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Cover: *Edriophus levis* (Bather, 1914) from the Middle Ordovician Trenton Group of Kirkfield, Ontario. ×2·5. Specimen in the Smithsonian Institution; photograph by H. B. Whittington.

DINOFLAGELLATE CYSTS FROM THE UPPER EOCENE-LOWER OLIGOCENE OF THE ISLE OF WIGHT

by M. LIENGJARERN, L. COSTA, *and* C. DOWNIE

ABSTRACT. The Upper Eocene and Oligocene succession of the Isle of Wight, southern England (Headon Beds to Hamstead Beds) has been studied palynologically. Seventy-one forms of dinoflagellate cysts are recorded, including two new genera, *Gerdiocysta* and *Vectidinium*, and ten new species, *Distatodinium scariosum*, *Eocladopyxis tessellata*, *G. conopeum*, *Glaphyrocysta paupercula*, *Phelodinium pachyceras*, *P. pumilum*, *Phthanoperidinium amiculum*, *P. flebile*, *Thalassiphora fenestrata*, and *V. stoveri*. The dinoflagellates (with the exception of *Vectidinium*) are marine and indicate six marine incursions or partial incursions in the sequence; the mid-Headon Beds, the Oyster Bed of the Bembridge Marls, the *Nematura* Band, and three episodes of the Upper Hamstead Beds. Correlation with the Paris Basin indicates that the base of the Stampian lies near the *Nematura* Band.

THE importance of dinoflagellate cysts in the stratigraphy of the Palaeogene has been emphasized in several recent papers. Many long-standing problems in the Upper Palaeocene and Lower Eocene have been resolved by their application, but problems of correlation at the Eocene/Oligocene boundary remain. This account describes the dinoflagellate cysts from the classical section on the Isle of Wight in southern England. The initial work was done by M. Liengjarern (1973) and has been revised recently by L. Costa.

STRATIGRAPHY

The sequences in the Isle of Wight span the Eocene/Oligocene boundary, and the placings of this boundary have varied according to the interpretation of different authors (see Curry *et al.* 1978) from the base of the Headon Beds to the base of the Hamstead Beds. The difficulties in correlation and interpretation are largely the consequence of the paralic nature of the deposits, which varied from open-sea to freshwater lacustrine in a complex coastal geography.

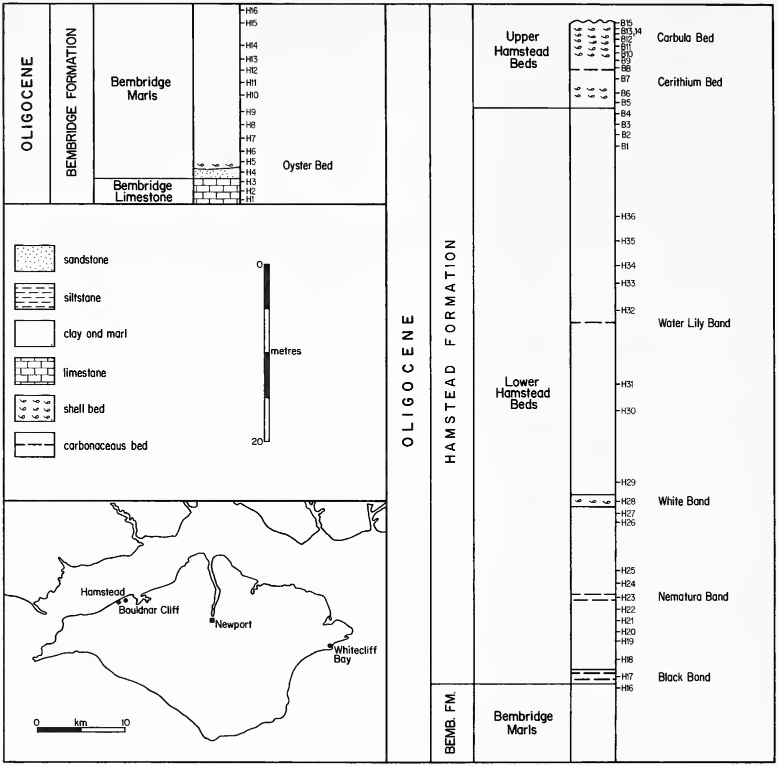
Two main localities are reported here. In the east of the island, the lower part of the succession, from the base of the Lower Headon Beds to the Bembridge Marls, is exposed continuously in the sea cliffs at Whitecliff Bay. In the west, the upper part of the succession (Bembridge Marls-Hamstead Beds) is exposed in Bouldnor and Hamstead cliffs as a continuous sequence (text-figs. 1 and 2).

PALYNOLOGY

All the samples were prepared by standard palynological methods. Only a few samples of fluvial sands were barren, the remainder yielded rich assemblages of palynomorphs, including pollen and spores, plant tissue, freshwater algae, dinoflagellate cysts, and acritarchs. Only the dinoflagellate cysts are dealt with in detail in this paper, but in each sample the proportions of pollen and spores, *Pediastrum*, dinoflagellates, and acritarchs based on counts of 200 individuals were noted. These results are shown in Tables 1 and 2. It should be noted that these counts were made after sieving through a 20 μm sieve and that consequently pollen is under-represented.

A complete list of the dinoflagellate taxa recorded and their distribution and relative abundances are shown in Table 1. Only new taxa or combinations, or taxa necessitating further comment are described here. The genera discussed are arranged in alphabetical order; suprageneric dinoflagellate cyst-taxa are not employed here.

[Palaeontology, Vol. 23, Part 3, 1980, pp. 475-499, pls. 53-54.]



TEXT-FIG. 1. Stratigraphic location of samples collected at Hamstead Cliff (prefix H) and at Bouldnor Cliff (prefix B).

The terms employed in the descriptions are those of Williams *et al.* (1973) and Evitt *et al.* (1977). In some species, the arithmetical mean of the measurements is indicated as a figure in parenthesis. The reference for holotypes and illustrated specimens is given with reference to their location in the 'England Finder' grid system.

Division PYRRHOPHYTA
Class DINOPHYCEAE Fritsch 1935
Order PERIDINIALES Haeckel 1894
Genus DISTATODINIUM Eaton 1976

Type species. Distatodinium craterum Eaton 1976

Distatodinium scariosum sp. nov.

Plate 54, fig. 3

Name derivation. Latin, *scariosus*, thin, papery.

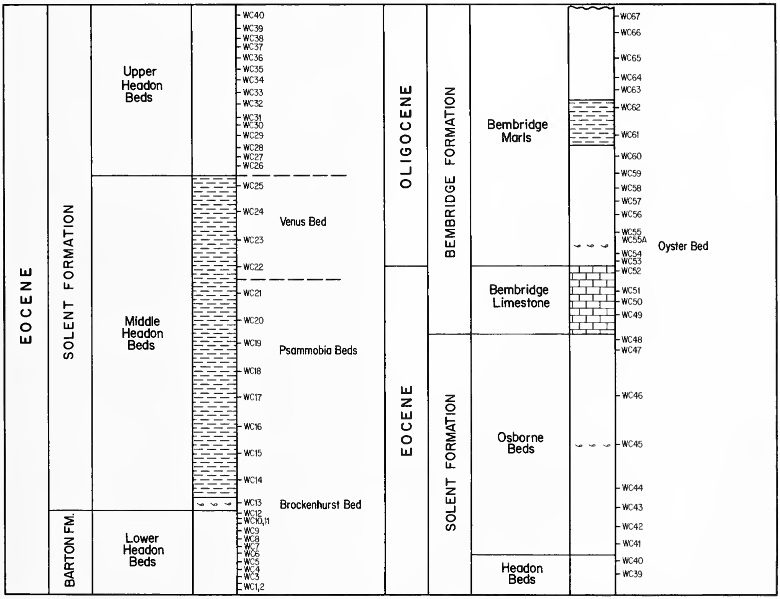
Diagnosis. *Distatodinium* with broad, hollow, intratabular processes (usually one per paraplate), oblate to subtriangular in cross-section, distally expanded, and bearing a variable number of thick secae on their distal margin. Cingular area devoid of processes.

Description. The central body ambitus is oval, antero-posteriorly elongate. Apex and antapex are rounded; the antapex may be prolonged into a corona formed by the expanded bases of the antapical processes.

The insertion of the processes on the central body is subcircular, oblate, or triangular. The processes occur one per paraplate, except on the antapical paraplate (1′′′′), where there may be two or more processes. The degree of compression of the processes varies on a single specimen; some processes are taeniate, but more commonly they are oblate to subtriangular and are open distally. The distal margin of the processes extends into a variable number of robust secae, sometimes prolonged into fine strands which might connect with those from near-by processes.

Two of the apical processes are considerably smaller than the other two. Cingular and sulcal zones are free of processes. When more than one antapical process occurs, their proximal sections coalesce, forming a corona which is apparently hollow.

Holotype. Slide ML 1456, R37/0, sample B11, Upper Hamstead Beds, Lower Oligocene, Bouldnor Cliff, Isle of Wight.



TEXT-FIG. 2. Stratigraphic location of samples collected at Whitecliff Bay (prefix WC).

TABLE 1. Distribution of dinoflagellate species

Species	Middle Headon Beds												Upper Headon		Bembridge Marls			Lower Hamstead			Upper Hamstead					
	WC13	WC14	WC15	WC16	WC17	WC18	WC19	WC20	WC21	WC23	WC24	WC25	WC34	WC35	WC55	H4	H6	H19	H23	H24	B6	B7	B8	B11	B14	B15
Achomosphaera ramulifera	6	3	6	2	4	5	6	2	3	2	×				×	×										×
A. cf. *grallaeformis*		×	×	×		×		×	×						2											
Adnatosphaeridium multispinosum	5	1	8	6	12	6	14	10	9	4	2	1														
A. reticulense	×	×		×															98		×					
Areosphaeridium diktyoplokus	×	3	1	×	×		×	×	×																	
A. fenestratum	×	×																								
A. multicornutum	×		×					×		×																
Deflandrea phosphoritica	×	1	×	×	×		×	1	1	1	4								×							×
D. spinulosa	×	×	×							×																
Dinopterygium fehmarnensis	3	2	2	1	×	2	1	×	3			3							×							
Diphyes colligerum	1		×	×			1	×		×		×												×		
Distatodinium craterum	1	×	×	×			×	×																×		
D. ellipticum	×	×	×	×	×	×	×	×																		
D. paradoxum	1	×	1	1	×		×	×				×											×	×		
D. scariosum																							×	×		
Emslandia sp.							5	5	×	×	×													×		
Eocladopyxis tessellata							×	3	2	1	1	42														
E. peniculata																					×			×		
Gerdiocysta conopeum																					×	3	×	25		10
Cordosphaeridium cantharellum	×	×		×	×	1	×	×	×		1															
C. funiculatum	×	×	×	×				×																		
C. inodes	×	×	×	×	1	×	×	×			1															
C. minimum	2	×	×																							
Glaphyrocysta microfenestrata	×	×	1	2	1	3	4	×	×	2		2			17	×	100			2	56	7	4	13		
G. paupercula																					3		78			
G. exuberans ellipsoidalis	×	×	×	1	1	6	2	×		×																
Heteraulacacysta campanula																								×		5
H. leptalea	×	×	×			×		×		×		×														
Homotryblium abbreviatum			×	×	5	3	×		3	2		2			7								×	3		1
H. oceanicum	3	×	1	1	×	×		1							×											
H. pallidum	4	3	6	6	4	5	3	8	5	17	5	2			11							×	1	37		×
H. plectilum	38	65	40	70	42	40	35	31	17	4	52	2														
Hystrichokolpoma cinctum		×	×			×		×	1																	
H. rigaudiae	×	×	×		×	×	×	×		×		×														

H. salacium	1	×	2	1	×	×	1	1	3	1		×										×	×		16
H.-sphaeridium cf. *pseudorecurvatum*	2	×	×		×			×	×	×															
Impletosphaeridium insolitum	4		7	×	2	1		5	3	3	3	7			1										
I. ?severinii	×	×					1	×							1										
Kisselovia coleothrypta	×	3	4		3	×	3	3	1		4							×							
Lejeunia hyalina																									6
L. tenella																							×		20
Lingulodinium machaerophorum	×	×		1	×	×	×	×							×										
Membranophoridium aspinatum	×	×	1	1	1	×	5	2	1		×				23										
Millioudinium tenuitabulatum																							10		
Operculodinium centrocarpum	×	×	×	×		×	×	×	1		×	×			×							×			
Palaeocystodinium golzowense	×	×	×		1	×	1	1	1																
Pentadinium laticinctum and *P. taeniagerum*																				×			1		
Phelodinium pumilum						×		1	7	6	×														
P. pachyceras																				8		×			
Phthanoperidinium amiculum												×													
P. amoenum																				×		×	×		15
P. comatum	14	3	4	2	5	4	5	6	8	32	5	20							20	26	3	12	×	100	
P. flebile																			75						
P. levimurum																99									
Rhombodinium draco	×	×	×				×																		
R. perforatum	×	×	3		2	×	×	×	3	4															
Vectidinium stoveri													100	100			100								
Spiniferites mirabilis		×						×																	
S. pseudofurcatus	×	×		×	×	×			×	1															
S. ramosus	6	5	5	×	2	5	2	4	10	4	6	2							3			×	2		×
Thalassiphora fenestrata	×	3	×	×	2	3	×	×	×	×															
T. pelagica		×	×		×					×															
T. velata	×	1	×	×	×	7	1	×	×																
Wetzeliella articulata							×																		
W. gochtii																						×	4		2
W. ovalis		×																							
W. symmetrica																						×	×		×
W. synmetrica incisa																							×		
Cyclopsiella elliptica																					×				
C. vieta																					×	×			
Paralaceniella indentata	2	×	2	×	2	5	×	3	7	3	8	8			27						2	×	×		
'*Micrhystridium*'							5	4		3					10					4	84	2	2		20

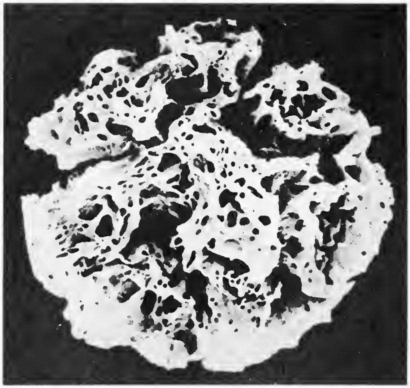
×—indicates that presence is below 1%.

