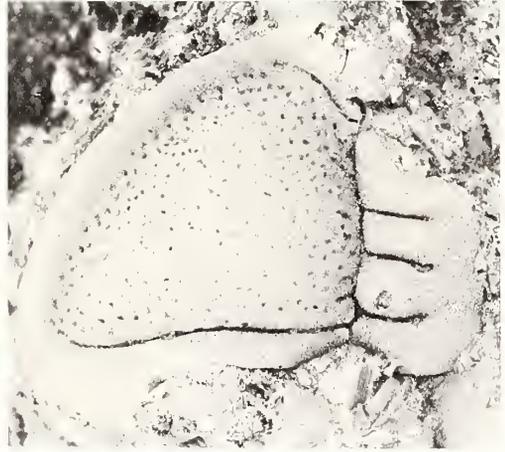
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11



12



13



14

mid-line. Glabellar expansion is less marked on small cranidia, and the frontal lobe is more broadly rounded. Glabellar furrows short, extending less than one-quarter of transverse glabellar width. 1P deepest, confining narrow (exsag.) 1P lobe; 2P and 3P lobes are progressively longer (exsag.). 2P furrow is directed slightly forwards, approaching axial furrow near its anterior end; 3P directed strongly forwards, finishing well inside the preglabellar furrow. Occipital ring deeply defined, and curving forwards medially. Axial furrows very deep and wide, like posterior border furrow. Because most of our specimens are internal moulds we do not know the dorsal expression of glabellar and other furrows. If they follow the usual pliomeric pattern (pliomericids usually have a very thick cuticle) furrows would have been narrower, but still deep on the dorsal surface. Intraocular cheeks very narrow (tr.) not exceeding one-quarter maximum glabellar width. Palpebral lobes are far back, centred on the 1P glabellar furrow, thereby constricting a narrow (exsag.) and short (tr.) postocular cheek. Anterior border not well-preserved on available material.

Pygidium almost twice as wide as long, pleural ribs deeply downward-curved peripherally. Axis tapers backwards gently and uniformly, the five axial rings decreasing greatly in convexity in the process. The fifth axial ring is incompletely defined posterolaterally. No distinct terminal piece is developed. The pleural ribs are relatively short for a pliomericid, swollen and sausage-shaped, terminating on a line as somewhat truncate-tipped spines.

Discussion. Legg (1976, p. 20) briefly distinguished the type species from other pliomericids; the inclusion of *G. brevis* in the genus modifies the original diagnosis. *G. brevis* differs from *G. wadei* in its forward-expanding and relatively wide glabella, with concomitantly shorter glabellar furrows, 3P being closer to the mid-line in the new species. *G. brevis* has more swollen pygidial pleural ribs than *G. wadei*. Both species share: very narrow fixed cheeks, with the palpebral lobes further back than in any other pliomericid; glabellar furrows similarly disposed, apart from the more adaxial 3P in *G. brevis*; wide pygidium with short ribs (steeply inclined distally, but not extended into long vertical spines). These characters are regarded as important in distinguishing *Gogoella* from other pliomericids. Legg emphasized a small median glabellar indentation on the type species, but this is a character which is widespread in pliomericids—although most strongly expressed in *Pliomera*. Inclusion of *G. brevis* in *Gogoella* means that a 'subelliptical glabella . . . with anterior furrow approximately at anterolateral angle of glabella' (Legg 1976, p. 19) cannot be used to distinguish the genus from *Pliomera*. The type species of that genus, *P. fischeri* (e.g. Neben and Krueger 1975, pl. 10, figs. 18–20), is more like *G. brevis* than *G. wadei*, but in *P. fischeri* the median cephalic indentation is developed as strongly as the (very short) 3P glabellar furrows, the palpebral lobes are further forward, and, as Legg pointed out, the structure of the cranial anterior border is quite different from that in *G. wadei*. The long (sag.) pygidium of *P. fischeri* is unlike that of *Gogoella*. We regard the cephalic similarities between *Gogoella* and *Pliomera* to be the result of convergence. Similarly, on *Pliomerops canadensis* (see Shaw 1968, pl. 1, fig. 4) the 3P glabellar furrows are far forwards, as in *G. brevis*, but the structure of the pygidium, with long, downturned spines, is quite different from the Australian forms. It seems that the anterior, adaxial migration of the 3P glabellar furrows is an evolutionary trend in pliomericids that was attained independently several times.

Legg (1976) reported only ten thoracic segments on *G. wadei*, the smallest number of any pliomericid known to us. The structure of the anterior border of this species is also unusual in the Pliomeridae, being thin and almost tucked beneath the frontal glabellar lobe. We lack information on the border structure of *G. brevis*, however.

Family PROSOPISCIDAE fam. nov.

Diagnosis. Blind Phacopina with broad, convex fixed cheeks covered with pitting. Glabella typically tapering in later species, but primitively subparallel sided. Broad anterior cranial border, often sloping back towards glabella. Eye ridges running immediately forward from 3P glabellar furrow to margin on primitive forms. Pygidium with six to eight segments, equally developed pleural and interpleural furrows; posterior pleural bands tending to fuse with border.

Discussion. *Prosopiscus* is the only genus assigned to the new family; it has hitherto been placed with the Encrinuridae or Cheiruridae. Our reasons for regarding it as a separate family are given with a discussion of its affinities in the following paragraphs.

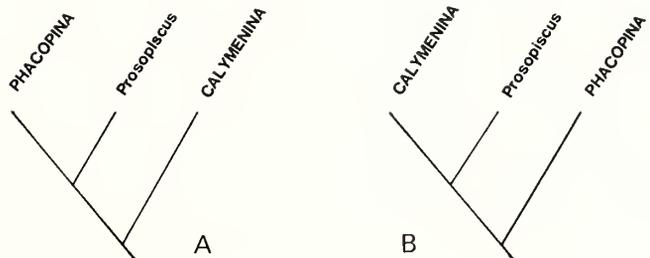
Genus *Prosopiscus* Salter, 1865

Type species. *Prosopiscus mimus* Salter, 1865, by original designation.

Discussion. The Nora Formation has yielded good material of this most extraordinary trilobite. The genus has hitherto been recorded from rocks of Llanvirn to Caradoc age; our species are therefore by far the oldest, and are appropriate for a consideration of the affinities of the genus. Lu (1975) discussed *Prosopiscus* at some length, and described well-preserved cephalic shields of three Chinese species. He concluded that the genus should be assigned to the Family Cheiruridae, Subfamily Areiinae Prantl and Přibyl. Lu and Chang (1974) figured a complete specimen of *P. latus*. We have also attributed the pygidium here, and this rules out any possibility of cheirurid affinities for *Prosopiscus* because the pygidium has up to eight segments, and an entire margin. The resemblance to *Areia* must be a matter of convergence. However, several features, particularly the pitted sculpture on the fixed cheeks and the form of the glabellar furrows, show that whatever its closest relatives *Prosopiscus* belongs to the Order Phacopida. The genus had a history extending through much of the Ordovician, and its earliest representatives are as old as any dalmanitacean, for example. In view of its curious combination of characters, and this long independent history, we regard *Prosopiscus* as belonging to a distinct family.

To which of the major groups of Phacopida is *Prosopiscus* most closely allied? We presume that the Cheirurina can be excluded, because of the entire pygidial margin of *Prosopiscus*, with the pleural ribs bisected by long, deep pleural furrows. This leaves two possibilities (A and B in text-fig. 13): *Prosopiscus* is more closely related to the Phacopina than the Calymenina, or vice versa. Blindness as a character is irrelevant, because it is capable of polyphyletic development. Later species of *Prosopiscus* have a markedly forward-tapering glabella, but this is not the primitive condition; our early species has a parallel-sided glabella, or even with slight expansion at the 3P glabellar lobe, and it is this form which must be compared with phacopines and calymenines. The ocular ridge is strongly defined, running forwards from the 3P glabellar furrow to the cranial margin. The anterolateral view of the specimen of *P. praecox* on Plate 46, fig. 2, shows that there was room for a minute, triangular free cheek adjacent to the cranial anterior border. However, the fact that no palpebral lobe is developed makes it very unlikely that there was even a rudimentary eye. The interpretation of the facial suture presents several problems. If a free cheek were present, then what appears to be the edge of the lateral cranial border is interpretable as a suture which may run some way towards the genal angle. In support of this interpretation is the fact that the anterior cranial border is distinctly rolled back into the doublure, whereas the 'border' on the fixed cheek is much narrower, not rolled and sharply truncated at its edge. The free cheek would then consist of the outer part of the border plus doublure. However, on species with broad lateral cranial borders (Pl. 46, fig. 7, and those in Lu 1975) the suture has presumably retreated to a completely marginal position, and this applies to all the younger species.

Of derived characters which might indicate calymenine affinities, one only is considered important: the structure of the anterior cranial border, which is robust, convex-forwards, and increases in width (tr.) away from the glabella. It may be compared with the structure of the preglabellar area of such early calymenids as *Neseuretus*. Although the tapering glabellae of calymenines and most



TEXT-FIG. 13. The two competing hypotheses for the closest related taxa to the peculiar trilobite *Prosopiscus*, as discussed in text.

Prosopiscus spp. are similar, this is clearly a secondary character in the latter, the primitive glabellar form being parallel-sided. The pygidium cannot be closely matched among calymenids, although some *Platycalymene* species are not dissimilar in general structure.

Derived characters which might indicate Phacopina are as follows: (1) The finely pitted surface sculpture on the fixed cheeks; such a sculptural type is present on many early Phacopina (Destombes 1972, pl. 4, fig. 1; Henry 1980, pl. 28, fig. 5b), while calymenids are apparently primitively granulate. (2) The form of the 3P glabellar furrow is typically phacopinoid, showing gently sigmoidal curvature and much greater forward inclination than the 2P furrow, making the 3L glabellar lobe longest (exsag.). (3) The pygidium is most like that of *Eudolaites* among phacopines (see *E. (Bamilaites)* aff. *dubius* figured by Destombes 1972, pl. 4, fig. 7) with regard to the development of pleural and interpleural furrows, and the retention of relict half-rings on the pygidial axis.

We conclude that more derived characters indicate the common ancestry of *Prosopiscus* and Phacopina than Calymenina. Pygidial details show that the Dalmanitidae include the closest forms. Since both *Prosopiscus* and Dalmanitidae are found in the Arenig, their common ancestor is of Tremadoc age or older but we know of no suitable candidate. The early origin and subsequent history of *Prosopiscus* indicates that its familial status is justified.

Note that other phacopids became blind: *Typhloniscus* is a Devonian genus which is homoeomorphic in some respects with *Prosopiscus* (Rennie 1930, pl. 10, fig. 12). In its glabellar furrows and pygidial features *Typhloniscus* is clearly a phacopid derivative, and there is no question of classifying it with *Prosopiscus*. It is interesting to observe, though, that the manner of eye loss appears to have been similar in both genera: forward migration of the facial sutures and (presumably) eventual elimination of the ocular part of the fixed cheek. *Areia* in the Cheiruridae may have lost its eyes in the same way.

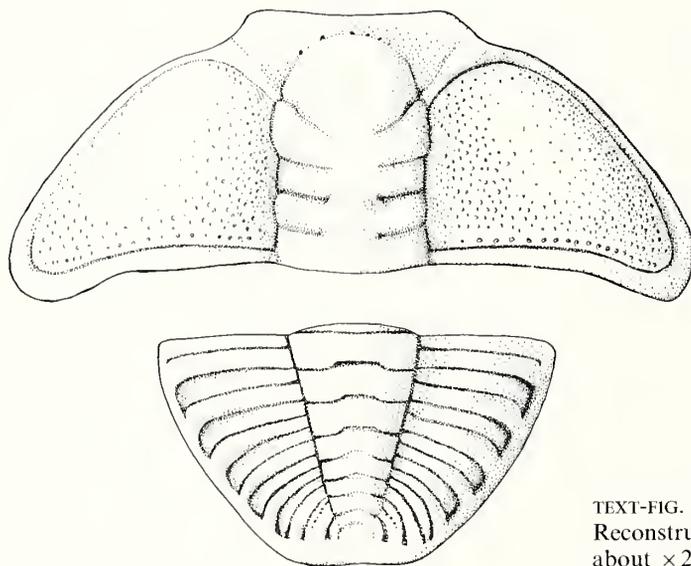
Prosopiscus praecox sp. nov.

Plate 46, figs. 1-6, 9; text-fig. 14

Diagnosis. *Prosopiscus* with glabella nearly parallel-sided; remnant eye ridges present; lateral border narrower than other species. Genal pitting very dense.

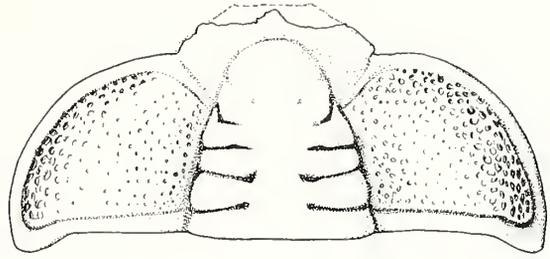
Derivation of name. Latin *praecox*, 'Spring', referring to its early appearance in the Nora Formation.

Holotype. Cranium, CPC 22762, from loc. 071/4.



TEXT-FIG. 14. *Prosopiscus praecox* sp. nov. Reconstruction of cephalon and pygidium, about $\times 2$.

TEXT-FIG. 15. *Prosopiscus minus* Salter. Reconstruction of the cephalon of the type species of *Prosopiscus*, based on fragments in the type collection in the British Museum (Natural History), about $\times 2$.



Other material. Cranidium, CPC 22763; pygidia, CPC 22764–22766, 22961.

Occurrence. Throughout most of Nora Formation, from locs. 071/4, 158/4, 158/9, 158/11.

Description. Cranidium deeply vaulted transversely, with lateral parts of cheeks steeply downsloping, and broad arch about the mid-line. Cheeks about one and a half times the maximum width of glabella, which is elevated above the cheeks rather than sunk between them, as in species such as *P. rugosus* Lu. Glabella almost parallel-sided, though with a tendency for the 3L lobe to bulge outwards slightly into axial furrow; frontal lobe with semicircular outline. First pair of furrows on glabella interpreted as lateral parts of occipital furrow, very shallow over mid-part of axis. Lateral glabellar furrows likewise extend far into glabella, defining a median glabellar lobe only about one-quarter width of glabella. 1P and 2P transverse (inner end of 1P deepened into an apodeme), glabellar lobe 2L slightly shorter (exsag.) than 1L. 3L is longer than either, adjacent to axial furrow, slightly inflated, delimited by 3P furrow which slopes inwards quite strongly, and is gently sigmoidal. Axial and preglabellar furrows nowhere deep, except for hypostomal pit, but there are four or five pits in the preglabellar furrow. Eye ridge almost continuing line of 3P glabellar furrow, furrow defining its posterior edge much the deeper, and continuing without a break into lateral border furrow. Although the eye ridge is slightly wider where it joins the border there is no palpebral lobe. Area in front of eye ridge continuous with cranidial anterior border (although the posterior part may well have a genal origin), which is narrowest medially and broadly 'rolled'. Anterior view shows a short section (Pl. 46, fig. 2) of the presumed facial suture terminating the anterolateral edge of the border. The question of whether a free cheek was present, and its probable extent, has been touched upon above. Lateral border narrow, no wider than the eye ridge; posterior border about twice as wide as lateral; genal angle rounded. Borders appear to lack the dense granulation that occurs everywhere else. Cheeks alone are densely pitted; the largest pits are concentrated in a line of about fifteen pits a little in front of the very narrow posterior border furrow.

Pygidia assigned here are two-thirds as long as wide, with slightly elevated axis, and distal part of pleural fields deeply downsloping. External mould shows seven segments clearly defined, and an eighth only indicated. Axis tapers gently almost to border, with seven rings and a small terminal piece. Long, narrow pleural furrows divide each segment into anterior and posterior bands, of which the anterior only merges with the slightly convex border. Posterior bands are sharply marked off from border by deep furrows. Narrow border widens and becomes more rounded where arched upward about mid-line. Internal moulds show that doublure was ventrally correspondent with border, forming marginal tube, widest posteriorly.

Discussion. The type species of *Prosopiscus*, *P. minus*, was redescribed by Reed (1912); the type material is fragmentary. We have used it as the basis for a new reconstruction shown in text-fig. 15. Compared with *P. praecox*, the borders are much wider and the glabella tapers strongly, differences which also apply to the several younger species figured by Lu (1975). The closest species is *P. edgarensis* Legg, 1976 (pl. 6, figs. 30, 35) from the early Llanvirn of the Canning Basin, north-western Australia. The specimens used to found this species are small and flattened, hence comparison is difficult with our material, but several differences are shown, not all accountable to preservation or size. The posterior border furrow of *P. edgarensis* is comparatively deep and wide, while the genal pitting is coarse. No lateral border is shown on the cranidia figured by Legg and according to him the border on this species is entirely librigenal: free cheeks 'narrow (tr.) and almost entirely consist of border only' (ibid., p. 23). *P. latus* Lu, in Lu and Chang 1974 from the late Arenig of south-west China, has a broad lateral cephalic border, and an acutely triangular pygidium with feeble interpleural furrows.

Our assignment of the pygidium to *P. praecox* is based on the following assumptions: having matched other pygidia and cranidia in the fauna, we were left with two kinds of *Prosopiscus* cranidia, and two types of pygidia, in approximately equal abundance scattered through the Nora Formation; the assumption that they belonged together seems reasonable. On morphology the assignment is consistent: low axial convexity is matched by glabella and pygidial axis, *P. praecox* has nearly horizontal fixigenal areas adaxially, distally turning downwards steeply, a profile which must have been reflected in the thorax, and which is shown also on the pygidium we assign to *P. praecox*. Note also that the axial arch along the mid-line is similar on cranidium and pygidium of *P. praecox*, and that the 'thickened' appearance of the anterior cranial border is matched also by the adaxial part of the pygidial border. The longer of the two types of pygidia was assigned to *P. praecox* because of its convexity and relatively narrow border; the wider type of pygidium was matched with *P. sp. A* (below), which is less convex, and with broad borders. Both are also generally similar to the pygidium in the complete specimen of *P. latus* Lu, in Lu and Chang 1974 (pl. 51, fig. 10).

Prosopiscus sp. A

Plate 46, figs. 7, 8, 10

Material. Cephalic shields, CPC 22767, 22768, 22962, 22963; pygidia, CPC 22769-22771, 22964-22966.

Occurrence. Nora Formation, locs. 071/4, 158/9, 308/1.

Discussion. Cephalic material of this species is insufficient to formally name it as new. It obviously differs from *P. praecox* in the following respects: (1) Lateral cephalic border is very broad; there is no question here of a narrow librigenal strip appearing dorsally and if there were any librigenal remnant it would have to be wholly ventral; overall cephalic convexity is lower than that of *P. praecox*. (2) Fixigenal pitting has about half the density of that on *P. praecox*; pits become large and sparse near lateral border. (3) Length (exsag.) of 2P glabellar lobe is relatively short in relation to 1P and 3P. (4) The pygidium is much more transverse and less convex than that assigned to *P. praecox*; only four (faint fifth) axial rings are present; pygidial pleural regions are greatly effaced compared with *P. praecox* and only the anterior segment is clearly defined. None the less the basic similarity of construction of the pygidia of the two species is apparent in the form of the borders and axial rings; internal moulds of pygidia of *P. sp. A* show similar pleural morphology to that observed on *P. praecox* dorsally.

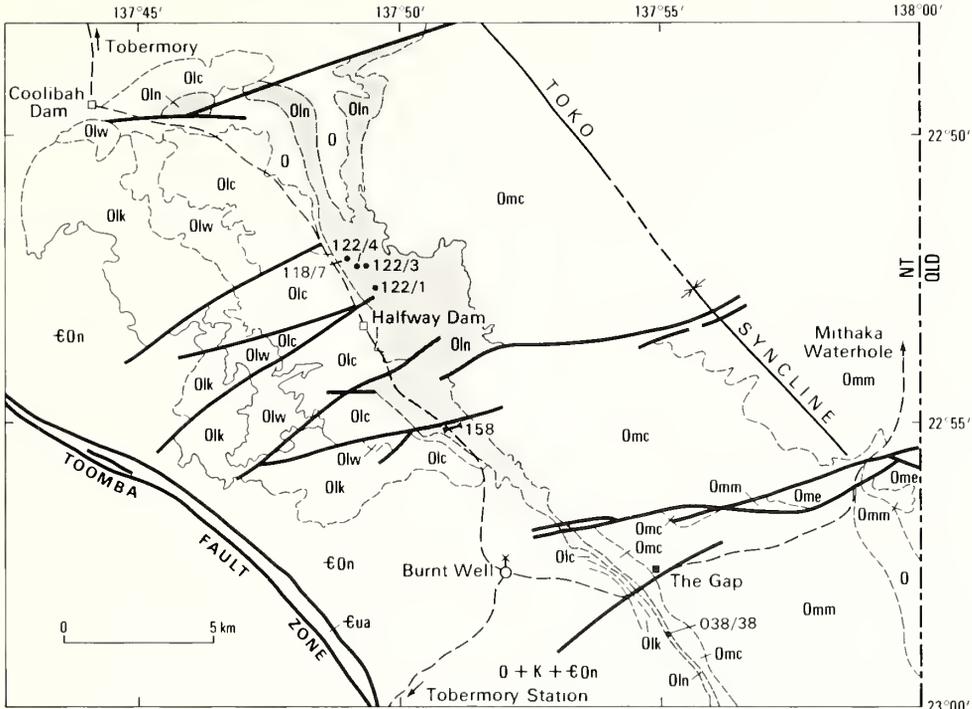
LOCALITY INFORMATION

Material described here has been collected from both single samples and measured sections, principally on the Toko, Abudda Lakes, and Mount Whelan 1:100 000 Geological Series Sheets, numbers 6452, 6551, and 6651, respectively. These sheets form portions of the Tobermory and Mount Whelan 1:250 000 Geological Series Sheets, SF/53-12 and SF/54-13, respectively. Localities are given grid references from the 1:100 000 scale series, and additional geographic references for location where only 1:250 000 scale sheets are available. They are listed numerically.

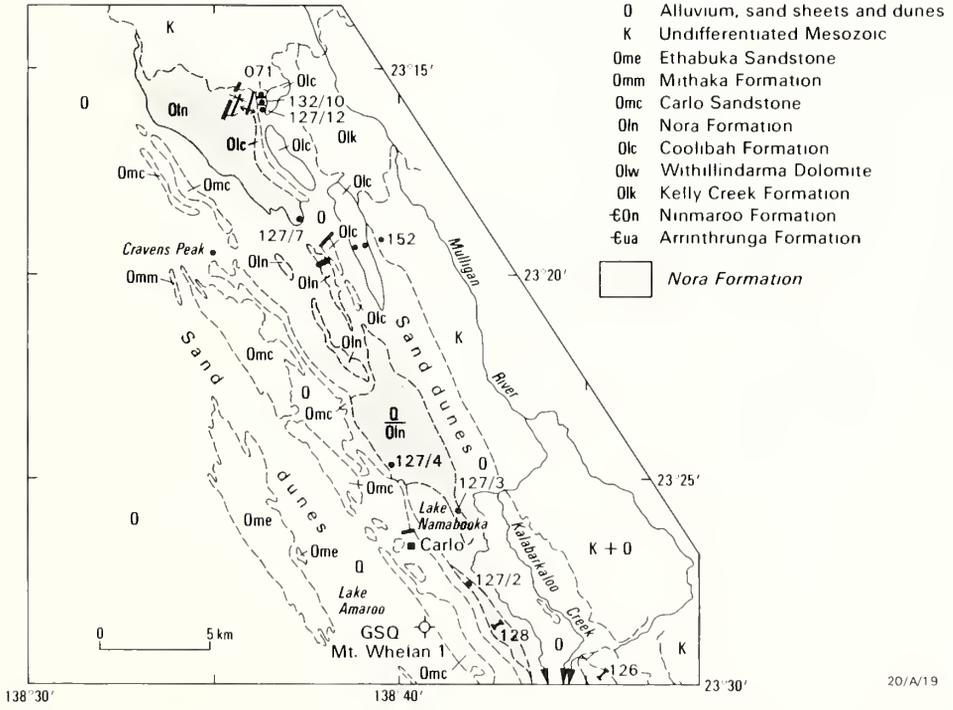
Locality 015/6: this refers to Stop 15 on the 1976 International Geological Congress field Excursion 4C (Shergold *et al.* 1976, p. 25, fig. 13), and is referred to more fully under Section 158 below. Samples numbered 015/6, 158/4, and 308/1 are all from the same layer.

Locality 038/38: specimens prefixed 038 are from spot sampling on the Toko and Neeyamba Hill 1:100 000 Geological Sheets 6452 and 6552, respectively. Sample 038/38 (text-fig. 16) is on the Toko Sheet at grid reference 79950 74563, geographic coordinates lat. 22°58'24" S. and long. 137°55'10" E., 6 km ESE of Burnt Well and 1.5 km SSE of The Gap Outstation. Brachiopods, bivalves, and gastropods occur with *Presbynileus* cf. *P. utahensis* in quartz sandstones from the upper part of the Nora Formation.

Section 071: Syncline (text-fig. 17), 14.5 km WSW of Rocky Waterhole, and 7.5 km due N. of Cravens Peak Homestead, Mount Whelan 1:100 000 Sheet, grid reference 25500 74256, geographic coordinates lat. 23° 15' 34" S., long. 138° 36' 19" E., containing a short sequence at the boundary between Coolibah Limestone and Nora Formation. At this locality the basal Nora Formation comprises poorly outcropping coarse pebbly



TEXT-FIG. 16. Detailed locality map for the Nora Formation in the Toko syncline. For key see text-fig. 17 below.



TEXT-FIG. 17. Detailed locality map for the Nora Formation in the Carlo-Cravens Peak district.

skeletal grainstone layers, interbedded with fine sandstone and siltstone, and generally concealed below alluvium. The following trilobite fauna occurs with gastropods, rostroconchs, bivalves, nautiloids, ostracodes, and an eocrinoid: *Amamitella strigifrons*, *Carolinites genacinaca*, *Prosopiscus praecox*, *P. sp. A.*, *Norasaphus (Norasaphus) skalis*, *Lycophron sp. A.*, *Phorocephala sp. aff. P. genalata*, and *Hungioides acutinasus*.

Section 118: 25 m sequence of fossiliferous grainstone overlain by fine-grained sandstone, 2 km N. of Halfway Dam, Toko Range 1:100 000 Sheet area. Horizon 118/7: sandstone containing *L. rex*, *C. cf. ekphymosus* (text-fig. 16), lying 21.5 m above base of section at geographic coordinates lat. 22°51'28" S., long. 137°48'46" E., lower part of Nora Formation.

Localities 122/1, 122/3, and 122/4 (text-fig. 16) refer to spot samples taken in the vicinity of Halfway Dam on the Toko 1:100 000 Sheet (text-fig. 16). 122/1 is 1.10 km ENE of Halfway Dam at grid reference 78980 74672, and geographic coordinates lat. 22°52'37" S., long. 137°49'29" E. 122/3 is 1.7 km N. of Halfway Dam at 78960 74679, lat. 22°52'23" S., long. 137°49'2" E. 122/4 is 1.8 km N. of Halfway Dam at 78920 74679, lat. 22°52'28" S., long. 137°48'42" E. Fine-grained sandstones occur at all three localities in the lower part of the Nora Formation, and these contain brachiopods, gastropods, nautiloids, and bivalves, together with *L. rex* (122/1, 122/3), *Fitzroyaspis irritans* (122/4), *N. (Norasaphites) monrocae* (122/1?), *N. (N.) vesiculosus* (122/1, 122/4), and *H. acutinasus* (122/1).

Section 126: this section (text-fig. 17) is located 10.5 km SE of Carlo Homestead, at grid reference 27110 73999 and geographic coordinates lat. 23°29'31" S., long. 138°45'20" E., on the Mount Whelan 1:100 000 Sheet. Some 20 m of varicoloured siltstone and sandstone layers are separated by intervals of no outcrop. Stratigraphically, the section is thought to lie slightly above that exposed at 071. Nautiloids, bivalves, brachiopods, ostracodes, and ichnofossils are associated with *L. rex* (126/1, 126/2, 126/3, 126/5), *H. acutinasus* (126/1, 126/3, 126/4, 126/5, 126/11), *A. strigifrons* (126/3), *C. cf. C. ekphymosus* (126/3, 126/4), *Nambeetella embolion* (126/3, 126/4, 126/5, 126/6, 126/7), *Presbnyileus cf. P. utahensis* (126/7), *F. irritans* (126/7), and *Norasaphus (Norasaphites) vesiculosus* (126/1, 126/2, 126/3, 126/4, 126/5, 126/6, 126/7, 126/11).

Localities prefixed 127 refer to spot samples collected along the length of the Toomba Range and western portion of the Toko Syncline.

127/2: spot sample located immediately S. of Lake Namabooka, 3 km SE of Carlo Homestead, Mount Whelan 1:100 000 Sheet area, grid reference 26450 74040, geographic coordinates lat. 23°27'30" S., long. 138°41'42" E. Fine-grained sandstone has yielded bivalves and *N. (Norasaphus) skalis*.

127/3: sample collected on eastern side of Lake Namabooka, 1.9 km NE of Carlo Homestead, Mount Whelan 1:100 000 Sheet area, grid reference 26370 74070, geographic coordinates lat. 23°25'45" S., long. 138°41'8" E. Fine-grained sandstone contains ichnofossils and *Phorocephala sp. aff. P. genalata*.