TABLE 1. Distribution of dinoflagellate species

Species	Middle Headon Beds												Upper Headon		Bembridge Marls			Lower Hamstead			Upper Hamstead					
	WC13	WC14	WC15	WC16	WC17	WC18	WC19	WC20	WC21	WC23	WC24	WC25	WC34	WC35	WC55	H4	H6	H19	H23	H24	B6	B7	B8	B11	B14	B15
Achomosphaera ramulifera	6	3	6	2	4	5	6	2	3	2	×				×	×										×
A. cf. *grallaeformis*		×	×	×		×		×	×						2											
Adnatosphaeridium multispinosum	5	1	8	6	12	6	14	10	9	4	2	1														
A. reticulense	×	×		×															98		×					
Areosphaeridium diktyoplokus	×	3	1	×	×		×	×	×																	
A. fenestratum	×	×																								
A. multicornutum	×		×					×		×																
Deflandrea phosphoritica	×	1	×	×	×		×	1	1	1	4								×							×
D. spinulosa	×	×	×							×																
Dinopterygium fehmarnensis	3	2	2	1	×	2	1	×	3			3							×							
Diphyes colligerum	1		×	×			1	×		×		×												×		
Distatodinium craterum	1	×	×	×			×	×																×		
D. ellipticum	×	×	×	×	×	×	×	×																		
D. paradoxum	1	×	1	1	×		×	×				×											×	×		
D. scariosum																							×	×		
Emslandia sp.							5	5	×	×	×													×		
Eocladopyxis tessellata							×	3	2	1	1	42														
E. peniculata																					×			×		
Gerdiocysta conopeum																					×	3	×	25		10
Cordosphaeridium cantharellum	×	×		×	×	1	×	×	×		1															
C. funiculatum	×	×	×	×				×																		
C. inodes	×	×	×	×	1	×	×	×			1															
C. minimum	2	×	×																							
Glaphyrocysta microfenestrata	×	×	1	2	1	3	4	×	×	2		2			17	×	100			2	56	7	4	13		
G. paupercula																					3		78			
G. exuberans ellipsoidalis	×	×	×	1	1	6	2	×		×																
Heteraulacacysta campanula																								×		5
H. leptalea	×	×	×			×		×		×		×														
Homotryblium abbreviatum			×	×	5	3	×		3	2		2			7								×	3		1
H. oceanicum	3	×	1	1	×	×		1							×											
H. pallidum	4	3	6	6	4	5	3	8	5	17	5	2			11							×	1	37		×
H. plectilum	38	65	40	70	42	40	35	31	17	4	52	2														
Hystrichokolpoma cinctum		×	×			×		×	1																	
H. rigaudiae	×	×	×		×	×	×	×		×		×														
H. salacium	1	×	2	1	×	×	1	1	3	1		×											×	×		16
H.-sphaeridium cf. *pseudorecurvatum*	2	×	×		×			×	×	×																
Impletosphaeridium insolitum	4		7	×	2	1		5	3	3	3	7			1											
I. ?severnii	×	×					1	×							1											
Kisselovia coleothrypta	×	3	4		3	×	3	3	1		4								×							
Lejeunia hyalina																										6
L. tenella																								×		20
Lingulodinium machaerophorum	×	×		1	×	×	×	×							×											
Membranophoridium aspinatum	×	×	1	1	1	×	5	2	1		×				23											
Millioudinium tenuitabulatum																								10		
Operculodinium centrocarpum	×	×	×	×		×	×	×	1		×	×			×								×			
Palaeocystodinium golzowense	×	×	×		1	×	1	1	1																	
Pentadinium laticinctum and *P. taeniagerum*																					×			1		
Phelodinium pumilum						×		1	7	6	×															
P. pachyceras																					8		×			
Phthanoperidinium amiculum												×														
P. amoenum																					×		×	×		15
P. comatum	14	3	4	2	5	4	5	6	8	32	5	20								20	26	3	12	×	100	
P. flebile																				75						
P. levimurum																99										
Rhombodinium draco	×	×	×				×																			
R. perforatum	×	×	3		2	×	×	×	3	4																
Vectidinium stoveri													100	100				100								
Spiniferites mirabilis		×						×																		
S. pseudofurcatus	×	×		×	×	×			×	1																
S. ramosus	6	5	5	×	2	5	2	4	10	4	6	2								3			×	2		×
Thalassiphora fenestrata	×	3	×	×	2	3	×	×	×	×																
T. pelagica		×	×		×					×																
T. velata	×	1	×	×	×	7	1	×	×																	
Wetzeliella articulata							×																			
W. gochtii																							×	4		2
W. ovalis		×																								
W. symmetrica																							×	×		×
W. symmetrica incisa																								×		
Cyclopsiella elliptica																						×				
C. vieta																						×	×			
Paralecaniella indentata	2	×	2	×	2	5	×	3	7	3	8	8			27							2	×	×		
'Micrhystridium'							5	4		3					10						4	84	2	2		20

× — indicates that presence is below 1%.

PLATE 53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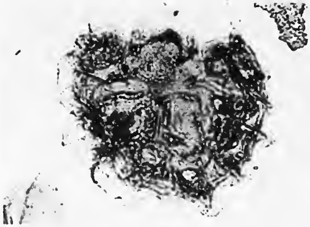
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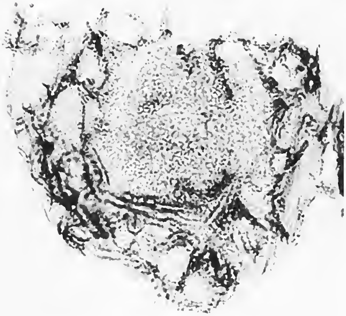
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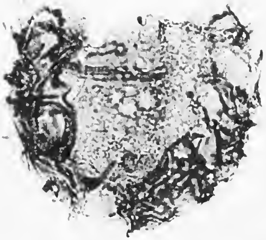
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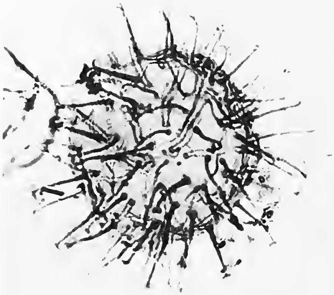
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LIENGJARERN *et al.*, Eocene/Oligocene dinoflagellates

Measurements. Holotype, central body length 51 μm including operculum (43 μm not including operculum), breadth 31 μm; process length 5–15·5 μm.

Range. Central body length 38–49 μm (not including operculum), breadth 26–31 μm; process length 5–16 μm. Specimens measured—8.

Comparisons. The broad, usually hollow and distally open processes, commonly unconnected distally, distinguish *D. scariosum* from other species in the genus.

Distribution. Samples B11, B15.

Genus EMSLANDIA Gerlach 1961

Type species. Emslandia emslandensis Gerlach 1961

Emslandia sp.

Plate 54, fig. 5

Remarks. This species of *Emslandia* has a bulging ventral hypocyst surface. The ambitus is subcircular to ovoid. The epicyst is distally rounded and is prolonged into a very short apical horn, subrectangular in outline, with distal ending truncate, bifid or sometimes produced into a variable number of short solid processes. The hypocyst may be rounded or somewhat pointed medially (?compression) and sometimes bears a very short, solid antapical projection.

The autophragm is robust but does not exceed 2 μm in thickness, it is apparently spongy, perforate, and its outer surface is scabrate. Linear thickenings of the wall appear scattered randomly on the autocyst; sometimes these coalesce on portions of the cyst producing irregular reticulate structures. Two parallel thickenings of the autophragm mark the cingular margins.

The archeopyle is large, type P. The operculum may remain attached along its cingular suture.

Emslandia sp. differs from *E. emslandensis* by its thinner autophragm and randomly scattered ornament of linear thickenings, in part reticulate. It is clearly a distinct species, but the material is too badly preserved to provide satisfactory types.

Distribution. Samples WC 19–21, 23; Middle Headon Beds, Whitecliff Bay, Isle of Wight.

Genus EOCLADOPYXIS Morgenroth 1966*b*

Type species. Eocladopyxis peniculata Morgenroth 1966*b*

Eocladopyxis tessellata sp. nov.

Plate 53, fig. 6

Name derivation. Latin, *tessellatum*, tessellated.

Diagnosis. Eocladopyxis distinguished by abundant, long, solid, intratabular processes which end distally in fine spines repeatedly furcated and reflexed. The central body is moderately compressed dorso-ventrally and its ambitus is circular. Archeopyle type $A+\overline{3A}+6P$. Additional sutures may occur randomly between any pair of paraplates.

EXPLANATION OF PLATE 53

Fig. 1. *Gerdiocysta conopeum* gen. et sp. nov., SEM showing the membrane connecting the distal ends of the processes, × 785.

Fig. 2. *Gerdiocysta conopeum* gen. et sp. nov., holotype, dorsal view showing apical archaeopyle, × 500.

Fig. 3. *Glaphyrocysta paupercula* sp. nov., holotype, × 1000.

Fig. 4. *Phthanoperidinium amiculum* sp. nov., holotype, × 1000.

Fig. 5. *Glaphyrocysta paupercula* sp. nov., specimen with reduced processes, × 1000.

Fig. 6. *Eocladopyxis tessellata* sp. nov., holotype, × 1000.

Description. The autocyst is moderately to strongly compressed dorso-ventrally with a circular ambitus. The autophragm is scabrate and is produced into solid intratabular processes, two to four, sometimes more, per paraplate. The processes are only slightly flexible, simple, somewhat expanded proximally, circular in cross-section; distally they flare into a number of fine spines which fork repeatedly; more rarely some of the processes may end in simple bifurcations. They are more or less strongly reflexed.

The archeopyle appears to be of the type $A+\overline{3A}+6P$ although it is possible that all apical plates separate in the formation of the archeopyle. Additional sutures commonly develop, apparently at random, between any other pair of paraplates, both on the epicyst and on the hypocyst.

The paratabulation formula may sometimes be determined on the basis of plate separation, and is 4′, 6″, 6c, ?5‴, 1 p.v., 1⁗, ?Xs. Two of the apical paraplates appear to be larger than the other two. The precingular paraplates are of roughly the same size, antero-posteriorly elongate, and pentagonal in outline. The cingular paraplates are narrow and subrectangular, and frequently bear only two processes each. The hypocyst appears to be formed by five large postcingular paraplates, a prominent posterior-ventral paraplate and an antapical paraplate, but these are only rarely evident since secondary sutures are uncommon on the hypocyst; a number of smaller sulcal paraplates also appear to be present.

Holotype. Slide ML 1451, T51/2, sample WC25, Middle Headon Beds, Upper Eocene, Whitecliff Bay, Isle of Wight.

Measurements. Holotype, central body diameter, 37 μm; process length 8–15 μm.

Range. Central body diameters 31–39 × 35–43 μm; process length 4·5–10 μm. Specimens measured—11.

Comparisons. The solid processes, paratabulation, and archeopyle type leave no doubt as to the generic allocation of *E. tessellata*; however, the archeopyle is not always observable, in which case the specimens closely resemble some species of the genus *Impletosphaeridium* Morgenroth 1966*b*.

E. tessellata differs from *E. peniculata* Morgenroth, the only other species so far allocated to the genus, in its larger size and longer processes. The process terminations in *E. tessellata* are more complex than in *E. peniculata.*

Genus GERDIOCYSTA gen. nov.

Name derivation. Latin, *gerdius*, weaver.

Type species. Gerdiocysta conopeum sp. nov.

Diagnosis. Cyst ambitus subcircular, posteriorly bilobed or rounded; dorso-ventral compression moderate to strong. Pericyst bearing solid penitabular to intratabular processes arranged into annular, soleate, or linear complexes. The process complexes support a reticulate or membraneous ectophragm, which on the dorsal face and laterally simulate the outline of the paraplates. On the ventral face, a median area of variable size is free of ornament and ectophragm. The processes on either side tend to be linearly oriented more or less parallel to the ambitus; the ectophragm on the ventral face may link processes from different paraplates.

Inferred tabulation formula: 4′, 6″, 6c, 5‴, 1 p.v., 1⁗, Os.

Archeopyle type $\overline{A}$, with zig-zag margins including a slightly offset sulcal notch. Operculum tetratabular, commonly free.

Comments. Gerdiocysta is similar to *Areoligera* Lejeune-Carpentier but differs strongly in the possession of an ectophragm, which, on parts or all of the dorsal surface of the cyst, simulates the shape of paraplates. In *Areoligera* the processes may be joined distally or laterally by trabeculae, but these are sparse and are loosely interconnected and do not constitute an outer reticulum or membrane.

The genus *Riculacysta* Stover 1977, resembles *Gerdiocysta* in shape and in possessing a membranous perforate to reticulate ectophragm. However, in *Riculacysta* the processes are not in complexes, and are restricted to the ventro-lateral and lateral zones of the cyst. The ectophragm on the dorsal surface of *Riculacysta* lies very close to or touches the autophragm and extends across the paraplate sutures in that region. In contrast there are the simulate dorsal complexes in *Gerdiocysta.*

Gerdiocysta conopeum sp. nov.

Plate 53, figs. 1, 2

Derivation of name. Latin, *conopeum*, mosquito net.

Diagnosis. Gerdiocysta characterized by a finely reticulate to membranous perforate simulate ectophragm developed over paraplates 1′–4′, 1″–5″, 2‴–4‴, 1 p.v., and 1⁗; an arcuate to soleate complex of very reduced processes, distally free, may be developed on paraplate 6″. The process bases are connected by microgranular thickenings of the cyst wall which form low ridges within the complexes; these thickenings are often further developed into an intratabular irregular, coarse reticulum. Individual processes are solid, slightly fibrous, and distally furcated. The median ventral area is large.

Description. The antapical bilobation of the central body may be moderately or only weakly marked. The dorsal convexity and ventral depression are moderate. The endophragm is finely granulose, apparently perforate. The periphragm, as seen on the process walls is slightly fibrous.

The process complexes are determined proximally by basal granulose thickenings on the cyst wall, which form a more or less continuous basal ridge. Distally, the simulate ectophragm is well developed over paraplates 1′–4′, 1″–5″, 2‴–4‴, 1 p.v., and 1⁗. The cingular paraplates 2c–4c may bear linear complexes of processes which may or may not be distally united. A narrow ectophragm may also be developed on the ventral surface, forming an arcuate wing bordering the central area free of ornament. The ectophragm is closely perforate and finely reticulate or membranous; both types may combine in the same species.

On some individuals, the processes are greatly reduced, no ectophragm is developed, but a coarse granulate basal reticulum extends over the dorsal plate surfaces; intermediate forms between these and normal specimens with well-developed processes and ectophragm are common.

Holotype. Slide ML 1456, E 29/2, sample B11, Upper Hamstead Beds, Lower Oligocene, Bouldnor Cliff, Isle of Wight.

Measurements. Holotype, central body length (operculum not included) 64 μm, breadth 73 μm, processes height up to 20 μm.

Range. Central body length (operculum not included) 47(54·7)64 μm, breadth 63(68)79 μm, process length 6–23 μm. Specimens measured—15.

Comparisons. No granulate proximal wall thickenings have been mentioned in the description of the only other species in the genus *G. cassicula* (Drugg) comb. nov., which also appears to differ from *G. conopeum* in having considerably longer processes and a more prominently bilobed antapex.

Benedek (1972, pl. 1, figs. 11*a–c*) illustrated examples as *Cyclonephelium pastielsii* which appear to be conspecific with *G. conopeum*.

Distribution. Samples B6, 7, 8, 11, and 15. Also in Lower Lintforter Beds and Ratinger Beds (early Rupelian), Germany and Calcaire de Sannois (early Stampian), France (Chateauneuf, pers. comm.).

Other species allocated to the genus: *G. cassicula* (Drugg) comb. nov. = *Areoligera cassicula* Drugg 1970, p. 811, figs. 2B, 3A–B.

Genus GLAPHYROCYSTA Stover and Evitt 1978

Type species. Glaphyrocysta retiintexta (Cookson 1975)

Glaphyrocysta paupercula sp. nov.

Plate 53, figs. 3, 5

Name derivation. Latin, *pauperculum*, diminutive of *pauperculus*, poor.

Diagnosis. Central body compressed, ambitus subcircular to quadrangular, with or without antapical indentation. Autophragm microgranular, finely reticulate. Processes developed along a peripheral band of varying width, leaving relatively prominent mid-dorsal and mid-ventral areas free. Processes solid, fibrous, simple or bifurcate. The processes may be isolated or arranged into linear, arcuate, soleate, or annular complexes. When in complexes the processes are joined by their expanded proximal parts; a few lateral (rarely distal) trabeculae may occur. The complexes have a ragged appearance distally. Processes from different complexes may be joined by basal ridge and/or medially by sparse trabeculae. Processes may be considerably reduced in number and in size.

Processes may occur on some or all of the paraplates 1′–4′, 1″–5″ (rarely on 6″), 1‴–5‴, 1 p.v., and 1⁗.

The archeopyle is apical tetratabular, type Ā; the operculum may be free or remain attached. The archeopyle suture has a sulcal notch a little offset from the mid-body line.

Description. The central body is moderately to strongly compressed; the ambitus varies from subcircular to quadrangular, the antapex is rounded, somewhat indented or produced into one or two unequal lobes. The autophragm appears microgranular in optical section and is finely reticulate in surface view.

The processes are variable in number, size, and shape, and are developed along an ambital line of variable width. The mid-dorsal and especially the mid-ventral areas are free of ornament and relatively prominent. Individual processes, when well developed, are solid, slightly fibrous (most noticeable at and near the base), slender, simple or bifurcate.

The processes may be isolated, although some alignment may often be evident, or arranged into complexes on parts of the cyst. When in complexes, the processes are joined proximally by low ridges formed by their expanded bases; sparse ribbon-like trabeculae with smooth margins may also occur laterally, and only rarely distally. Processes from different complexes may also be united proximally by ridges and laterally by sparse trabeculae. Process complexes are normally present and better defined on the apical, dorsal precingular, and antapical zones of the cyst.

All apical paraplates bear processes, normally arranged into four or three annular or soleate complexes; when four, two are smaller and tend to coalesce into a single elliptical complex. Linear to arcuate complexes may occur on the precingular paraplates 1″–5″ (occasionally, processes occur on paraplate 6″). Towards the periphery of the dorsal face (2″ and 4″) the complexes may be soleate. On the ventral face, linear or somewhat arcuate complexes may be clear but sometimes the peripheral processes may coalesce with those from postcingular paraplates and become part of a more or less continuous complex parallel to the ambitus. On the postcingular paraplates process complexes tend to lose definition and to form a number of lines running antero-posteriorly near the periphery of both dorsal and ventral faces. The posterior ventral processes may join in these lines or be separate as an arcuate complex. A soleate complex is frequently observable on paraplate 1⁗.

These forms with more or less well-defined complexes of well-developed processes constitute one end of the range of variation observed in this species. The other end includes forms with some isolated processes reduced to simple spines scattered along the peripheral and dorsal precingular zones, tending to form two to four loosely defined lines parallel to the cyst ambitus. The variability between both extreme types is continuous in the same assemblage and cannot be applied to further taxonomic division.