127/4: locality situated approximately 3 km N. of Carlo Homestead, Mount Whelan 1:100 000 Sheet area, grid reference 26110 74090, geographic coordinates lat. 23°16'30" S., long. 138°39'55" E. Fine-grained sandstone contains ichnofossils and *N. (N.) skalis*.

127/7: a spot sample 4.4 km NE of Cravens Peak Homestead, Mount Whelan 1:100 000 Sheet area, at grid reference 25700 74200, geographic coordinates lat. 23°18'35" S., long. 138°37'22" E. The locality contains a sequence of sandstone with calcareous lenses in the lower part of the Nora Formation. Ostracodes and bivalves occur with *L. rex* and *Nambeetella embolion*, and the conodonts *Trigonodus* and *Drepanoistodus* spp.

127/12: this locality is adjacent to 132/10 at the southern end of the synclinal structure 1 km S. of section 071, at grid reference 25500 74250, geographic coordinates lat. 23°16'18" S., long. 138°36'30" E. (text-fig. 17), Mount Whelan 1:100 000 Sheet area. Varyingly indurated, lateritized sandstone, siltstone, and carbonate occurs at these localities. Nautiloids and a bivalve are associated with *L. rex* and *Norasaphus (Norasaphus) skalis*.

127/15: spot sample at S. end of Ilanama Swamp, 21.5 km NW of Cravens Peak Homestead, Mount Whelan 1:100 000 Sheet area, grid reference 24520 74387, geographic coordinates lat. 23°8'22" S., long. 138°30'41" E. Fine-grained sandstone contains ichnofossils, brachiopods, nautiloids, and *N. (N.) skalis*.

Locality 132/10: see 127/12 (above).

Locality 139/4: this locality lies at the SE corner of Ilanama Swamp, 22.3 km NNW of Cravens Peak Homestead, Mount Whelan 1:100 000 Sheet area, at grid reference 24550 74394, geographic coordinates lat. 23°8'0" S., long. 138°30'55" E. A skeletal, peloidal clast grainstone sequence about 10 m thick, contains brachiopods, bivalves, and *N. (Norasaphites) vesiculosus*.

Section 152: this is a long and discontinuous line of section running from the top of the Kelly Creek Formation (152/1) into the lower Nora Formation (152/10), commencing 7.5 km due east of Cravens Peak outstation and terminating 4.2 km from the same (text-fig. 17), on the Mount Whelan 1:100 000 Sheet, grid reference 26050 74192 to 25770 74180, geographic coordinates for 152/9, lat. 23°19'37" S., long. 138°37'55" E. Locality

152/9 comprises varying indurated micaceous sandstone containing bivalves, nautiloids, and brachiopods associated with *L. rex* and *H. acutinasus*, and two species of the conodont *Trigonodus*.

Section 156: this section line runs from the Coolibah to the Nora Formation, commencing 7.5 km WSW of Mount Harriet on the Abudda Lakes 1:100 000 Sheet area, grid references 20350 74176 to 20280 74177, and geographic coordinates approximately lat. 23°19'23" S., long. 138°5'40" E. to lat. 23°19'28" S., long. 138°6'4" E. Nora Formation comprises some 42 m of quartz sandstone and skeletal pelletal grainstone yielding brachiopods and *N. (N.) vesiculosus* throughout.

Section 158: this section (text-fig. 16) was initially spot sampled and the numbers 308/1, 308/2, and 015 also refer to it. Section 158 is located 5 km NNW of Burnt Well, and 8.5 km NW of The Gap outstation in the Toko 1:100 000 Sheet area, grid references 79180 74625 to 79420 74625, and geographic coordinates lat. 22°55'8" S., long. 137°50'43" E. to lat. 22°55'5" S., long. 137°51'2" E. The section (see also Shergold *et al.* 1976, p. 25, fig. 13) exposes some 26 m of resistant ferruginized carbonate layers significantly devoid of trilobites, overlain by a further 30–40 m of flaggy bedded sandstone and siltstone with occasionally more calcareous interlayers, now decalcified, which contain the richest faunas (e.g. horizon 158/4, = 308/1, = 015/6). These sandstones represent the lower portion of the upper Nora Formation. A variety of molluscs, bivalves, gastropods, a rostroconch, and brachiopods occur on section 158. Trilobites, occurring in the interval between 26–40 m, include *A. brachyops*, *C. cf. C. ekphymosus*, *F. irritans*, *Gogoella brevis*, *H. acutinasus*, *L. rex*, *N. (N.) monroae*, *N. (N.) vesiculosus*, *Presbynielus cf. P. utahensis*, *Prosopiscus praecox*, and *P. sp. A.*

Localities 308/1 and 308/2: see section 158 (text-fig. 16) above.

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THE UPPER CARBONIFEROUS TETRAPOD ASSEMBLAGE FROM NEWSHAM, NORTHUMBERLAND

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ABSTRACT. The Upper Carboniferous amphibians from Newsham in Northumberland constitute one of only five large, compact tetrapod assemblages known from the Westphalian of Europe and North America. The environment in which the Newsham tetrapods were preserved appears to have been a large and deep freshwater lake occupying a stretch of abandoned river channel. The lake was apparently surrounded by swamp-forest dominated by arborescent lycopods; sphenopsids, including *Calamites*, probably grew around its shoreline.

A revised list of the (eight) Newsham tetrapods which are certainly determinate at least to family level is presented. Specimens probably representing three additional species, including a colosteid temnospondyl, are described. A census of tetrapod specimens from the site facilitates distinction of the abundant endemic species from those representing erratics from environments other than that in which they were preserved. The eogyrinid embolomere *Eogyrinus attheyi* Watson, the loxommatid *Megalocephalus pachycephalus* (Barkas) and the keraterpetontid nectridean *Batrachiderpeton reticulatum* (Hancock & Atthey) seem to have been endemic in life to the Newsham lake. The aistopod *Ophiderpeton nanum* Hancock and Atthey, a lysorophid and a urocorylid nectridean are each represented by only a single specimen and are regarded as possible erratics from water bodies smaller and shallower than the Newsham lake. The colosteid specimen is probably also derived from a shallow-water/swamp-lake environment, as may be the material representative of the medium-sized eogyrinid *Pteroplax cornutus* Hancock and Atthey. The only Newsham tetrapod which appears to represent an erratic from a terrestrial/marginal environment is the anthracosaurid embolomere *Anthracosaurus russelli* Huxley.

The structure of the, fish-dominated, open-water/lacustrine community which includes the three endemic Newsham tetrapod species is briefly discussed. Finally, the Newsham assemblage is compared with the only other large, compact tetrapod assemblage of Westphalian B age known, that from Joggins in Nova Scotia. In direct contrast to those known from Newsham, the Joggins tetrapods appear to represent only the more terrestrial elements of the Westphalian B lowland tetrapod fauna of the southern margin of Laurasia. It is therefore suggested that, in view of their close contemporaneity, the assemblages from Newsham and Joggins may be regarded as complementary.

TETRAPOD fossils of Carboniferous age are of rare occurrence and have so far been recorded only from Europe and North America. Within the Westphalian stage of the Upper Carboniferous, only five large, compact tetrapod assemblages are known (A. R. Milner 1980*b*). Two, those from Linton, Ohio, and Nýřany in Czechoslovakia, are of upper Westphalian D age. The assemblage from Jarrow, Eire, is from the middle Westphalian A and the remaining two, from Joggins, Nova Scotia, and Newsham, Northumberland, are both lower Westphalian B in age (data from Rayner 1971, which see for further stratigraphic and palaeoenvironmental details). The Newsham amphibians are of particular importance as constituting the largest taxonomically diverse assemblage of well-preserved tetrapods yet yielded by the Westphalian Coal Measures of the north-west European paralic belt.

Tetrapod specimens from Newsham were first recorded by Kirkby and Atthey (1864), who figured (as '*Rhizodus lanciformis*') a skull fragment of the loxommatid amphibian *Megalocephalus*. Further tetrapod material was described by Hancock and Atthey (1868, 1869*a, b*, 1870*a, b*, 1871*a*), Barkas (1873), Embleton and Atthey (1874), Atthey (1876, 1877, 1884) and Embleton (1889). Much of the loxommatid and eogyrinid material was described by Watson (1912, 1926), who also gave a detailed account of the Newsham keraterpetontid nectridean *Batrachiderpeton* (Watson 1913). With the exception of a short description of the sole recorded Newsham aistopod specimen by Steen (1938),

subsequent work on the tetrapods from the site has been confined to the past two decades. The eogyrinid embolomeres have been restudied by Panchen (1964, 1966, 1970, 1972) and Boyd (1978, 1980a), *Megalocephalus* by Beaumont (1971, 1977), the keraterpetontid material by A. C. Milner (1978, 1980) and the aïstopod by Boyd (1982a). Specimens representing three taxa hitherto unrecorded from the site have also recently been described. These comprise a lysorophid 'lepospondyl' (Boyd 1980b), the anthracosaurid embolomere *Anthracosaurus* (Panchen 1981), and a urocordylid nectridean (Boyd 1982b).

Most previous publications on the Newsham tetrapods have been morphological and taxonomic studies of individual taxa. Comparison with other Westphalian tetrapod assemblages has been hampered by the fact that the Newsham assemblage has never been reviewed in detail as a single entity and no precise information as to the relative frequency of the species represented has been published. In the present paper the nature of the palaeoenvironment in which the Newsham tetrapods were preserved is considered and the, hitherto unpublished, plant and invertebrate material from the site is briefly described. A revised list of the tetrapod taxa so far recorded from Newsham is given and specimens probably representing three further amphibian taxa are described. A census of Newsham tetrapod specimens follows and an attempt is made to identify ecological associations within the assemblage, employing the methods used by A. R. Milner (1980b) in his study of the Nýřany tetrapods. Finally, the Newsham assemblage is compared with the only other large, compact assemblage of Westphalian B tetrapods known, that from Joggins in Nova Scotia.

The following abbreviations are used for institutions and organizations in this work: BRM, Bradford Museums; BM[NH], British Museum (Natural History); IGS, Institute of Geological Sciences; NCB, National Coal Board; RSM, Royal Scottish Museum, Edinburgh. All specimens referred to by museum registration numbers without one of the above institutional prefixes are in the Hancock Museum, Newcastle upon Tyne.

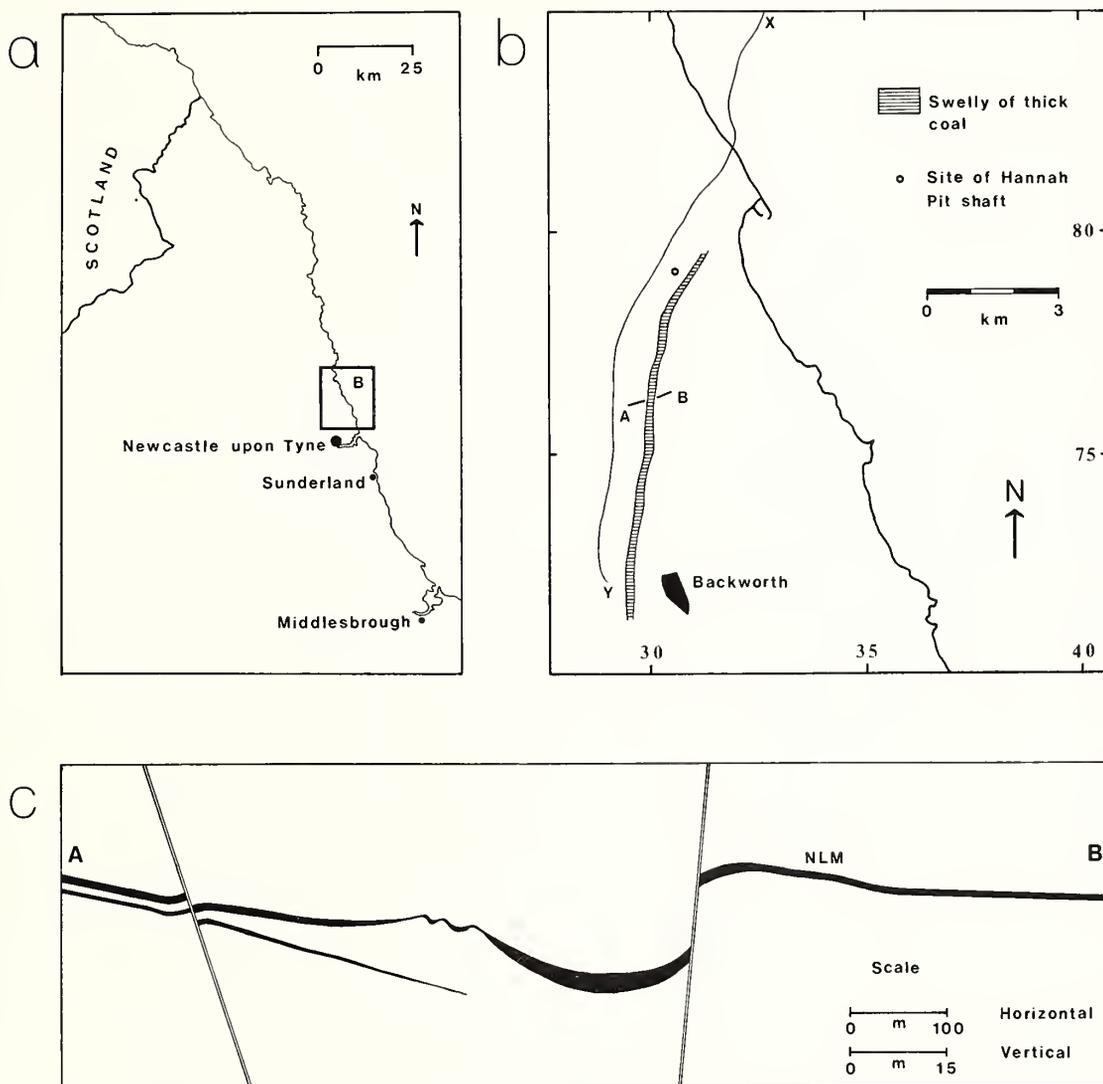
PALAEOENVIRONMENT

The Newsham tetrapod assemblage was collected entirely from the workings of Hannah Pit, Newsham Colliery (NZ 306791), which was situated at South Newsham, approximately 1 km south of Blyth in Northumberland. Hannah Pit was sunk in 1860 and remained operational until 1914; however, most of the vertebrate specimens known from the site were collected prior to 1880, by the amateur palaeontologist Thomas Atthey. All are from a bed of black shale immediately overlying the Northumberland Low Main Seam. This horizon lies within the upper *Modiolaris* non-marine lamellibranch zone of the Middle Coal Measures (Land 1974) and is lower Westphalian B in age. During the Westphalian the Newsham area formed a small part of the Pennine depositional province, itself a part of the north-west European paralic belt (Calver 1969).

The shale in which the Newsham tetrapods are preserved is a highly carbonaceous sediment, always well bedded and having, according to Atthey (1877), a thickness of between 7.5 cm and 10 cm. Pyrite is abundant in the shale and is often closely associated with the vertebrate specimens. The presence of pyrite and the high organic content of the shale suggest deposition as an anaerobic sapropel, either in the centre of a lake or during a period of low input of inorganic detritus. As Panchen (1970, p. 66) has noted, the presence of xenacanth and other sharks at Newsham suggests that the surface waters, at least, were adequately oxygenated and the lake may have been thermally stratified, with a warm aerobic epilimnium and a cooler anaerobic hypolimnium.

The lateral extent of the highly fossiliferous area of the black shale worked at Newsham is not certainly known. However, a clue to the nature and extent of the lake in which it was deposited may be afforded by the presence, in the Newsham area, of a linear trough-like 'swelly' of thick coal within the Low Main Seam. The recorded length of this structure, which ranges between approximately 120 m and 185 m in width, extends some 8 km southward from Newsham to the vicinity of Backworth (text-fig. 1b). The 'swelly' appears to terminate at its northern end in the Newsham area, but its southern end has not been explored. The structure of the 'swelly' will be apparent from text-figure 1c. About 0.8 km west of the structure the seam, here between 1.2 m and 1.8 m thick, splits. The lower leaf

thins out completely before reaching the 'swelly'. The upper leaf also thins, to between 0.4 m and 0.9 m, before thickening into the 'swelly' itself (data from Land 1974, p. 59). The 'swelly' has been described by Hurst (1860), who pointed out that strata above and below it are not affected and attributed it to pencontemporaneous deformation, and by Land (1974). The latter, although arriving at no firm conclusion as to the origin of the structure, noted that its direction is in line with that of contemporary depositional currents. Interestingly, Elliot (1965) has described almost precisely similar 'swilleys' [*sic*] within seams in the *Modiolaris* and *Similis-pulchra* zones of the



TEXT-FIG. 1. Location and structure of 'swelly' in Northumberland Low Main Seam. A, Map of north-east England showing area (B) covered by text-fig. 1b. B, Map of the Newsham area showing recorded course of 'swelly' and site of Hannah Pit shaft. Line X-Y indicates course of split in seam to west of 'swelly' (after Land 1974). C, Section through 'swelly' between points A and B on text-fig. 1b. Double lines represent faults (after Hurst 1860). NLM, Northumberland Low Main Seam.

Nottinghamshire Coal Measures. These are convincingly demonstrated by Elliot to represent river courses which became established and were abandoned within the period of deposition of the seams concerned. It seems very likely that the Newsham 'swelly' originated in this manner and that, after reflooding (presumably due to local subsidence) of the old channel to submerge the peat which had accumulated therein since its abandonment, the linear lake thus formed was the environment of preservation of the Newsham tetrapods. It is particularly interesting to note that in the Nottinghamshire Abdy Seam 'swilley' described by Elliot (1965) the thick coal of the 'swilley' trough is roofed by a dark pyritic shale containing fish and lamellibranch fragments. That the trough coal of the Newsham 'swelly' was, at least in certain areas, also roofed by a black shale is evidenced by the strata recorded in the shafts of A and B Pits, Seaton Delaval Colliery (NZ 299 763), which were sunk to the Low Main Seam where it forms the western slope of the 'swelly' trough (Borings and Sinkings 1878-1910, no. 1691).

Unfortunately, it is not certain that the Newsham vertebrates were collected from the roofing shale associated with the thick coal of the 'swelly' trough. The 1893 Abandonment Plan (NCB No. 8566) of the Newsham Colliery Low Main Seam workings indicates that Hannah Pit did work the 'swelly' coal, but the writer has been unable to trace any documentary or other evidence linking the 'swelly' and the vertebrate material. Mining in the area has now ceased, precluding the possibility of examining the 'swelly' underground. However, the occurrence within the workings of one small colliery of a large assemblage of (mostly aquatic) vertebrates and a structure interpretable as an abandoned stretch of river channel is a very remarkable coincidence if the two were not directly associated.

As Panchen (1970) and A. R. Milner (1980*b*) have pointed out, the presence at Newsham of the large embolomere *Eogyrinus* and of crossopterygians up to 6 m long implies a lake large and open enough to sustain the biomass required for the support of such large ultimate consumers. The size of some of the, apparently endemic, vertebrates and the presumed thermal stratification also suggest a water-body of some depth. It will therefore be assumed in the present study that the Newsham vertebrates were preserved in the bottom sediments of a single large lake. However, as Hannah Pit worked approximately the northernmost 1.5 km of the 'swelly's' recorded length it is conceivable that two or more adjacent lakes may have been involved.

Invertebrates. The only invertebrate specimens from the Newsham black shale which are known to the writer pertain to ostracods and the bivalve genus *Naiadites*. All are preserved on two small shale slabs, in the Hancock Museum. G162.46 bears several fragmentary *Naiadites* specimens and ostracods representing two species of *Carbonita*; all are too poorly preserved for specific identification. G162.47 bears a single specimen of *Carbonita* cf. *humilis* (Jones and Kirkby) and a second ostracod referable to *Geisina*. The presence of *Carbonita* is of some importance as an indicator of the salinity of the Newsham lake. Whereas *Geisina* is known to have been tolerant of very brackish (and occasionally marine) conditions within the Coal Measures (Calver 1968), *Carbonita* species appear to have been oligohaline, tolerating only fresh to slightly brackish water (Pollard 1966). *Naiadites* species seem to have been euryhaline and Calver (1968) has suggested that the members of this genus may have lived by byssal attachment to floating vegetation. Their presence in the area of deposition of the Newsham black shale, even as living individuals, is thus not necessarily ruled out by the presumed low oxygen tension of the bottom sediments and hypolimnium. None of the, several hundred, specimens of the Newsham black shale examined by the writer shows any convincing evidence of the activity of benthonic invertebrates. In view of the nature of the sediment it is likely that this absence reflects a genuine scarcity of benthonic animal life in the area of its deposition.

Plants. The Atthey collection in the Hancock Museum includes a suite of undescribed plant specimens from the Newsham black shale. Of the seventy specimens examined by the writer, fifty-one are determinate at least to generic level. The high proportion of well-preserved, and hence determinate, specimens in the sample may, however, merely reflect collector bias. The taxa present are listed below; the values in brackets indicate the number of specimens present.

LYCOPSIDA

Sigillaria tessellata (1)
Sigillaria sp. (3)
Lepidophloios acerosus (3)
Lepidodendron aculeatum (3)
Lepidodendron sp. (3)
Lepidostrobus sp. (23)

SPHENOPSIDA

Calamites cisti (1)
Calamites sp. (11)

PTERIDOSPERMS

Trigonocarpus sp. (3)

With the exception of three *Calamites* specimens (notably G162.45) preserved as pith-casts in a micaceous siltstone, all are compression fossils. The lycopod material, apart from the well-preserved and usually entire strobili, consists of leafy shoots and fragments of large branches. The *Calamites* specimens all represent lengths, mostly less than 10 cm, of stem or branch.

Scott (1977, 1979, 1980) has emphasized the need to relate fossil plant assemblages to depositional environments, and to consider the possible transport history of specimens, before attempting interpretation of the assemblages in terms of the communities they derive from. In the case of the known Newsham plant material it seems likely that most of the specimens represent the flora of the lake margins and have undergone minimal transport. This is suggested by:

1. The well-preserved nature and large size of many of the plant fragments.
2. The relatively large number of intact lycopod strobili.
3. The paucity of taxa represented.

There is, moreover, much evidence to suggest that arborescent lycopods comprised the dominant flora of Westphalian swamp-forests and that *Calamites* grew around the margins of lakes (Scott 1979, 1980).

Nonetheless, the *Calamites* specimens preserved as siltstone pith-casts embedded in the black shale were presumably transported some distance. The same may apply to the pteridosperm seeds; only three are present in the sample and these were probably the parts of the plants in question best suited to surviving transport in a recognizable form. In addition, Scott (1980) has noted that pteridosperms appear to have been characteristic inhabitants of river flood-plains and levée banks in the Westphalian. A swamp-forest or lake margin origin for the Newsham *Trigonocarpus* specimens thus appears unlikely.

The nature of the small lenticular structures from Newsham, described by Hancock and Atthey (1869c) as fungi (*Archagaricon* spp.), is uncertain and the material needs re-study.

Fishes. Most of the known Newsham vertebrate material pertains to fishes, which dominate the total assemblage from the site in terms of both number of specimens and number of species represented. Much of the Newsham fish assemblage needs re-study, but a list of twenty-five of the twenty-eight species so far reported from the site has been given by Dr. S. M. Andrews (*in Land* 1974, p. 61); the remaining three species, all haplolepid actinopterygians, were described by Westoll (1944). In addition to the haplolepids, the fish assemblage includes palaeoniscoid and platysomoid palaeoniscids, dipnoans (currently being studied by Dr. T. R. Smithson (University of Newcastle upon Tyne)), rhizodontid and osteolepid crossopterygians, the coelacanth *Rhabdoderma*, climatiid and ischnacanthid acanthodians and a number of elasmobranch genera.

In summary, the environment of preservation of the Newsham tetrapods appears to have been a large and deep freshwater lake of linear shape (but unknown length), occupying a stretch of abandoned river channel in which peat had previously accumulated. Many species of fish inhabited the lake, as did ostracods and, possibly, the bivalve *Naiadites*. The lake was probably surrounded by swamp-forest, composed largely of arborescent lycopods and sphenopsids; the latter may have been especially abundant around the shoreline.

THE TETRAPOD ASSEMBLAGE

Eight tetrapod species, all amphibians, have so far been described from Newsham:

Order TEMNOSPONDYLI

Loxommatidae: *Megalocephalus pachycephalus* (Barkas, 1873)

Note. The above 'traditional' classification of the Loxommatidae as a family of the Order Temnospondyli is for convenience of listing only, and should not be taken to indicate disagreement with the recent suggestions of Panchen (1980) and Smithson (1982) that the Loxommatidae as a whole should be removed from this order.

Order BATRACHOSAURIA (*sensu* Panchen 1980)

Eogyrinidae: *Pteroplax cornutus* Hancock and Atthey, 1868

Eogyrinus attheyi Watson, 1926

Anthracosauridae: *Anthracosaurus russelli* Huxley, 1863

Order NECTRIDEA

Keraterpetontidae: *Batrachiderpeton reticulatum* (Hancock and Atthey, 1869)

Urocordylidae: Urocordylid *gen. et sp. indet.*

Order AISTOPODA

Ophiderpetontidae: *Ophiderpeton nanum* Hancock and Atthey, 1868

Order LYSOROPHIA

Lysorophidae: Lysorophid *gen. et sp. indet.*

However, three further amphibian species from Newsham appear to be represented, each by a single specimen, in the collections of the Hancock Museum. Although none is strictly determinate, even to family level, they will now be described for the sake of completeness.

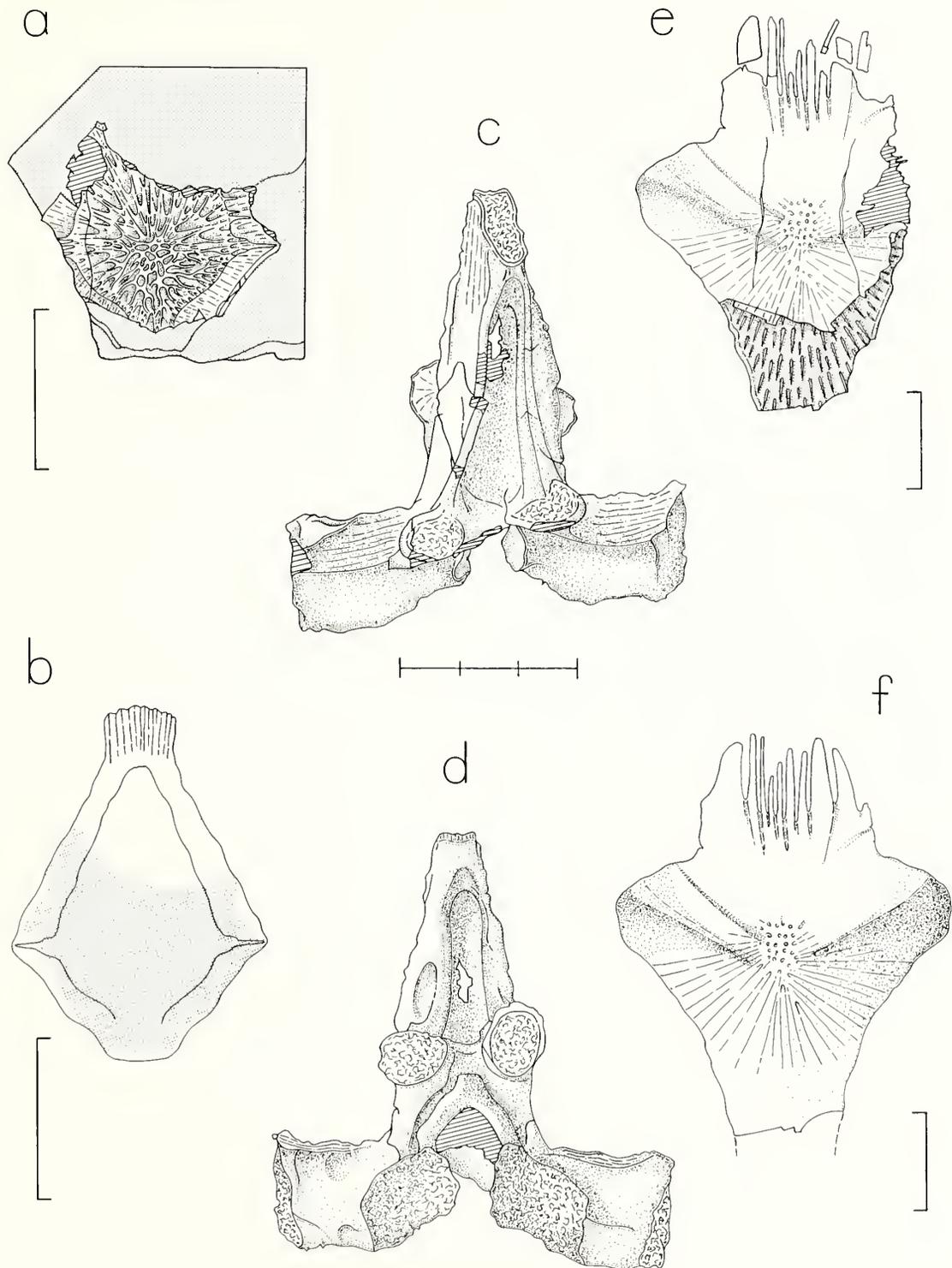
Order TEMNOSPONDYLI

?Colosteidae: colosteid *gen. et sp. indet.*

Specimen G24.98 consists of an incomplete interclavicle preserved with its ventral surface exposed on a small slab of shale (text-fig. 2a). The anterior, posterior and right lateral extremities of the element are absent. The form of the posterior part is, however, apparent from an impression in the matrix and the right lateral extremity may confidently be restored as the mirror-image of the left. Except on the clearly defined, anterolateral, areas of clavicular overlap and on the narrower posterolateral marginal areas, the interclavicle bears a well-developed ornament of pits and ridges radiating from the presumed centre of ossification of the bone. Near the ossification centre, the pits are circular or oval and completely enclosed. Towards the margins of the element, however, the pits become more elongate and are deepest mesially, becoming shallower at their, open, distal ends. Bystrow (1935) has noted that differential growth of ornamented dermal bones produces elongation of the pits in the direction of the greatest growth rate. In G24.98, as preserved, the degree of elongation of the pits is greatest anterior to the centre of ossification, suggesting that the complete bone originally extended further in this direction than posteriorly.

G24.98 does not appear referable to any of the eight previously described Newsham amphibians which are determinate at least to family level. Its size is such that it could only have been derived from a very small juvenile of *Eogyrinus*, *Pteroplax*, *Anthracosaurus* or *Megalocephalus*. However, the nature of the ventral ornament would seem to preclude reference of G24.98 to any of the embolomeres. No certainly associated interclavicle has been described for *Megalocephalus*, but the ornament of G24.98 does not resemble the 'honeycomb' pit and ridge ornament characteristic of much of the dermal skull roof in this genus (Beaumont 1977, fig. 6). In addition, the well-ossified nature of the interclavicle and its well-developed ornament do not suggest that it derives from a very young animal. Nor is it likely that the specimen pertains to any of the four 'lepospondyl' species recorded from

TEXT-FIG. 2. Isolated skeletal elements of Newsham tetrapods. A-B, Interclavicle G24.98: A, As preserved. Stippling represents matrix; B, Restoration. Stippling represents area actually preserved (ornament omitted). C-D, neural arch G25.03 as preserved: C, Anterior view; D, posterior view. E-F, Interclavicle G94.65. E, As preserved. Stippling indicates area preserved as impression only. F, Restoration. All scale bars graduated in centimetres. Cross-hatching indicates broken bone surface.



Newsham. The interclavicle is not known for adult specimens of *Batrachiderpeton*, but the interclavicle of the juvenile figured by Watson (1913, text-fig. 167 (as '*Ceraterpeton*')) has the form of an antero-posteriorly elongate ovoid. Moreover, the dermal skull roof ornament of adult *Batrachiderpeton* specimens (e.g. Watson 1913, pl. XCVI) is very different from the ornament of G24.98. The Newsham urocordylid, represented in the study sample by only a single vertebra, appears to be a member of the *Ptyonius*-group of Bossy (1976), which comprises the described genera *Ptyonius*, *Urocordylus*, and *Ctenerpeton* (Boyd 1982b). The interclavicles of *Ptyonius* (Bossy 1976, fig. 57b) and *Urocordylus* (Bossy 1976, fig. 77b) are, like those of juvenile *Batrachiderpeton* specimens, ovoid in outline, tapering most acutely to their anterior ends. The ventral ornament in both cases differs from that of G24.98. No interclavicle has been described for *Ctenerpeton* but there is no reason to suppose it to have been radically different in form or ornament from those of *Ptyonius* and *Urocordylus*. Lysorophid limbs and limb-girdles are very small in relation to body size (e.g. Sollas 1920, fig. 1, Carroll and Gaskill 1978, fig. 132B) and G24.98 thus seems far too large to have pertained to a lysorophid of the dimensions of the single Newsham specimen (Boyd 1980b) representative of this group. An interclavicle may have been present in *Ophiderpeton nanum* (Boyd 1982a), but it seems unlikely that G24.98 could have been derived from an individual of this species. Although the only known specimen of *O. nanum* may be a juvenile which could have grown to a size compatible with the possession of an interclavicle of the dimensions of G24.98, the shape of the element tentatively identified as an interclavicle in this form (Boyd 1982a, fig. 1) does not resemble that of G24.98.

Specimen G24.98 does, however, appear closely to resemble the interclavicles known for members of the temnospondyl family Colosteidae. Colosteids have been described from the upper Viséan of Scotland (*Pholidogaster*: e.g. Panchen 1975), the upper Viséan or lower Namurian of West Virginia, U.S.A. (*Greererpeton*: e.g. Carroll 1980; Smithson 1982) and the Westphalian D of Linton, Ohio (*Colosteus*: e.g. Romer 1930). Their occurrence at Newsham would thus not be unexpected from a stratigraphic point of view. Moreover, the Westphalian A tetrapod assemblage from Jarrow, Eire, includes undescribed colosteid specimens, whose dimensions seem roughly compatible with those of G24.98 (A. R. Milner 1980a, p. 135 and pers. comm.).

Among points of particular resemblance between described colosteid interclavicles and G24.98 may be noted:

1. The nature, degree of development and distribution of the ventral ornament (e.g. Carroll 1980, fig. 2).
2. The proportions of the element, partly inferred in the case of G24.98, which extends further anterior to the point of maximum width than posterior to it (e.g. Romer 1930, fig. 8; Carroll 1980, fig. 2).
3. The distinctive shape of the posterior tip of the element, clearly indicated by an impression in the matrix in G24.98 (e.g. Romer 1930, fig. 8). The writer would, therefore, suggest that interclavicle G24.98 probably pertains to a colosteid temnospondyl. The restoration of the element (text-fig. 2b) is based on the form of the interclavicle in *Greererpeton* and *Colosteus*.

Order TEMNOSPONDYLI

Family *incertae sedis*

Specimen G25.03 is an isolated neural arch (text-fig. 2c-d) which, although otherwise well preserved, has suffered severe antero-posterior compression during preservation. In the course of this compression the anterior face of the arch has been shifted, in the morphologically vertical plane, relative to the posterior face, so that the dorsal edge of the neural spine now slopes downward from posterior to anterior. In addition, the diapophyses have been rotated in such a fashion that their originally antero-dorsal surfaces now face anteriorly.

The height of the neural spine, together with the form and span of the diapophyses, suggest, by comparison with *Eryops* (Moulton 1974), that the arch is that of an anterior dorsal vertebra. The neural spine is a high, narrow structure in its lateral aspect and is deeply excavated both anteriorly and posteriorly by an upwardly tapering groove. Dorsally, the anterior and posterior grooves are linked by a canal piercing the neural spine. The margins of the canal are irregular; whether it is entirely an artefact, produced by breakage of the very thin bone in this region, or a genuine supra-neural canal enlarged by damage to its periphery is uncertain. In view of its small size, the former seems the more likely explanation. The top of the neural spine is slightly expanded and terminates in an originally dorsally-directed, concave facet, whose irregular surface suggests a covering of cartilage in life. The facet may originally have abutted against a dermal ossification. Moulton (1974, p. 15) has noted that the expanded and rugose tips of the dorsal neural spines in mature *Eryops* specimens probably lay in the dermis. He points out, moreover, that in some cases their appearance suggests formation by fusion of the original spine tips with overlying osteoderms. The zygapophyses of G25.03 are large. Unfortunately the *post-mortem* compression of the specimen prevents determination of their original orientation.

Of the eight described Newsham amphibians determinate to family level, only the four 'labyrinthodont' species are large enough to have possessed neural arches of the dimensions of G25.03. The specimen is most unlikely to pertain to any of the embolomeres. The presacral neural spines of *Eogyrinus*, as evidenced by the

vertebrae associated with the lectotype of *E. attheyi* (G13.72), and of *Pteroplax*, as evidenced by the attributed vertebrae described by Boyd (1980a), differ markedly from G25.03. They are relatively short and more massive structures, roughly rectangular in lateral view and lacking expanded tips or dorsal facets. No certainly associated vertebrae have been described for *Anthracosaurus*, but the posterior trunk vertebrae figured by Panchen (1977, fig. 12(a)) as possibly pertaining to *A. russelli* have neural spines resembling those of *Eogyrinus*. Little is known of the vertebrae of *Megalocephalus* or any other loxommatid. However, Baird (1957) described a series of vertebral elements, including apparently five neural arches, associated with a skull of *M. lineolatus* (Cope) from Linton, Ohio. These have been figured by Beaumont (1977, fig. 16b), who has also attributed a very similar, isolated neural arch (G37.88) from Newsham to *M. pachycephalus* (Tilley (Beaumont) 1971, fig. 32). All differ markedly from G25.03 in the possession of narrower neural spines, which appear to lack dorsal facets, and in the size and form of the diapophyses. While it is possible that these differences merely reflect regional variation within the vertebral column of *Megalocephalus*, the evidence at present available is not such as to warrant attribution of G25.03 to this genus.

Of described amphibian neural arches, G25.03 seems most closely to resemble those of the anterior dorsal vertebrae of *Eryops* as figured by Moulton (1974, fig. 2). Points of particular resemblance include the proportions of the diapophyses and the presence, anteriorly and posteriorly, of strongly developed ridges extending dorsally and mesially from the zygapophyses to enclose an upwardly tapering groove in the neural spine. Nonetheless, the neural spines of *Eryops* appear to be somewhat higher than that of G25.03 and, moreover, no diagnostic *Eryops* material of pre-Stephanian age has been described. It is, however, possible that G25.03 pertains to an edopid, rather than eryopid, temnospondyl. *Edops* itself is of lower Permian age and no certainly associated neural spine has been figured. However, edopids occur in the Westphalian D at Linton and Nýřany (A. R. Milner 1980b, p. 463) and the Westphalian A assemblage from Jarrow includes an *Edops*-like form whose vertebrae, since they are apparently rhachitinous in type, may well have borne neural arches not dissimilar to those of *Eryops* (A. R. Milner, pers. comm.). It is interesting to note also that two large rhachitinous vertebrae, in many respects resembling those of *Eryops*, are known from the upper Viséan or lower Namurian of Greer, West Virginia (Smithson 1982, p. 30).

Order BATRACHOSAURIA

Family *incertae sedis*

Specimen G94.65 is an incomplete interclavicle preserved with its dorsal surface uppermost on a small shale slab (text-fig. 2e). The right lateral and posterior extremities of the element are absent; the shape of at least part of the latter region is, however, apparent from a very clear impression remaining in the matrix. The impression unfortunately terminates abruptly at the edge of the slab, making it impossible to determine with certainty whether or not a parasternal process was originally present. It is apparent from the impression that the ventral surface of the interclavicle bore, at least posteriorly, a weakly developed ornament of elongate shallow pits, presumably radiating from the centre of ossification. The anterior margin of the bone is very markedly fimbriated.

The size of G94.65 is such that, if it were to be referred to any of the eight certainly determinate Newsham amphibians listed above, it could only pertain to a small individual of one of the four 'labyrinthodont' species. No certainly associated interclavicle has been described for *Megalocephalus*, but the ornament of G94.65 could hardly be more different from that of the dermal skull roof of *M. pachycephalus* (e.g. Beaumont 1977, fig. 6). Moreover, the isolated Newsham interclavicle (G13.81) referred to this species by Tilley (Beaumont) (1971, fig. 33) differs from G94.65 in shape, ornament and the absence of a distinctly fimbriated anterior margin. Although the ornament of G94.65 suggests that the specimen pertains to a batrachosaur, rather than a temnospondyl, it is not possible to attribute it with certainty to any of the three known Newsham embolomeres. No certainly attributable interclavicle has been described for *Eogyrinus attheyi* but that present in the holotype specimen of *Pholiderpeton scutigera* Huxley, which is probably in fact at least congeneric with the former species, resembles in form the interclavicle of the Permian embolomere *Archeria* as figured by Romer (1957, fig. 1) (J. A. Clack, pers. comm.). It thus differs from G94.65 in both shape and the lack of a 'comb-like' anterior margin. No certainly associated interclavicle has been described for *Pteroplax* or *Anthracosaurus*; the almost total lack of ornament on the dermal skull bones in the latter genus (e.g. Panchen 1977, fig. 1), however, makes it unlikely that G94.65 pertains to this form. While it is just possible that G94.65 derives from a small individual of *Pteroplax*, it must, in the absence of any positive evidence to support such an attribution, be regarded simply as a batrachosaur interclavicle at present indeterminate below ordinal level. The restoration of the specimen (text-fig. 2f) is based upon an assumption of bilateral symmetry and, in part, upon the impression in the matrix.

CENSUS OF TETRAPOD SPECIMENS

In order to assess the relative abundance of the various tetrapod species represented in the Newsham assemblage a census of specimens from the site has been carried out. Almost all of the known tetrapod material from Newsham is stored in the Hancock Museum (Boyd and Turner 1980), but the census sample also includes specimens in the British Museum (Natural History).

Only specimens referable with some certainty to one of the eight Newsham tetrapod species which are certainly determinate at least to family level have been included in the census sample. The numerous isolated 'labyrinthodont' ribs from the site have thus been excluded. Moreover, the recent recognition of cranial material of *Anthracosaurus* from Newsham (Panchen 1981) means that isolated elements of large embolomeres can no longer be attributed with any certainty to *Eogyrinus*. The large numbers of isolated *Megalocephalus* teeth present in the two museum collections examined for census purposes have also been excluded from the census sample, as many may have been lost in the course of normal tooth replacement during life.

Most of the tetrapod material consists of skulls, isolated skull and postcranial elements or, at best, incomplete articulated skeletons (Boyd and Turner 1980). The assessment of the relative abundance of the taxa present has therefore been made employing the principle of the minimum number i.e. by determining the minimum number of individuals of each species necessary to account for all the specimens referable to that species in the census sample. This method compensates for possible inaccuracies due to one species possessing more skeletal elements, or a more easily disarticulated skeleton, than another (Ager 1963, p. 249).

The results of the census are presented in text-fig. 3; the numbers of individuals of each species estimated to be present in the sample are given in histogram form. A card index comprising details of all 105 tetrapod specimens in the census sample is held by the writer and a copy has been deposited in the Hancock Museum.

IDENTIFICATION OF ASSOCIATIONS

As A. R. Milner (1980*b*) has pointed out, there are four main types of information inherent in Westphalian tetrapod assemblages, such as that from Nýřany, which permit identification of ecological associations within them:

1. The relative frequency of the various taxa present.
2. The size distribution and degree of articulation of the specimens.
3. The functional morphology of the animals themselves.
4. The environmental and faunal contexts in which the taxa present occur elsewhere.

TAXON	NO. OF SPECIMENS	MINIMUM NUMBER OF INDIVIDUALS IN SAMPLE
<i>Megalocephalus pachycephalus</i>	61	11
<i>Batrachiderpeton reticulatum</i>	21	9
<i>Eogyrinus attheyi</i>	11	4
<i>Anthracosaurus russelli</i>	3	2
<i>Pteroplax cornutus</i>	6	1
<i>Ophiderpeton nanum</i>	1	1
Lysorophid gen. et sp. indet.	1	1
Urocordylid gen. et sp. indet.	1	1

TEXT-FIG. 3. Results of census of Newsham tetrapods.

On the basis of the above types of information, Milner recognized three associations, derived from different environments, within the Nýřany assemblage. These associations, which were further defined by Milner (1980*b*, pp. 471–473) in terms of the most consistently occurring tetrapod families characteristic of each at Nýřany and other Westphalian sites, comprised:

1. A terrestrial/marginal association, characterized by dendrerpetontid and dissorophid temnospondyls (the latter family apparently replacing the former in post-Westphalian B localities), gymnarthrid, hapsidopareiontid and tuditanid microsaur, romeriid captorhinomorphs, and ophiacodontid pelycosaur.
2. A shallow-water/swamp-lake association, characterized by ophiderpetontid aistopods and urocordylid neotridaeans.
3. An open-water/lacustrine association, characterized by loxomatids and eogyrinid embolomeres.

Using the four types of information listed above, the Newsham tetrapods may also be divided into three ecological associations, derived from different environments.

1. *Terrestrial/marginal association.* The terrestrial/marginal 'association' known from Newsham appears to include only *Anthracosaurus russelli*, represented in the census sample by three specimens. The specimens comprise the incomplete left mandibular ramus (G24.35) described by Panchen (1981), an undescribed right jugal (G24.39) noted by Boyd and Turner (1980, p. 13) and an isolated skull table (G13.78). The skull table was originally figured by Atthey (1877, pl. XIII) as that of *Pteroplax cornutus*, but was later referred by Watson (1926) to *Eogyrinus attheyi*; the latter attribution was endorsed by Panchen (1970, 1972). However, comparison of G13.78 with the skull table of the holotype of *A. russelli* indicates that it actually pertains to this species (J. A. Clack, pers. comm.). Its almost unornamented dorsal surface is thus not due, as has been suggested (Panchen 1964), to *post-mortem* erosion but is probably merely characteristic of *Anthracosaurus* (e.g. Panchen 1977, fig. 1). At least two individuals are represented by the three Newsham *Anthracosaurus* specimens. The jaw ramus apparently derives from a somewhat smaller animal than is represented by the, 40 cm long, holotype skull of *A. russelli* (Panchen 1981, p. 89), but the jugal and skull table are closely similar in size to those of the holotype. They could, therefore, both be derived from one individual.

No certainly associated post cranial remains have been described for *A. russelli* but several aspects of its known cranial morphology suggest that the adults, at least, may have been largely terrestrial in habit. Thus, the skull is massively built and reptiliomorph in appearance, with orbits facing more laterally than is the case in *Eogyrinus*, and lateral line sulci are absent save for possible traces on the jugals. Naso-labial grooves, regarded by Panchen (1967) as probably primitive for tetrapods and serving, in conjunction with ventrally placed external nares, to keep the buccal cavity free of excess water, are absent. The teeth are massive, roughly conical structures and are recurved to a much lesser extent than those of the, probably largely piscivorous, *Eogyrinus* (data from Panchen 1977). Moreover, the mid-point of insertion and line of action of the adductor muscles of the lower jaw were further forward in relation to the tooth row in *Anthracosaurus* than in *Eogyrinus*, increasing the static pressure capable of being exerted on prey items when the jaw was near closure (Panchen 1981). Olson (1961) has suggested that the static pressure system of jaw closure was originally developed in tetrapods as an adaptation to terrestrial feeding, upon invertebrates such as insects and molluscs. It seems likely, however, that adults of *Anthracosaurus* fed also upon other tetrapods, possibly around the margins of lakes and rivers.

Specimens of *A. russelli*, the sole known member of the family Anthracosauridae, have been described only from the Westphalian of England and Scotland (Panchen 1977); no certainly anthracosaurid material has been reported amongst the tetrapod assemblages from Linton, Nýřany, Jarrow, or Joggins. The absence of anthracosaurids from the Joggins assemblage, which is almost precisely contemporary with that from Newsham and is composed primarily of terrestrial tetrapods, is of some interest and is discussed elsewhere in the present study (see below).

In summary, the relative rarity of *A. russelli* specimens in the census sample and the functional

morphology of the animal, so far as it is known, suggest that this species was not endemic in life to the environment of preservation of the Newsham tetrapods. It is presumed to have formed part of a terrestrial/marginal tetrapod community, of which it is the only representative so far known from the site (text-fig. 4). While it is possible that the Newsham *A. russelli* material, which all appears to pertain to adult animals, is derived from individuals which were visiting the lake to breed, the fragmentary nature of the known specimens suggests rather that they are erratics, having been transported to the site *post-mortem*.

2. *Shallow-water/swamp-lake association*. The three Newsham tetrapods regarded with some confidence as comprising this association are the ophiderpetontid aïstopod *Ophiderpeton nanum*, a urocordylid nectricean and a lysorophid. Each is represented by only a single specimen in the census sample. The urocordylid and the lysorophid are not certainly determinate below family level.

The specimen of *Ophiderpeton nanum* consists of a poorly preserved skull and incomplete postcranial skeleton, the latter including the most anterior forty-three vertebrae in an articulated series (Boyd 1982a, fig. 1). The vertebral count in an entire specimen of this species is not known, but Baird (1964, p. 6) has given a figure of 100 + for a juvenile of *O. granulosum* Fritsch. The first forty vertebrae of the *O. nanum* specimen together measure 11.2 cm; on the assumption the vertebral count of the complete animal was similar to that of *O. granulosum*, the total length of its vertebral column may very roughly be estimated at somewhat in excess of 28 cm. The skull appears to have been approximately 1 cm in length.

A restoration of the probable appearance of *Ophiderpeton* in life has been published by A. R. Milner (1980b, fig. 5). The body in this genus is highly elongate and snake-like, and the tail very short (Zidek and Baird 1978). Although an interclavicle may be present in the Newsham *O. nanum* specimen (Boyd 1982a), there is no convincing evidence of the presence of limbs in any described aïstopod (Baird 1964; Wellstead 1982). The skull of *Ophiderpeton* is narrow and elongate with the orbits placed well forward, anterior to large temporal fenestrae (Steen 1931; Thomson and Bossy 1970). The body bears a ventral armour of elongate, needle-like gastralia arranged *en chevron*, and the dorsal and lateral surfaces of both body and tail are covered by an armour of small, pebble-like osteoderms. The latter armour also extends forward to cover the temporal fenestrae (Baird 1964). Examination of a skull (BM(NH) R2657) of *O. amphiuminum* (Cope) from Linton indicates that the small marginal teeth are not, as described by Steen (1931), merely erect and cylindrical, but possess horizontal chisel-like edges and resemble in form those of the lower Permian embolomere *Archeria* (e.g. Panchen 1970, fig. 4b). Like those of *Archeria*, the marginal teeth of *Ophiderpeton* appear to have been closely set and of roughly uniform height over most of the length of the tooth row. As A. R. Milner (1978) has pointed out, such a dentition provides a continuous surface for gripping, rather than piercing, prey and it is probable that *Ophiderpeton* fed largely upon soft-bodied invertebrates considerably smaller than itself. While it is clear that *Ophiderpeton* had a lateral undulatory propulsive system (Lund 1978), conflicting opinions have been expressed as to the primary environment in which the system was used. Thus, Romer (1930) considered that both phlegethontiïd and ophiderpetontid aïstopods were entirely aquatic whereas Gregory (1948) argued for a burrowing mode of life for *Ophiderpeton*, and Thomson and Bossy (1970) merely noted that, whether on land or in water, aïstopods obviously 'swam'. However, as A. R. Milner (1980b) has noted, *Ophiderpeton* has not been reported from any primarily terrestrial tetrapod assemblage but is of frequent occurrence at Jarrow, Linton, and Nýřany. Furthermore, at the latter two localities this genus would appear, from published data (Romer 1930, p. 140; A. R. Milner 1980, p. 454), to be considerably more abundant than the phlegethontiïd aïstopod *Phlegethontia*, which has been convincingly demonstrated by Lund (1978) to have been primarily terrestrial. Thus, although the serpentiform body, short tail, small orbits and heavy dermal armour of *Ophiderpeton* may indicate derivation from burrowing ancestors it would seem likely that the known members of this genus were very largely, if not entirely, aquatic in habit. Gregory's (1948) objection to an aquatic mode of life for *Ophiderpeton*, on the grounds that the caudal vertebrae lack the high neural and haemal spines seen in the tail of urocordylid nectriceans,

seems of little moment. In *Ophiderpeton* the trunk is very elongate and the tail short (Zidek and Baird 1978) whereas the reverse of this arrangement is exhibited by the urocordylids, in which the tail is markedly longer than the trunk (A. C. Milner 1980) and clearly constituted the major propulsive organ in aquatic locomotion. It is, moreover, possible that the posterior body and tail of *Ophiderpeton* species bore dorsal and ventral fin-like membranes without skeletal supports, such as are present in some (almost tailless) aquatic apodans of the family Typhlonectidae. Indeed, *Ophiderpeton* species may parallel the typhlonectids in being secondarily aquatic, limbless amphibians derived from ancestors adapted for a burrowing mode of life.

The presumed mode of life of *Ophiderpeton*, the presence of only a single specimen at Newsham and the relative abundance of this genus at Jarrow, Linton, and Nýřany together suggest that *O. nanum* was not endemic in life to the environment of preservation of the Newsham tetrapods but is to be regarded as probably an erratic derived from a shallow-water/swamp-pool environment. The poorly preserved and incomplete nature of the specimen may indicate *post-mortem* transport (text-fig. 4).

The Newsham urocordylid specimen is an isolated posterior caudal vertebra which, although indeterminate at generic level, appears, as noted above, to pertain to a member of the *Ptyonius*-group of Bossy (1976). Comparison with the caudal vertebrae of the *Urocordylus wandesfordii* holotype as figured by Bossy (1976, fig. 73), which measures approximately 55 cm in total length, suggests that the Newsham vertebra derives from an animal of closely similar size. Like other urocordylids, the *Ptyonius*-group members were principally, if not entirely, aquatic in habit, swimming by sinusoidal flexure of the body and long laterally compressed tail (A. C. Milner 1980). *Ctenerpeton* is known only from the posterior trunk and tail, but in *Urocordylus* and *Ptyonius* the trunk was shorter than in the *Sauroleura*-group urocordylids (*Sauroleura*, *Lepterpeton*, and *Crossotelos*: Bossy 1976), having a maximum of twenty-two vertebrae. The tail, which in *Urocordylus* includes over eighty vertebrae, was particularly deep in vertical profile, being of constant depth for the anterior two-thirds of its length and then tapering rapidly to its tip (A. C. Milner 1980, after Bossy 1976). Bossy (1976) has suggested that *Urocordylus* and *Ptyonius* were adapted for sustained powerful swimming, although having a lower initial acceleration than the *Sauroleura*-group genera. The skull of *Ptyonius*-group urocordylids is adequately known only in *Ptyonius* itself, but that of *Urocordylus*, as restored by Bossy (1976), appears similar in being broader and shorter-snouted than is the case in the *Sauroleura*-group. Cranial kinesis in *Ptyonius* was apparently restricted to the supratemporal-squamosal line and Bossy (1976) suggests that the jaw mechanics of this genus tended towards the static-pressure system of Olson (1961), thus differing from the specialized type of kinetic inertial system found in *Sauroleura* and its allies. The teeth of *Ptyonius* are smaller and more numerous than those of *Sauroleura* and differ also in not being recurved. It thus seems likely that *Ptyonius*-group urocordylids were adapted for feeding on relatively smaller and less vigorous prey than that of *Sauroleura*-group members, and their diet may have consisted in large part of soft-bodied invertebrates.

Although rare at Newsham, urocordylids are relatively abundant at Nýřany (at least thirty-two specimens of *Sauroleura scalaris* Fritsch), Linton (many specimens of *Sauroleura pectinata* Cope, at least eight specimens of *Ctenerpeton remex* Cope and at least fifteen specimens of *Ptyonius marshii* (Cope)) and at Jarrow (four specimens of *Urocordylus wandesfordii* Wright and Huxley and two specimens of *Lepterpeton dobbsii* Wright and Huxley) (data from A. C. Milner 1980). It is therefore probable that, although known urocordylids were clearly largely aquatic in habit, the species represented by the single Newsham specimen was not endemic in life to the environment in which the Newsham tetrapods were preserved but is an erratic from a shallow-water/swamp-pool environment (text-fig. 4). The nature of the specimen suggests that transport to the site of preservation may have been *post-mortem*.

The lysorophid specimen from Newsham consists of twenty-one articulated vertebrae, apparently from the anterior trunk region, most of which are associated with their respective rib pairs (Boyd 1980b, fig. 1A). The vertebrae are almost identical in size with the anterior trunk vertebrae of the *Lysorophus* specimen described by Sollas (1920), which has a skull length of slightly less than 2 cm.

Seventy-two presacral vertebrae are present in the articulated specimen of *Cocytinus* figured by Carroll and Gaskill (1978, fig. 132B). On the assumption that a similar number was originally present in the animal represented by the Newsham specimen, the length of its presacral vertebral column may very tentatively be estimated at approximately 35 cm, although this makes no allowance for regional variation in centrum length. The snout-vent length of the Newsham lysorophid was thus probably about 37 cm and, if the tail was like that of *Lysorophus* (Olson 1971) in being roughly one-sixth as long as the body, the overall length would have been in the region of 43 cm.

The known lysorophids were apparently largely aquatic, although Olson (1971) has suggested that *Lysorophus* may have been capable of some overland travel by wriggling. Lysorophid limb girdles and limbs are very small relative to body size (e.g. Sollas 1920, fig. 1; Carroll and Gaskill 1978, fig. 132B) and the latter were probably functionally insignificant in both aquatic and terrestrial locomotion. There is little doubt that the animals were active swimmers, moving by sinusoidal flexure of the long body and short, laterally compressed, tail. The skull is completely open in the orbital and temporal regions (Sollas 1920) suggesting that lysorophids were not habitual burrowers; the presence of *Lysorophus* specimens preserved in aestivation burrows in the lower Permian of Oklahoma (Olson 1971) does, however, indicate some capability in this respect. As Olson (1971) has pointed out, the ability to aestivate would also seem to suggest that, although lysorophids exhibit well-ossified branchial arches and may have been perennibranchiate, functional lungs were also present. Lysorophid premaxillae and maxillae were freely moveable on the rest of the skull (Carroll and Gaskill 1978) and the teeth of *Lysorophus* are relatively large, few in number and slightly recurved (Sollas 1920, fig. 38). It would thus seem likely that lysorophids were active carnivores, feeding on relatively large and vigorous prey. Coprolites containing the bones of a small temnospondyl, a small captorhinomorph reptile and palaeoniscid fishes, in addition to lamellibranch shells, have been attributed to *Lysorophus* by Olson (1971). As Olson notes, insects and various aquatic invertebrates doubtless also formed part of the diet of *Lysorophus*, which probably had a mode of life in many respects similar to that of the extant urodele *Amphiuma*.