The archeopyle is apical, tetratabular; the opercula may be free or may remain in place. A rather shallow sulcal notch, relatively little offset from the mid-cyst line is observable on the archeopyle margin.

Holotype. Slide ML 1455 P44/1, sample B8, Upper Hamstead Beds, Lower Oligocene, Bouldnor Cliff, Isle of Wight.

EXPLANATION OF PLATE 54

Fig. 1. *Thalassiphora fenestrata* sp. nov., holotype, dorsal view, showing archaeopyle and fenestrations, × 250.

Fig. 2. *Phelodinium pumilum* sp. nov., holotype, dorsal view showing archaeopyle and small cavities at the horns, × 1000.

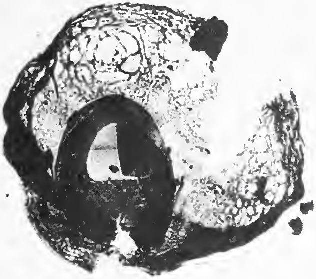
Fig. 3. *Distatodinium scariosum* sp. nov., holotype, × 1000.

Fig. 4. *Phelodinium pachyceras* sp. nov., holotype, × 1000.

Fig. 5. *Emslandia* sp. Middle Headon Beds, sample WC20, showing precingular archaeopyle and cingulum, × 500.

Fig. 6. *Phthanoperidinium flebile* sp. nov., holotype, × 1000.

Fig. 7. *Vectidinium stoveri* gen. et sp. nov., holotype, × 1000.



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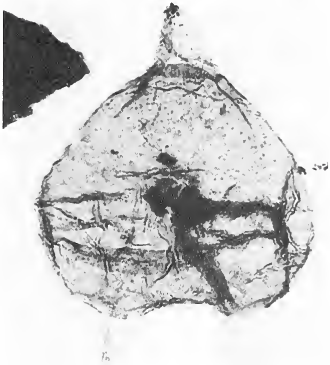

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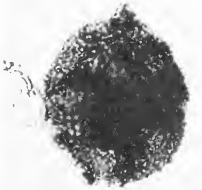

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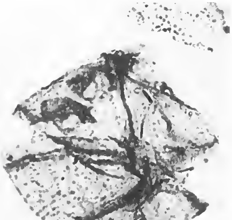

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LIENGJARERN *et al.*, Eocene/Oligocene dinoflagellates

Dimensions. Holotype, central body length 50 μm, breadth 59 μm, maximum length of processes 10 μm.

Range. Central body length 41(47·6)52 μm, breadth 48(57·4)64 μm, processes length (maximum) 6–20 μm. Specimens measured—20.

Comparison. In the ragged distal appearance of the ornament, this species resembles *Glaphyrocysta divaricata* (Williams and Downie 1966), but no process complexes are defined in the latter where the processes are united distally by trabeculae bearing free aculei and/or by perforated membranes in a more complex fashion than in *G. paupercula.*

G. paupercula also resembles *G. intricata* (Eaton 1976), *G. texta* (Bujak 1977), and *G. microfenestrata* (Bujak 1977), where individual process complexes may also be distinguished. However, the distal connections between processes in those species are always more complex than in *G. paupercula*, while the processes are rarely, if at all, united distally. *G. paupercula* may be a degenerate offshoot of this lineage.

Genus IMPLETOSPHAERIDIUM Morgenroth 1966*b*

Type species. Impletosphaeridium transfodum Morgenroth 1966*b*

Impletosphaeridium severinii (Cookson and Cranwell 1967) comb. nov.

1967 *Baltisphaeridium severinii* Cookson and Cranwell, p. 208, pl. 3, figs. 1, 2.

Comments. This species is transferred to *Impletosphaeridium* in view of its solid processes. Some specimens appear to show archeopyle sutures; if these eventually prove to be consistent, then *I. severinii* may have to be transferred once more possibly to *Eocladopyxis.*

Genus PHELODINIUM Stover and Evitt 1978

Type species. Phelodinium pentagonale (Corradini 1973) Stover and Evitt 1978

Phelodinium pachyceras sp. nov.

Plate 54, fig. 4

Name derivation. Greek, *pachys*, large, *keros*, horn.

Diagnosis. Phelodinium characterized by apical and antapical horns, triangular in outline, proximally broad, and distally rounded. Thin-walled cysts moderately compressed dorso-ventrally. Endocyst sub-circular, with low apical and antapical lobes. Apical and antapical pericoels well developed; a narrow ambital pericoel may occur between the horns.

Pericyst ornament atabular of reduced spinules. Pericingulum margins indicated by folds on the periphragm. Perisulcus broad and shallow.

Description. The cyst is thin-walled and usually compressed dorso-ventrally. The ambitus has convex sides and is projected into three prominent horns; these are triangular, with a broad base and a blunt distal ending, and are subequal in size. The epipericyst is more or less conical and somewhat larger than the hypopericyst; the posterior margin of the hypopericyst is straight or slightly concave.

The endocyst is rounded, only weakly bilobed posteriorly; a rounded, low projection into the base of the apical horn may occur. The pericoels are well developed beneath the horns, a narrow pericoel is commonly present between the antapical horns. The ornament is reduced to small spinules or granules, apparently atabular in distribution. Cingulum relatively wide, not indented; its margins are marked by two parallel folds on the periphragm. The sulcus is very broad posteriorly but narrows markedly towards the cingular zone.

The archeopyle is difficult to observe due to the opercula remaining nearly always in place, but the wide posterior archeopyle suture (H4), lying very close to the cingular margin, is evident on most specimens observed.

Holotype. Slide ML 1454, H19/0, sample B6, Upper Hamstead Beds, Lower Oligocene, Bouldnor Cliff, Isle of Wight.

Dimensions. Holotype, pericyst length 75 μm, breadth 53 μm, endocyst length 46 μm, breadth 53 μm, apical horn 12 μm, left antapical horn 15 μm, right antapical horn 13 μm.

Range. Pericyst length 57(65)77 μm, breadth 45(51·6)56 μm, apical horn 6(9)12 μm, left antapical horn 9(12)14 μm, right antapical horn 8(10)13 μm. Specimens measured—12.

Distribution. Upper Hamstead Beds (B6, B8), ?Middle Headon Beds WC19.

Comparisons. The prominent broad horns and reduced ornament, as well as a strong dorso-ventral compression, distinguish *P. pachyceras* from the other species allocated to this genus.

Phelodinium pumilum sp. nov.

Plate 54, fig. 2

Name derivation. Latin, *pumilus*, dwarf.

Diagnosis. Phelodinium of small size, ambitus bilaterally asymmetrical with reduced antapical horns, right antapical broadly rounded, may be absent. Apical horn small, cylindrical with prominent distal pore. Pericingulum relatively wide, marked by folds. Sulcus distinct.

Description. The ambitus varies from subcircular to distinctly peridinioid: the bilateral asymmetry of the cyst is nearly always evident. The dorso-ventral compression is strong. The pericoels, if observable, are restricted to the cavities beneath the horns. The cylindrical apical horn is distinctive, its truncated distal tip bears a prominent pore bordered by a thickening of the periphragm. The left antapical horn is always developed and is sharply pointed distally. The right antapical horn is often absent but commonly it is represented by a broad lobe.

The periphragm is very thin and transparent and is often folded. The cingulum is only very slightly helicoid, wide in relation to the over-all size of the cyst; anterior and posterior cingular sutures are indicated by low smooth ridges formed by folding of the periphragm. The perisulcus is distinct.

The archeopyle is of a type and shape seen in species of *Phelodinium*. Peri- and endoperculum are indistinguishable. The operculum may remain attached along its posterior suture.

Holotype. Slide ML 1450, Q45/4, sample WC 23, Middle Headon Beds, Upper Eocene, Whitecliff Bay, Isle of Wight.

Dimensions. Holotype, pericyst length 64 μm, breadth 54 μm, apical horn 6 μm, left antapical horn 5 μm, right antapical horn 8 μm.

Range. Pericyst length 50(55)62 μm, breadth 41(46·5)54 μm, apical horn 3·5(4·5)6·4 μm, left antapical horn 2·7(4·5)6·5 μm, right antapical horn 0(1)3 μm. Specimens measured—11.

Comparisons. The small size, rounded ambitus, bilateral asymmetry, and distinctive apical horn distinguish this species from all known *Phelodinium* species. Allocation to *Phelodinium* is based on the archeopyle shape and relative size, the absence of well-defined pericoels and the very strong dorso-ventral compression.

Distribution. Samples WC18, 20, 21, 23, and 25.

Genus PHTHANOPERIDINIUM Drugg and Loeblich 1967

Type species. Phthanoperidinium amoenum Drugg and Loeblich 1967.

Phthanoperidinium amiculum sp. nov.

Plate 53, fig. 4

Name derivation. Latin, *amiculum*, cloak.

Diagnosis. Phthanoperidinium with ambitus rounded-pentagonal to suboval. Epicyst with convex sides, terminating in a short apical horn, hypocyst also rounded, produced into one, very occasionally two, antapical horns. Peri- and endophragm very closely appressed except beneath the horns, where restricted pericoels develop. Periphragm ornamented with intratabular spinules and penitabular to hyaline sutural ridges with smooth to slightly denticulate free edges. Laevigate to striate pandasutural lines may be distinct. Pericingulum and perisulcus laevigate, bordered by membranes.

Description. The pericyst is fusiform in lateral view; the ambitus is rounded-peridinoid to subcircular or suboval. The apical horn is short, trangular and distally blunt. The left antapical horn is usually well developed. On some specimens, a right antapical horn, very much reduced, may occur; on most specimens, a projection of the sutural ridges takes the place of the right antapical horn.

The intratabular spines are small and solid, distally short or somewhat capitate; those closer to the paraplate periphery may be arranged in a penitabular ring. The ridges are hyaline and imperforate, their free margins are entire or very slightly serrate to denticulate; the height of the ridges normally does not exceed 3 μm, except along the cingular sutures where they may be up to 5 μm in height. The ridges may be parasutural or penitabular in position. Narrow laevigate pandasutural zones are normally observable on parts of the pericyst and, on some specimens, very faint striations, perpendicular to the margin of the paraplate, may be observable.

The paratabulation formula and shape of the paraplates are normal for the genus. The pericingulum is helicoid, its ends being offset about one pericingular width; its surface is laevigate. The perisulcus is relatively narrow, moderately excavated, extending anteriorly to nearly a half of the epicyst height. The archeopyle is formed by the detachment of paraplate 2a, but it is only rarely observable. Occasionally, additional sutures occur along the margins of all three intercalary plates.

Holotype. Slide ML 1451, K23/4, sample WC25, Middle Headon Beds, Upper Eocene, Whitecliff Bay, Isle of Wight.

Dimensions. Holotype, pericyst length 63 μm, breadth 48 μm, apical horn 7 μm, left antapical horn 5·5 μm.

Range. Pericyst length 47(55·5)63 μm, breadth 40(43)48 μm, apical horn 3(5·5)7 μm, left antapical horn 3(5·5)7 μm. Specimens measured—10.

Comparisons. *P. eocenicum* (Cookson and Eisenack 1965) appears to have sutural ridges and intratabular granules, and thus resembles *P. amiculum* in the style of ornament; but the ambitus in *P. eocenicum* is fusiform to subpolygonal, less rounded than *P. amiculum* and the left antapical horn lies closer to the median axis; in addition both intratabular granules and sutural ridges are much more reduced than on the present species.

P. alectrolophum Eaton 1976 resembles *P. amiculum* in possessing sutural–penitabular ridges, but these bear well-developed spines on their free margins and the intratabular paraplate surfaces are smooth.

Distribution. Only in sample WC25.

Phthanoperidinium flebile sp. nov.

Plate 54, fig. 6

1978 *Geiselodinium* cf. *geiseltalense* Krutzsch, Chateauneuf 1978.

Name derivation. Latin, *flebilis*, pathetic.

Diagnosis. *Phthanoperidinium* with ?partial (not continuous) endophragm occasionally developed beneath the horns. Ornament intratabular of small echinae or setae, laevigate sutural bands may be observable. Cingulum indicated by a relatively broad equatorial band free of ornament.

Description. The autocyst ambitus is subcircular to oval, but is frequently folded and the ambitus may appear somewhat fusiform; the ambital outline is little affected by the horns. The apical horn is very short, subtriangular to rectangular in outline; its apical margin may be smooth or may bear a tuft of short spines, to which sometimes the entire horn is reduced. The hypocyst is posteriorly rounded, and may bear a very short, sharp, antapical horn slightly to the left of the median line.

The autophragm is thin and bears a variable number of small setae or echinae, sometimes reduced to granules, atabular to intratabular in distribution; on some specimens the number of spines is reduced, and these may adopt a penitabular arrangement. Sutural bands, when observable, are smooth and of variable width.

The cingulum, observable on some specimens, appears as a relatively wide band free of ornament; it is not indented. The sulcus has only been seen on one specimen, appearing as a very broad, slightly depressed area with ornament more sparse than on the rest of the ventral autocyst face.

The archeopyle, rarely observable, is intercalary and formed by the loss of paraplate 2a; additional splitting may sometimes develop along the lateral sutures of paraplate 3″, but only very rarely, along the sutures of the remaining paraplates in the intercalary series.

Holotype. Slide ML 1453, X27/3, sample H24, Lower Hamstead Beds, Lower Oligocene, Hamstead, Isle of Wight.

Dimensions. Holotype, autocyst length 39 μm, breadth 28 μm, apical horn 5 μm, antapical horn 1 μm.

Range. Autocyst length 31(35)42 μm, breadth 22(27)31 μm, apical horn 1(3)5 μm, antapical horn 0(1)2 μm. Specimens measured—20.

Distribution. Sample H24; Lower Hamstead Beds.

Discussion. *P. echinatum* most closely resembles *P. flebile* in its ornament of spines, but in *P. echinatum* these are sutural to penitabular (distribution as a single simulate ring), whereas they are intratabular to atabular in *P. flebile*.

Occurrence. Sample H24, and at base of Sannoisian in Paris Basin (Argile Verte de Romainville).

Genus THALASSIPHORA Eisenack and Gocht 1960

Type species. *Thalassiphora pelagica* (Eisenack 1938) Eisenack and Gocht 1960

Thalassiphora fenestrata sp. nov.

Plate 54, fig. 1

Name derivation. Latin, *fenestratus*, windowed.

Diagnosis. *Thalassiphora* with partial fenestration of the periphragm. The fenestration is restricted to the lateral and ventral areas of the periphragm. The extent of the fenestrated area is variable, but it never extends over the whole dorsal region. The perforations are large, more or less circular, and may be closely packed forming an irregular reticulum. The ventral flange of the pericyst is narrow and is fenestrated throughout.

Description. This species is similar to *T. pelagica* in shape and in wall structure but the extension of the periphragm on the ventral side appears to be more reduced than is common in *T. pelagica*, that is, the ventral lacuna is larger. Perforations develop in the periphragm in ventral and lateral areas and disappear towards the mid-dorsal area. Between these perforations, the fibres are more loosely packed. A large number of smaller perforations occur between the larger fenestrations, the latter are of variable diameter tending to be larger closer to the ambitus. Ventrally, the pericyst occurs as a relatively narrow flange which is strongly fenestrate throughout. The antapical keel may often be reduced or, sometimes, absent.

Holotype. Slide ML 1449 U16/2, sample WC14, Middle Headon Beds, Whitecliff Bay, Isle of Wight.

Measurements. Holotype, endocyst 81 × 67 μm, pericyst diameter 150 μm.

Range. Endocyst 73(77)89 × 59(67)77 μm, pericyst diameter 126(154)182 μm. Specimens measured—10.

Comments. This species, which is apparently restricted in distribution to the latest Eocene and ?early Oligocene, seems to be an intermediate form between *T. reticulata* Morgenroth 1966*a*, which is characteristic of younger Oligocene deposits and whose pericoel is fenestrate virtually all over, and *T. pelagica*.

Distribution. Samples WC13–23.

Genus VECTIDINIUM gen. nov.

Name derivation. Latin, *Vectis*, Roman name for the Isle of Wight.

Type species. Vectidinium stoveri sp. nov.

Diagnosis. Single-walled proximate peridinioid cysts, moderately compressed dorso-ventrally, ambitus subpentagonal or subcircular to oval or somewhat fusiform. Epicyst and hypocyst of approximately equal size. Epicyst may or may not extend into a short apical horn; apical pore always present. Hypocyst semicircular or bilobed; left antapical horn present or absent, right antapical horn commonly present.

Autophragm with atabular or intratabular to penitabular ornament of small granules, spinules or baculae, which may be reduced in size and/or number. Narrow laevigate pandasutural zones may be observable. Paratabulation formula, when determinable, 4′, 3a, 7″, Oc, 5″, 2‴, Os. When observable paraplate 1″ is rhombic, antero-posteriorly elongate, and relatively large.