The presence of only a single, incomplete, lysorophid in the census sample and the inferred mode of life of the members of the group together suggest that the Newsham specimen was derived from an aquatic environment other than that in which it was preserved. Lysorophids have been reported from few localities in the Westphalian. They do, however, occur at Linton, where the group is represented by the genera *Molgophis* and *Cocytinus* (Steen 1931), and may also be present at Jarrow (Carroll and Gaskill 1978, p. 187), although the poor preservation of the material from the latter site makes identification uncertain. It thus seems likely that the Newsham lysorophid specimen represents an erratic transported from a shallow-water/swamp-lake environment (text-fig. 4). A. R. Milner (1982, p. 661) has suggested a similar origin for the single *Cocytinus* specimen recorded as part of the Westphalian D tetrapod assemblage from Mazon Creek, Illinois.

Two further Newsham amphibian taxa may also, although less certainly, represent erratics from shallow-water/swamp-lake environments. The first is the medium-sized, almost certainly eogyrid, embolomere *Pteroplax cornutus*, apparently represented in the census sample by six specimens. Of these, only the isolated skull table (G15.72) designated the lectotype of *P. cornutus* by Romer (1963) is certainly referable to this species. However, as the five attributed specimens could all, in theory, be derived from the same individual as the lectotype, the slight uncertainty as to their pertaining to *P. cornutus* does not affect the assessment of the minimum number of individuals represented by the material. The attributed specimens comprise: a trunk pleurocentrum, intercentrum and one indeterminate central element in association with two neural arches and three ribs (G83.68); seven articulated trunk vertebrae in association with four ribs (G15.73); a caudal intercentrum (G4.83); an isolated left pterygoid (G25.45) and a right nasal with associated premaxilla (G24.40). The last specimen is, if correctly attributed to *P. cornutus*, of some importance as the premaxilla bears four recurved teeth (Boyd 1978, fig. 10) of the shape characteristic of eogyrid, rather than archeriid or anthracosaurid, embolomeres (Panchen 1970). Reasons for attributing the above five specimens to *P. cornutus* have been set forth elsewhere (Boyd 1978; 1980a). There can be little doubt that *P. cornutus* was largely aquatic: the skull table bears well-developed lateral line sulci (Panchen 1970, fig. 14A), as

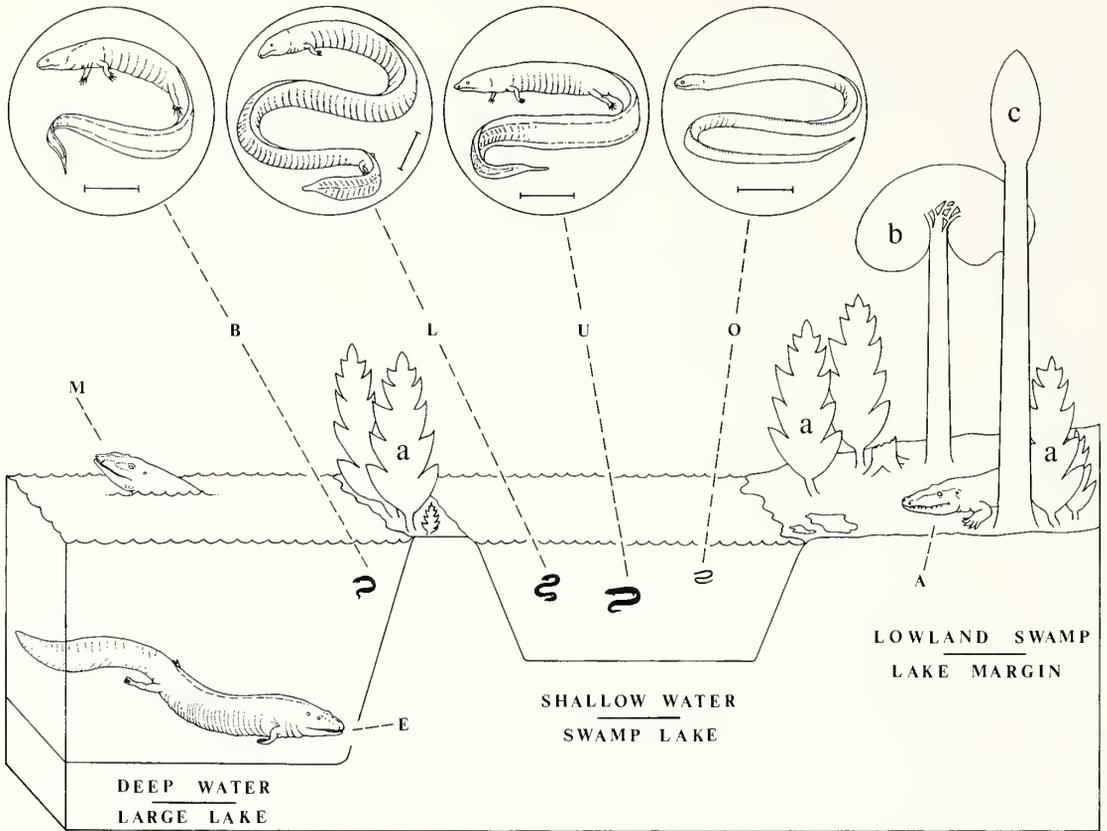
do the attributed nasal and premaxilla. The structure and mode of life of eogyrinid embolomeres have been discussed by Panchen (1970; 1972), who regards the members of this family as aquatic carnivores, swimming in anguilliform manner by sinusoidal flexure of the elongate body and long, laterally compressed, tail. The teeth of *P. cornutus*, if correctly attributed to this species, suggest a piscivorous habit. The inferred mode of life of *P. cornutus*, its rarity at Newsham and the nature of the few specimens known from the site together suggest the possibility that the species may not have been endemic to the environment of preservation but represents an erratic from another aquatic environment, possibly of the shallow-water/swamp-lake type. A second and, in view of the rarity of embolomere specimens at Nýřany (A. R. Milner 1980*b*) and Linton (Panchen 1977), perhaps more likely possibility is that *P. cornutus* was primarily a river-dwelling species.

If the isolated amphibian interclavicle (G24.98) described above as probably that of a colosteid temnospondyl is correctly so designated, it too may represent a transported erratic from a shallow-water/swamp-lake environment. Described colosteids were clearly largely aquatic in habit: the skull bore a well-developed lateral line system (e.g. Romer 1930, fig. 11; Smithson 1982, fig. 7) and the vertebral column, where known, includes approximately forty presacral vertebrae (Smithson 1982, p. 31). Colosteids have not been reported from any primarily terrestrial tetrapod assemblage, such as that from Jogjins, and in the Westphalian occur at Jarrow and Linton (A. R. Milner 1980*a*, p. 135; Romer 1930).

As A. R. Milner (1980*b*) has pointed out, the haplolepid actinopterygians known from Newsham are probably also to be regarded as erratics from a shallow-water/swamp-lake environment. Haplolepid is rare at Newsham: Westoll (1944) described the remains of only four individuals, representing three species, from the site. The haplolepid-aïstopod-nectridean 'facies fauna' of Westoll (1944) has been equated by A. R. Milner (1980*b*, p. 474) with the latter's shallow-water/swamp-lake association and redefined, in more precise terms, as a haplolepid-ophiderpetontid-urocordylid association. However, the recent recognition of urocordylid material from Newsham (Boyd 1982*b*) means that, despite Milner's more restricted definition of the haplolepid 'facies fauna', Westoll's (1944) statement that members of all three constituent groups occur as occasional individuals at the site still holds true.

3. *Open-water/lacustrine association.* The three Newsham tetrapod species regarded as comprising this association, and as having been endemic in life to the environment of their preservation, are *Megalocephalus pachycephalus*, *Batrachiderpeton reticulatum*, and *Eogyrinus attheyi*. These are the most abundant species in the census sample, each being represented by more than ten specimens (text-fig. 3).

Megalocephalus pachycephalus is the most frequent tetrapod in the sample studied. Sixty-one specimens are present, representing the remains of at least eleven individuals. Interestingly, all the Newsham material certainly referable to *M. pachycephalus* consists of skulls, skull fragments, isolated cranial elements, and teeth (Boyd and Turner 1980), although a few postcranial bones from the site have been attributed to this species. The latter comprise an isolated neural arch (G37.88), an interclavicle (G13.81) and an ilium (RSM 88.33) figured by Tilley (Beaumont) (1971, figs. 32–34), and a number of isolated centra figured in part by Panchen (1980, fig. 9*d–e*). In view of the relative abundance of *M. pachycephalus* at Newsham, the absence of certainly associated postcranial remains is somewhat surprising. However, a similar state of affairs has been noted by A. R. Milner (1980*b*, p. 448) at Nýřany, where many of the medium to large amphibian specimens consist only of isolated skulls or skulls in association with disarticulated pectoral elements. Milner suggests that this is due to the combination in the animals concerned of a large dense skull and pectoral girdle anteriorly and a potentially autolysing hind-gut posteriorly, resulting in the bodies and tails of the corpses disintegrating or floating away while the denser anterior ends remained stationary. The almost total lack of even isolated postcranial material plausibly referable to *M. pachycephalus* at Newsham may conceivably be due to most of the floating, headless, bodies having been carried from the lake by excurrent streams. Alternatively, many of the 'missing' postcranial elements may be preserved in areas of the Newsham black shale which have not been collected.



TEXT-FIG. 4. Restorations of tetrapod taxa recorded from Newsham. The animals are depicted in diagrammatic representations of the environments they are considered to have inhabited in life. Abbreviations: M—*Megaloscephalus* (after A. R. Milner 1980b, fig. 3), B—*Batrachiderpeton* (postcranial proportions based on those of *Keraterpeton* as figured by A. C. Milner 1980, fig. 4A). Scale bar represents 5 cm, E—*Eogyrinus* (after A. R. Milner 1980b, fig. 3), L—lysorophid (proportions based upon those of *Cocytinus* skeleton figured by Carroll and Gaskill 1978, fig. 132B). Scale bar represents 3 cm, U—urocordylid (restoration based upon skeleton of *Urocordylus* as figured by Bossy 1976, fig. 73). Scale bar represents 6 cm, O—*Ophiderpeton* (after A. R. Milner 1980b, fig. 5). Scale bar represents 3 cm, A—*Anthracosaurus* (postcranium hypothetical). Plant symbols partly after Scott (1979). Abbreviations: a—*Calamites*, b—*Lepidodendron*, c—*Sigillaria*.

The total lengths of the Newsham *M. pachycephalus* skulls in which such measurement is possible range between approximately 35 cm and 40 cm, although the dimensions of one incomplete specimen (BM(NH) R3417) are suggestive of an even greater original length (Beaumont 1977). The presence at the site of sub-adult individuals of the species is suggested by an isolated right jugal (G140.81) measuring only 72 mm in length; that of the roughly 35 cm long, skull figured by Beaumont (1977, fig. 8) measures approximately 150 mm. The skull of *M. pachycephalus* is crocodile-like in shape and bears well-developed lateral line sulci, suggesting that the animal spent a considerable amount of time in water. Such a habit is also suggested by the ventrally placed external nares, which are separated from the jaw margin by distinct naso-labial grooves (*sensu* Panchen 1967, p. 413). The slender, lanceolate marginal teeth of *M. pachycephalus*, the shagreen of denticles on the parasphenoid and dermal palatal elements and the kinetic inertial system of jaw closure (Beaumont 1977) all suggest that this species was an aquatic feeder and probably largely piscivorous. Although it is possible that,

as A. R. Milner (1980*b*) has suggested, loxommatids such as *Megalocephalus* lived a crocodile-like existence, entering the water to feed but otherwise resting around lake and river margins, the large amount of *M. pachycephalus* material from Newsham might be taken to indicate a more thoroughly aquatic mode of life for this species at least. Loxommatids appear to occur only rarely in tetrapod assemblages from shallow-water/swamp-lake environments. Thus, A. R. Milner (1980*b*) reported only one specimen representative of this family, a skull of *Baphetes*, amongst approximately 400 tetrapod specimens from Nýřany. Beaumont (1977) listed only five loxommatid specimens from Linton and one, a *Megalocephalus* skull, from Jarrow; the second Jarrow skull (BM(NH) R8465) cited by Beaumont, and considered by her to be possibly that of a juvenile *Megalocephalus* specimen, actually pertains to the aïstopod *Ophiderpeton* (A. R. Milner, pers. comm.).

Batrachiderpeton reticulatum is the second most frequent tetrapod species in the census sample; twenty-one specimens are present, representing at least nine individuals. Both adults and juveniles are represented in the material (Boyd and Turner 1980, pp. 18–19) and there appears to be a correlation between the size and degree of disarticulation of the specimens. The adult *B. reticulatum* material consists almost entirely of isolated skulls, skull fragments and isolated mandibular rami and vertebrae, although in one specimen (G25.39) part of the pectoral girdle is associated with an incomplete skull. Of the four juvenile specimens, however, two consist of skulls in association with much of the postcranial skeleton. This size-linked disintegration may have been a result of the larger animals having had a greater, potentially autolysing, volume of hind gut, capable of producing more gas before decomposition was inhibited by the anaerobic conditions on the lake bottom (A. R. Milner 1980*b*, p. 448). Like all other known keraterpetontid neotriassicans, *B. reticulatum* was clearly largely, if not entirely, aquatic in habit, swimming by sinusoidal flexure of the body and the long, laterally compressed tail. The skull, which in the restoration figured by A. C. Milner (1980, fig. 5*f*) measures approximately 5 cm in length, is short-snouted with an akinetic skull table firmly sutured to the, relatively deep, cheek region. The marginal teeth are of moderate size and conical in form, with incurved tips. Teeth only slightly smaller are present on the coronoids and the lateral dermal palatal elements; in addition, the pterygoids bear a shagreen of denticles anteriorly. The mandible bears a well-developed retroarticular process (data from A. C. Milner 1980). A. C. Milner (1978; 1980) has suggested that the jaw mechanism of keraterpetontids tended towards the static pressure type and that the animals were adapted for seizing and crushing small invertebrates with shells or hard exoskeletons. *B. reticulatum* appears to have possessed a, probably ligamentous, connection between the tabular horn and cleithrum on each side; these connections probably served to dampen lateral oscillatory movements of the head during swimming and thus to facilitate a straight-line approach to prey (A. C. Milner 1980, p. 389). It seems quite probable that, as A. R. Milner (1980*b*, p. 477) has suggested, this species lived around the margins of the Newsham lake, possibly in stands of marginal vegetation including *Calamites*.

The relative abundance of *B. reticulatum* at Newsham and the nature of the known material both strongly suggest that this species was endemic to the site. Indeed, A. R. Milner (1980*b*) has suggested that keraterpetontids should be regarded as forming part of the Westphalian open-water/lacustrine tetrapod association, although not occurring uniformly enough with loxommatids and eoogyrinid embolomeres to be included with the latter two taxa in the familial characterization of this association. Keraterpetontids are absent from Nýřany (A. R. Milner 1980*b*) and rare at Linton (only eight reported specimens of *Diceratosaurus brevisrostris* (Cope): A. C. Milner 1980, p. 404). At least twenty-four specimens of *Keraterpeton galvani* Wright and Huxley are known from Jarrow (A. C. Milner 1980) but A. R. Milner (1980*b*, p. 473) interprets these as constituting a 'juvenile swarm' and, presumably, as inhabiting a water body shallower than those preferred by the adults.

Eogyrinus attheyi is represented in the census sample by eleven specimens; these include the remains of at least four individuals. All the specimens in the sample, with the exception of the lectotype of *E. attheyi*, are skull fragments and isolated cranial elements. The lectotype consists of an almost complete skull with both mandibular rami (Panchen 1972, fig. 2), in association with at least twelve anterior trunk vertebrae, six ribs, a number of dermal scutes and a limb bone interpreted by Panchen (1972) as a femur. The presence of only a few anterior vertebrae with the lectotype skull and

the absence of associated postcranial remains with the other *E. attheyi* skull specimens may, as has been suggested in the case of the Newsham loxommatid material, be due to the disintegration or floating away of the, less dense, postcrania as a result of gas generation by hind-gut autolysis. As has been noted above, the, fairly numerous, isolated elements of large embolomere vertebrae from Newsham (e.g. Boyd & Turner 1980, pp. 13–16) have been omitted from the census sample on the grounds that some may pertain to *Anthracosaurus russelli* rather than *E. attheyi*. The same applies to the large isolated dermal scutes (e.g. Panchen 1972, fig. 15) from the site. However, even if most or all of these vertebrae and scutes are in fact derived from *E. attheyi*, as is statistically likely to be the case, they are not sufficient in number for their exclusion from the study sample to make any difference to the assessment of the minimum number of individuals of this species based upon skull material.

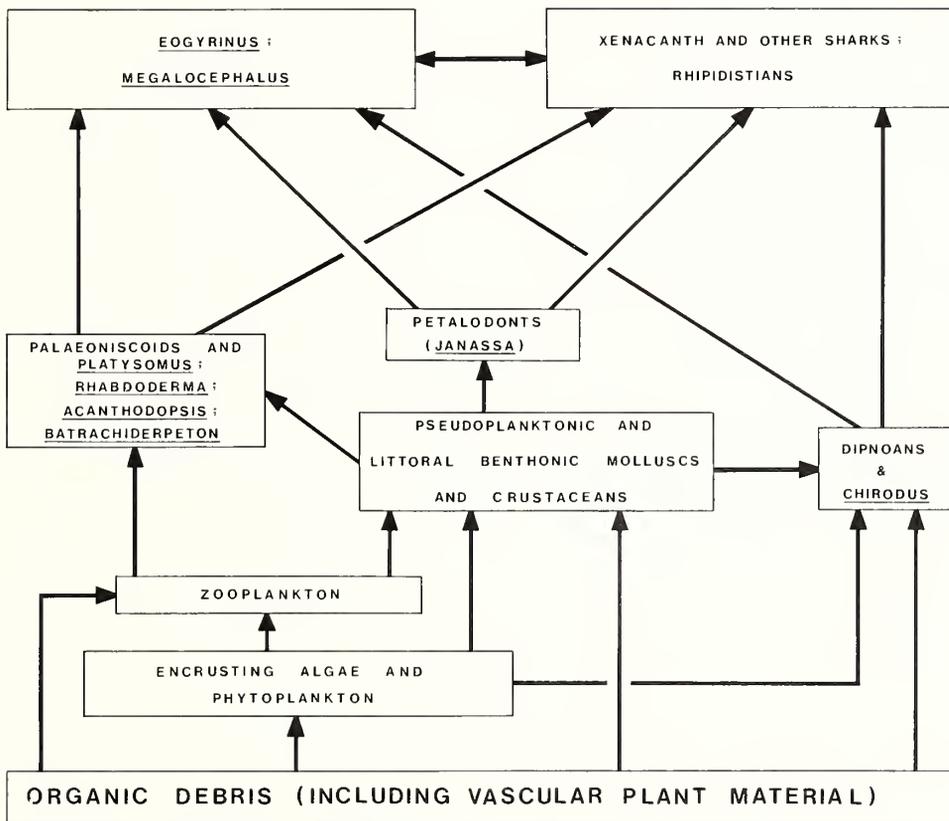
E. attheyi was probably the largest of the apparently endemic Newsham tetrapods and one of the largest vertebrates known from the site; the lectotype skull has an overall length of 41 cm and the complete animal may have been up to 4 m long (Panchen 1972). The fact that this species is apparently much less abundant at Newsham than are *Megalocephalus* and *Batrachiderpeton* is consistent with its greater size and presumed status as an ultimate consumer. The skull bears well-developed lateral line sulci and naso-labial grooves are present below the external nares; there can thus be little doubt that *E. attheyi* was, as suggested by Panchen (1970), largely aquatic in habit, swimming by sinusoidal flexure of the elongate body and long, deep, tail. The marginal teeth are of moderate size and recurved at their tips. A row of similar teeth is present on each ectopterygoid, which, like the palatine, bears tusks anteriorly. The form of the teeth and the shagreen of tiny denticles on the pterygoids and coronoids are suggestive of a diet largely of fish and the presence in *E. attheyi* of a kinetic inertial system of jaw closure (Panchen 1970) might be taken to indicate that aquatic feeding was the norm for this species. Moreover, as Atthey (1876, p. 165) pointed out, amongst the vertebrae and ribs associated with the *E. attheyi* lectotype are preserved a toothplate, rib, and several scales referable to the dipnoan genus *Ctenodus*, which may represent gut contents. In addition, the holotype specimen of the large eogyrinid *Pholiderpeton scutigerum* Huxley (BRM NS.111.81) is associated with two scales of the crossopterygian *Megalichthys* which, to judge from their situation and eroded condition, are probably also derived from ingested prey (J. A. Clack, pers. comm.). Although *E. attheyi* was probably mainly piscivorous, it seems highly likely that it fed also upon other aquatic tetrapods; there is, however, no direct evidence for this. A. R. Milner (1980b) has suggested that eogyrinids may have been adapted for swimming and/or crawling among dense *Calamites* stands around lake margins.

Eogyrinids appear to be scarce in tetrapod assemblages from shallow-water/swamp-lake environments. Only two incomplete specimens of the, doubtfully eogyrinid, embolomere *Diplovertebron punctatum* Fritsch were reported by A. R. Milner (1980b) from Nýřany. Panchen (1977) noted only six specimens of *Leptophractus obsoletus* Cope from Linton. No precise published data are available concerning the frequency of eogyrinids in the Jarrow assemblage; however, Panchen (1970, p. 64) reported a mere two embolomere specimens from the site. Interestingly, the tetrapod assemblage from Joggins, which is composed mostly of terrestrial tetrapods (see below), includes a few specimens of the tiny, probably eogyrinid (Panchen 1970), embolomere *Calligenethlon watsoni* Steen. They are, however, relatively rare components of the assemblage (Carroll 1967) and, while the mode of their preservation suggests that they were capable of terrestrial locomotion, it is doubtful if larger eogyrinids were habitual overland travellers.

In summary, the relative frequency of *Megalocephalus*, *Batrachiderpeton*, and *Eogyrinus* specimens in the Newsham tetrapod assemblage, the nature of the material and the presumed mode of life of the animals themselves together suggest that these taxa were endemic in life to the environment of preservation. The scarcity of loxommatids, keraterpetontids, and eogyrinids in shallow-water/swamp-lake tetrapod assemblages would seem to confirm that the Westphalian members of these families were characteristic inhabitants of larger and deeper water bodies, such as the Newsham lake (text-fig. 4).

The structure of the Newsham open-water/lacustrine community has been discussed by A. R. Milner (1980b, pp. 475–479), who suggests that the ultimate energy sources in Carboniferous open-

water bodies such as the Newsham lake were probably organic detritus and algae, the former being fed upon by a wide range of invertebrate primary consumers and the algae, both planktonic and encrusting, mainly by ostracods and gastropods. Milner further suggests that all the endemic fish species at Newsham, with the possible exception of the platysomid palaeoniscid *Chirodus*, were, like the amphibians, secondary and tertiary consumers which fed upon other vertebrates and invertebrates. As noted elsewhere in the present paper, the only invertebrate taxa known from Newsham are ostracods and bivalves; the other invertebrate groups noted by Milner as possible carnivores (chelicerates) and primary consumers (palaeocarid crustaceans and gastropod molluscs) in open-water/lacustrine communities have not been reported from the site. However, all three are known from Westphalian non-marine deposits (e.g. Calver 1968; Schram 1976) and their absence from the Newsham assemblage may merely be due to non-preservation or non-collection. While generally in agreement with A. R. Milner's (1980b) conclusions with respect to the structure of the Newsham open-water/lacustrine community, the present writer would suggest that *Chirodus* (represented by a very few articulated specimens of *C. striatus* (Hancock and Atthey)) may not have been the only vertebrate primary consumer at the site. Two species of dipnoan, the ctenodontid *Ctenodus cristatus* Agassiz and the sagenodontid *Sagenodus inaequalis* Owen, have been reported from Newsham (S. M. Andrews *in Land* 1974, p. 61) and the latter, at least, may have been partly, if



TEXT-FIG. 5. Hypothetical food-web of the Newsham open-water/lacustrine community. The food-web is much simplified, for the sake of clarity, and does not attempt to show all possible interactions involving juveniles and larvae. Format based upon that employed by A. R. Milner (1980b, fig. 9).

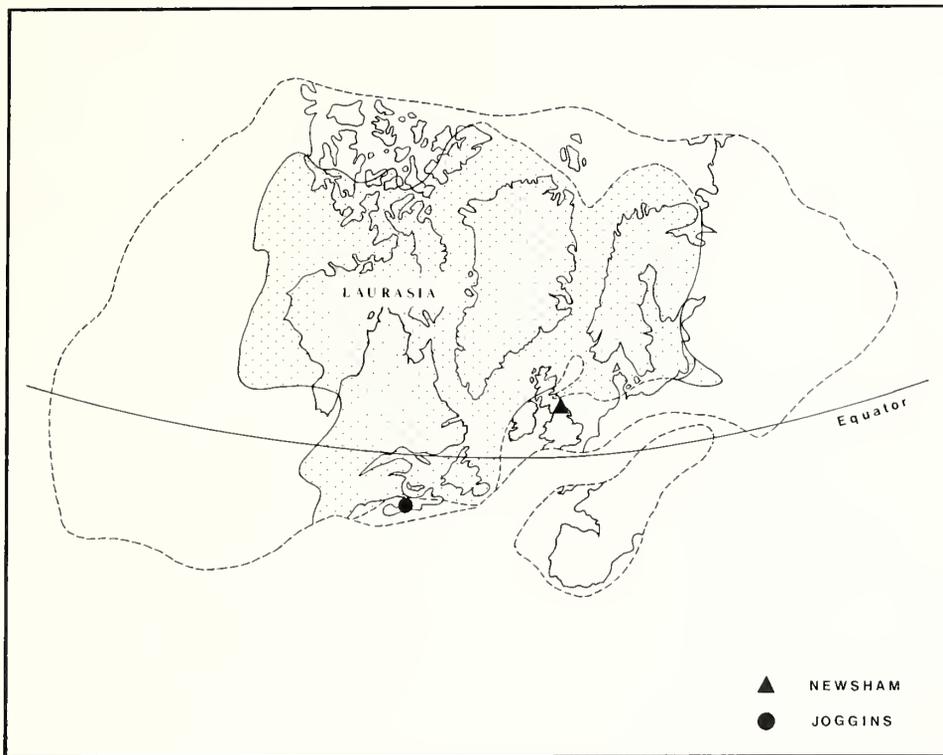
not entirely, herbivorous. Unlike the tooth-plates of *Ctenodus*, which appear to have been specialized for crushing, those of *Sagenodus* bear a reduced number of ridges and denticles and were probably mainly sectorial in function (Moy-Thomas and Miles 1971, p. 152). It is interesting to note, moreover, that both juveniles and adults of *Neoceratodus*, structurally the most primitive of the living Dipnoi, are known to take vegetable, as well as animal food. Indeed, Günther (1880, p. 357) noted that the stomach of *Neoceratodus* specimens usually contains large quantities of leaves derived from plants growing on river banks, which are evidently eaten after falling into the water. If one or both of the Newsham dipnoans included significant amounts of plant material in their diet, they must have been much more important as primary consumers than the, rare, *Chiroodus striatus*; a cursory survey of the extensive Newsham fish collections in the Hancock Museum suggests that the Dipnoi may be the most abundantly represented group. Moreover, Hancock and Atthey (1871*b*, p. 197) note that Atthey's collection at that date included at least 400 isolated dipnoan tooth-plates from Newsham, representing a minimum of 100 individuals. Like *Neoceratodus*, the juveniles of the Newsham lungfish may have eaten filamentous algae and the adults may have taken both living and dead vascular plant material, including, perhaps, *Calamites* growing around the lake margins.

Text-fig. 5 is a hypothetical food-web of the Newsham open-water/lacustrine community, which incorporates the above suggestions.

THE JOGGINS TETRAPOD ASSEMBLAGE

As noted above, only one other large, compact tetrapod assemblage of Westphalian B age is known, that from Joggins in Nova Scotia (text-fig. 6). All described tetrapod specimens from this site were collected from within Division 4 (*sensu* Logan 1845) of the lower Westphalian B Cumberland Group, on the south side of Chignecto Bay at the head of the Bay of Fundy (Carroll 1967). Division 4 of the Cumberland Group includes approximately forty horizons at which erect stumps of arborescent lycopods, including *Sigillaria*, occur. All but a very few of the Joggins tetrapods were found within these stumps. As Carroll (1967, p. 112) has pointed out, 'the preservation of the stumps in an erect position is apparently a result of very rapid deposition. In the cases where vertebrates are found within the trees, it is probable that the bases of the trees were covered but most of the trunk remained exposed. The portion of the trees remaining above the new ground level then fell over, and the centre of the stumps (pulpy even in the living trees) rotted out. The resulting hollow cylinders served as traps for animals living on the new land surface.' Rayner (1971, p. 463), however, has suggested that at least some of the Joggins tetrapods may have deliberately entered the hollow stumps in search of food. The Joggins assemblage has been briefly reviewed by Carroll *et al.* (1972, pp. 64-80).