Cingulum and sulcus distinct. The cingulum is wide relative to over-all autocyst size, not indented, non- or moderately helicoid. Sulcus shallow and broad on the hypocyst. Archeopyle combination type 3I 3P 3″–5″, accessory sutures may occur along cingular margin of the remaining precingular paraplates. Opercula free.

Comparisons. Vectidinium differs from *Palaeoperidinium* Deflandre 1934, and from *Saeptodinium* Harris 1975, in that the apical paraplate 3′ is not included in the archeopyle. From *Saeptodinium* it also differs in being single walled and usually having intratabular or penitabular ornament. From *Palaeoperidinium* it differs in the presence of ornament and its much smaller size.

Ginginodinium Cookson and Eisenack 1960, *Laciniadinium* McIntyre 1975, and *Lunatodinium* Brideaux and McIntyre 1973, all have a 3I 3P 3″–5″ archeopyle, and they also resemble *Vectidinium* in the type of ornament. *Ginginodinium* is double walled, and in the formation of the archeopyle the three dorsal precingular paraplates (3″–5″) always remain attached along their cingular margins (Lentin and Williams 1975, p. 95). *Laciniadinium* has a single opercular piece 3I 3P 3″–5″ which always remains attached to the cyst along its posterior margin, like a flap. In *Vectidinium* whenever the archeopyle is present, the operculum is detached and some doubt remains as to whether this is simple or compound. *Lunatodinium* (a Lower Cretaceous genus) was described as having an archeopyle formed by the loss of the three dorsal precingular paraplates. However, Lentin and Williams (1975, pp. 96 and 116) included this genus in the pericysts, possessing a 3I 3P archeopyle. This appears to be so from the original illustration of *Lunatodinium* (Brideaux and McIntyre 1973, figs. 1–13). The genus is stated to have a circular or subcircular outline.

Cysts of the Recent freshwater dinoflagellate *Peridinium* resemble *Vectidinium* in the type and distribution of the ornament, but they are normally cavate and the archeopyle is formed by the detachment of plates along a transapical suture, type A3I3P.

Vectidinium stoveri sp. nov.

Plate 54, fig. 7

Name derivation. This species has been named after Lew Stover.

Diagnosis. As for the genus.

Description. The dorso-ventral compression of these cysts is normally slight, and some specimens may be oriented in apical or antapical view; in lateral view the cysts are somewhat fusiform or oval. The epicyst has strongly convex sides which may merge imperceptibly in a very short, blunt apical horn with a solid tip on which sits a pore; the apical horn may be absent, and the epicyst apex is then invaginate. The hypocyst is commonly broadly rounded posteriorly, but some specimens may show a weak bilobation on the antapex. The short, eccentrically located left antapical horn may be present or absent.

The ornament varies in density and shape. When the ornament is baculate or of short processes their distal endings are often T-shaped and may be linked to those from near-by processes, giving the appearance of a tectum supported by columellae in optical section; sometimes the ornament is very reduced in size and mostly consisting of granules. The ornament may be densely or sparsely arranged on the paraplate surface, the most peripheral elements tending to be arranged along simulate rings. Laevigate pandasutural zones, usually narrow, are present but are not always clearly visible.

Cingulum and sulcus are distinct, both being marked by low ridges or folds on the autophragm. The cingulum is relatively wide, slightly helicoid or circular, not indented; intratabular ornament and smooth pandasutural zones may be observable on the cingular surface, but the number of cingular paraplates has not been determined with certainty. The sulcus is also broad and shallow, and extends approximately half-way to the apex. The shape and relative size of individual paraplates are difficult to determine because of very small size and transparent autophragm of these cysts.

When present, the archeopyle is formed by complete detachment of plates 1a–3a, 3″–5″. On some specimens, accessory archeopyle sutures develop along most of the anterior margin of the cingulum, but both portions of the cyst usually remain attached along a narrow band, presumably corresponding to the sulcus. The operculum is always free, but it has not been possible to determine whether this is formed by a single piece or is compound, since isolated opercula have not been observed—a fact suggesting that the operculum may be compound, disintegrating into the very small individual paraplates which would easily be lost in sieving of the organic residue during preparation.

Holotype. Slide ML 1452, U43/3, sample WC34, Upper Headon Beds, Upper Eocene, Whitecliff Bay, Isle of Wight.

Measurements. Holotype, autocyst length 37 μm, breadth 42 μm, apical horn 1 μm, left antapical horn 1 μm, width of cingulum 4 μm.

Range. Autocyst length 30(35·5)41 μm, breadth 24·5(31)42 μm, apical horn 0(2)4·2 μm, left antapical horn 0(1)4·5 μm, width of cingulum 2·7(3·6)4 μm. Specimens measured—24.

Distribution. The distribution of *Vectidinium stoveri* in the section studied deserves some special attention since it constitutes monospecific assemblages at some horizons, and has not been found in association with any other dinoflagellate cysts. These horizons yield ostracod assemblages of type III (Keen 1972, 1977); these have been stated by Keen to indicate brackish-water conditions (salinity 3–9‰). *V. stoveri* is thought to be a non-marine dinoflagellate cyst, and possibly a good indicator of oligohaline conditions; it is recorded from samples WC34, 35, and H19.

PALYNOLOGICAL ASSEMBLAGES AND DEPOSITIONAL ENVIRONMENTS

The Upper Eocene–Lower Oligocene of the Isle of Wight was deposited under widely variable environmental conditions. The area of deposition has been likened to an embayment, limited to the north and south by the Portsdown and the Sandown–Brixton anticlines respectively, and opening towards the sea to the east and south-east. At times this sea penetrated into the basin. At other times an eastward flowing river system occupied the area (Keen 1977). The conditions ranged from shallow, near-shore open sea, to brackish-water lagoons—with or without connection to the sea—to freshwater lacustrine or fluviatile environments. These changes are reflected in the palyno-assemblages, and are especially noticeable in the relative proportions of different classes of palynomorphs as well as in the composition of the microplankton assemblages where these occur.

Palaeoecological studies of palynomorph assemblages and particularly of dinoflagellate cysts are currently in their preliminary stages, and no work on the palaeoenvironmental interpretation of Tertiary palyno-assemblages from paralic areas has yet been published. However, the assemblages recovered here may be correlated to particular environmental conditions by using, as a control, the existing information on the distribution of dinocysts in Tertiary to Recent sediments, as well as the sedimentological and faunal evidence available from the sections studied. The foraminifera (Murray and Wright 1974), molluscs (Daley 1973), and ostracods (Keen 1972, 1977; Haskins 1969) from the Upper Eocene–Lower Oligocene sections of the Isle of Wight have yielded a considerable volume of data that can be used in assessing the meaning of the palynological assemblages recovered.

The major components of the palynological assemblages are indicated in Table 2. They clearly fall into two groups, one with marine dinoflagellates present; the other non-marine samples contain only terrigenous freshwater or lagoonal elements.

The non-marine group shows considerable variation, particularly in the proportions of *Pediastrum* Meyen, which may contribute from 0 to over 90% of the assemblage. In some samples there is also a considerable contribution from non-marine dinoflagellates. These non-marine samples are associated with various lithologies ranging from limestone through to sands and no particular pattern has so far been determined. It is evident, particularly from the work of Keen, that the salinities vary from fresh to oligohaline water. The environments of deposition include evidently freshwater lacustrine, fluvial, flood-plain, and bay-head situations. The control over the relative abundance of *Pediastrum* Meyen is not understood. It is notably more common in the Bembridge Marls in the west of the island. In marine sediments it is present only in very small numbers and is probably allochthonous. It is most abundant in situations that could be interpreted as oligohaline water.

TABLE 2. General character of palynological assemblages. P & S—pollen and spores; Ped—*Pediastrum* spp.; MD—marine dinoflagellates; fd—freshwater dinoflagellates; 'r' indicates that dinoflagellates are all reworked from older strata.

Sample	% P & S	% Ped	% MD	% fd
Whitecliff Bay				
Bembridge Marls				
WC67	99	—	1(r)	—
WC66	99	1	×(r)	—
WC65	94	2	4(r)	—
WC64	99	1	×(r)	—
WC63	91	8	1(r)	—
WC62	74	26	—	—
WC61	100	—	—	—
WC60	100	—	—	—
WC59	97	3	—	—
WC58	100	—	—	—
WC56	99	1	—	—
WC55	13	80	7	—
WC55A	16	84	×	—
WC54	100	—	—	—
WC53	100	—	—	—
Bembridge Limestone				
WC51	100	—	—	—
WC49	100	—	—	—
Osborne Beds				
WC47	100	—	—	—
WC46	58	42	—	—
WC45	36	64	—	—
WC44	100	—	—	—
WC43	100	—	—	—
WC42	10	90	—	—
WC41	97	3	—	—
Upper Headon Beds				
WC40	22	78	—	—
WC39	86	14	—	—
WC38	97	3	—	—
WC37	93	6	—	1
WC36	99	1	—	×
WC35	62	1	—	37
WC34	73	14	—	13
WC33	94	6	—	—
WC31	62	38	—	—
WC30	100	—	—	—
WC29	61	39	—	—
WC28	90	10	—	—
WC26	100	—	—	—
Middle Headon Beds				
WC25	74	—	26	—
WC24	84	—	16	—
WC23	54	—	46	—
WC21	58	2	40	—
WC20	40	—	60	—
WC19	31	—	69	—
WC18	28	—	72	—
WC17	38	—	62	—
WC16	29	—	71	—
WC15	25	—	75	—
WC14	20	—	80	—
WC13	37	×	37	—
Lower Headon Beds				
WC12	72	28	—	—
WC9	80	20	—	—
WC8	45	55	—	—
WC7	25	75	—	—
WC6	100	—	—	—
WC5	7	93	—	—
WC4	80	20	—	—
WC3	96	4	—	—
WC2	100	—	—	—
WC1	98	2	—	—

Sample	% P & S	% Ped	% MD	% fd
Hamstead Cliff				
Lower Hamstead Beds				
H36	54	46	—	—
H35	55	45	—	—
H34	88	12	—	—
H33	82	18	—	—
H32	75	25	—	—
H31	63	37	—	—
H30	81	19	—	—
H29	41	59	—	—
H28	64	36	—	—
H27	97	3	—	—
H26	96	4	—	—
H25	96	3	—	—
H24	94	1	6	—
H23	42	13	45	—
H22	84	16	—	—
H21	87	13	×	—
H20	78	22	—	—
H19	63	29	—	8
H18	76	24	—	—
H17	73	27	—	—
Bembridge Marls				
H16	76	24	—	—
H15	34	66	—	—
H14	67	33	—	—
H13	64	36	—	—
H12	36	64	—	—
H10	34	66	—	×
H9	57	43	—	×
H8	75	25	—	×
H7	73	27	—	—
H6	35	6	59	—
H4	49	×	51	—
H3	44	56	—	—
Bembridge Limestone				
H2	16	84	—	—
H1	100	—	—	—
Bouldnor Cliff				
Upper Hamstead Beds				
B15	92	—	8	—
B14	94	—	6	—
B13	96	4	—	—
B12	100	—	—	—
B11	24	2	74	—
B10	75	25	—	—
B9	42	58	—	—
B8	8	3	89	—
B7	28	2	70	—
B6	52	29	19	—
B5	63	37	×	—
Lower Hamstead Beds				
B4	100	—	—	—
B3	100	—	—	—
B2	100	—	—	—
B1	52	48	—	—

Non-marine dinoflagellates are represented by a single species, *Vectidinium stoveri* which is present only in three samples, WC34, 35, and H19. It is associated with ostracod assemblage III of Keen, indicating brackish-water conditions.

Marine samples are characterized by the presence of marine dinoflagellate cysts and acritarchs. They can be classified into a number of types according to their diversity and the dominant species. Since these types occur in stratigraphic order and are associated with a series of marine incursions it is convenient to discuss them in stratigraphic sequence.

The Middle Headon Beds transgression

Four assemblage types are present:

Assemblage 1. The Brockenhurst Bed and *Psammobia* Beds (samples WC13–21) are characterized by assemblages with forty or more species of dinoflagellate cysts dominated by *Homotryblium plectilum* which makes up 30–70% of the microplankton; other abundant species are *Spiniferites ramosus*, *Adnatosphaeridium reticulense*, and *Phthanoperidinium cometum*. These assemblages are associated with ostracod assemblage type VI and indicate open-sea conditions, the major transgressive episode in the sequence studied.

Assemblages 2–4. The succeeding *Venus* Bed contains three different assemblage types showing a marked reduction in the number of species present and in their relative abundance.

Type 2, occurring in sample WC23, has less than thirty species and is dominated by *H. pallidum* and *P. cometum*, the latter a species evidently tolerant of reduced salinities in estuarine or lagoonal environments.

Type 3, occurring in sample WC24, has only seventeen species and is dominated by broken species of *H. plectilum* associated in assemblage 1 with open-sea conditions. Here these are thought to be allochthonous. *H. pallidum* is the next most common species.

Type 4, occurring in sample WC25, is dominated by *Eocladopyxis tessellata* and *P. cometum*.

These three assemblages appear to indicate a period of regression with restriction of marine access to the area. Keen refers the ostracod assemblages in these beds to his type V, indicating salinities in the range of 16·5–33‰.

The Lower Bembridge Marl transgression

Assemblage types 5–7 are associated with the Oyster Bed.

In the east, sample WC55 yielded assemblage type 5, where dinoflagellates made up only 7% of the palynomorphs. No clearly dominant species was present, the commonest being *Chiropteridium aspinatum*, *Glaphyrocysta microfenestrata*, *Homotryblium pallidum*, and *Paralecaniella indentata*.

In the west, assemblage type 6 is monospecific; *Phthanoperidinium levimurale* makes up 51% of the palynomorphs in sample H4. Assemblage type 7 is also monospecific, *G. microfenestrata* making up 59% of the palynomorphs in sample H6.

The significance of these three diverse assemblages from the Oyster Bed is made clearer by consideration of the fauna. Molluscs, foraminifera, and ostracods all indicate brackish estuarine conditions. Assemblage type 5 is associated with Keen's type V indicating near-marine conditions; the assemblages from the west, however, are associated with his type IV, indicating lower salinities (9–16‰). This seems to mean that the monospecific assemblages with *P. levimurale* and *G. microfenestrata* are composed of more or less stenohaline species, since both also occur in open marine conditions. They appear to have flourished in this estuarine situation since they are particularly abundant, more so than any of the species in the east, where the assemblage, although poorer in relative numbers, has a greater variety of marine species and, although still estuarine, appears to have better connection with the open sea.

The Lower Hamstead Bed transgression

Assemblage types 8 and 9 are associated with a marine incursion at the horizon of the *Nematura* Band.

Assemblage type 8, sample H23, contains only four species and is dominated by *Adnatosphaeridium reticulense*. Only 13% of the palynomorphs are dinoflagellates. Assemblage type 9, an even poorer assemblage from H24 immediately above, is on the other hand dominated by *P. flebile*. Ostracods from the *Nematura* Band show the presence of assemblage type IV characteristic of mesohaline conditions.

The Upper Hamstead Bed transgressions

Six different dinoflagellate assemblages (types 10–15) have been found in the Upper Hamstead Beds and the palynology appears to show the presence of three different invasions of saline water.

The first incursion corresponds to the *Cerithium* Bed and contains assemblage types 10–12. Assemblage type 10, sample B6, contains 19% dinoflagellates with only a few species represented and is dominated by *G. microfenestratum* and *P. cometum*, both of which, although known from other marine sediments, have previously been noted in assemblage types 7 and 4 and 2, with reduced salinities associated with Keen's types IV and V. Keen (1972) finds that the *Cerithium* Bed also yields assemblages of types IV and V. Assemblage type 11 in sample B7 is also impoverished in species, but is dominated by small acritarchs of the *Micrhystridium* group, which accounts for about 60% of the palynomorphs. Assemblage type 12, sample B8, is more varied and richer in numbers, but *G. paupercula* accounts for most of these.

Taken together these three samples indicate a marine influence, which, however, did not achieve fully marine conditions in this locality, the area remaining meso- to polyhaline.

The second incursion is represented only by assemblage type 13, sample B11. That it is a separate episode is indicated by the intervention of samples B9 and 10 which contain only terrigenous pollen and spores and the ?freshwater alga *Pediastrum*. Assemblage type 13 appears to represent more fully marine conditions with many new species appearing. The dominant species is *H. pallidum*, which also dominates in assemblage type 2 (*Venus* Bed) and is abundant in type 5 (Oyster Bed, Whitecliff Bay). Here it is associated with *Gerdiocysta conopeum*. The conditions indicated are still not yet fully marine, but must closely approach that condition.