Comparison of the tetrapod assemblages from Newsham and Joggins is of some interest in view of the fact that they are closely contemporaneous but preserved in sediments deposited in two very different micropalaeoenvironments within broadly similar (coal-swamp basin) macropalaeoenvironments. The fact that the Joggins lycopod stump tetrapods were collected from a number of different horizons within over 450 m of strata (Carroll *et al.* 1972), whereas the Newsham assemblage derives entirely from one bed of shale no more than 10 cm thick (Atthey 1877), is probably of less significance for such a comparison than initial consideration might suggest. The Newsham black shale was apparently laid down during a period of very low detrital input into (at least the centre of) the Newsham lake and sedimentation may have been very slow. Conversely, the presence at Joggins of erect lycopod stumps up to 9 m in height is, as noted by Carroll (1967) and Rayner (1971), indicative of very rapid sedimentation. The lengths of time represented by the tetrapod-bearing deposits at the two localities may thus not be so widely disparate as suggested by the differing thicknesses of strata involved. The ten valid tetrapod species so far recorded from the Joggins lycopod stumps are listed below. Where possible, data (derived from the literature) on the frequency of each species at the site have been included, as has an indication of size. The latter is, in most cases, given as skull length, as many of the Joggins tetrapods are known only from disarticulated and incomplete skeletons.



TEXT-FIG. 6. Map of Laurasia during mid-Carboniferous times to show approximate positions of Joggins and Newsham relative to one another and to the southern margin of the continent. Stippling indicates terrestrial hinterland; unstippled area of continent comprises shelf seas and marginal environments (map modified from Johnson 1981, fig. 4).

Order TEMNOSPONDYLI

Dendrerpetontidae: *Dendrerpeton acadianum* Owen—'about 100 specimens' (Carroll 1967, p. 111). The largest described skull of this species from Joggins has a midline length of 102 mm and, as restored by A. R. Milner (1980a, fig. 3D), a total length of about 120 mm.

Order BATRACHOSAURIA

Eogyrinidae: *Calligenethlon watsoni* Steen—'less than a dozen specimens' (Carroll 1967, p. 111). Carroll (1967) estimates the skull of this species to have been between 50 mm and 75 mm in length.

Order MICROSAURIA

Tuditanidae: *Asaphestera intermedia* (Dawson)—twenty identifiable specimens. The larger skulls have a total length of about 42 mm (Carroll and Gaskill 1978).

Pantylidae: *Trachystegos megalodon* Carroll—five identifiable specimens (Carroll and Gaskill 1978). The total length of the skull as restored by Carroll (1966, fig. 11B) is 53 mm.

Gymnarthridae: *Leiocephalikon problematicum* (Dawson)—ten identifiable specimens. The total length of the skull appears to have been about 21 mm (Carroll and Gaskill 1978).

Gymnarthridae: *Hylerpeton dawsoni* Owen—fourteen identifiable specimens (Carroll and Gaskill 1978). The total length of the skull is not known but the left mandibular ramus figured by Carroll (1966, fig. 6A) is 37 mm long.

Hapsidopareiontidae: *Ricnodon* sp.—four identifiable specimens (Carroll and Gaskill 1978). The total length of the skull is unknown but the isolated dentary figured by Carroll (1966, fig. 19B) measures about 9 mm in length.

Order CAPTORHINOMORPHA

Romeriidae: *Hylonomus lyelli* Dawson—eighteen specimens (Carroll *et al.* 1972). The skull of the type specimen is 33 mm in length (Carroll and Baird 1972).

Romeriidae: *Archerpeton anthracos*—sixteen specimens (Carroll *et al.* 1972). This species is known from very incomplete remains; it is, however, clearly substantially smaller than *Hylonomus* (Carroll and Baird 1972).

Order PELYCOSAURIA

?Ophiacodontidae: *Protoclepsydrops haplous* Carroll—four specimens (Reisz 1972). The skull is not known in its entirety but the humeral length of this species is only slightly less than that of the Westphalian D ophiacodont pelycosaur *Archaeothyris florensis* (Reisz 1972, fig. 18), which has a skull about 92 mm in length.

All the above listed species, with the possible exception of *Calligenethlon watsoni*, appear to have been largely terrestrial in habit (e.g. Carroll 1967; Carroll and Gaskill 1978; Carroll and Baird 1972; Reisz 1972) and are members of families regarded by A. R. Milner (1980*b*) as belonging to the Westphalian terrestrial/marginal tetrapod association. *C. watsoni* is, as noted above, the smallest described embolomere and may have been more terrestrial than other known eoogyrinids.

The Eogyrinidae, represented at Joggins by *C. watsoni*, is the only tetrapod family common to both this assemblage and that from Newsham. Microsaur (*sensu* Carroll and Gaskill 1978), pelycosaur and captorhinomorph reptiles and dendrerpetontid temnospondyls have not been reported from Newsham. Loxommatids, keraterpetontid and urocordylid nectrideans, lysorophids, ophiderpetontid aistopods and anthracosaurid embolomeres are not known from the Joggins erect stumps. The differences in the composition of the two assemblages clearly reflect their differing environments of preservation. Most, if not all, of the Joggins tetrapods were primarily terrestrial forms whereas the Newsham assemblage is composed almost entirely of amphibians which were either endemic to the lake in whose bottom sediments they were preserved or derived from other aquatic environments. However, a second difference exists between the tetrapod assemblages from the two sites. Whereas the Newsham assemblage includes both small and very large amphibian species, that from Joggins is composed only of relatively small tetrapods. The largest species reported from the erect stumps appears to be *Dendrerpeton acadianum*, with a recorded skull length of up to 120 mm. A. R. Milner (1980*a*, p. 126) has suggested that the known members of this genus probably grew to about one metre in total length. The absence of larger tetrapods at Joggins is, as suggested by Carroll *et al.* (1972, p. 71), probably due to the manner in which the assemblage was preserved; tetrapods above a certain size would have been unlikely to fall into the, 0.9m–1.2 m diameter, hollow lycopod stumps or, if they did so, may have been able to extricate themselves. The operation of this filter, controlling the size of the animals preserved, may explain the absence from the Joggins assemblage of the only terrestrial/marginal tetrapod species known from Newsham, the large anthracosaurid embolomere *Anthracosaurus russelli*, or any other representative of the Anthracosauridae.

Of the seven tetrapod families represented at Joggins but not at Newsham, all but one (Pantylidae) occur also in the Westphalian of Europe, either at Jarrow (Dendrerpetonidae: A. R. Milner 1980*a*) or at Nýfany (Tuditanidae, Gymnarthridae, Hapsidopareiontidae, Romeriidae, Ophiacodontidae: A. R. Milner 1980*b*, p. 453). Similarly, all but one (Anthracosauridae) of the six families occurring at Newsham, but not Joggins, are present in the North American Westphalian at Linton, Ohio (Loxommatidae, Keraterpetontidae, Urocordylidae, Lysorophidae, Ophiderpetontidae: Romer 1930). It thus seems likely that the constitutional differences between the tetrapod assemblages from Joggins and Newsham are largely, if not entirely, due to the differing coal-swamp basin micropalaeoenvironments represented by the tetrapod-bearing deposits at the two sites. The writer

would, therefore, suggest that the two assemblages may be regarded as complementary, and as together providing a more balanced and complete picture of the Westphalian B lowland tetrapod fauna of southern Laurasia than either does alone.

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Note added in proof. Since the present paper went to press, preparation of a hitherto enigmatic specimen (Hancock Museum, no. G.2484) from Newsham has enabled it to be identified as the skull table of a romeriid reptile. This new reptile forms an addition to the terrestrial/marginal tetrapod assemblage. A full description of the material will shortly be published.

COMPUTER-BASED STORAGE AND RETRIEVAL OF PALAEOLOGICAL DATA AT THE SEDGWICK MUSEUM, CAMBRIDGE, ENGLAND

by DAVID PRICE

ABSTRACT. The computer-based data handling system at the Sedgwick Museum is a specialized application of the GOS program package, geared to the requirements of a large palaeontological collection. Rigorous analysis and careful structuring of palaeontological data facilitate the automatic production, by machine processing, of hard-copy catalogues, labels, and a variety of indexes. The system goes beyond the capabilities of the standard GOS package in that a number of extra programs are geared to direct access information retrieval. The Information Retrieval System incorporates a solution to the problem of variant forms of single catalogue terms and can be used to answer rapidly many queries about the collections which formerly would either have been virtually impossible or have required extensive physical searches. Those aspects of the Sedgwick System of interest and potential use to palaeontologists and biostratigraphers are described.

MANY museums are using or beginning to use computer-based methods for cataloguing and the production of collection indexes (see, for instance, Roberts and Light 1980). The computer-based procedures described in this paper will be of particular interest to palaeontologists in that they are geared to the documentation requirements of the Sedgwick Museum, whose large palaeontological collections are of international scope and contain a high proportion of type, figured, and cited specimens; many represent classic pieces of research.

HISTORICAL DEVELOPMENT

The long history of Cambridge as a centre of palaeontological and biostratigraphic research ensured that the value of well-organized and accessible collections was appreciated at an early date (see Rickards 1979). Such appreciation led to the development, particularly during the pioneering regime of A. G. Brighton (Curator, 1931–1968), of a curatorial system whose outstanding characteristic was its exceptionally high standard of collection documentation. Specimens were comprehensively labelled, fully and systematically catalogued, and taxonomically indexed; there was also a supporting Curator's library of annotated scientific periodicals, monographs, and reprints, together with collector's original catalogues, notebooks, field-slips, and museum correspondence. This Sedgwick manual system has been described elsewhere (Price 1981; see also Orna and Pettitt 1980, pp. 152–153).

The Sedgwick Museum became a centre for the early development of ideas on computer-based data handling in museums, through the work of J. L. Cutbill, from the mid-1960's onwards (Cutbill 1971; Cutbill *et al.* 1973). Many characteristics of the Sedgwick manual system had an important influence on those ideas. But the 'computerization' of the Sedgwick Museum came to be only a partial aim of the several Sedgwick-based projects through which Cutbill's work developed. Those projects increased in scope to embrace a multidisciplinary approach to the analysis and recording of museum data, and the development of a computer program package for handling museum data which was equally flexible. While this broader approach led in 1977 to the setting up of the Museums Documentation Association, and the subsequent release by MDA of the GOS program package, the move of the final Sedgwick-based project team to their new MDA headquarters (Duxford,

Cambridgeshire) took place before the Sedgwick manual catalogue had been entirely transcribed to machine-readable computer files and indeed before all the necessary procedures for maintaining and updating a computerized catalogue had been fully developed and tested.

The gap between 1977 and the revival of the Sedgwick computerization project in 1981 only served to emphasize differences between the MDA's 'all-embracing' approach, with its broadly conceived data standard, and the rather specialized documentation procedures used in earlier phases of work at the Sedgwick Museum. Differences of approach have further increased during the completion and refinement of the Sedgwick System, because the final phase had the sole aim of deriving a working system specific to the needs of the museum. The final Sedgwick System is based on the GOS program package (with extra programs related to the Information Retrieval System described below), but is a specialized application of that package to a large palaeontological collection. Porter (1982) has given a more technical overview of the general capabilities of GOS. At the time of writing, the Sedgwick System's computer catalogue file contains details of 451 000 specimens, representing approximately 10 000 man-hours of typing and checking catalogue data.

It is not appropriate to describe here the Sedgwick System in its entirety. It is a complete working system covering all aspects of museum documentation, including the automatic production of labels and the recording of specimen loans. This paper attempts merely to describe those characteristics and capabilities of the Sedgwick System which will be of interest and potential use to palaeontologists and biostratigraphers.

GENERAL STRUCTURE OF DATA

Palaeontological data is stored in a precisely structured, machine-readable form within the computer file which now constitutes the Sedgwick Museum catalogue. To enable manipulation by the various programs ('processors') of the GOS package, each record is broken down into a large number of discrete data-categories or *fields*; each field is labelled or *tagged* so that it can be identified by the programs operating on it. The nature and relationships of all the fields considered necessary to contain the data in any Sedgwick Museum catalogue record are described by the *SM Format*, a complex hierarchical arrangement of fields derived from a rigorous analysis of existing manual catalogue entries, together with a consideration of what other kinds of data it might be useful to record for each specimen. The SM Format is described in the Appendix.

RETRIEVAL OF DATA

Indexes

The original purpose of rigorously analysing the data in each record into tagged fields (in the way outlined in the Appendix) was to enable the generation of collection indexes on a very large number of keyword terms. The possible use of any of the tagged keyword terms in the format to sort and order the records permits the construction of complex taxonomic indexes, donor indexes, collector indexes, locality indexes, stratigraphic indexes, bibliographic indexes, and so on. The generation and use of such indexes for data retrieval was indeed central to all thinking about data-handling in the Sedgwick Museum up until the most recent phase of 'computerization'. The Sedgwick System still retains the ability to produce all these indexes, but their use in practice has involved a number of difficulties.

Most indexes have proved very unwieldy in use, particularly so when two or more large indexes are used in conjunction. Problems of this kind can be reduced somewhat by using the great flexibility of the GOS package to produce 'multiple' indexes. An example index is shown as text-fig. 1 arranged primarily geographically, but including also basic stratigraphy and taxonomic names. Another way of easing the problems of handling large indexes is to reduce their bulk by producing them as microform output (COM), in our case as 127 × 76 mm microfiche at a 42 × reduction. Even so, difficulties with hard copy indexes remain.

It should be emphasized at this point that much of the machine-readable catalogue at the Sedgwick Museum was simply transcribed, word for word, from a manual catalogue which had grown

British Somaliland, Biyo Gora.		
Eocene,		
(Fish) Cichlid (indet.);	(Sect. 1).	<u>C. 80131</u>
(Fish) <u>Ogygiochromis</u> sp.;	(Sect. 1).	<u>C. 80130</u>
Lower Eocene,		
(Fish) Pycnodont;	(2628-2646 m below), (strata section i), 10 d 22' N., 45 d 12' E., loc: sigma 35.	<u>C. 73153</u>
(Fish) Sparoid;	(2755-2781 m below top - strata section i), 10 d 22' N., 45 d 12' E., loc: sigma 42.	<u>C. 73157-73158</u>
Middle Eocene,		
(Fish) <u>Odontaspis</u> sp.;	(1960 m. below top - strata section i), loc: sigma 25.	<u>C. 73155</u>
Tertiary,		
(Fish) <u>Aplocheilus</u> sp. nov.;	(922-923 m. below top of strata section i), loc: sigma 17.	<u>C. 76120-76132</u>
	(970-976 m. below top of strata section i), loc: sigma 18.	<u>C. 76133-76134</u>
	(1179-1184 m. below top of strata section i), loc: phi 21.	<u>C. 76135</u>
(Fish) <u>Tilapia?</u> sp. nov.;	(111-116 m. below top of strata section i), loc: phi 13.	<u>C. 76087</u>
	(210-212 m. and 271-285 m. below top of strata section i), loc: phi 14.	<u>C. 76088-76096</u>
	(strata section i), loc: phi 14.	<u>C. 76097-76103</u>
	(270-274 m. below top of strata section i), loc: sigma 15.	<u>C. 76104</u>
	(329-330 m. and 420-422 m. below top of strata section i), loc: phi 15.	<u>C. 76105</u>
	(583-589 m. below top of strata section i), loc: phi 151.	<u>C. 76106-76108</u>
	(922-938 m. below top of strata section i), loc: sigma 17.	<u>C. 76109-76115</u>
	(970-976 m. below top of strata section i), loc: sigma 18.	<u>C. 76116</u>
	(1179-1184 m. below top of strata section i), loc: phi 21.	<u>C. 76117</u>
	(1199-1203 m. below top of strata section i), loc: phi 23.	<u>C. 76118</u>
	(1326-1328 m. below top of strata section i), loc: phi 149.	<u>C. 76119</u>
	(1179-1184 m. below top of strata section i), loc: phi 21.	<u>C. 76136-76157</u>
	(1199-1203 m. below top of strata section i), loc: phi 23.	<u>C. 76158-76165</u>
British Somaliland, Biyo Gora, Daban Corner.		
Eocene,		
(Fish) Cichlid (indet.);	(Sect. 1).	<u>C. 80129</u>
British Somaliland, Rhabka.		
Eocene,		
(Fish)	(section), 10 d 10' N., 45 d 19' E., loc: sigma 14.	<u>C. 73159-73161</u>
Buckinghamshire, Brickhill.		
Lower Greensand,		
(Fish) <u>Asteracanthus</u> sp.;		<u>B. 26675-26676</u>
(Fish) "Edaphodon" sp.;		<u>B. 58620</u>
(Fish) <u>Ischiodus townsendii</u> (Buckland);		<u>B. 26759</u>
(Fish) <u>Lepidotus maximus</u> Wagner;		<u>B. 26765-26766</u>
(Fish) <u>Otothus</u> sp.;		<u>B. 26549-26553</u>
(Fish) <u>Oxyrhina</u> ;		<u>B. 26790-26792</u>
(Fish) <u>Pycnodus</u> sp.;		<u>B. 26639</u>
(Fish) <u>Pycnodus couloni</u> Agassiz;		<u>B. 26648</u>
(Fish) <u>Sphenonchus</u> sp.;		<u>B. 26637</u>
(Fish) <u>Strophodus</u> sp.;		<u>B. 26618-26619</u>
		<u>B. 26716</u>
		<u>B. 26595</u>
Buckinghamshire, Pitstone, Upper Icknield Way.		
Turonian,		
(Fish) <u>Scapanorhynchus subulatus</u> (Agassiz);	(pit on S. side), (600 yds. E.S.E. of church), grid ref: 42/946147.	<u>B. 91737</u> 4.20

gradually over almost fifty years. Data quality is thus rather variable. Over the full range of the catalogue, locality names may have several different spellings or differ in orthography. Geographical information for a single locality may be given in different records in different hierarchical sequences, in one case say 'farm name — village — town — county', in others 'farm name — town — county', or just 'village — county'. Such variation can cause a single locality to appear in many different places on a single index. The same is true for stratigraphic horizons.

Because of all these difficulties with indexes, and to obviate the need for reprinting large numbers of indexes at each updating of the catalogue, the Sedgwick Museum has now reduced the number of routinely used indexes to just one: a taxonomically based index divided up into sections on the basis of convenient suprageneric groups. An example of the layout and contents of part of the 'Fish' section of this index is shown in text-fig. 2. This taxonomic index in the form of microfiche (currently 90 fiche), together with a fiche version of the entire catalogue in alphanumeric order (117 fiche), are the only fixed hard-copy documents which play any important part in the Sedgwick System. The need for a variety of other indexes has been obviated by the use of an Information Retrieval System (IR System), which is now central to all Sedgwick Museum procedures.

Acanthodes sp.

(bone-bed - conglomeratic sandstone - Bed 2), Downtonian (base); Lower Wolton Farm, Woolhope Inlier, Herefordshire.

Listed, Gardiner, 1927, Q.J.G.S., lxxxiii, pp.517, 527 p.527.

A. 45356

Coal Measures, Carboniferous.

E. 3969

Coal Measures, Carboniferous; Newcastle, Northumberland.

Identified, Traquair, R.H.

E. 3970

Lancashire, 40 yds Mine, Coal Measures, Carboniferous; Bacup. styliform, bone.

E. 3971

Acanthodes mitchelli Edgerton

Mesacanthus mitchelli (Edgerton)

Old Red Sandstone, Devonian; Reswallie, Forfar.

H. 4465-4467

Old Red Sandstone, Devonian; Forfar.

H. 4468

Acanthodes nitides A.S.Woodward

Cement Stone Group, Calciferous Sandstone Series, Carboniferous; Esk R., Glencartholm, Langholm, Dumfries, Scotland.

Topotype,

E. 4965

Acanthodes wardi Edgerton

Coal Measures, Carboniferous; Longton, Staffordshire.

E. 3950

Coal Measures, Knowles Ironstone, Carboniferous; Fenton, Staffordshire. Identified, Traquair, R.H., spine.

E. 3951-3954

Coal Measures, Carboniferous; Longton, Staffordshire. Identified, Traquair, R.H., pectoral, spine.

E. 3955

Coal Measures, Better Bed, Carboniferous; Low Moor, Yorkshire. Identified, Traquair, R.H., spine.

E. 3956-3959

Coal Measures, 40 yds Mine, Carboniferous; Bacup, Lancashire. Identified, Traquair, R.H., spine.

E. 3960-3961

Identified, Traquair, R.H., pectoral, spine.

E. 3962

Coal Measures, Carboniferous; Longton, Staffordshire. trunk.

E. 3963-3965

Information Retrieval System

The entire catalogue can be searched rapidly on-line using the IR System, on the basis of pre-determined search criteria which may be very complex. The IR System responds initially by giving the number of *specimens* found in all records conforming to the search criteria. It can then be asked to list all such specimens by number, or a 'job' can be submitted to the computer to retrieve the actual records from a magnetic disc version of the catalogue. The job may take fifteen minutes or so to run.

Each specimen in the catalogue is indexed by a set of *terms* which are generated automatically from the GOS record describing the specimen. A term has the form of an initial upper case letter followed by a series of up to 23 lower case letters, digits, commas or full stops, but with all other characters, including spaces, discarded e.g. 'Ajones,o.t.1948', 'Roxfordclay'. The initial letter indicates the nature of the term: 'A', for instance, indicating authorship. The list below explains the significance of each upper case initial and shows also from which field or fields of a record each term is derived (field-tags, such as *a1 or *gn, relate to the SM Format given in the Appendix).

Term category	Example	Term derived from (see Appendix)
A = authorship	'Abarker,r.w.1927'	first *a1 and *ryear in *doc in each *re
D = donor	'Dstricklandcoll.'	each *ps1 in *oh
F = function word	'Fholotype'	each *fl containing 'fig'd' or ending in 'type'
G = group	'Gtrilobite'	each *gn
K = keyword	'Kcranidium'	individual words in each *kw1
L = locality	'Lrobinhoodsbay'	each *loc1
N = informal name	'Ngoniatite'	each *taxs with no formal taxonomic name components
O = lithology	'Oblackshale'	each *lith1
P = preservation	'Preplacement'	each *pres1
Q = age	'Qjurassic'	each *age1
R = rock	'Rcornbrash'	each *rk1
S = store	'Sxxx.n.39'	each level (between stops) in each *store1
T = genus	'Thildoceras'	each *gen
U = species	'Ublumenbachii'	each *spec

In addition every catalogued specimen is indexed as 'I'. The way in which such index terms are generated from an actual record is illustrated by an example in the Appendix.

Within the system each term has a *term number*, *n*, which merely indicates its position within the current index, and a *frequency*, *f*, which is the number of specimens indexed by that term. Terms are usually printed in *n* — term — *f* order, with *f* in brackets, e.g.

593 = Gforaminiferan (5424)
2027 = Lperu (1921)

The simplest possible retrieval request is based on a single term. The query a-q <'Gammonoid'> asks what ammonoids there are in the collection. More complex queries combine terms together according to the rules of Boolean logic, using the operators '&' (= logical and), '|' (= logical or), and '-' (= logical subtraction). Further, actual terms may be replaced in queries by the term number, *n*, or by a specimen identity number, or by a range of such numbers. The query a-q <'Gammonoid' & 'Qoxfordian'—[F.1-23000]> asks for all British ammonoids of Oxfordian age (British since all 'foreign' Mesozoic specimens, of which there are just over 22,000, have specimen numbers prefixed with 'F.'). Of course, an actual retrieval request would be more complex than this, since not all records for ammonoids of Oxfordian age would necessarily contain 'Oxfordian' as an age term, particularly if they had been transcribed from the earlier part of the manual catalogue. In practice it would be necessary to retrieve also on rock terms such as 'Roxfordclay', 'Ramphillclay', 'Rwestwaltonbeds', 'Rbrorasandstone', etc. Similar problems arise when locality names appear in different guises in different parts of the catalogue.

The problem of variant forms of a single term. This is another aspect of the problem discussed earlier in relation to the use of hard-copy indexes; only in the case of index terms in the IR System there is a solution. The IR System has a facility for listing all index terms which show similarity to a given term. Each term in the term index is broken into fragments of four characters and separately indexed under all of these fragments, e.g. 'Cambridge' generates the fragments 'camb', 'ambr', 'mbri', 'brid', 'ridg', and 'idge'. The measure of similarity between terms is based on the number of fragments they have in common. A list can be requested which will give similar terms in decreasing order of similarity up to any number specified by the user. The list may either be restricted to terms of a particular category (e.g. age terms, genus names) or may include all terms irrespective of category.

The usefulness of this 'similar term' facility can be illustrated by an actual example. An IR query asking what specimens in the collections were donated by F. R. Cowper-Reed might be expected to take the form a-q <'Dcowperreed,f.r.'>. In fact, the submission of such a query should be preceded by a request for similar terms. If the ten most similar donor terms are requested by a-simt <Dcowperreed, f.r. >, the system responds with:

(cfterms)

Dcowperreed,f.r.:	3271 = Dcowperreed,f.r.	(804)	3269 = Dcowperreed	(22)
	3272 = Dcowperreed,f.r.coll.	(1)	4752 = Dreed,f.r.c.	(1225)
	3270 = Dcowperreed,f.	(3)	4753 = Dreed,f.r.c.coll.	(61)
	3254 = Dcooperreed,f.r.	(3)	4751 = Dreed,f.c.r.	(1)
	4754 = Dreed,f.r.cowper	(48)	5484 = Dwoodward,f.r.	(1)

The first nine of the above terms are indeed variations on F. R. Cowper-Reed ('cooperreed' is a misspelling; 'coll' is an abbreviation for collection). Using term numbers, the original query could now be replaced with a-q <3271 | 3272 | 3270 | 3254 | 4754 | 3269 | 4752 | 4753 | 4751 >. The original query would have yielded only 804 specimens, but the more complex query now yields 2168.

The IR System can be used to answer many enquiries about the collections which would have been virtually impossible to answer using the manual system. Enquiries which formerly could only have been answered by physically searching the collections (exploiting a lay-out which reflects both stratigraphy and geography) can now be answered in a minute fraction of the time such a physical search would have taken—and much less fallibly.

DISCUSSION

Major benefits of 'computerization'

As a result of adopting computer-based data handling techniques, the Sedgwick Museum has acquired a wide range of new capabilities. Many of these are of strictly curatorial interest in that they are aimed at facilitating and improving management of the collections. Even here though external users will derive some benefit; for example, from rapid automatic processing of loans. Most of the main benefits to external users, however, are implicit in the preceding description of data retrieval, particularly in the illustration of the great variety of queries about the collections which can now be rapidly answered using the IR System. One major use of the IR System has been to provide palaeontologists with what might be termed 'specialist catalogues': retrieving and printing-out for instance the records of vertebrates from the Oxford Clay, Ordovician ostracodes, British Liassic, Callovian and Kimmeridgian corals, or Wealden reptiles from Brook on the Isle of Wight (all actual examples).

The complete museum catalogue and the taxonomic index are both on microfiche, and can therefore be very quickly and cheaply reproduced (in whole or in part) and readily distributed. Diazo copies from the COM fiche originals at present cost between 12p and 14p, depending on the numbers involved. At such a rate, a copy of the entire catalogue costs approximately £16, the taxonomic index approximately £13. Each section of the taxonomic index (e.g. 'trilobites', 'graptolites', 'bivalves') is usually only a few fiches in length.

Specimen security and locality conservation

The possibility of easy reproduction and distribution of catalogues and indexes raises problems of data security. At present the main concern must be with data about specimen storage. Data 'in the computer' is reasonably secure because it is only accessible to those at once familiar with the general working of the Cambridge Data Network, with the general working of GOS, and with the esoteric command syntax for the Sedgwick System; and who, in addition, are in possession of (or able to obtain) the passwords which safeguard access. Such data is also safe from loss because there are duplicated magnetic tape versions of the catalogue stored separately from the primary version and, of course, hard-copy fall-back in the form of fiche.

It is hard-copy output which potentially leads to the greatest security risk. Internal 'working' Museum hard-copy needs to carry storage locations; the present policy is to ensure that all hard-copy for external use is produced from GOS files which have had the *store field stripped out. It would be possible to strip out also detailed locality information, including grid-references or latitude and longitude. At present we see little point in doing this since the information is usually readily available in scientific papers and monographs, and because catalogue information is only distributed to bona fide research workers.

Future developments

Direct access to the museum database is restricted at present to the Curators who alone decide what information to release and to whom. It may be possible in the future to permit some form of access to external users at other computer sites linked to the Cambridge Network, or through a dial-up link. Such access would be via the IR System and, we envisage, would be restricted to the IR System indexes, thus enabling external users to make full use of the fiche versions of the catalogue and indexes while still safeguarding access to museum storage data (and any other data deemed 'sensitive' in the GOS database). Ideally any such arrangements would include reciprocal arrangements with other museums.

The Sedgwick Museum has acquired a complete, working, computer-based documentation system earlier than many other museums. It is now open to palaeontologists and palaeontological curators elsewhere to appraise the system in relation to their own requirements. It is our strong hope at this early stage that it might find wider application. Thoughts of a unified palaeontological database, involving the collections of many major institutions, may seem Utopian at present but we believe that in our work at the Sedgwick there lies one opportunity for such a future. Opposed to this opportunity is the very real danger that soon each institution will develop its own computer-based system, with its own data standard, and that mapping data from one system to another will become virtually impossible. In the field of computer-based museum documentation as a whole in Britain, it is already apparent that various factors (not least political and economic ones) have conspired to force such a pluralistic future. Perhaps for the major palaeontological collections this can yet be avoided.

Acknowledgements. My enormous indebtedness to Martin Porter, prime architect of the computer-based system described in this paper, will be obvious. He, Dr. W. D. I. Rolfe, and Mr. R. H. Hughes kindly read earlier typescripts and made useful suggestions for improvements.

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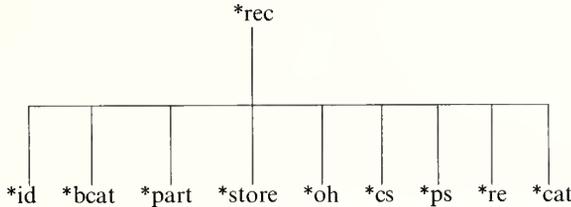
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APPENDIX

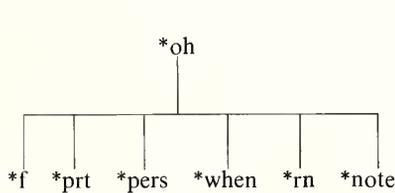
Details of data structure

The SM Format is a much modified version of the 'General Index Format' devised by J. L. Cutbill during the early stages of work at the Sedgwick Museum. It can be visualized as an irregularly branching tree-like structure. The main trunk represents a complete record, and this is progressively divided into increasingly restricted data categories until the terminal branches represent *basic* data fields which, unlike the *group* data fields nearer the trunk, cannot be divided further and contain the actual items of data making up the record, either as strings of characters or as numeric variables. Basic fields are either *keyword* fields containing essential data, or *detail* fields containing data elaborating the keywords. If each data field is represented by its tag, the point where the trunk of the format first divides can be represented as follows:



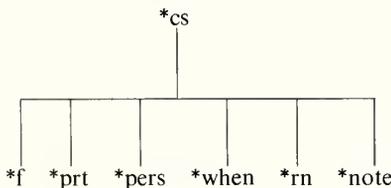
- *rec denotes the complete *record* in SM Format
- *id the record *identity* (= specimen catalogue number)
- *bcat the *broad category* of objects to which the specimen belongs (implicitly 'fossil'; otherwise 'replica', 'artefact', 'rock specimen', or 'inorganic' explicitly stated)
- *part a declaration that the specimen comprises two or more *parts*
- *store the *storage location*
- *oh the *ownership history* (mode of acquisition by the Sedgwick Museum, and previous ownership)
- *cs a *collection statement* (saying by whom the specimen was collected and when)
- *ps a *provenance statement*
- *re a *research event* (anything from an informal identification to the designation of the specimen as a type)
- *cat *cataloguer* information

Of these nine data fields, *oh, *cs, *ps, and *re contain by far the bulk of the data in the record, and are accordingly known as the *main data groups*. They represent major branches of the format which are worth following separately. First, *ownership history*:



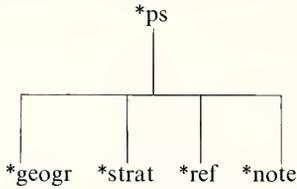
- *f a *function* word (e.g. 'presented', 'exchanged', 'purchased')
- *prt the part(s) of the specimen concerned
- *pers the person or institution concerned
- *when the date or a time period (range of dates)
- *rn the reference number of the specimen in any previous collection
- *note a general detail field

*f and *pers are each made up of keyword and detail fields, *when contains *date denoting a single date (field repeated for a period) and is broken further into separate fields for day, month, and year (each containing a two digit number), with a detail field for terms like 'circa', 'not later than' etc. The *collection statement* field has a similar structure:



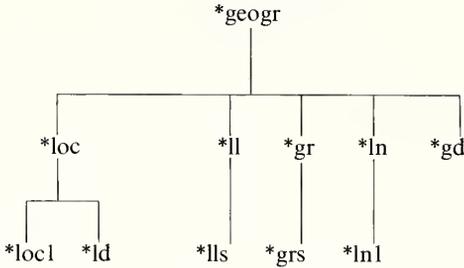
but for this field the function (*f) word 'collected' is automatically generated by the GOS 'display' processor rather than put in as data.

The *provenance statement* has the structure:

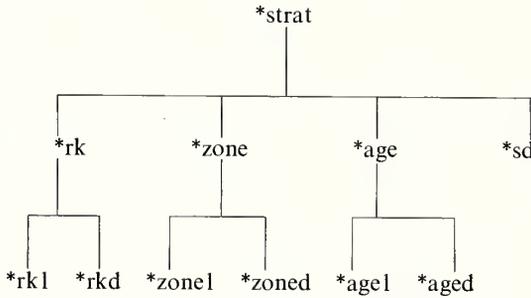


- *geogr contains *geographical* information
- *strat contains *stratigraphical* information
- *ref contains *documentary* information (e.g. bibliographic references)

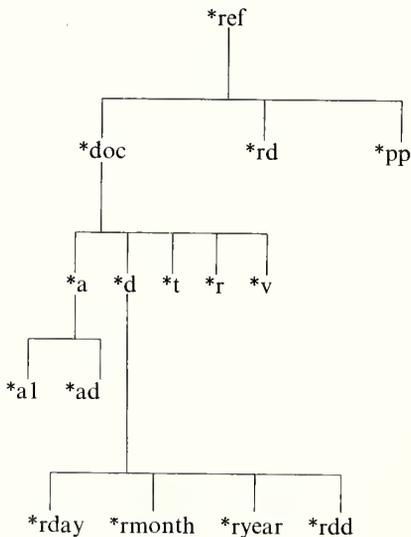
These fields have the following structure:



- *loc place names
- *loc1 a specific place name (keyword)
- *ld detail for *loc1 (e.g. 'near', '3 km NW')
- *ll *latitude and longitude*
- *lls text for *ll
- *gr *grid reference*
- *grs text for *gr
- *ln locality number
- *ln1 text for *ln
- *gd general geographical detail

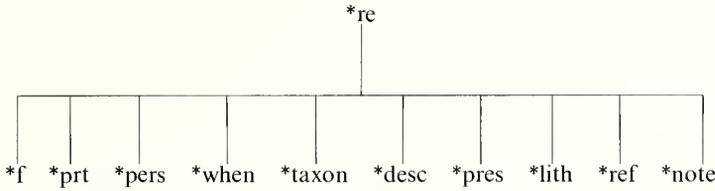


- *rk *lithostratigraphic* information
- *rk1 name of rock unit (usually a formational name)
- *rkd detail for *rk1 (e.g. 'basal')
- *zone *biostratigraphic* information
- *zone1 name of zone or sub-zone
- *zoned detail for zone1 (e.g. 'topmost')
- *age *chronostratigraphic* information
- *age1 name of period, stage, etc.
- *aged detail for *age1
- *sd general stratigraphic detail



- *doc document
- *a *author*
- *a1 name of author
- *ad detail for *a1
- *d date
- *rday day (as a two digit number)
- *rmonth month (as a two digit number)
- *ryear year (as a two digit number)
- *rdd any qualifying details for date
- *t title
- *r journal
- *v volume
- *rd reference detail
- *pp page number, plate, and figure information

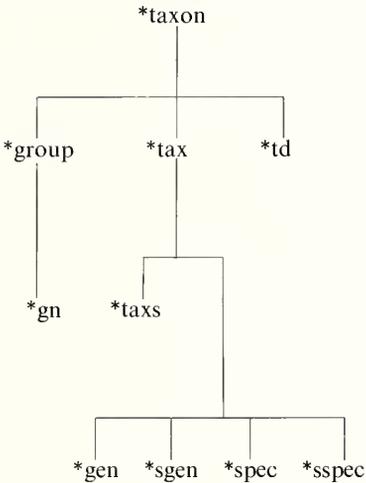
The *research event* is structured thus:



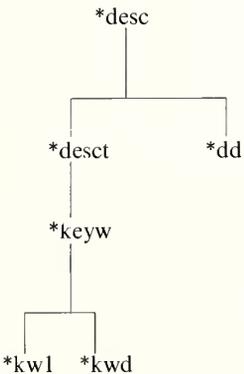
In the **re* field, **f* contains words such 'described', 'mentioned', 'fig'd', 'holotype', 'paratype', etc.

- *taxon* *taxonomic* information
- *desc* *descriptive* information (morphology)
- *pres* *preservational* information
- *lith* *lithological* information (matrix)

**pres* and **lith* are simply made up of keyword and detail fields; **taxon* and **desc* are structured as follows:



- *group* suprageneric classification } arbitrary museum scheme
- *gn* name of suprageneric group } only
- *tax* formal taxonomic nomenclature
- *taxs* full taxonomic name with author(s)
- *gen* *genus*
- *sgen* *subgenus*
- *spec* *species*
- *sspec* *subspecies*



- *desct* descriptive term
- *keyw* keyword information
- *kw1* actual keyword (e.g. 'cranidium', 'phragmacone')
- *kwd* detail for **kw1* (e.g. 'incomplete', 'distal end')
- *dd* description detail (e.g. 'atypically convex', 'shows doublure')

In designing the SM Format we have tried to produce a data structure which gives much scope for improved specimen documentation; for instance, by incorporating fields for morphological, preservational, and lithological data. The only major data category not catered for is biometric data, and we have considered this to be beyond the scope of a general museum database. It would, of course, be possible to produce specialized databases to contain biometric data for particular groups of organisms for which standardized measurement schemes had been agreed.

The rationale of the SM Format can be illustrated by considering its application to a hypothetical specimen from the *Schloenbachia varians* Zone of the lower Chalk (Cenomanian) of Burwell, Cambridgeshire, collected by J. Bloggs in 1970, identified by him as the external mould of the right valve of the bivalve *Agenus beta* Smith and presented to the Sedgwick Museum in the same year. The specimen is subsequently selected by T. Jones as the holotype of his new species *Agenus nova* Jones, 1975 (*Geol. Mag.* vol. 200, p. 16, pl. 1, fig. 3). Supposing that a catalogue number A1 had been applied to the specimen, and that it had been stored in drawer x.t.114 of the museum, then it would ultimately have a record in the computer-file catalogue with the following structure:

```

*rec
  *id
    *key
      *code
        *elem A
        *elem2 1
        *elem2 0 (this indicates a single
                  specimen)
    *bcat fossil (implicit—data not actually
                present)
  *store
    *store1 x.t.114
  *oh
    *f
      *f1 presented
    *pers
      *ps1 Bloggs, J.
    *when
      *date
      *wyear 1970
  *cs
    *f
      *f1 collected (implicit—data not
                    actually present)
    *pers
      *ps1 Bloggs, J.
    *when
      *date
      *wyear 1970
  *ps
    *geogr
      *loc
        *loc1 Burwell
        *loc1 Cambridge
    *strat
      *rk
        *rk1 Chalk
        *rkd lower
      *zone
        *zone1 /USchloenbachia/N
              /Uvarians/N Zone†
    *age
      *age1 Cenomanian
      *age1 Cretaceous

```

```

*re
  *f
    *f1 identified
  *pers
    *ps1 Bloggs, J.
  *when
    *date
    *wyear 1970
  *taxon
    *group
    *gn Bivalve
  *tax
    *taxs /UAgenus/N /Ubeta/N Smith†
    *gen Agenus
    *spec beta
  *desc
    *desct
    *keyw
    *keyw1 right valve
  *pres
    *pres1 external mould
*re
  *f
    *f1 fig'd
    *f1 holotype
  *taxon
    *group
    *gn Bivalve
  *tax
    *taxs /UAgenus/N /Unova/N Jones†
    *gen Agenus
    *spec nova
*ref
  *doc
    *a
      *a1 Jones, T.
    *d
      *ryear 1975
    *r Geol. Mag.
    *v 200
    *pp p.16, pl.1, fig.3
  *cat
    *catn Price, D.
    *catd 1972

```

(† /U and /N are 'flags' controlling underlining)

This example illustrates an important feature of GOS-based data handling: that fields can be repeated, if necessary many times over. For example, complicated locality descriptions can be broken down into a series of *loc keywords or complicated modes of preservation described by a series of *pres keywords. This feature is of

particular importance in the Sedgwick System in respect to the *re (research event) field. Repetition of this field allows a record to contain all the taxonomic names ever applied to a specimen so that the specimen could be retrieved on any one of them. The hypothetical record with the structure illustrated above would, in fact, generate the following catalogue entry:

A.1 store: x.t.114

Presented, Bloggs, J., 1970.

Collected, Bloggs, J., 1970.

Lower Chalk, *Schloenbachia varians* Zone, Cenomanian, Cretaceous; Burwell, Cambridgeshire.

Identified, Bloggs, J., 1970, as bivalve *Agenus beta* Smith; right valve, external mould.

Fig'd, Holotype, Jones, T., 1970, Geol. Mag., 200, p. 16, pl. 1, fig. 3, as bivalve *Agenus nova* Jones.

[Catalogued Price, D./1972]

With respect to the Information Retrieval System, this hypothetical record would generate the following index terms (from the fields listed on p. 397 above):

'I'	'Rchalk'	'Krightvalve'
'Sx.'	'Qcenomanian'	'Pexternalmould'
'Sx.t.'	'Qcretaceous'	'Ffig'd'
'Sx.t.114'	'Gbivalve'	'Fholotype'
'Dbloggs,j.'	'Tagenus'	'Ajones,t.1970'
'Lburwell'	'Ubeta'	
'Lcambridgeshire'	'Unova'	

PTEROSAUR REMAINS FROM THE KAYENTA FORMATION (?EARLY JURASSIC) OF ARIZONA

by KEVIN PADIAN

ABSTRACT. Two records of pterosaurs, the earliest from the Western Hemisphere, are reported from the Kayenta Formation (?Early Jurassic) of north-eastern Arizona. The first specimen represents a new genus and species, *Rhamphinion jenkinsi*. It consists of three pieces of a skull, including an occipital region, most of a left jugal, and two teeth associated with a possible fragment of the dentary; it is difficult to diagnose because it is so fragmentary and because the occipital region of early pterosaurs is not well known, but may be recognized by the position and configuration of the orbital and antorbital borders of the jugal. The second specimen is the left-wing (fourth) metacarpal of a rhamphorhynchoid; it is well-preserved but cannot be classified more precisely.

OVER the past few years, field parties from the Museum of Comparative Zoology at Harvard University (MCZ), the Museum of Northern Arizona (MNA), and the Museum of Paleontology of the University of California at Berkeley (UCMP) have renewed intensive palaeontological exploration of the Kayenta Formation of northern Arizona. The Kayenta Formation was prospected sporadically since the 1930s, but its white to orange-red sandstones and grey-purple siltstones yielded few specimens. The recent finds, however, have greatly increased our knowledge of the faunal diversity of the Kayenta, which now includes large and small ornithischian and saurischian dinosaurs (Welles 1954; Colbert 1980; Attridge *et al.* MS.), several kinds of crocodylians, (Crompton and Smith 1980), testudinales, lizards, amphibians, tritylodontid mammal-like reptiles (Lewis 1958; Kermack 1982), and several kinds of mammals (Jenkins *et al.* 1983). Most remains of the smaller vertebrates have been recovered by screen-washing sediment and hand-picking the sieved residue; most of this work has been ably carried out by Mr. William R. Downs of the Museum of northern Arizona. The results of these labours, in addition to an expanded faunal list, include a better understanding of the biostratigraphical relationships among the fossiliferous horizons of the Kayenta and other early Mesozoic formations. While the exact age of the Kayenta Formation is not certain, the general faunal composition and the consistent absence of Triassic marker species now appear to argue for Early Jurassic (Olsen and Galton 1977), although difficulties with this assignment may remain (Colbert 1980). Most Kayenta vertebrates, at the taxonomic levels so far determined, do not permit of a precise stratigraphical correlation. Dinosaurs, testudinales, crocodylians, lizards, and perhaps mammals are known both from Late Triassic and Early Jurassic sediments. Until the phylogenies of the early members of these groups have been elucidated, we shall be unable to comment on the stratigraphical and geographical distribution of certain sub-groups of each, which may indeed be restricted and therefore diagnostic.

This note describes the first remains of pterosaurs (flying reptiles) from the Kayenta Formation. These are the earliest known from the Western Hemisphere, but not the oldest in the world; *Eudimorphodon ranzii* Zambelli 1973 and *Peteinosaurus zambellii* Wild 1978, from the Norian (Upper Triassic) sediments of northern Italy, are older. Pterosaurs are exceptionally light-boned animals and therefore do not preserve well. It is indeed fortunate to recover their remains from the Kayenta Formation; pterosaurs are best preserved in low energy, fine-grained marine or lacustrine sediments, and their record in any kind of terrestrial sediment is poor. Although the quality of the specimens at hand is not very good, I believe there is sufficient evidence to assign them to the Order Pterosauria, as outlined below.

SYSTEMATIC PALAEOLOGY

Class REPTILIA

Order PTEROSAURIA

Sub-order RHAMPHORHYNCHOIDEA

Family *Incertae sedis*Genus *Rhamphinion* gen. nov.*Type species. Rhamphinion jenkinsi*, sp. nov.

Etymology. *Rhampho-*, comb. form of *rhamphos*, Gr., 'beak', used in other rhamphorhynchoid names; *inion*, Gr., 'nape of the neck'; referring to the occipital region comprising much of the present specimen.

Diagnosis. The material is diagnostic of the Order Pterosauria because of the large, long, strap-like quadrate, the relatively small occipital condyle, the thin, laminar cranial bones, the large lower temporal fenestra, the shape and orientation of the ascending process of the jugal, and the form of the teeth. Without better preservation it is difficult to specify characters that diagnose the Sub-order Rhamphorhynchoidea, although the shape of the jugal is not at all similar to those of pterodactyloids. The genus is characterized by nearly rounded antorbital and orbital margins next to the ascending process of the jugal. The apparent suture between the maxilla and the jugal has a long, low sloping contact and the orbit is situated at approximately the same height above the tooth row as is the antorbital opening.

Remarks. The shape of the quadrate is reminiscent of that of *Eudimorphodon* (see Wild 1978, fig. 1 and pl. 3), as is the general shape of the jugal and the participation of the lacrimal (prefrontal of Wild 1978) in the anterior margin of the orbit. The present specimen has single-cusped teeth that are slightly recurved and tapered at both ends. Such teeth occur in juvenile *Eudimorphodon* (Wild 1978), and are found in the maxillary region of *Dimorphodon macronyx* (Buckland) (Owen 1870; Padian, in press) and most other rhamphorhynchoids. Family division and nomenclature among the Pterosauria are greatly in need of revision, as is the generally accepted phylogeny of the group and its evolutionary position with respect to other archosaurs. Hence, no family designation is given here. The genus is generally similar to several early rhamphorhynchoids, including *Eudimorphodon*, *Dimorphodon*, and *Dorygnathus*.

Rhamphinion jenkinsi, sp. nov.

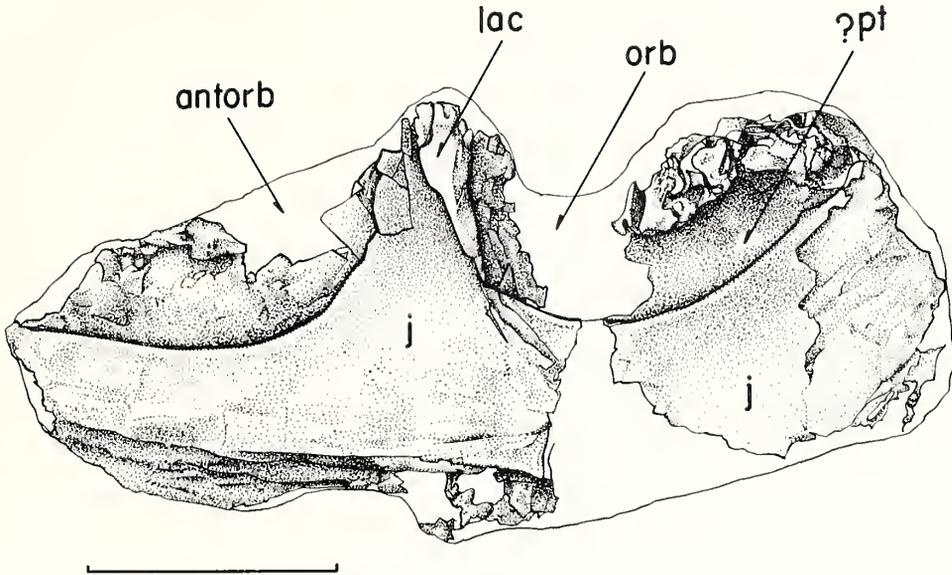
Text-figs. 1-3

Etymology. Named in honour of Dr. Farish A. Jenkins Jr., who discovered the specimen and very kindly made it available to me for description.

Material and occurrence. Holotype, MNA V 4500, consisting of four pieces: an occipital region, a left jugal fragment, a possible mandibular fragment with two associated teeth and the impression of a third, and an unidentifiable bone fragment. Middle Kayenta Formation (Lower Jurassic) of north-eastern Arizona, at the locality known as 'Foxtrot Mesa', the southern side of Sand Mesa, along the Adeii Eechii cliffs, Ward's Terrace, Little Colorado River Valley. Approximate coordinates 35°41'43" N., 111°0'25" W. The remains were found in surface float of the silty facies of the Kayenta; the horizon cannot be precisely traced. Collected by Dr. Farish A. Jenkins Jr. and his field party from the Museum of Comparative Zoology at Harvard University and the Museum of northern Arizona. With this material, which was given the field number 23/78A, were a few other scraps of as yet unidentified bone, lighter in colour and more robust in structure, and not pterosaurian.

Diagnosis. As for the genus.

Description. The preserved fragment of the left jugal (text-fig. 1) is 40 mm long and 19 mm wide at its highest point on the ascending process. The horizontal, sub-orbital portion widens posteriorly and ascends slightly. The rounded bottom of the orbit curves more gently posteriorly, whereas the base of the antorbital opening curves more gently anteriorly. The lower borders suggest that the antorbital opening may have been larger than the orbit, as in most pterosaurs. Along the posterior border of the ascending process is a splint of bone identifiable as



TEXT-FIG. 1. *Rhamphinion jenkinsi*, gen. et sp. nov. Left jugal with associated fragments. Part of holotype, MNA V 4500. Scale = 10 mm. Abbreviations: antorb = anterior orbital opening; j = jugal; lac = lacrimal; orb = orbital opening; ?pt = possible fragment of pterygoid.

the lacrimal (following Wellnhofer's (1978) terminology; Wild (1978) calls this the pre-frontal). This splint is about 7 mm long, and it tapers as it descends.

Most of the bone has been worn away beneath the very front of the orbit, but the remaining bone seems to be undisturbed. The lower border of the jugal appears to slope upwards and forwards, and 22 mm of the maxillary suture is preserved. Anteriorly the bone is broken away, and posteriorly it is hidden by a support compound applied during preparation, that might be difficult to remove without damage to the specimen. Parts of internal skull bones can be seen within the openings, but these have been crushed beyond recognition.

The occipital fragment (text-fig. 2A) is about the same size as the jugal fragment. It preserves the occipital condyle with part of the adjacent basioccipital and exoccipital regions, the medial part of the left paroccipital process, an underlying fragment which may be the prootic, and two descending rami of bone that seem to be portions of the quadrates. It is difficult to estimate the size of the complete skull from these remains, but in relation to the other bones the occipital condyle is small, a characteristic of pterosaurs and birds (Seeley 1901; Wellnhofer 1978). Text-fig. 2B, based on the skull of *Rhamphorhynchus*, shows the parts of the occipital region represented in this specimen. A great deal of crushing and dislocation has taken place, and the identification of many features must be regarded as tentative.

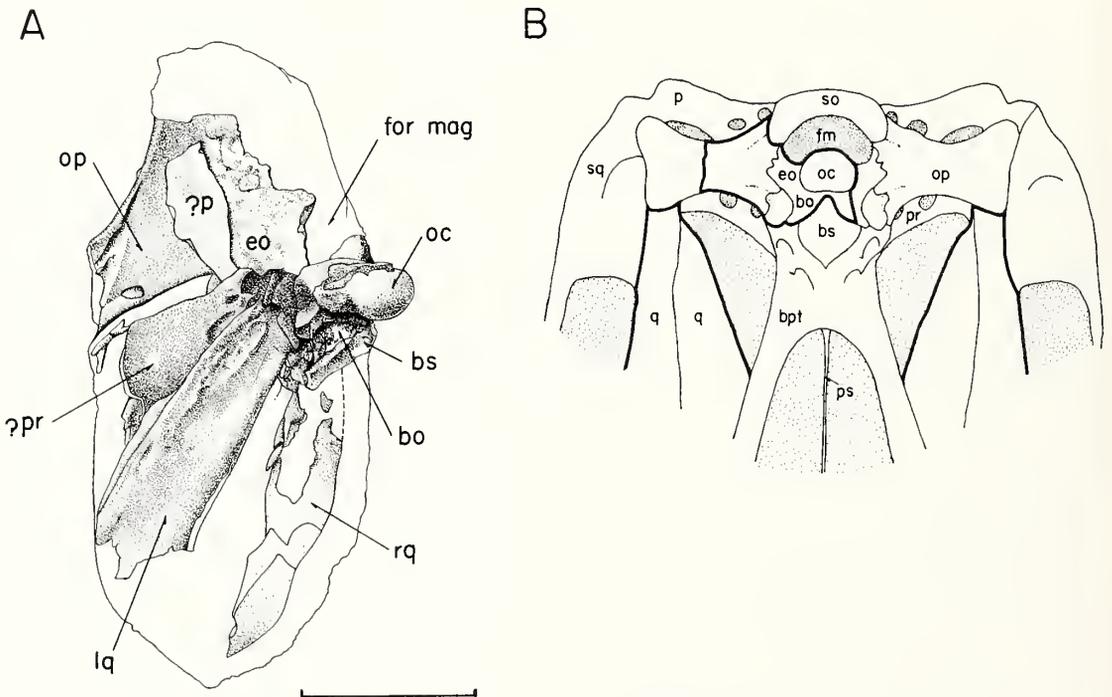
The occipital condyle is ovate in shape; it lacks some of its dorsal portion, but is otherwise fairly complete. Portions of the left exoccipital can be seen ventral and lateral to the condyle, including the basal tubera that connect the exoccipital with the basisphenoid and the basioccipital, and the lateral flange that meets the opisthotic or paroccipital process. Along its lateral border there is a recess in which the most posterior cranial foramina should be located, but no details of this region are preserved. Most of the basioccipital region is missing, and only a few bone fragments of dubious origin remain. Lateral and dorsal to this region is the medial portion of the left opisthotic or paroccipital process. Its dorsal and ventral borders are well-formed, and the positions of the post-temporal foramen and the foramen magnum can be inferred from its preserved relationship to the other bones of the occipital region. About 15 mm, or roughly half the length of the entire bone, appears to have been preserved. There is no trace of the supraoccipital. A portion of another bone, perhaps displaced from the skull roof, overlies the medial section of the opisthotic, but it has no diagnostic feature.

A wide, strap-like lamina of bone runs lateroventrally from just below and to the left of the occipital condyle, widening until its disappearance at the lower left edge of the specimen. Medially it tapers somewhat, but this end

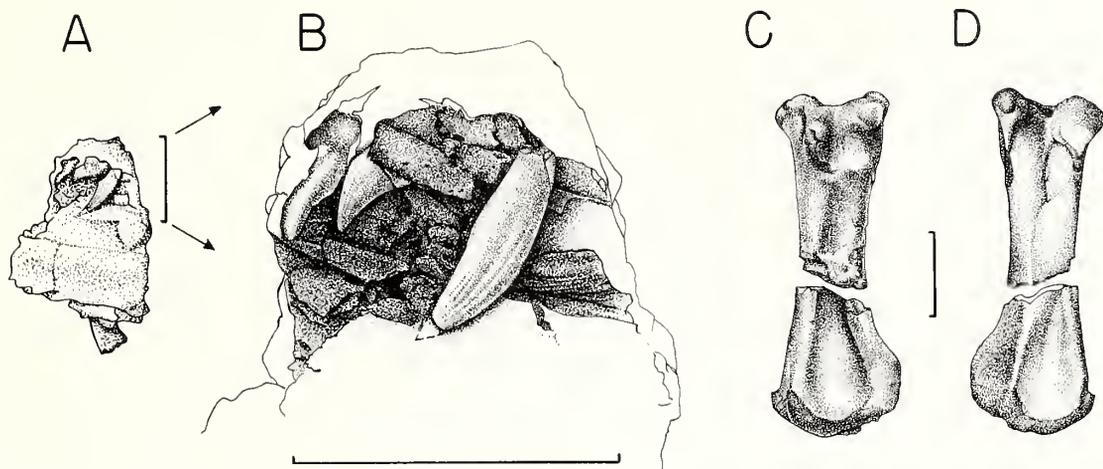
is obscured by overlying portions of the exoccipital region; it appears to be part of the left quadrate. Another similar fragment, apparently the right quadrate, is located behind the occipital region and is mostly obscured by compound applied in preparation. The quadrates in pterosaurs, though quite large, are light in structure; their apparent displacement in this specimen does not facilitate identification of their major features. They superficially resemble the basiptyergoid processes, which are unusually large in pterosaurs (Wellnhofer 1978, fig. 3). However, the structures on the specimen at hand widen as they descend from the occipital region, unlike the basiptyergoid processes, which are of fairly uniform width throughout.

In the space bounded by the paroccipital and the quadrate, and overlain by both bones, there is a small segment of bone that, from its position, I take to be part of the prootic; however, there are no identifying features of the bone, and no foramina are evident.