The third incursion is represented by assemblage types 14 (sample B14) and 15 (sample B15). That this is a separate episode is indicated by the intervention of the purely terrigenous palynological assemblages in samples B12 and 13. The second and third incursions together form the *Corbula* Bed. Assemblage type 14 is a poor monospecific one comprising only *Phthanoperidinium cometum*. It probably indicates low salinities. Type 15, however, is somewhat richer and is particularly so in the variety and lack of any clearly dominant species. *Micrhystridium*, *Lejeunia tenella*, *Hystrichokolpoma salacium*, and *P. amoenum* are prominent, the last three being known only from open marine sediments. It is believed that these two samples B14 and B15 represent the beginning of a major transgression, the culmination of which is not represented due to erosion of the succeeding beds.

DINOFLAGELLATE CYST STRATIGRAPHY

The distribution of dinoflagellates is shown in Table 1.

The first dinoflagellate assemblages appear in the Brockenhurst Bed associated with the Middle Headon transgression. Detailed comparison between the dinoflagellate assemblages from the Solent Formation and the marine sediments of the underlying Barton Formation is not possible at present, since little information on the dinoflagellate content of the Barton Beds has so far been published (Bujak 1976). However, from unpublished evidence (Bujak 1973), it appears that, notwithstanding the intervening regression represented by the Becton and Lower Headon Beds, only minor changes take place in the composition of the assemblages between the uppermost marine beds of the Barton Formation and the lower part of the Solent Formation (Middle Headon Beds). The number of species that first appear in the Middle Headon Beds is very small, but they include *Rhombodinium perforatum* and *Thalassiphora fenestrata*, and the possibility remains that some of these may also occur in the Barton Beds; the number of apparent extinctions is also limited, and their stratigraphic significance, which may be only local, cannot be assessed at this stage.

As the assemblages become impoverished towards the upper part of the Middle Headon Beds, among the dinoflagellate species disappearing from the assemblages are *Areosphaeridium diktyoplokus*, *Cordosphaeridium funiculatum*, *Distatodinium ellipticum*, *Palaeocystodinium golzowense*, *R. draco*, *R. perforatum*, and *T. velata*.

Other taxa, *Emslandia* sp., *Eocladopyxis tessellata*, and *Phelodinium pumilum*, make their first appearance in the section here. These species first appearing within the upper part of the Middle Headon Beds are all new and so their stratigraphic value, if any, cannot be stated.

The Bembridge transgression, represented by the Oyster Bed, yields poorly diversified assemblages. These, in terms of their species content, show a somewhat closer relationship to the Middle Headon Beds than to the Upper Hamstead Beds. The Bembridge Oyster Bed at Whitecliff Bay registers the last known occurrence in England of *Chiropteridium aspinatum*, *Impletosphaeridium severinii*, *Homotryblium oceanicum*, and *Leptodinium incompositum*.

The Lower Hamsted Bed transgression, represented by a thin sequence including the *Nematura* Bed, also provides a poor assemblage consisting mainly of long-ranging species. One species, *Phthanoperidinium flebile* is, however, apparently confined to this horizon.

A very pronounced break in the dinocyst succession is evident in the final transgressions of the Upper Hamstead Beds. Out of a total of sixty-eight dinoflagellate species recorded, only nineteen are common to the Solent and Hamstead Formations; thirty-four species disappear below the base of the Hamstead Beds, and fifteen species are first recorded within the latter. The marked renewal of the assemblages registered between the two main marine episodes in the sequence is to some extent environmentally controlled, since some of the species missing in the Headon Bed are known to persist elsewhere into the Oligocene, such as *C. aspinatum*, *Cordosphaeridium cantharellum*, *D. ellipticum*, *Hystrichokolpoma rigaudiae*, *Kisselovia coleothrypta*, *R. draco*, *T. velata*, and *T. pelagica*. Two species, however, which fail to reappear are *R. perforatum* and *A. diktyoplokus*, whose absence seems to be stratigraphically important.

A number of species make their first appearance here and some of them are thought to be stratigraphically important. These are *Gerdiocysta conopeum*, *Heteraulacacysta* cf. *companula*, *Phthanoperidium amoenum*, *Wetzeliella gochtii*, and *W. symmetrica incisa*. Other appearances of possible significance are *Phelodinium pachyceras* and *D. scariosum*.

CORRELATION WITH OTHER EUROPEAN AREAS

Paris Basin

Curry *et al*. (1978) correlate the Middle Headon Beds with part of the Marnes à Pholadomya ludensis, i.e. with the deposits of the Ludian transgression of the Paris Basin. Both formations yield rich dinoflagellate assemblages. A description of those from France has been given by Chateauneuf (1978). Most of the species recorded by him are present in the Middle Headon Beds but there is none of sufficiently restricted range to allow confident correlation on the basis of the dinoflagellates, except that *R. perforatum* (which appears for the first time in the mid-Headon Beds in England) also appears for the first time in small numbers in the top Marinesian and more commonly in the Ludian. *R. perforatum*, previously mentioned from the Barton Beds (Costa and Downie 1976) is in fact a separate species (Bujak, in press). A marked distinction between the Ludian assemblages and those from the Headon Beds is the remarkable abundance of *H. plectilum* in the Isle of Wight and its apparent absence from the Ludian.

The impoverished assemblages from the Bembridge Oyster Bed yield little of correlative value, but the abundance of *C. aspinatum* does correspond with the prominence of this species in assemblages from the Ludian Marnes à Lucines (Chateauneuf 1978).

The equally poor assemblages from the vicinity of the *Nematura* Band do, however, show some marked similarities to those of the Argile Verte de Romainville at the base of the Stampian. The lower of the English samples (H23) is dominated by *Adnatosphaeridium reticulense*, which is also a dominant form in the Argile Verte. The upper English sample (H24) is dominated by *Phthanoperidinium flebile*, which is restricted to this horizon in England and has also been found to be abundant in the Argile Verte by Chateauneuf (1978) and recorded by him under the name of *Geiselodinium* cf. *geiseltalense*. This strongly suggests a correlation between the *Nematura* Band and a horizon within the Argile Verte de Romainville.

The Upper Hamstead Beds can be correlated with the Calcaire de Sannois and the lower part of the Marnes à Huitres. This correlation is supported by the appearance of *Gerdiocysta conopeum* (= *Cyclonephelium reticulosum* Gerlach, Chateauneuf 1978), *W. gochtii* (Chateauneuf, pers. comm.), *P. amoenum*, and the increased abundances of *W. symmetrica* and *Pentadinium taenigerum* (Chateauneuf 1978) in both areas.

The overlying Sables de Fontainebleau have a rich and varied dinoflagellate assemblage with species such as *Chiropteridium lobospinosum* and *C. partispinatum* (Chateauneuf 1978). In England there is no representative of this assemblage, which has marked similarities to those from the Rupelian of Germany (Benedek 1972).

Belgium

Weyns (1970) described two assemblages from the Sables de Grimmertingen (Lower Tongrian). He listed forty-seven forms of dinoflagellate cysts. Of these thirty-six are apparently present in the Middle Headon Beds, and the assemblages have a general similarity, particularly in the prominence of *Homotryblium* and *Spiniferites*.

In comparison with the Hamstead Beds assemblages, there are major differences. The many species appearing for the first time in the Hamstead Beds are not listed in Weyns's assemblages. Only a few of the species listed by Weyns appear to have stratigraphic significance. *Glaphyrocysta microfenestrata* (= *C. semicirculatum* in Weyns) does not appear until late in the Chama Beds of the

Bartonian (Bujak 1976). *G. exuberans ellipsoidalis* and *Areosphaeridium diktyoplokus* are absent above the Middle Headon Beds. The correlation that best fits these circumstances is between the Sables de Grimmertingen and the Middle Headon Beds. This is in agreement with recent work on the nanoplankton correlation (Cavelier 1975). A notable difference between the Belgian and English assemblages is the presence of *Leptodinium* and *Nematosphaeropsis* in the former. These are forms found to be more prominent in open-sea situations.

Two samples, one from 20 m and the other from 30 m above the base of the Rupel Clay in the type section, yielded rich dinoflagellate assemblages. These showed marked similarities to those from the Upper Hamstead Beds, in particular containing *W. gochtii*. However, they also contain *C. lobospinosum*, *C. partispinatum* and other species which are not present in the Isle of Wight, but are characteristic of the Sables de Fontainebleau in the Paris Basin, and the Rupelton in Germany. These samples are clearly younger than any from the Isle of Wight.

THE EOCENE/OLIGOCENE BOUNDARY IN THE ISLE OF WIGHT

Establishment of a standard for this stratigraphic boundary is the subject of continuing debate. In France, it has commonly been placed at the base of the Stampian Stage, i.e. at the base of the Argile Verte de Romainville (Chateauneuf 1978). Accepting this, the correlations between the Isle of Wight succession and the Paris Basin based on dinoflagellates indicate that the boundary lies closely below the *Nematura* Band. The boundary clearly lies between the *Nematura* Band and the Middle Headon Beds. The Oyster Bed, although it has a poor assemblage, has greater similarity to the Headon Beds than to the succeeding assemblage.

Therefore, if the French view is accepted the boundary lies between the base of the *Nematura* Band and the top of the Oyster Bed. Since the Argile Verte de Romainville marks the first important marine incursion after the episode of the Marnes a Lucines it seems very likely that the *Nematura* Band represents the same transgression. The Bembridge Marls then correlate with the Supra- and Upper Gypsiferous Groups (1st and 2nd mass) and the Osborne Beds with the 3rd mass of gypsum. The base of the Oligocene could conveniently be taken at the base of the Hamstead Beds, some 9 km below the *Nematura* Band.

An alternative, widely held, view is that the base of the Oligocene originally selected in Germany should be adopted. This is marked by the transgression associated with the Latdorf (Lattorf) Sands (NP21), which correlate readily with the Sables de Grimmertingen in Belgium.

Dinoflagellates have not been described from the Latdorf Sands, but from the Sable de Grimmertingen assemblages very like those from the Middle Headon Beds have been described by Weyns (1970). If this correlation is accepted the Middle Headon Beds would be Oligocene. However, the Brockenhurst Bed has given evidence of an NP20 age, which indicates that the base should be higher. There is, however, no apparent break in the Middle Headon Beds sequence, only a progressive increase in terrigenous influence in the *Venus* Beds (samples WC22–25). No suitable location for a boundary is evident.

The next marine incursion in the Isle of Wight succession, the Bembridge Oyster Bed, did not yield any dinoflagellates of much value in correlation. Those that are present are not inconsistent with a correlation with the Sables de Grimmertingen and consequently with the placing of the base of the Oligocene immediately above the Bembridge Limestone, as is done by Curry *et al.* (1978).

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DICTYODORA FROM THE SILURIAN OF PEEBLESSHIRE, SCOTLAND

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ABSTRACT. The meandering trace fossil *Dictyodora* Weiss, 1884 occurs in deep water greywacke/shale sequences in the Gala Group (lower Silurian) of Thornylee and Grieston Quarries, Galashiels. Two species are recognized; *D. scotica* (M'Coy, 1851) and *D. tenuis* (M'Coy, 1851); the former is distinguished by a more regular meandering form. These traces were originally named *Crossopodia scotica* and *Myrianites tenuis*. It is suggested that *C. scotica* be rejected as the type species of *Crossopodia*.

THORNYLEE QUARRY (Grid ref. NT 4200 3635) (formerly spelt Thornyly, Thorney Lee, Thornielee, Thornilee) is situated on the north bank of the River Tweed, 8 km east of Galashiels and 8 km west of Innerleithen. The quarry is located on a steep slope above a layby on the A72 (Peebles-Galashiels) road. Between the quarry and the road is a dismantled railway with cuttings which provide a 300 m long section through Upper Llandovery greywackes and shales (Gala Group of Lapworth 1870). The first geological description of Thornylee was given by Nicol (1850) who noted some graptolites and abundant 'annelid impressions'.

Grieston Quarry (NT 3130 3618) was also described by Nicol (1850), who noted the abundant graptolite fauna and the trace fossils. More recently the fauna and sediments of this quarry have been described by Toghill and Strachan (1970) and Trewin (1979). The thin greywackes and shales of Grieston also lie within the top of the Gala Group of Lapworth (1870), but are not exactly the same age as those at Thornylee on the basis of the graptolite fauna.

This study stemmed from work on H. A. Nicholson's trace fossil collection in Aberdeen (Benton and Trewin 1978). The following descriptions are based on large collections made at Thornylee and Grieston in April and June, 1977. Comparisons have been made with the type material of M'Coy and Nicholson. Repository abbreviations used are: AUGD, Aberdeen University, Department of Geology and Mineralogy Palaeontology Collection; BMNH, British Museum (Natural History); GSM, Geological Survey Museum, I.G.S., London; HM, Hunterian Museum, Glasgow; SM, Sedgwick Museum, Cambridge.

DEPOSITIONAL ENVIRONMENT AND ASSOCIATED FAUNA

At both localities deep water, interbedded greywacke/shale sequences are exposed in which the coarser lithologies are of turbidite origin. The trace fossils at Thornylee are more abundant in the shale-rich parts of the sequence rather than in association with greywacke beds. There seems to be a greater frequency of meandering traces in the purple rather than the green shales. At Grieston the greywackes are fine-grained and contain abundant ripple-lamination, possibly the results of reworking; other beds are characterized by numerous transported graptolites which produced delicate tool marks on bed bases (Trewin 1979). The greywackes at Thornylee are usually medium grained, graded, and sometimes show tool marks and load casts on the sharp bed bases. Internally, Bouma sequences of structures are frequently seen. The general aspect of the lithofacies is of a low-energy turbidite environment with thin greywacke turbidites and abundant shale.

At both localities graptolites are present but they are much more abundant in the finer grained rocks of Grieston Quarry, where the majority have been transported and deposited in thin turbidites.

[Palaeontology, Vol. 23, Part 3, 1980, pp. 501-513.]

Tail spines of *Ceratiocaris* occur at Grieston, but no other fauna was noted. The ichnofauna dominated by meandering feeding burrows is typical of deep water muds and belongs to Seilacher's *Nereites* facies.

THE ICHNOFAUNA

Introduction. The ichnofauna is dominated by the meandering burrows of two species of *Dictyodora*, which are described below. The small burrow *Caridolites* Etheridge, Woodward and Jones, 1890 is common at both localities. Rare examples of *Nereites* were found at Thornylee and stuffed burrows, cf. *Planolites*, are also present. The meandering traces are described below with more emphasis placed on *Dictyodora scotica* in view of its taxonomic importance. A redescription is given of *Caridolites* and the association with *Nereites* briefly discussed.

Genus DICTYODORA Weiss, 1884

Taxonomic discussion of Dictyodora

Geinitz (1867) founded the species *Dictyodora liebeanum* for a 'plant' from the Culm (Lower Carboniferous) of Gera, East Germany, and Weiss (1884*a*, *b*) proposed the genus *Dictyodora* for this species. He was unable to decide if it was of plant or animal origin.

Zimmermann (1889, 1891) discussed the taxonomic problems associated with German Carboniferous *Dictyodora*, noticing that as with the British examples, different horizontal (bedding parallel) sections had been given distinct names at different times. Zimmermann (1892) gave a detailed account of the type species *D. liebeana*, and considered that the vertical wall contained no infill, but noted longitudinal and oblique streaks. Zimmermann noted that the wall tends to slope inwards towards the top, giving tighter loops than those of the basal burrow, but was puzzled by walls intersecting without disturbance. *D. liebeana* has vertical walls up to 180 mm high and a well-defined over-all cone shape distinguishing it from *D. scotica* and *D. tenuis*. Zimmermann (1892) briefly described a species, *D. hercynica*, which has a looser structure and walls 1-3 cm high, found in the Upper Devonian of the Harz mountains. It has apparently not been figured.

D. simplex Seilacher, 1955 from the Lower Cambrian of the Salt Range of Pakistan is a simple, loose structure about 6 mm deep. However, this is a structure built from successive sloping layers and Seilacher proposed that the trace was produced by a worm-like animal travelling through the sediment in an oblique position. There is no basal burrow in Seilacher's reconstruction and the 'vertical wall' is of equal width from top to bottom. We consider that these differences are sufficient to exclude *D. simplex* from the genus *Dictyodora.* No alternative generic assignment is suggested without examination of the original material.

Seilacher (1967, p. 77) figured a *Dictyodora* evolutionary sequence from relatively loosely structured forms in the Lower Palaeozoic to tightly spiralling patterns in the Carboniferous. In grade of organization, *D. tenuis* appears similar to Seilacher's most primitive type (a) and *D. scotica* is slightly more advanced.

Pfeiffer (1959) reviewed previous work on *D. liebeana* and gave good three-dimensional reconstructions of Carboniferous examples. Müller (1962) also described the morphology of German Lower Carboniferous *Dictyodora* in detail with many figures, and Ruchholz (1967) gave further examples from the Harz mountains. Pfeiffer (1968) gave a synonomy list for *D. liebeana* (Geinitz, 1867). Müller (1971) discussed the formation of *Dictyodora* meanders, emphasizing that the trace was a feeding structure formed relatively rapidly, since the basal burrow does not change in diameter in any single specimen and since it maintains a constant depth and does not rise gradually to keep up with sedimentation.