A third piece of matrix, encrusted with haematite, bears a sheet of bone with the remains of three teeth (text-fig. 3A, B). These teeth do not appear to be in position, and so the bone cannot be positively identified as either maxilla or dentary; its depth and general surface character, however, suggest the latter (cf. *Dimorphodon macronyx*, Owen 1870, pls. XVII and XVIII). Most of two teeth and an impression of a third are preserved. No alveoli are visible. The larger of the two preserved teeth is 6.0 mm long, missing about 0.5 mm at the tip of its crown. It shows the slightly compressed and recurved, unserrated shape of the mid-maxillary teeth of the approximately contemporaneous *Dimorphodon* (Owen 1870; Padian 1980, 1983). There are faint longitudinal striations on the tooth, and its tip is only slightly sharper than its root. A second tooth is smaller, with only 2.5 mm of the tip of the crown exposed. Next to this is a shallow impression about 5.0 mm long of most of the main body of a third tooth, preserving some detail of the longitudinal striations. Similar teeth can be found



TEXT-FIG. 2. *Rhamphinion jenkinsi*, gen. et sp. nov. Occipital region. A, part of holotype, MNA V 4500. Scale = 10 mm. Abbreviations: bo = basioccipital; bs = basisphenoid; eo = exoccipital; for mag = foramen magnum; lq = left quadrate; oc = occipital condyle; op = opisthotic; ?p = possible fragment of parietal; ?pr = possible fragment of prootic; rq = right quadrate. B, posteroventral view of occipital region of *Rhamphorhynchus* (Carnegie Museum of Natural History CM 11434; actual breadth 32 mm), schematic diagram. bpt = basiptyergoid; ps = parasphenoid; so = supraoccipital; sq = squamosal. Portions represented by the corresponding region in *Rhamphinion jenkinsi* are heavily outlined.



TEXT-FIG. 3. A, B, *Rhamphinion jenkinsi*, gen. et sp. nov. Jaw fragment with two disarticulated teeth and one tooth impression. Part of holotype MNA V 4500. B is an enlargement of indicated part of A. C, D, left fourth metacarpal of a rhamphorhynchoid pterosaur, Kayenta Formation, UCMP 128227, in medial (C) and lateral (D) view, distal end up. Scale bars = 10 mm.

in other archosaurs, but are normally serrated or keeled, whereas they never are in pterosaurs. The general shape of the teeth, particularly the relative proportions and relationships of the root and crown, is indistinguishable from that of several Jurassic pterosaurs including *Dimorphodon* and *Campylognathoides* (Wellnhofer 1974), but is not reported in any other Lower Mesozoic.

ADDITIONAL PTEROSAUR REMAINS FROM THE KAYENTA FORMATION

In the Autumn of 1981 James M. Clark, a graduate student at the University of Chicago, discovered two fragments of a haematite-encrusted bone that he suspected were from a pterosaur. These proved to be the nearly complete left fourth (wing) metacarpal, about 42 mm long as reconstructed, of a rhamphorhynchoid pterosaur (UCMP 128227). It was found at the 'Airhead West' locality (V82374), not far from where the crocodylian *Eopneumatosuchus colberti* was collected by an MCZ field party in 1979 (Crompton and Smith 1980, p. 197). The horizon is near the base of the Kayenta Formation in Coconino County, Arizona, 11 miles NE of Cameron between the southern two tributaries of Five Mile Wash. The two pieces were preserved in a green siltstone with a thin sandstone stringer; no other remains were found.

The wing-metacarpal (text-fig. 3C, D) is diagnostic of rhamphorhynchoid pterosaurs because of its short, flattened shape and the topography of its articular surfaces. The pterodactyloid metacarpal is relatively longer, rounded in cross-section, and lacks the pronounced ventral flange present at the proximal end of rhamphorhynchoid metacarpals; it is often the longest, or one of the longest, segments of the pterodactyloid wing, whereas in rhamphorhynchoids it is nearly always the shortest.

Galton (1981) has recently described in detail a superbly preserved rhamphorhynchoid wing metacarpal from Como Bluff, Wyoming (Brushy Basin Member of the Upper Jurassic Morrison Formation). He named it *Comodactylus ostromi*, assigning separate generic status because of its large size and corresponding proportional differences from the metacarpals of other, smaller rhamphorhynchoids. In pterosaurs the fourth metacarpal appears to have rotated its position through 90° with respect to the other metacarpals, so that its distal condyles faced laterally instead of ventrally. As such, the wing-finger flexed and extended in a horizontal plane from its articulation with mc IV, and the first three metacarpals were also arranged in a horizontal plane (Wellnhofer 1978,

figs. 11 and 12; Wild 1978, pls. 1, 2, and 9g). This adaptation has led to some confusion in the terms used to describe orientation: the natural 'dorsal' face, for example, is properly regarded as 'medial' in orientation.

The proximal end of UCMP 128227 is badly worn and lacks most surface detail. The groove interpreted by Galton (1981) as for an extensor of the wing-finger is recognizable, but the ventral (or medial, in Galton's sense) flange near the proximal end has been mostly worn away. As in *Comodactylus* and other well-preserved metacarpals of both rhamphorhynchoid and pterodactyloid pterosaurs, the dorsal (lateral) condyle of the distal end is the larger and is skewed away from the axis of the shaft (see Wellnhofer 1978, fig. 12). There are deep ginglymal facets on both sides of the distal end.

The wing metacarpal is one of the poorest indicators of wing length in pterosaurs. In fact, no individual bone is a very good indicator because relative proportions vary among genera. However, the relative proportions of any two wing bones (except for the metacarpals and the last phalanx of the wing-finger) are almost without exception diagnostic to the generic level (Padian, unpublished). In size and proportions the present specimen resembles the larger specimens of *Dimorphodon* in the British Museum (Natural History), which have a wing span of approximately 1.5 m.

This specimen, and the cranial material of *Rhamphinion jenkinsi* described above, provide the third and fourth (and also the earliest) records of rhamphorhynchoid pterosaurs in the Western Hemisphere: the others are *Nesodactylus hesperius* Colbert 1969, from the Upper Jurassic of Cuba, and *Comodactylus ostromi*, also from the Upper Jurassic.

Acknowledgements I thank Dr. Farish A. Jenkins Jr., who presented the *Rhamphinion* material to me for study; Mr. James M. Clark, who collected the metacarpal during field work sponsored by the Museum of Paleontology, University of California; and the National Geographic Society which funded both expeditions. Mr. William Amaral prepared MNA V 4500, and Mr. Mark Goodwin prepared UCMP 128227 from its haematite crust. Ms. Augusta Lucas-Andrae illustrated text-figs. 1, 2A, and 3. I should also like to thank Mr. Charles Schaff of the Museum of Comparative Zoology for locality information on MNA V 4500, and Drs. A. J. Charig, Wann Langston Jr., and John H. Ostrom for reviewing the manuscript.

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ORDOVICIAN RECEPTACULITID ALGAE FROM BURMA

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ABSTRACT. *Fisherites burmensis* sp. nov., is described from the Lower-Middle Ordovician Wunbye Formation in the western part of the southern Shan State, Burma. This extends the geographic range of receptaculitids known from North America, Europe, and Australia to south-eastern Asia, where they have hitherto been poorly known.

SINCE the first publication 179 years ago (Hüpsch 1805) receptaculitids have had a vagrant history. Like a pendulum they have swung from sponges to algae with brief pauses in a considerable variety of animal Phyla. However, most workers preferred to banish them to a remote place of retirement among sponges, and Rauff (1892) alone argued that they were algae. The oscillations of this systematic pendulum have stopped only in the mid 20th century. Byrnes (1968), Rietschel (1969), and Nitecki (1972), among others, produced new and convincing evidence that receptaculitids are plants. However, Byrnes's (1968) arguments that they were dasyclads and Nitecki's (1976 and subsequent) propositions that, although not dasyclads, they were nevertheless an independent order of green algae within siphonous complex of Chlorophyceae, cannot any longer be maintained (Rietschel 1977). A detailed demonstration of the algal nature of receptaculitids will be presented elsewhere; suffice it to say here that the arrangement of branches in whorls or circlets and the calcification of the thallus are common features not only of chlorophytes, but also of certain other groups of algae. Furthermore, since we do not know the exact nature of receptaculitid reproduction, we cannot assign them with any degree of certainty to any specific group of thallophytes.

Receptaculitids range from Lower Ordovician to Permian but they are most abundant in the Ordovician, particularly in North America, where they are very common and are frequently used as index fossils. They decline rapidly in the Middle Devonian, and are known only from single localities in the Carboniferous (Roemer 1897) and Permian (Parona 1933). Receptaculitids are known from all continents except Antarctica.

In many North American localities receptaculitids are a major component of organic buildups (Toomey and Nitecki 1979). They are not well studied in South America and are known only from the Ordovician of Argentina (Nitecki and Forney 1978) and the Devonian of Bolivia (Branisa 1965).

Although rather rare in Europe, receptaculitids have been studied there for a considerable period of time; many taxa have been described, and their morphology is well understood. The entire stratigraphic range of receptaculitids is represented in Europe, but the best known European ranges are the Silurian and Devonian (Rietschel 1969).

African receptaculitids have been figured from the supposed Ordovician of Morocco (Termier and Termier 1950) and from the Devonian of Algeria (Le Maitre 1952). In Australia, receptaculitids are less common than in North America but considerably more abundant than in Europe. Their stratigraphic range is more restricted than, but otherwise similar to, the North American distribution (Byrnes 1968).

The least well-known receptaculitids are from Asia. Except for single taxa known from: (1) Soviet Asia, particularly the Ordovician of Siberia, where receptaculitids have been described in detail (Miagkova 1965); (2) the Ordovician of Manchuria (Endo 1932); (3) the Devonian of Iran (Flügel 1961); and (4) the Devonian of Afghanistan (Nitecki and De Lapparent 1976), Asian receptaculitids have either been misidentified or are poorly known. Kobayashi (1960) illustrated, but did not

otherwise describe, Ordovician *Receptaculites* from Vietnam. He also described a sponge, *Archaeoscyphia*, from Malaya (Kobayashi 1959); this last taxon is an undoubted *Calathium*. Their (1973) listed *Receptaculites* from the Ordovician of the southern Shan State in Burma.

The new receptaculitids from the Middle Ordovician of Burma described here are the first receptaculitids from south-east Asia available for detailed description; they thus extend the geographic range of these fossils and fill a gap in their global distribution.

SYSTEMATIC PALAEOLOGY

Class RECEPTACULITAPHYCEAE Weiss 1954

Order RECEPTACULITALES James 1885

Family RECEPTACULITACEAE Eichwald 1860

Genus FISHERITES Finney and Nitecki 1979

Fisherites burmensis sp. nov.

Pl. 47, figs. 1, 2

Diagnosis. Thallus subglobular to globular; nuclear area of small and very numerous meroms; intercalation asymmetrical, occasionally symmetrical; meroms of two distinct sizes.

Holotype. Nuclear hemisphere FMNH PP 20079.

Other material. Eight more or less incomplete specimens FMNH PP 20076 to FMNH PP 20083.

Derivation of name. From Burma.

Terminology. The terminology used in descriptions of receptaculitids was confused in the past mainly due to the conflicting interpretations of the nature of receptaculitids. When receptaculitids were considered sponges, sponge terminology was used (e.g. Hinde 1884); when they were believed to be dasyclads (e.g. Byrnes 1968), dasyclad terminology was applied. Now that we can be certain that they are algae (although independent of Dasycladales), a terminology has evolved which in many ways is unique to this group of fossils. The terminology in this paper follows Fisher and Nitecki (1982) as modified from Rietschel (1969).

Shape and size of thalli. The specimens are preserved only as flat, incomplete discs, a very common state of preservation of receptaculitids. They were certainly neither conical nor cylindrical and were probably subglobular to globular in the adult stage; the small specimens (FMNH PP 20081 and PP 20083) appear to have been globular. The diameter of the preserved thallus is between 6 cm (3 specimens) and 10 cm (1 specimen). Due to the fragmentary nature of the specimens, maximum diameter is unknown. We assume that the adult thallus was at least 12 cm in diameter.

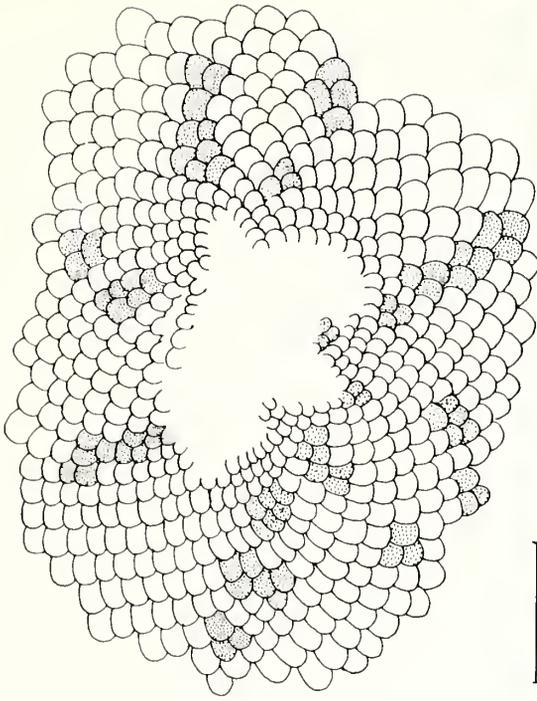
Nucleus. Nuclear area is preserved only on the outer side of the intervallum (FMNH PP 20079). Although the nucleus itself is obscure, a large number of small meroms is discernible (Pl. 47, fig. 1*b*). The plates in this area were not more than 0.3 to 0.4 mm in largest dimensions.

Lacunar hemisphere. Not preserved in any specimens available.

Nuclear hemisphere. Intercalation is predominantly either dextral or sinistral and thus asymmetrical (in the terminology of Fisher and Nitecki 1982) or $M\frac{3}{4}$ (in the terminology of Rietschel 1970). Occasionally, the intercalation is in both directions, and thus symmetrical or $M\frac{3}{2}$. Orthostichies are pronounced, and

EXPLANATION OF PLATE 47

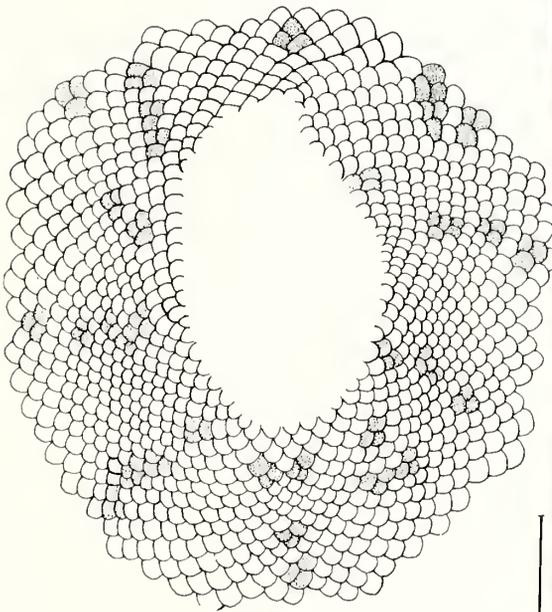
Figs. 1, 2. Nuclear hemispheres of *Fisherites burmensis* sp. nov.; Middle Ordovician, Wunbye Formation; southern Shan State, Burma. 1, holotype; FMNH PP 20079; bar = 3.29 cm. 2, FMNH PP 20082; bar = 1.78 cm.



1a



1b



2a



2b

intercalations are clustered along them. Intercalations are thus not distributed at random, and areas of thallus free from intercalary meroms are pronounced. In the holotype (Pl. 47, fig. 1a) there are 29 visible asymmetrical intercalations, 14 sinistral and 15 dextral, and thus left and right intercalations are approximately of equal number. In FMNH PP 20082 (Pl. 47, fig. 2a) there are 35 intercalary meroms of which 15 are asymmetrical sinistral, 18 asymmetrical dextral, and 2 symmetrical.

Meroms. The size of the merom plates increases away from the nucleus and can be estimated from the positions of merom shafts. Thus, plates range from very minute in the nuclear area to 2.5 mm in largest dimension at the preserved edge of the thallus. Complete meroms are observed in only three specimens, and their distances from the nucleus are unknown: (1) on the weathered outer surface of FMNH PP 20078 the height of the merom is 8.5–10.0 mm; thickness 2.0 mm; plate size 2.5 mm; foot, largest dimension 2.1 to 2.2 mm; (2) on the polished surface of FMNH PP 20081 the length of the merom is 10 mm and the thickness 1.8 mm (maximum); (3) on FMNH PP 20080 the height of the merom is at least 3.5 mm and the thickness is greater than 2.3 mm. The sizes of meroms do not increase greatly on individual specimens because intercalations are relatively abundant, allowing the sizes of plates to remain relatively constant. There are about 1,100 meroms visible on FMNH PP 20082 (Pl. 47, fig. 2), and about 600 on the holotype (Pl. 47, fig. 1). The meroms have well-developed heads and feet; plates are poorly preserved; and the stellate structures are stout and short.

Discussion. In the past, the criteria used in the definitions of receptaculitid taxa were: (1) the shapes and relative ratios of length to width of meroms; (2) the outlines of plates; and (3) the general shapes of thalli. However, these features of morphology are not sufficient, and other characters now used in receptaculitid systematics include: (4) the intercalation pattern; (5) the morphology of stellate structures; and (6) the relative size of meroms with respect to the size of plates. The pattern of intercalation, which reflects morphogenesis, is now considered of prime importance.

Because our taxon agrees in all but one of these aspects (the length of meroms) with the genus *Fisherites*, and it agrees in only very limited aspects with other taxa, we are assigning it to *Fisherites* Finney and Nitecki 1979.

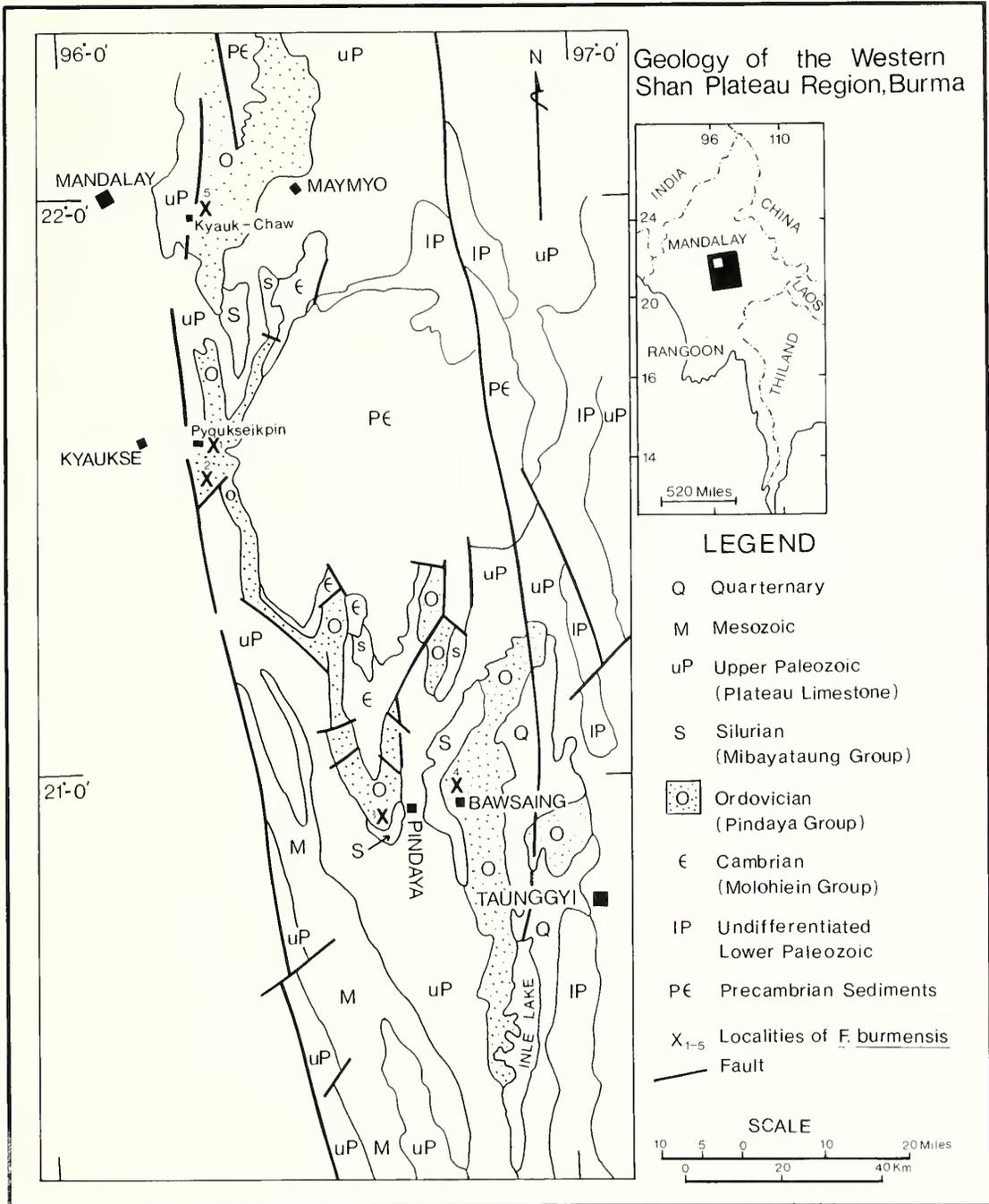
Stratigraphy and lithology. *F. burmensis* (sp. nov.) occurs in the Wunbye Formation (Lower–Middle Ordovician) of the Pindaya Group (Ordovician) of the western part of the Shan Plateau region of Burma (text-fig. 1). According to Thein (1973) the Wunbye Formation, the principal formation of the Pindaya Group, is distributed extensively in the Bawsaing and Pindaya ranges, Yengan, Myogyi, and Pyaukseikpin areas at Kyaukse East, and between Mandalay and Maymyo in the north. It consists of a succession of thick-bedded limestones, siltstones, and dolomites. The limestones are finely crystalline, grey to bluish grey, sometimes oolitic, and with pink, buff, or yellow silty materials in the forms of burrows, specks, pellets, or irregular and regular laminations; burrow structure is so typical of these limestones that locally the limestone is called the Burrow Limestones. The siltstone sub-units are thin, medium to thick-bedded, yellow to light grey, and soft to indurated. The dolomite sub-units are usually thick-bedded, often massive, but generally with fine laminations, and with highly jointed surfaces in criss-cross pattern; colour is usually bluish grey or grey with submetallic lustre, but dull on weathered surfaces. They are finely crystalline although often oolitic, and do not usually extend laterally for long distances.

F. burmensis occurs in the Burrow Limestone sub-units of the Wunbye Formation. It is not abundant and is distributed locally. The five major localities in the western part of the Shan Plateau region of Burma (text-fig. 1) are listed below.

Specimen No.	Locality No.	Location
FMNH PP 20076, 20079, 20080, 20081	X ₁ and X ₂	2.4 km due east (X ₁) and 2.8 km due south-east (X ₂) of Pyaukseikpin village, east of Kyaukse town.
FMNH PP 20077, 20078, 20083	X ₃	4.8 km south-west of Pindaya town; 2.4 km north of Wabya village.
FMNH PP 20082	X ₄	Just north of Yebyukan village, 5.2 km north-east of Bawsaing.
No specimens collected	X ₅	0.8 km north-east of Kyauk-Chaw village.

F. burmensis occurs in association with *Helicotoma*, *Lophospira*, *Cyrtolites*, *Paurorthis*, *Actinoceras*, and *Ormoceras*.

Acknowledgements. We are grateful to the Field Museum of Natural History for financial support to Rietschel during his 1981 tenure of Visiting Scientist position at the Geology Department of the Museum.



TEXT-FIG. 1. Geological map of the area south-east of Mandalay, Burma showing the geology of the western Shan Plateau region and the localities where *Fisherites burmensis* have been found.

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USE OF ETHANOLAMINE THIOGLYCOLLATE IN THE CONSERVATION OF PYRITIZED FOSSILS

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ABSTRACT. The neutralization and removal of decay products from pyritized fossil material with ethanolamine thioglycollate is described. Its use on a wide range of material is a significant improvement over previous techniques which, although satisfactory, were complex and hazardous to the preparator.

THE deterioration and even complete decomposition of pyritized fossils through oxidation is a common problem in collections throughout the world. Various conservation treatments have been described, e.g. Rixon (1976). Howie (1977*a*) reviewed these techniques, together with many of the hypotheses put forward to explain the decay process, and showed that pyrite breakdown is initiated in storage or exhibition environments solely by high relative humidity. Howie (1979*a, b*) also demonstrated that where specimens incorporating reactive pyrite (i.e. with a micro-crystalline structure) are exposed to relative humidities above 60 per cent, visible deterioration due to oxidation may occur within a few weeks.

The practice of protecting the surface of specimens from the air by coating with lacquer or resin is now considered ineffective as a safeguard since such coatings are permeable to both oxygen and water vapour. This can be readily observed by studying the surface of decayed, coated specimens (text-fig. 1A). The coating will usually have been ruptured by the sulphuric acid produced during oxidation, exposing earthy textured iron sulphate breakdown products beneath. Thus, it is advisable to remove as much of the coating as possible to expose the specimen surface for effective re-treatment. In some cases this may result in the specimen breaking up and care must be taken in noting where the pieces belong for reassembly after treatment. In most instances pyrite oxidation breakdown products are easy to identify on the surface of the specimen (Howie 1979*a*). In cases where the operator is unsure whether or not pyrite breakdown has occurred, a simple test with universal indicator paper moistened with distilled water and pressed against the affected area, will confirm this if the pH is less than or equal to 3.

The method described here replaces the ammonia neutralization process (Rixon 1976; Howie 1979*a*) and morpholine treatments (Rixon 1976) hitherto used in the British Museum (Natural History) and other laboratories. The substance now used, ethanolamine thioglycollate, is of comparatively low toxicity and can be safely employed where calcareous material or water soluble compounds, such as animal glue, are present.

ETHANOLAMINE THIOGLYCOLLATE

This material, originally developed for use in hair-perming preparations (see Robinson Brothers Limited, Technical Bulletin 210868 PAL) has three important characteristics that are relevant in the conservation of pyritic fossil material.

1. Ethanolamine is alkaline and in solution will react with and effectively wash out acidic pyrite oxidation products (i.e. sulphuric acid).

2. Thioglycollates will react with soluble and insoluble iron compounds (though not stable pyrite) and chelate or complex iron in solution as a violet-coloured ferrothioglycollate.

3. Ethanolamine thioglycollate is readily soluble in ethanol or propan-2-ol (isopropanol), as are the products of its reactions with those of pyrite oxidation; thus contact of specimens with reagents containing more than a small proportion of water, which may be damaging, can be avoided.

The chemistry of the formation of iron-thiol compounds has been described in detail (Leussing and Tischer 1963) and thioglycollic acid is currently used as a successful technique in the preparation of vertebrate fossils encrusted with haematite (Howie 1974). A major advantage of using ethanolamine thioglycollate is its solubility in organic solvents which, coupled with its high pH and the ready solubility of the violet coloured ferrothioglycollates in solvents, makes it an effective neutralization and dry-cleaning treatment for oxidized pyrite. Ethanolamine thioglycollate is supplied commercially as an aqueous solution containing 40 per cent thioglycollic acid. This material is an alkaline, colourless to pale pink viscous liquid, miscible in all proportions with water, ethanol or isopropanol. Despite its relatively low toxicity, precautions should be taken against the possible hazards associated with its use. The manufacturer's product safety data sheet should be consulted for full specifications, but generally its corrosive action necessitates the use of PVC gloves and goggles for eye protection. Its use should be restricted to a well ventilated area, preferably a fume cupboard.

METHOD

Actively decomposing specimens should initially be placed, together with containers and any associated labels, in an environment of 40–50 per cent relative humidity until treatment can commence. It may be necessary to use a desiccator for this purpose. Specimens should then be examined and note taken of their general condition, whether they are very friable or largely intact. If a specimen is very friable then the immersion procedure discussed below should be avoided as this may do more harm than good.

Loose breakdown products can be removed by either gentle brushing or scraping. Sturdier specimens can be cleaned using an 'Airbrasive' with sodium bicarbonate powder; however, this should be carried out carefully to avoid damaging any surviving original surface. Old coats of varnish and laquer can also often be removed by this process. Any wax-based adhesives or fillers should be removed by the application of methylene chloride soaked tissues or pads (Rixon 1976; Howie 1979a) as these can impair treatment. Where the original shell is preserved, particular care is needed to avoid damage when physical cleaning methods are used; in many such cases it is better not to carry out initial cleaning and proceed directly to ethanolamine thioglycollate treatment.

After cleaning, each specimen is completely immersed in a solution of between 2 per cent and 5 per cent ethanolamine thioglycollate in 95 per cent industrial methylated spirit, or alternatively absolute ethanol or anhydrous iso-propanol. The higher concentration is used on more oxidized material. The small quantities of water present in the final solution are not enough to endanger specimens during treatment. Glass beakers are ideal containers for immersion as one can observe both the iron complexing reactions and the general state of the specimen. The ethanolamine thioglycollate solution should cover the specimen by 5–6 cm to ensure adequate dilution of the reaction products, and ideally the specimen should not touch the side of the beaker. Each immersion should last between one and four hours depending on how badly decayed the specimen is. The clear colourless solution will turn a violet colour as neutralization and iron complexing occurs. The solution should be changed after a maximum of four hours immersion to prevent the violet coloured complex ferrothioglycollate anion from oxidizing to a brown insoluble precipitate which will coat the specimen. Treatment can be repeated if necessary, provided the specimen is 'washed' in clean dry alcohol between immersions. The specimen should be washed at least three times longer than the treatment time to ensure removal of reaction products.

Once reaction has slowed down or ceased altogether, i.e. when little or no violet ferrothioglycollate complex forms, the specimen should be given a final wash and allowed to dry in air. When the specimen has dried, the surface should be carefully examined and cleaned with the 'Airbrasive' to remove any remaining oxidation products. Alternatively, if the more persistent black coatings (which are usually mixtures of microcrystalline pyrite and iron oxides) remain, a further course of treatment using a more concentrated solution of ethanolamine thioglycollate (e.g. 10–15 per cent) may be effective. Cleaned fragments can be reassembled and glued using Butvar B76 in acetone (1:1 by volume) or other solvent-based cement.