There is thus an extensive, mainly German, literature on *Dictyodora* which establishes the characteristic features of the genus as the meandering basal burrow and the dorsal striated wall. The species *D. scotica*, described below, has previously been given the name *Myrianites tenuis* for sections for the vertical wall and *Crossopodia scotica* for the basal burrow.

The genus *Myrianites* MacLeay, 1839 was established for a meandering track with small leaf-like extensions at the sides. The type species, *M. macleayii* Murchison, 1839 (type specimen: GSM Geol. Soc. Coll. 6824) appears to be a small *Nereites*. Species from Spain described by Delgado (1910) as *Myrianites* are certainly *Dictyodora* but are not described or figured well enough to establish synonymy with the material described here.

M'Coy (1851*a*, *b*) founded the species *M. tenuis* based on specimens of small meandering traces from Grieston Quarry. Nicholson (1978, pp. 42, 43) identified wall sections of *D. scotica* from Thornylee as *M. tenuis*, but the specific name *tenuis* is retained here for M'Coy's original material redescribed below as *D. tenuis*.

M'Coy (1851*a*, *b*) also founded the genus *Crossopodia* for two Silurian trace fossils. *C. lata* from Llandeilo, Wales, is a 2 cm wide trail with clear transverse striations and a 'fringe' which better resembles the *Crossopodia* of modern usage. *C. scotica*, however, is the form redescribed here as *D. scotica* and M'Coy's type (SM A45575a–c) clearly shows the diagnostic features (text-fig. 2). The figure of the type of *C. scotica* in M'Coy 1851*b*, pl. 1D, fig. 15, appears to be a composite of the three specimens SM A45575a–c. Fortunately all are of the same species and A45575a is more suitable as the lectotype showing well all the major features. M'Coy's figure has been reversed in the engraving process. Unfortunately, Häntzschel (1962, p. W189) designated *C. scotica* as the type species of *Crossopodia* and repeated this with a mislabelled figure of '*C. scotia*' (*sic*) in Häntzschel (1975, fig. 34, 2b). This figure is derived from Schimper and Schenk (1879, p. 52, fig. 40) and is clearly not the *C. scotica* of M'Coy (1851*a*, *b*) and Nicholson (1978).

In order to preserve the normally accepted usages of *Crossopodia* and *Dictyodora* we propose that *C. scotica* be rejected as the type species of *Crossopodia*. *C. lata* M'Coy (1851) (type specimen SM A37733) would then become the type species of *Crossopodia*. An application to this effect will be made to the I.C.Z.N. or other appropriate body, when agreement has been achieved on the rules of trace fossil nomenclature. Further revision of the genus *Crossopodia* is required, but is outside the scope of this paper.

Dictyodora scotica (M'Coy, 1851)

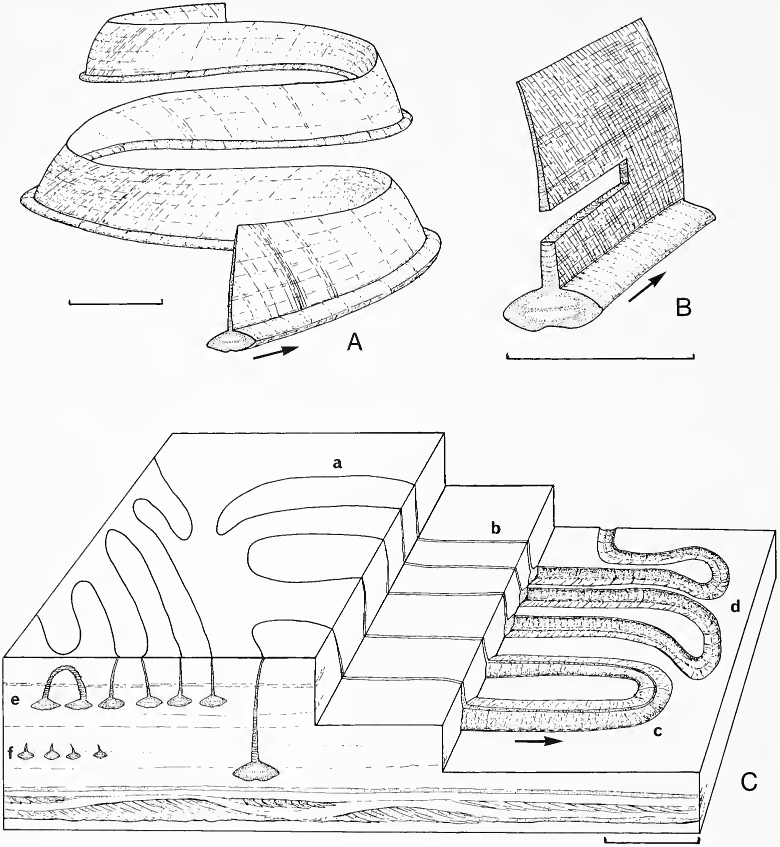
Text-figs. 1, 2, 3

v*1851*a*	*Crossopodia scotica* M'Coy, p. 395.
v*1851*b*	*Crossopodia scotica* M'Coy; M'Coy, p. 130, pl. 1D, fig. 15.
?1855	*Crossopodia scotica* M'Coy; Harkness, p. 475.
non 1879	*Crossopodia scotica* (M'Coy); Schimper and Schenk, p. 52, fig. 40.
non 1962	*Crossopodia scotia* (M'Coy) (*sic*); Häntzschel, p. W189, fig. 118, 2.
non 1975	*Crossopodia scotia* (M'Coy) (*sic*); Häntzschel, p. W54, fig. 34, 2b.
v1978	*Crossopodia scotica* M'Coy; Nicholson, p. 36, pl. 3, fig. 1, pl. 6.
v1978	*Myrianites tenuis* M'Coy; Nicholson, p. 42, text-fig. 7, *non* pl. 4, fig. 1. [The same specimen as in Benton and Trewin 1978, pl. 2, fig. 2.]
v1978	*Crossopodia scotica* M'Coy; Benton and Trewin, p. 8, pl. 2, fig. 1.

Lectotype. Here designated, SM A45575a, the original of M'Coy (1851*b*, pl. 1D, fig. 15). Gala Group, Upper Llandovery, lower Silurian, Thornylee Quarry, nr. Innerleithen, Peeblesshire, Scotland. Refigured here, text-fig. 2.

Other material. More than two hundred examples from the type locality, a representative selection of which are catalogued as AUGD 10693 to 10710. Also: AUGD 8819, 8820, 10606, 10723, Mus. Coll. 956, 957; BMNH 39451, 58169 (1, 2); GSM 104247, 104249, 104250, RU 2970; HM X871/1–2, X1003/1–7.

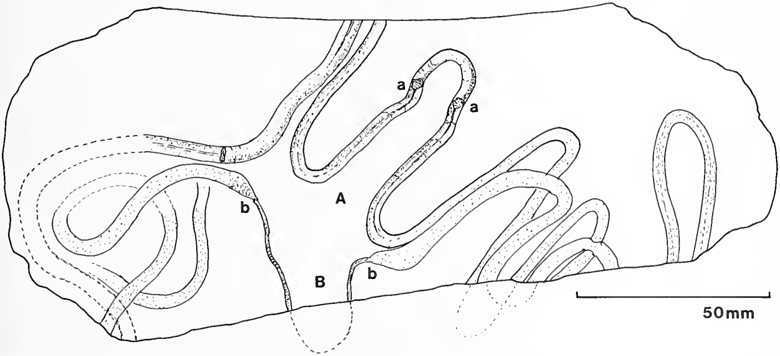
Description. The burrow system illustrated in text-fig. 1 consists of a basal burrow, generally preserved with a lenticular cross section, and having a vertical or inclined longitudinal wall arising from the dorsal mid-line of the basal burrow. The basal burrow varies from 1·5–6 mm wide and up to 3 mm high in slate lithologies, but when developed in fine sand may have a nearly circular cross section due to the small degree of compaction. The wall is up to 13 mm high and tapers upwards from a width of 1–2 mm at the base. The taper is most rapid in small examples. The typical burrow system (text-fig. 3C, D, E) consists of 5–10 parallel meanders each 10–80 mm long



TEXT-FIG. 1. Scale bars 10 mm at front faces of figures. Arrows indicate direction of travel of *Dictyodora* organism. A, general morphology of *Dictyodora* meanders showing basal burrow and wall; wall curves inwards at meander bends. B, section of burrow to show features of burrow and wall fill, horizontal striations and curved vertical/oblique striations of wall surface. C, block diagram illustrating different preservational aspects of the burrow in plan and section; *a*, narrow sections at top of wall; *b*, wider sections near base of wall; *c*, convex top of basal burrow with base of wall fill preserved on top; *d*, concave impression of underside of burrow with fill removed, a weak median ridge may be present; *e*, smaller example showing effect of sectioning the inclined wall at meander turn; *f*, juvenile burrow in section. The style of ripples and fine parallel lamination present is also illustrated on the front face of C.

(usually 30–50 mm) and internally measured at basal burrow level as 0–20 mm apart (usually 5–15 mm). Where successive meanders touch, a tight turning circle is present at the meander turn. The meanders may also be irregular and broad as in text-fig. 3A, B. The relevant features of the type specimen are illustrated in text-fig. 2.

The burrow shows various preservational aspects (text-fig. 1C) dependent on the level at which it is sectioned. Sections of the wall appear as meandering lines up to 2 mm wide, occasional sharp turns are seen in sections close to the top of the wall (text-fig. 3E) but nearer the basal burrow the wall displays smooth curves. The wall has a finite thickness and the burrow may break either side of the wall as shown in text-fig. 3B. Sections at the top of the basal burrow show the entire infill with a median ridge marking the base of the wall (text-fig. 1C). Specimens showing the lower surface of the basal burrow display a smooth groove which is sometimes double, with a weak median ridge (text-fig. 1C). The burrow may also split within the burrow fill giving very little relief to the preserved trace. Internally, a distinct pattern is frequently seen in polished or etched cross-sections of the burrow fill resulting from reorientation of platey minerals (text-fig. 1B).

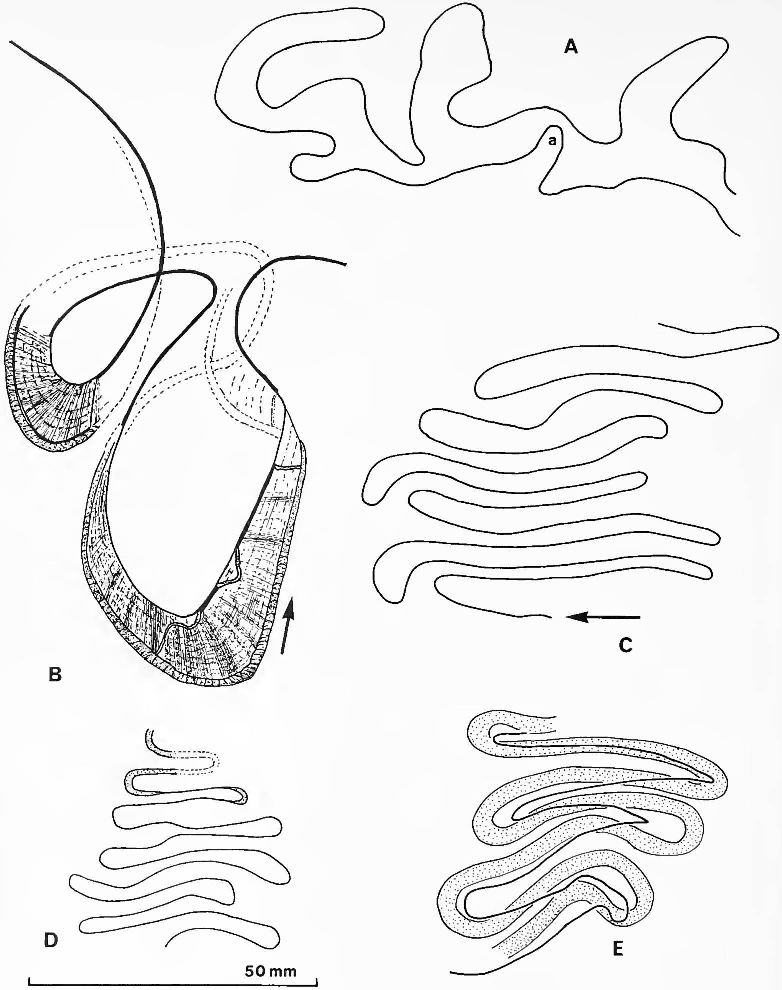


TEXT-FIG. 2. Sketch of lectotype of *Dictyodora scotica*, SM A45575a showing the lower surface of the specimen. Trace A shows the typical meander pattern. Most of the specimen displays the lower surface of the burrow but at *a* the burrow fill is broken out to show a mould of the upper surface of the basal burrow. The wall of A is 5 mm high and is not seen on the top of the slab. Trace B is larger than A and later since it clearly crosses A. At *b* the transition from basal burrow to wall can be seen. The wall passes through the full 8 mm thickness of the slab and is seen on the top of the specimen (not illustrated).

The burrows are indistinct in places due to the presence of several crossing burrows, and fracture irregularities on the surface of the slab which have been omitted for clarity.

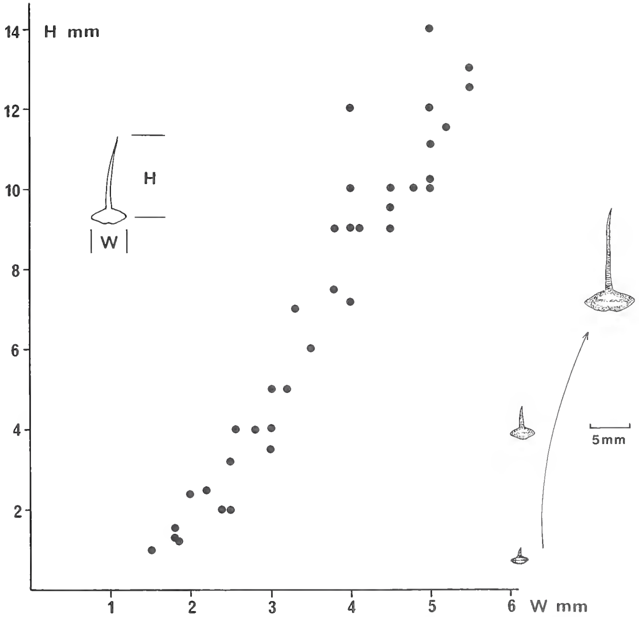
The wall is normally vertical above straight stretches of burrow, but curves inwards at meander bends (text-figs. 1A, C, 3B, E). Fine bedding parallel striations are present on the surface of the wall closely spaced at 4 per mm. A similar bedding parallel banding due to platey mineral orientation occurs within the wall fill, and is not related to sedimentary laminae. Curved vertical/oblique striations are also present on the wall surface normally spaced at 3·5 per mm. Internally the wall may show fine curved structures marked by reoriented platey minerals and resembling backfill within the wall (text-figs. 1B, 3B). Detailed observation of features is difficult in the wall fill but it is likely that the possible backfill structures seen normal to bedding occur between the bedding parallel bands.

The smallest forms recognized have a basal burrow 1.5 mm wide and a wall only 1 mm high, and a full gradation exists up to the larger forms with a progressive increase in wall height relative to burrow width (text-fig. 4). Detailed measurement of the morphology and meander patterns of over 170 specimens using principal components analyses failed to differentiate any groups with significantly different characters, and we consider that all the meandering burrows of this type are growth stages of a single species.



TEXT-FIG. 3. *Dictyodora scotica*; examples of burrow morphology. A, irregular meanders (section of burrow wall) with example of avoidance of previously formed burrow at *a*, AUGD 10693. B, irregular burrow which crosses previously formed burrow; plan view shows wall above basal burrow to be partly broken away, and inward slope of wall at meander curves; thickness of slab 10 mm; AUGD 10697. C, D, typical regular meander forms, hooked ends to meanders seen in C; both on AUGD 10694. E, plan view of basal burrow (stipple) and position of top of wall (solid line); sharp bends present at top of wall become smooth curves at lower levels close to the basal burrow; AUGD 10698. All examples from Thornylee Quarry.

Occurrence. Dictyodora scotica is common at Thornylee Quarry and scarce at Grieston Quarry. It is probably common in the Llandovery strata of the Southern Uplands since Peach and Horne (1899) mention '*Crossopodia*' and '*Myrianites*' from at least twenty localities in the Galashiels–Hawick region. It also occurs in the Llandovery of Penwhapple Glen, Girvan (Nicholson and Etheridge 1880, pp. 304–318). P. Doughty (pers. comm.) also records *Dictyodora* from the Silurian of Co. Down, Northern Ireland.



TEXT-FIG. 4. *Dictyodora scotica*. Relationship of width of basal burrow W with burrow height H to show range of variation and the relative increase in wall height in the larger examples.

Dictyodora tenuis (M'Coy, 1851)

Text-fig. 5

v*1851*a* *Myrianites tenuis* M'Coy, p. 394.
v*1851*b* *Myrianites tenuis* M'Coy; M'Coy, p. 130, pl. 1D, fig. 13.
v1978 *Myrianites tenuis* M'Coy; Nicholson, pl. 4, fig. 1, *non* text-fig. 7.
v1978 *Myrianites murchisoni* Emmons; Nicholson, p. 43, pl. 5, fig. 1.

Lectotype. Here designated, SM A45579a, the original of M'Coy (1851*b*, pl. 1D, fig. 13). Gala Group, Upper Llandovery, Lower Silurian, Grieston Quarry, nr. Innerleithen, Peeblesshire, Scotland (text-fig. 5A).

Other material. AUGD 9224, 10329, 10607, 10612, and 10711 to 10720 from Grieston Quarry and AUGD 10710 from Thornylee Quarry.

Description. *Dictyodora* with broad irregular meanders, as in text-fig. 5, which frequently have a secondary sinuosity with a wavelength of 3–15 mm which may develop into meanders with length roughly equal to breadth in larger examples. The basal burrow is from 1·5 to 3 mm wide and the wall has not been observed to exceed 10 mm in height. The wall is 0·2–0·7 mm wide and striated in the same manner as in *D. scotica*. Traces range from tiny 'scribbles' (text-fig. 5E) up to large examples as in text-fig. 5B, D.

Trace endings are observed as in text-fig. 5B where lengths of trace as short as 10 mm occur between inclined circular burrows 3 mm in diameter; other traces can be followed for over 200 mm without interruption.

Discussion. The distinction of *D. tenuis* from *D. scotica* can be made on maximum size and on the meandering pattern, which is more regular and smooth in *D. scotica* compared with the irregular meanders with secondary sinuosity displayed by *D. tenuis*.

In the past specimens displaying sections of the wall have been identified as *Myrianites* and specimens showing the basal burrow as *Crossopodia* or *Nemertites*. The specimens from Grieston called *M. murchisoni* by Nicholson (1978, p. 43, pl. 15, fig. 1) are not synonymous with the American form described by Emmons (1844) and are ascribed here to *D. tenuis*.

Occurrence. Common in the Upper Llandovery (*griestoniensis* Zone) of Grieston Quarry, nr. Innerleithen, Peeblesshire, and also present in association with much commoner *D. scotica* at Thornylee Quarry. The form illustrated by Raup and Seilacher (1969, fig. 1a) from the Ordovician of Barrancos, Portugal, appears to be *D. tenuis*.

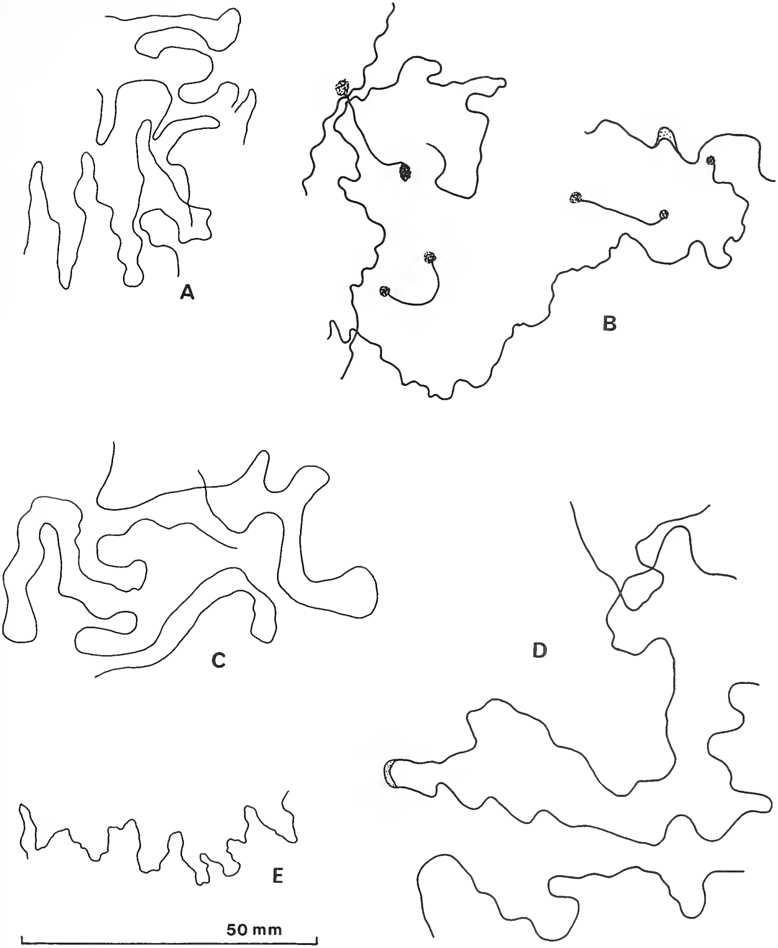
THE *DICTYODORA* ANIMAL AND ITS BEHAVIOUR

The meandering burrow of *Dictyodora* resembles the meandering burrows and trails produced by worms and molluscs efficiently utilizing an area as a food source. The tightly packed meanders of *Dictyodora* were probably formed during feeding, and the looser irregular meanders may have been the result of searching for areas rich in food. We assume that the body of the animal occupied the basal burrow, and probably progressed by peristaltic movement. Since individual burrows cannot be traced from small to large size, and considering that the burrows are sometimes seen to end by rising through the sediment it is likely that the animal moved from place to place on or above the sediment surface. Thus the burrows are considered to be produced by short periods of food search and utilization at a constant level within the sediment.

The animal appears to have maintained contact with the surface by means of an organ which was responsible for the production of the striated wall on the dorsal burrow surface; this we term the wall-organ to avoid assumptions implicit in the use of known zoological terms such as 'siphon'. The curved vertical striations on the wall and the fill of the wall indicate that the wall-organ moved regularly through the sediments, maintaining a constant convex-forward edge and followed the movement of the animal in the burrow; thus wall-organ traces occasionally touch or cross each other while the corresponding burrows do not.

The behaviour of animals that form meandering traces has been discussed by several authors. Seilacher (1967) suggested that the *Dictyodora* animal measured its meander length by the length of its body. It maintained contact with a previously formed burrow (thigmotaxis) until its body was straight and then the animal was 'programmed' to make a sharp U-turn (homostrophy) as its tail straightened, and to follow beside the last-formed portion of the burrow. However, this explanation does not satisfactorily explain individual burrows where meander length varies, or the Carboniferous *Dictyodora* where the meanders spiral out from a central point, each meander being longer than its predecessor.

Seilacher based his interpretation on the classic work of Richter (1924, 1928), who studied the Cretaceous/Tertiary *Helminthoida labyrinthica* Heer, 1865 which forms similar meandering feeding traces. Richter's interpretation differs from Seilacher's in one important way: he defined the homostrophic turning stimulus as caused by loss of contact with a former trace and not by tail straightening. The animal followed a former trace and could at times curve in front of previous meander ends (e.g. text-fig. 3C) before turning back when it lost contact with disturbed mud. In text-fig. 3 meander length varies from 30 to 80 mm and was clearly not measured by the body length of the



TEXT-FIG. 5. *Dictyodora tenuis*. Examples of burrow morphology shown by sections of the wall of the burrow. A, small meandering trace with irregular meanders showing secondary sinuosity; part of lectotype SM 45579a. B, parts of typical irregular meanders, together with short lengths of burrow terminated by inclined sections of basal burrow; AUGD 10719. C, D, E, irregular meanders of various sizes to show variation in meander morphology; C, E AUGD 10716; D AUGD 10718. All from Grieston Quarry.

animal. The reactions of the animal while feeding in meanders as listed by Seilacher (1967) and Raup and Seilacher (1969) may be modified to:

(1) Move horizontally keeping within a single stratum of sediment (?controlled by wall-organ length);
(2) Always keep in touch with previously formed burrow while feeding (thigmotaxis);
(3) Never come closer to a previously formed burrow than a particular distance 'd' (phobotaxis);
(4) If contact is lost with a former burrow, make a 180° turn (homostrophy/strophotaxis).

These 'rules' appear to apply reasonably well, and obvious cases of burrow avoidance can be found (text-fig. 3A). Traces made by individuals at different levels in the sediment frequently cross each other, but the basal burrows in such cases are normally at different levels. In the Thornylee examples population density was probably low and thus there was no need for attempting to utilize an area more than once.

If the meandering burrows are formed during feeding then the question arises of how feeding was accomplished. The wall-organ could have been a food collector at the surface, with the animal protected in its burrow, or the animal could have fed by sediment ingestion at burrow level leaving the wall-organ to perform a respiratory function. The second of these suggestions seems most favourable since the basal burrow has a definite burrow fill which corresponds to the sediment type at basal burrow rather than surface level. The apparently passive motion of the wall-organ does not accord with a function as a feeding organ, and it is more likely to have had a respiratory function and to have controlled burrow depth.

In laminated sediment the fill of the wall roughly matches the characteristics of the immediately adjacent sediment, with only slight downward movement of sediment during filling occasionally seen in thin section. Thus the wall-organ does not seem to have had a significant sediment transport function. No annulation of the burrow fill is seen and the constant fine spacing of the striations formed by the wall-organ would seem to indicate a slow regular movement through the sediment. The wall-organ may have been ciliated to facilitate its progress through the sediment. The striations and structured fill of the wall indicate that the organ was not merely dragged through the sediment but that the thin wall of sediment was packed in both horizontal and vertical increments by the wall-organ.

The *Dictyodora* animal was probably a worm or shell-less mollusc which fed by sediment ingestion and maintained contact with the over-lying water by means of the wall-organ which controlled burrow depth and possibly aided respiration.

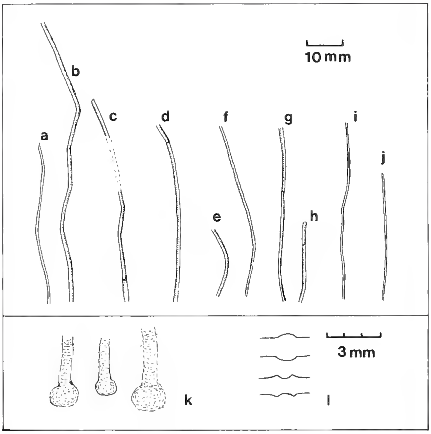
OTHER TRACES PRESENT

Caridolites wilsoni Etheridge, Woodward and Jones, 1890

Text-figs. 6, 7

The name *Caridolites wilsoni* was first mentioned in Nicholson (1873) and a brief description appeared in Etheridge, Woodward and Jones (1890), which must rank as the type description. Nicholson's original (1872) manuscript with a description and figure of *C. wilsoni* has been published recently together with a discussion (Benton and Trewin 1978, p. 10, pl. 3) in which Nicholson's interpretation that the trace was made by the tail spines of shoals of swimming *Ceratiocaris* is rejected.

The traces are generally about 1 mm wide and may consist of a slight central ridge bounded by hollows or a single ridge, or the counterpart of either. The traces are generally nearly straight for from 10–50 mm before disappearing or turning fairly sharply on a new course. Typical examples are shown in text-fig. 6*a–j* and typical profiles in text-fig. 6*l*. In cross section the traces are seen to be burrows with a vertical depth of up to 5 mm and consist of a basal tunnel with a narrower vertical extension (text-fig. 6*k*). These traces thus resemble minute *Dictyodora* without the meanders. *Caridolites* frequently covers bedding surfaces with a confusion of burrows as in text-fig. 7.



TEXT-FIG. 6. *Caridolites wilsoni*. *a–j*, typical burrow traces as seen on bedding surfaces; *a–c*, AUGD 10675; *d–f*, AUGD 10748; *i*, *j*, AUGD 7055, Grieston Quarry; *g*, *h*, AUGD 10723, Thornylee Quarry. *k*, typical vertical cross sections of burrows. *l*, profiles of surface expressions of the burrows.

TEXT-FIG. 7. *Caridolites wilsoni*. Bedding surface covered with typical examples, × 1, AUGD 10674, Grieston Quarry.

Caridolites is abundant at both Grieston and Thornylee and is frequently associated with both *D. scotica* and *D. tenuis*. It seems possible that *Caridolites* represents the activities of juvenile *Dictyodora* animals which had not developed sufficiently to meander. Certainly the observed size ranges of the traces fit this possibility.

Genus NEREITES MacLeay, 1839

Nereites is rare in the Thornylee–Grieston assemblage, with only two clear examples of this surface trace seen. Sediment surface texture was probably not suited to preservation of surface trails and most were probably removed by turbidity currents. The slaty muds and silts generally do not split at the top surfaces of beds. The common association of *Nereites* surface traces in sequences with *Dictyodora* burrows of similar width raises the speculation that *Nereites* could be a surface trace of the *Dictyodora* animal moving from one feeding spot to another.

CONCLUSIONS

The deep water ichnofauna of the greywacke/shale turbidite facies of the Llandovery in southern Scotland is dominated by two species of *Dictyodora.* The small burrow *Caridolites* is probably the juvenile burrow of the '*Dictyodora*' animal. *Nereites* is also present but rare, probably owing to original sediment texture and preservation.

Crossopodia scotica is shown to be a *Dictyodora*, and it is suggested that it should be rejected as the type species of *Crossopodia*, being replaced by *C. lata.*

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LOWER CRETACEOUS TEREBRATULIDAE FROM SOUTH-WESTERN MOROCCO AND THEIR BIOGEOGRAPHY

by FRANK A. MIDDLEMISS

ABSTRACT. The terebratulid brachiopods contained in the Gentil and Whitaker Collections from the Lower Cretaceous of south-west Morocco have been revised. Although the majority of the species are confined to south-west Morocco, the affinities of the fauna are with the faunas of the shallow marine regions bordering Tethys, such as the Jura region, eastern Spain, the Crimea, and the northern Caucasus; the Tethyan pygopid brachiopods characteristic of the Rif in northern Morocco are almost absent. The fauna thus constitutes a Jura-type assemblage situated on the southern side of Tethys. In the systematic section a new genus *Paraboubeithyris* is erected; also seven new species: *Loriolithyris melaitensis*, *L. marocensis*, *Boubeithyris tibourrensis*, *B. pleta*, *Paraboubeithyris plicae*, *Kutchithyris kennedyi*, and *Juralina ecruensis*. The genera *Kutchithyris* and *Juralina*, previously described from the Jurassic, are shown to have survived into the Lower Cretaceous. *Terebratula subsella* Leymerie is referred to *Kutchithyris*.

THIS paper consists mainly of a revision of the terebratulids contained in two important collections, the Gentil Collection in the Collection de Paléontologie of the Université Pierre et Marie Curie, Paris, and the Whitaker Collection in the British Museum (Natural History), London. All the specimens came from the Lower Cretaceous (Berriasian to Aptian inclusive) of an area at the seaward end of the High Atlas in south-western Morocco, extending some 40 kilometres inland between Agadir in the south, Essaouira (Mogador) in the centre, and Safi in the north.

Louis Gentil, who was born at Algiers in 1868 and died in Paris in 1925, was a pioneer in the study of the geology of Morocco. His first major contribution was the exploration of the Tafna basin. Later he became a member of the Segonzac exploratory mission to the Atlas Mountains and eventually head of the mission. He was the author of numerous publications, particularly on the geology of the Atlas, almost up to the time of his death including, most notably, the first geological map of Morocco, which appeared in 1923. J. J. S. Whitaker was not a geologist but a Christian missionary who worked in Morocco during the early years of this century. His collection was made at one locality only (see p. 519 below) and very probably on one occasion. Figured specimens are in the British Museum (Natural History) (BM) or the Collection de Paléontologie, Université Pierre et Marie Curie, Paris (Gentil Coll.).