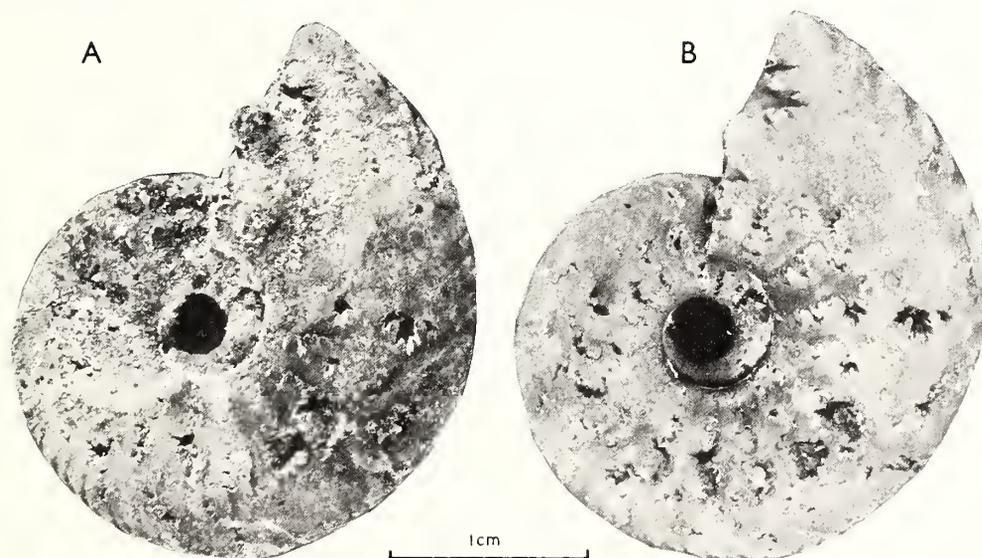
Friable and other specimens which would be damaged by immersion can be neutralized in the following manner. Place the specimen on a flat surface in a well-ventilated area and apply a paste composed of 3–5 per cent ethanolamine thioglycollate in spirit added to sepiolite in about equal portions. The area requiring treatment or the whole specimen should be covered by the paste and then by polythene or aluminium foil to prevent rapid evaporation of the solvent and left for one to three hours. Immersion of the sturdier specimens in clean alcohol is a recommended method of washing. If the specimen cannot be immersed the ferrotioglycollate complex may be removed by applications of I.M.S./sepiolite paste until clean. Consolidation of treated but friable specimens is often advisable although this will not offer protection against exposure to high relative humidity. Such consolidants as polyvinyl acetate (5–10 per cent in ethyl methyl ketone) or polyvinyl butyral (e.g. 5–10 per cent Butvar B98 dissolved in isopropyl alcohol, or 5–10 per cent Butvar B76 dissolved in acetone) are recommended. Thin coats should be applied and if more than one is necessary, adequate drying time should be allowed between each coat.

Specimen containers should be replaced where possible and labels coated or wiped clean with a tissue. Badly damaged labels can be treated by exposing to ammonia fumes or by washing in a very dilute 1 per cent ethanolamine thioglycollate solution in alcohol, and subsequently coated in a polymethyl methacrylate emulsion (Primal AC 73), or alternatively, inserted into small polythene sachets which can be pressure or heat sealed. Storage of treated material should be in a low humidity environment (40–55 per cent relative humidity), which will help prevent further decay. Howie (1979a) and Thompson (1978) described methods for controlling and modifying storage and exhibition environments using various techniques.

Conclusion

The use of ethanolamine thioglycollate in palaeontological conservation has provided a satisfactory method of treating decaying pyritized fossils. As well as being an effective reagent for the removal of pyrite oxidation products, without endangering calcareous structures, it is safer and easier to use than previous techniques. It can also be readily adapted to suit the requirements of individual specimens.

Supplier of ethanolamine thioglycollate. Robinson Brothers Limited, Phoenix Street, West Bromwich, West Midlands B70 0AH



TEXT-FIG. 1. Dimorphophoplitid ammonite from the Gault Clay (Albian, lower Cretaceous; Folkstone, Kent) preserved in pyrite. A, before treatment, showing typical areas of pyrite oxidation speckled white. B, after removal of pyrite oxidation products with ethanolamine thioglycollate.

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DICHOGRAPTID SYNHRABDOSOMES FROM THE ARENIG OF BRITAIN

by J. A. ZALASIEWICZ

ABSTRACT. Dichograptid synrhabdosomes are reported for the first time. Synrhabdosomes of *Didymograptus* aff. *simulans* Elles and Wood from Arenig Fawr, North Wales and *Azygograptus lapworthi* Nicholson from near Keswick, Lake District, are described, both from the Arenig Series (*extensus* Zone). Possible reconstructions of synrhabdosomes of *D.* aff. *simulans* are attempted. It is suggested that synrhabdosomes acted as mechanisms to promote rapid breeding in short-lived, highly favourable environmental conditions.

SYNRHABDOSOMES are comparatively rare associations of graptolite rhabdosomes. Individual rhabdosomes are generally linked at the free distal ends of their virgulae or nemata, although in one recorded instance (Bjerreskov 1976) linkage involves the free ends of proximal virgellae. Biserial (diplograptid) graptolites make up the bulk of known examples (e.g. Ruedemann 1947), but synrhabdosomes have also been recorded amongst uniserial monograptids (e.g. Rickards 1975, p. 414); possible synrhabdosomes of *Dictyonema* (Bulman 1927–1967, p. 27; Ruedemann 1947, pl. 2, fig. 11), and *Corynoides* (Ruedemann 1947, pl. 58, fig. 25) have also been figured. Dichograptid synrhabdosomes have not been described previously. The figured specimens are deposited in the Sedgwick Museum, Cambridge (SM).

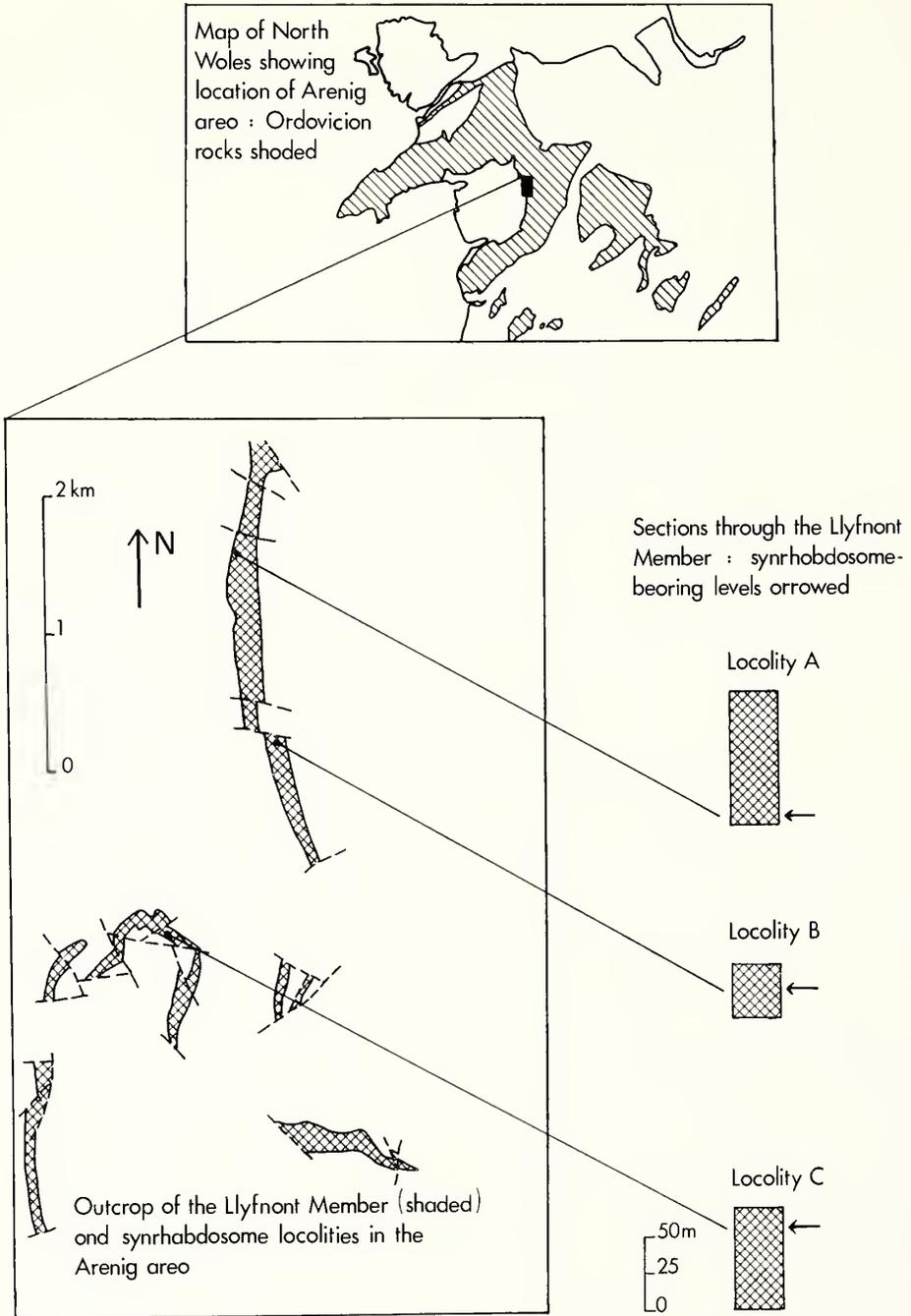
DESCRIPTION OF SYNHRABDOSOMES

Didymograptus aff. *simulans* Elles and Wood, 1901

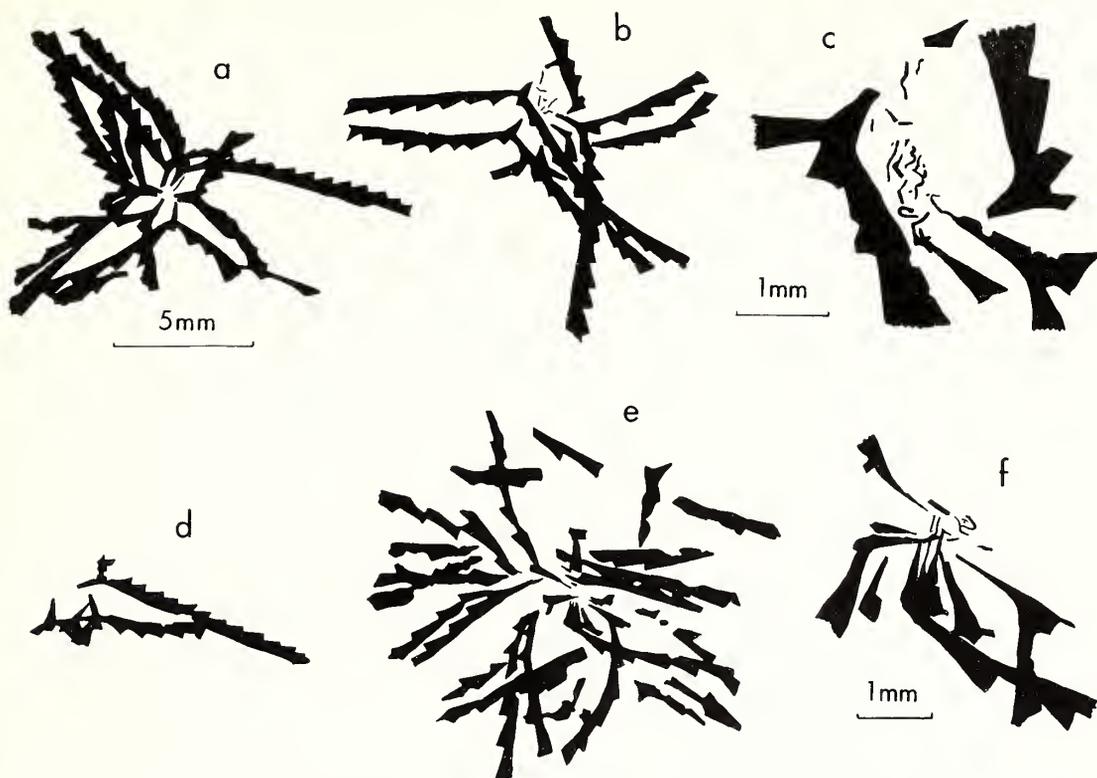
Material. Five synrhabdosomes from three localities in the Llyfnant Member of the Carnedd Iago Formation (lower Arenig Series, *extensus* Zone) of Arenig Fawr, North Wales (text-fig. 1; Zalasiewicz, in press). The Llyfnant Member is dominated by interlayered sandstones and mudstones, containing burrows, loadcasts, and a few ripples (Zalasiewicz 1981). There is little or no grading of individual layers or evidence, such as mudcracks and rainprints, of subaerial exposure. The environment was probably shallow marine subtidal. The only body fossil found *in situ* was *D.* aff. *simulans*, which is locally abundant.

Description. *D.* aff. *simulans* from Arenig Fawr differs from the type material in having a slightly smaller angle between the stipes. The synrhabdosomes are made up of from four to eight rhabdosomes, radially to subradially arranged. The apices of the siculae point towards the centre of the synrhabdosome (text-fig. 2*a, b, d*), and give rise to short, tangled nemata (text-fig. 2*c*). Nemata within synrhabdosomes are locally thickened, up to 0.036 mm across, while nemata of unassociated rhabdosomes do not exceed 0.027 mm across. Preservation of the synrhabdosomes is not good enough to state whether their constituent rhabdosomes are all at the same stage of development.

Discussion. The difference between the nemata of unassociated rhabdosomes and those that form part of a synrhabdosome appears to represent a functional adaptation. However, this does not seem to have been simply a strengthening of the nemata in order to hold the synrhabdosome together, as the thickening is only local (text-fig. 2*c*). In any case, it is likely that synrhabdosomes were held together by soft tissue rather than by the nemata themselves (Rickards 1975, p. 416). Possible reconstructions of synrhabdosomes of *D.* aff. *simulans* are shown in text-fig. 3. The major alternatives are between an ordered (text-fig. 3*a*) and a disordered (text-fig. 3*b*) structure. An ordered structure would have been preferable if most or all *D.* aff. *simulans* rhabdosomes spent most or all of their lifespans as members of synrhabdosomes. However, if synrhabdosomes were temporary structures, or were not formed by all rhabdosomes of *D.* aff. *simulans*, then it may not have been necessary to attain an ordered structure. These general questions are addressed below.



TEXT-FIG. 1. Location and stratigraphic position of synrhabdosomes of *Didymograptus* aff. *simulans* Elles and Wood. Loc. A, spoil from old pits south of Hafotty Ffilltirgerig, NGR SH 8167 3844. Loc. B, 200 m south-east of Beudy Nant-y-pysgod, NGR SH 8202 3703. Loc. C, east face of Moel Llyfnant, NGR SH 8116 3575.



TEXT-FIG. 2. Synrhabdosomes. *a-d*, *Didymograptus* aff. *simulans* Elles and Wood. *a*, SM A102852a–A102860a, loc. B. *b*, SM A102893b–A102898b, loc. A. *c*, proximal part of *b*. *d*, SM A102971–A102975, loc. C. *e*, *Azygograptus lapworthi* Nicholson, SM A17963–A17970, Hodgson Howe Quarry, near Keswick, Cumbria. *f*, proximal part of *e*. *a*, *b*, *d*, *e* to same scale.

Azygograptus lapworthi Nicholson (*ex* Lapworth MS), 1875

Material. One synrhabdosome in a grey mudstone from the middle Skiddaw Slates (lower Arenig Series, *extensus* Zone) of Hodgson Howe Quarry, near Keswick, Cumbria, England.

Description. At least fifteen rhabdosomes, radially arranged (text-fig. 2*e*). The centre of the synrhabdosome is poorly preserved, but fragments of tangled nemata are visible (text-fig. 2*f*).

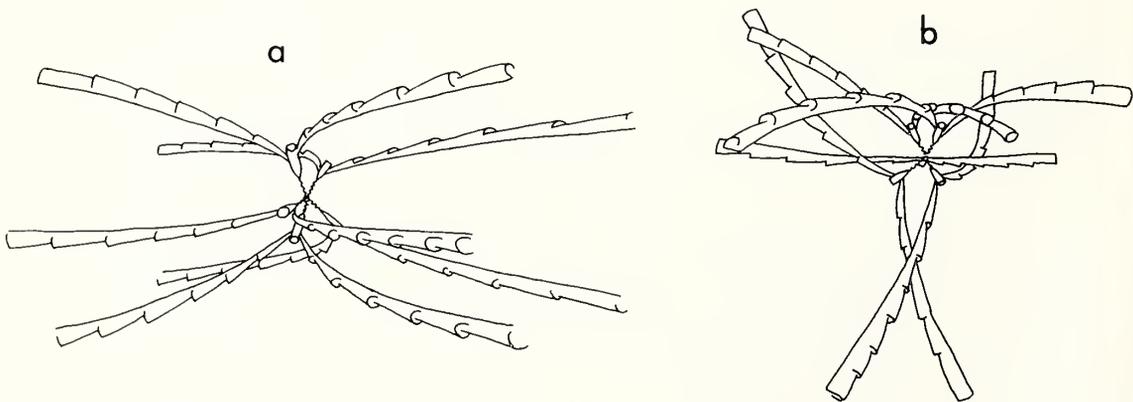
ABUNDANCE, FORM, AND FUNCTION OF SYNHRABDOSOMES

Synrhabdosomes are paradoxical: few species are known to form them, although these species are nevertheless widely scattered both in time and within the graptolite orders. It is commonly implied that this rarity is illusory. Many reconstructions of the Ordovician sea show graptolite synrhabdosomes in the plankton, suspended by their 'floats' (such 'floats' are now known to be artefacts: see Rickards 1975, p. 416). In this view, synrhabdosomes are rare due to post-mortem break-up with, in addition, many synrhabdosomes being overlooked as 'chance associations'. Several features suggest that this view is probably not true. First, where synrhabdosomes have been found they tend to be present in numbers, as in those of *D.* aff. *simulans* described above, and the examples of synrhabdosomes figured by Ruedemann (1947, e.g. pl. 81, fig. 33). Secondly, even moderately well-preserved synrhabdosomes are striking fossils, unlikely to be taken as chance associations. Thirdly,

many species appear to have been physically incapable of forming synrhabdosomes, e.g. *Dicranograptus*, and species of *Dicellograptus* in which the nema is absent or embedded in the dorsal wall of one of the two stipes; in any hypothetical *Cyrtograptus* synrhabdosome the individual graptolites must have been stacked one on top of the other like pancakes—an unlikely structure. Fourthly, any widespread occurrence of graptolites as synrhabdosomes would contradict a most marked evolutionary trend in graptolites, that of the progressive reduction through time in the number of stipes. It follows that synrhabdosomes were relatively rare, yet they possessed advantages that must have overcome the 'disadvantage' of a marked increase in stipe number.

Consider a synrhabdosome-forming species of graptolite. In *Didymograptus* aff. *simulans* it appears that rhabdosomes were not members of synrhabdosomes all of the time, since unassociated rhabdosomes have a straight slender nema, unlike the short, twisted and locally thickened nemata of those within synrhabdosomes. It is also unlikely, for two reasons, that these unassociated rhabdosomes were bound up in synrhabdosomes at some point in their life-cycle. First, the graptolite would have had to discard its nema and grow another to suit its new life-style. Secondly, a numerical argument can be applied: in the case of *A. lapworthi*, several hundred specimens were present on the slabs examined, and only one synrhabdosome was discovered; in the case of *D.* aff. *simulans*, some 120 specimens included five synrhabdosomes. The formation of synrhabdosomes emerges as a strategy indulged in by only some members of a population for what must have been quite particular reasons.

Ruedemann (1895, 1947) described diplograptid synrhabdosomes that included rhabdosomes at all stages of development. In contrast, the rhabdosomes of *Rhaphidograptus toernquisti* joined at their virgellae, that make up the remarkable synrhabdosomes described by Bjerreskov (1976), were all at the same stage of development. Previously suggested modes of development of synrhabdosomes envisage either budding from the apical part of the original sicula (Kozłowski 1949), or the development of a number of siculae from within a mass of extrathecal tissue (Bjerreskov 1976). These imply that the members of any synrhabdosome were either genetically identical, as in the former instance, or were at least kin to each other. Since the most plausible function of the synrhabdosome was to aid sexual reproduction (Rickards 1975, p. 416), both modes of development would have resulted in presumably disadvantageous inbreeding. This disadvantage would have arisen through a reduction in the interchange of genetic material rather than through 'genetic mistakes', a few of which could have been afforded in the likely *r*-selective reproductive regime of the graptolites (D. Grzywacz, pers. comm.). However, if the members of synrhabdosomes were not genetically related, then some



TEXT-FIG. 3. Possible reconstructions of synrhabdosomes of *Didymograptus* aff. *simulans* Elles and Wood. *a*, an ordered structure composed of symmetrically positioned graptolites. *b*, a disordered structure, with randomly positioned graptolites.

clustering together of 'automobile' graptolites must have occurred, perhaps under the influence of some graptolite pheromone. Whether graptolites were capable of 'automobility' (Kirk 1969) remains in doubt (Rickards 1975).

I conclude therefore that the graptolites making up synrhabdosomes were indeed genetically related, that the function of synrhabdosomes was to aid sexual reproduction, and that synrhabdosomes formed only under environmental conditions in which the joint 'disadvantages' of a multi-stipe colony and inbreeding were over-ridden by special circumstances. The special circumstances might have been short-lived, highly favourable conditions, in which synrhabdosomes acted as a mechanism to promote rapid breeding. Given such a function, there would have been little need for synrhabdosomes to obtain the stable ordered structure necessary for an optimum feeding strategy, and those of *D. aff. simulans* would have had the disordered structure shown in text-fig. 3b.

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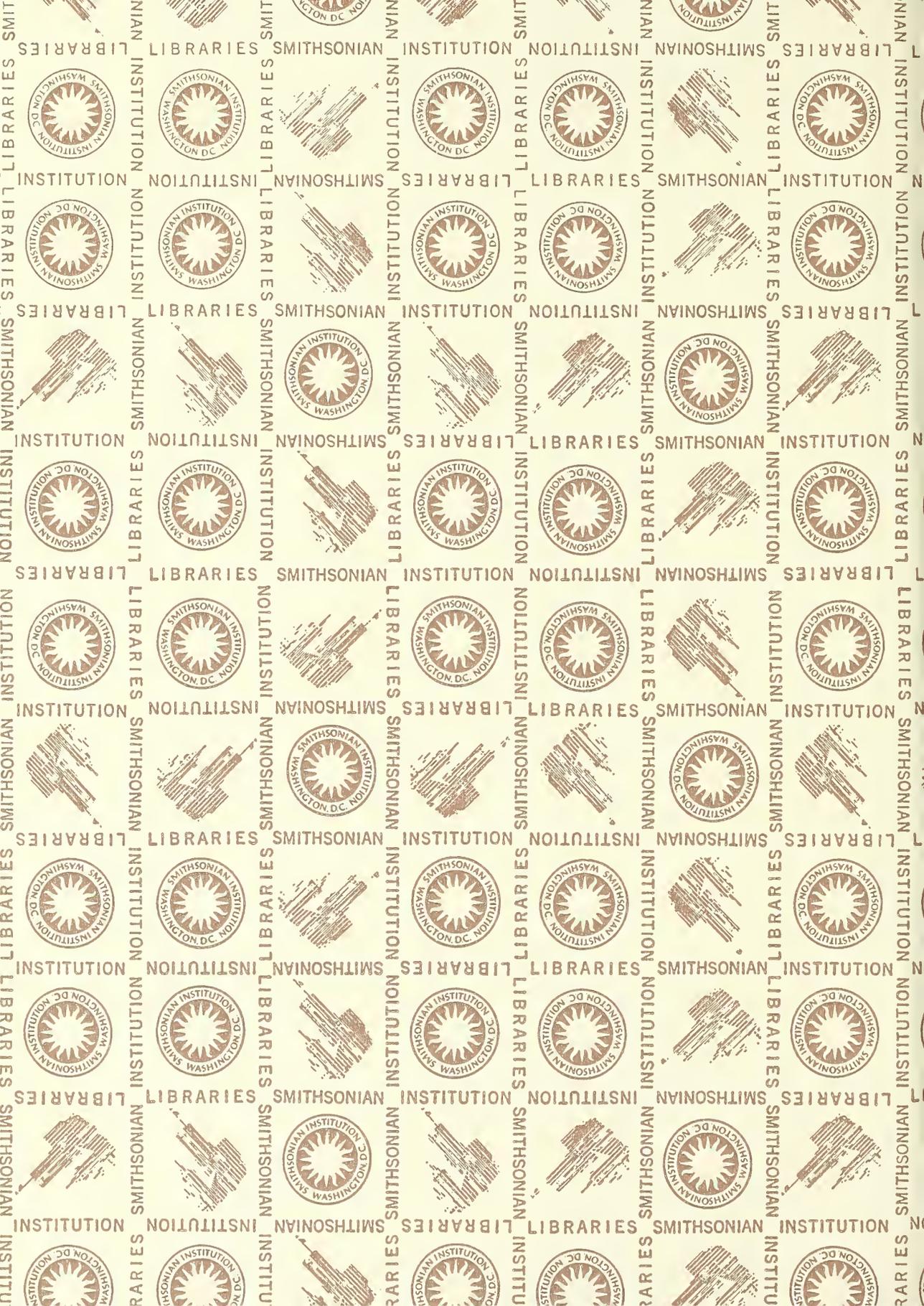
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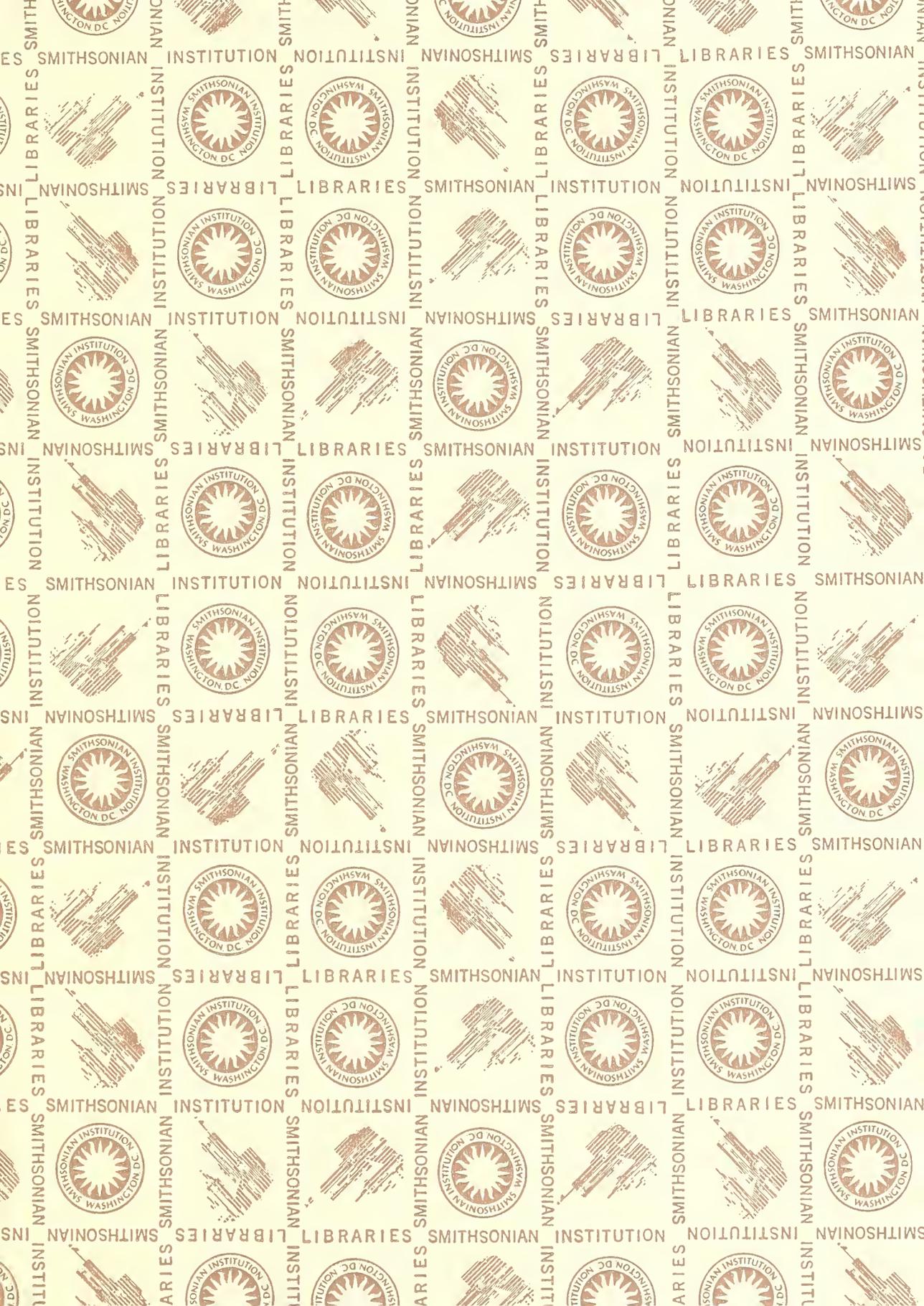
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