THE LOWER CRETACEOUS OF SOUTH-WESTERN MOROCCO

The Lower Cretaceous geology of the area was described by Roch (1930) and that of the southern part by Ambroggi (1963); Gigout (1951) included the extreme northern part, around Safi, in his survey; Ager (1974) gave a brief summary in English. All agree that south-western Morocco was, in Lower Cretaceous times, a marine depositional basin opening westwards towards the ocean, cut off from the marine deposits of the same age, but quite different lithofacies and fauna, in the Rif arc to the north by the interposition of the positive block of the Moroccan Meseta and from the marine area of the Algerian high plateaux by the emergent central massif of the High Atlas. At each stage of the Lower Cretaceous the most fully marine conditions, presumably indicating the deepest water, are found in the extreme west, around Cap Ghir and northwards to the neighbourhood of Cap Tafelney. Passing north-eastwards, eastwards, and south-eastwards from this region one finds increasingly

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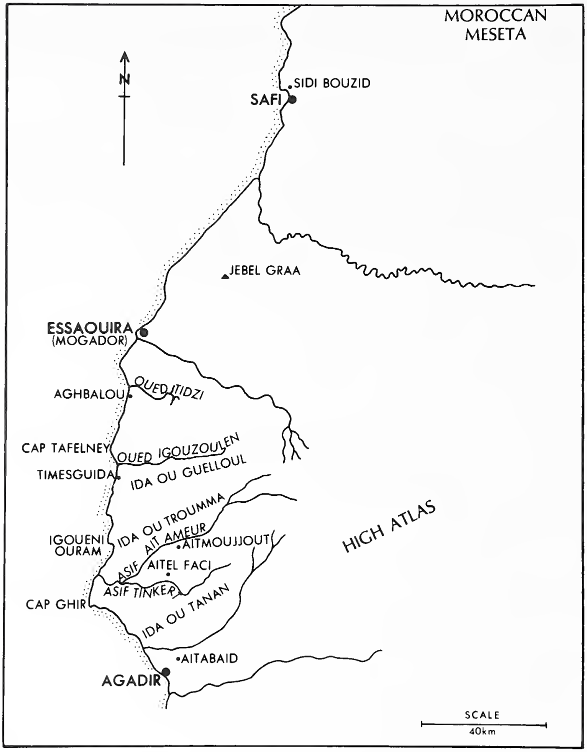


TEXT-FIG. 1. Locality map of south-west Morocco.

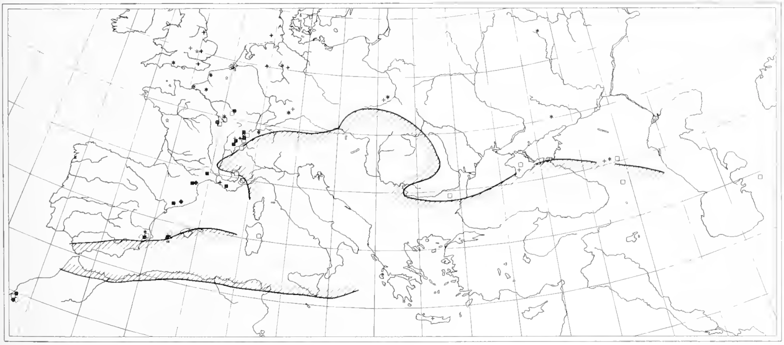
shallow-water lithofacies and biofacies and, usually within 40 or 50 kilometres, non-marine deposits.

The deep-water facies around Cap Ghir consists of green marls and marly limestones with ammonites. These pass eastwards into the more sandy and calcareous beds, with brachiopod and mollusc faunas, of what Roch significantly calls a 'jurassian facies'. These pass eventually into sub-continental red beds. The lithological succession differs markedly from the monotonous lithofacies of the 'bathyal' Lower Cretaceous, seen in the Rif and the Betic region, and has a general resemblance to the successions seen in the Pre-Betic zone of Spain, north-east Spain (Sitges), east-central Sardinia, Provence, and Portugal. It exhibits a very striking difference from these, however, in the absence of the massive urgonian limestones, which are characteristically developed in the Barremian and Aptian of those regions, and of the rudists. In these respects, the south-west Moroccan succession is most comparable to the Lower Cretaceous of central Texas and parts of Coahuila (Mexico). The Aptian, as in northern Spain and England, is transgressive, the Gargasian overlapping the earlier divisions on to the flanks of the High Atlas. To the south lies the coastal Cretaceous basin of Tarfaya, at first sight similar in situation to the Agadir–Essaouira basin, but here the earlier part of the Cretaceous is non-marine, marine sedimentation starting only with the Apto-Albian (Choubert *et al.* 1967).

PALAEOBIOGEOGRAPHICAL RELATIONSHIPS OF THE TEREBRATULID FAUNA

Endemicity. The fauna contains a high proportion of endemic species: of the eleven species described eight are new and seven of these are so far known only from south-west Morocco. This is not unusual. The terebratulids tend to produce local, allopatric species. For example, of the sixteen terebratulid species in the English Aptian thirteen are known only in south and south-central England, of which three occur at one locality only (Middlemiss 1959). I have recently (Middlemiss 1979) pointed to the contrast between such local species and widespread species such as (in the Moroccan fauna) *Loriolithyris valdensis* and suggested that these differences were probably due to differing lengths of the free-swimming larval stage. Evidence for the palaeobiogeographical relationships of the fauna comes mainly from the occurrence elsewhere of the widespread species but also from the taxonomic relationships of the local species.

Loriolithyris. L. valdensis is the most widespread species of this genus, occurring in the Lower Cretaceous of eastern Spain (and the Balearic Islands), Sardinia, southern France, the Jura, south-east Paris Basin, north-east Bulgaria, the Crimea, northern Caucasus, Kopet Daga, and perhaps Algeria. *L. russillensis* shares the western part of this distribution—eastern Spain, the Balearic Islands, southern France, the Jura, and south-east Paris Basin. *L. melaitensis* and *L. marocensis* are local offshoots from the stock, not at present known outside the south-west Moroccan basin.



TEXT-FIG. 2. Palaeobiogeographical relationships of the Lower Cretaceous terebratulids of south-west Morocco. Distribution of south-west Moroccan Lower Cretaceous species which occur elsewhere: ■ *Loriolithyris russillensis*, □ *Loriolithyris valdensis*, ◆ *Cyrtothyris middlemissi*, ◇ *Kutchithyris kennedyi*. Distribution of other Lower Cretaceous species of *Cyrtothyris*: ✦ . Distribution of Aptian–Cenomanian species of *Boubeithyris*: ☆ . Generalized occurrence of *Kutchithyris subsella* in the Upper Jurassic and Lower Cretaceous: ∗ . Generalized occurrence of Jurassic species of *Juralina*: + . Generalized boundary of the Tethyan pygopid fauna shown by diagonal shading.

Boubeithyris and *Paraboubeithyris*. The three species here ascribed to these genera are all local to south-west Morocco but the genus *Boubeithyris*, of which *Paraboubeithyris* is perhaps a specialized development, is represented by a species in the Aptian of the Jura, by two species in the Albian of England and by one species in the Cenomanian of Belgium and western France.

Cyrtothyris. *C. middlemissi*, the south-west Moroccan species, is known also in eastern Spain and southern France. The genus is more widespread, being represented by species in the early Cretaceous of north Germany, north-east England, and east Greenland and the Aptian of the Jura and southern France. Imlay's species *Terebratula sillimani* and *T. tamaulipana* (Imlay 1937), from the Valanginian–Hauterivian of northern Mexico, probably belong to this genus.

Kutchithyris. *K. brivesi* is a highly distinctive form confined to south-west Morocco but *K. kennedyi* is known also in the Lower Cretaceous of eastern Spain, the Balearic Islands, and southern France, the southern part of the same distribution area as *L. russillensis*. Other species of the genus are found in the Middle Jurassic of India and, according to Buckman (1918), Europe. I here refer *Terebratula subsella* Leymerie to this genus. This species has a widespread occurrence in the Upper Jurassic of Europe and is known (but undescribed) in the Lower Cretaceous of eastern Spain.

Juralina. This genus, as interpreted by recent authors (especially Boullier 1976), occurs in the Upper Jurassic of a wide area of Europe north of the Alps from England to Russia and also of Crete (*J. immanis*—see Bonneau, Beauvais, and Middlemiss 1975) and Sicily (Boullier 1976). *J. ecruensis* is the first species of the genus to be described from the Cretaceous.

Discussion. The Lower Cretaceous terebratulids of Europe can be divided into three geographical faunas: the boreal fauna in the north, the Tethyan fauna with its distinctive Pygopinae, and between them the Jura fauna. The last is so named after the area in which the fauna is richest and best known, but the character of the Jura fauna is essentially that of a neritic assemblage occupying an optimum situation on the border of the deeper-water Tethyan region and extending approximately parallel to the border of Tethys from the Iberian Peninsula eastwards to Turkmenistan. In this sense, the Lower Cretaceous fauna of south-west Morocco falls into place as an extension of the Jura fauna to the south of the Tethyan fauna which is so strongly developed in the Rif.

The affinities of our terebratulids are essentially with the Jura brachiopod fauna. This is generally true of the cephalopods listed and figured by Roch, Ambroggi, and Gigout. Characteristic Tethyan genera such as *Lytoceras* (Valanginian–Hauterivian), *Phylloceras* (Hauterivian), *Desmoceras* (Barremian), *Pulchellia* (Barremian), *Duvalia* (Valanginian), *Hibolites* (Valanginian) occur but are almost confined to the deep-water region of the extreme west. Further east the cephalopods are noted by Roch as being of 'Jura type' and include such genera as *Acanthodiscus* and *Leopoldia*. There is scarcely a trace in the pre-Aptian Cretaceous of the Tethyan pygopines which characterize the Rif and the Betic region (Geyssant 1966). The 'jurassian' affinities of the faunal facies were clearly recognized by Roch and Gignoux (1955). Ager (1974) has recorded the discovery of *Nucleata* cf. *jacobi* in the Aptian or Albian near Tamzargout. This seems to be the only recorded occurrence of pygopine brachiopods in the Lower Cretaceous of south-west Morocco—a feeble sign of southward 'Tethyan spread' simultaneous with those transgressions which were causing northward movement of southern species into north Spain, England, and north Germany (Middlemiss 1979). The specimen from Safi figured by Gigout (1951, pl. 9, figs. 35–38) as *T. euthymi* is a terebratellidine related to '*Terebratula*' *moreana* d'Orbigny.

Kutchithyris, in the Lower Cretaceous, does not occur north of southernmost France and is one of those sub-Tethyan forms (Middlemiss 1979) which are sensitive indicators of the advance and retreat of the Tethyan fauna. *K. subsella* shows this well. In the Oxfordian, a period of major expansion of the Tethyan fauna (Arkell 1956), it is found throughout a large part of central Europe—England, northern France, northern and south-western Germany, southern Poland, the Russian Platform. By Kimmeridgian times it extended no further north than the Boulonnais. The Volgian saw a further southward retreat to the Pays de Bray, its place in England and the Boulonnais being taken by boreal forms. In the Lower Cretaceous it has so far been found only in the Pre-Betic region of Spain, on the margin of Tethys. *Juralina* may also be a sub-Tethyan genus whose history is possibly similar to that of *K. subsella.*

Reconstruction of plate positions as they were in Lower Cretaceous times shows the area of the Jura faunas as much more linear than it is now. Provence, eastern Spain, Sardinia, the Balearic Islands, and south-west Morocco form a linear belt which, extended westwards, would include the western Gulf region of the U.S.A. and the northern parts of Mexico. The neritic Lower Cretaceous of these latter regions is in this sense an extension of the area of the Jura fauna. Unfortunately brachiopods are rare but Imlay (1940) remarked of the Neocomian faunal assemblage of northern Mexico that it was remarkably similar to that of France, England, and Switzerland and belonged decidedly to the 'Mediterranean' province. His species *T. coahuilensis* is certainly close to and probably synonymous with *Sellithyris carteroniana* d'Orbigny, one of the most characteristic Jura species. It seems a reasonable forecast that neritic Lower Cretaceous brachiopod assemblages of 'Jura fauna' affinities will some day be found in the south-eastern or Gulf continental shelf deposits of the U.S.A. or the north-western continental shelf deposits of Africa. Unfortunately those of the offshore part of the Tarfaya basin have yielded no brachiopods.

STRATIGRAPHIC AGES OF SPECIMENS IN THE WHITAKER AND GENTIL COLLECTIONS

Whitaker left no record of the age of the strata from which he made his collection and it has not so far proved possible to trace the exact locality. All the specimens were obtained from one locality, recorded as: 'Ecru, Mogador, Morocco. 500 ft. on plateau edge of 1000 ft. elevation'. The age can only be assessed on the internal evidence of the fauna and appears to be either Hauterivian or Barremian. The species represented all occur elsewhere in south-west Morocco in both the Hauterivian and the Barremian, whereas not all occur in the Valanginian or Aptian.

Four species are represented in the Whitaker Collection, in the following numbers: *Loriolithyris russillensis*, 57; *L. valdensis*, 39; *Juralina ecruensis*, 46; *Kutchithyris kennedyi*, 1. The predominance of *L. russillensis* would suggest, on analogy with the occurrence of the species in Switzerland and France, a Barremian age. The distribution of these four species in the Gentil Collection is as follows:

L. russillensis	Hauterivian	7	*J. ecruensis*	Valanginian	25
	Barremian	39		Hauterivian	2
	Aptian	9		Barremian	15
L. valdensis	Valanginian	25	*K. kennedyi*	Hauterivian	2
	Hauterivian	63		Barremian	1
	Barremian	104			
	Aptian	16			

In general these statistics again support a Barremian age for the Whitaker Collection but they may reflect nothing more than the accidents of collection.

I have followed stratigraphic ages given on the labels of the Gentil Collection because it was not possible to check each locality in the field, but there are some arguments supporting the general validity of these labels, even though there must be a number which are wrong. Analysis of all the localities given on the labels shows that all the specimens from any one locality are assigned consistently either to a single stage or to two, or rarely three, adjacent stages. Thus a logical series of localities can be set out, ranging from those credited with yielding only Berriasian and Valanginian fossils to those credited with yielding fossils only of Clansayesian age.

SYSTEMATIC PALAEONTOLOGY

Order TEREBRATULIDA Waagen, 1883
Suborder TEREBRATULIDINA Waagen, 1883
Superfamily TEREBRATULACEA Gray, 1840
Family TEREBRATULIDAE Gray, 1840
Subfamily SELLITHYRIDINAE Muir-Wood, 1965

Remarks. Loriolithyris and *Boubeithyris* are closely related sellithyridine genera. The corniced hinge plates which are the most distinguishing feature of *Boubeithyris* are essentially the same in detailed structure as the piped hinge plates of *Loriolithyris*. Both genera essentially have *small* crural bases (attached to the inner edges of the hinge plates) which become encased in successive layers of secondary skeletal tissue (Pl. 60, fig. 2; Pl. 61, figs. 2, 3). The function of this is presumably to strengthen the junction of hinge plates and crural bases. These structures are not inner hinge plates, which some authors claim to be present in *Terebratula*, although Muir-Wood (1965, p. H775) denies their presence in that genus, because they show no sign of having taken part in any way in the attachment of the dorsal pedicle muscles. *Boubeithyris* and *Loriolithyris* differ mainly in the shape of the hinge plates—concave and corniced in *Boubeithyris*, concave to sigmoid and piped in *Loriolithyris*. Externally *Boubeithyris* is distinguished especially by the close spacing of the plicae of the anterior commissure. Both differ from *Sellithyris* in having accessory structures (cornicing or piping) on the hinge plates and in their much less pentagonal external form.

Paraboubeithyris has an internal structure which is closely related to that of *Boubeithyris*. Externally *P. plicae* looks different at first sight from *Boubeithyris* spp. but similarities include the convex cardinal slopes, small size of the median sinus, and the late development of folding. The external differences, however, seem too great to allow the species to be included in *Boubeithyris*. *P. plicae* is here regarded as a specialized local offshoot from the *Boubeithyris* stock.

Genus LORIOLITHYRIS Middlemiss, 1968

Type species. Terebratula russillensis de Loriol, 1866.

Species included. T. russillensis de Loriol, *T. valdensis* de Loriol, *L. melaitensis* nov., *L. marocensis* nov. Range: Berriasian to Aptian.

EXPLANATION OF PLATE 55

Figs. 1–4. *Loriolithyris russillensis* (de Loriol). Whitaker Coll. 1*a–d*, typical form, plaster cast of specimen sectioned (see text-fig. 5), BM BB 76544. 2*a–c*, wide *latifrons*-like form, plaster cast of specimen sectioned (see text-fig. 7), BM BB 76552. 3*a–d*, small sharply folded form, plaster cast of specimen sectioned (see text-fig. 6) BM BB 76543. 4*a–d*, thick *latifrons*-like form, BM B 17293.

Figs. 5–9. *Loriolithyris valdensis* (de Loriol). 5*a–c*, typical form, plaster cast of specimen sectioned (see text-fig. 11), BM BB 76545. Whitaker Coll. 6*a–d*, juvenile rectimarginate form, BM BB 76546, Whitaker Coll. 7*a–d*, juvenile incipiently biplicate form BM BB 76549, Whitaker Coll. 8*a–d*, elongate adult form, BM BB 76554, Whitaker Coll. 9*a–d*, wide adult form, S.546/1/12, Gentil Coll., Upper Hauterivian, loc. unknown.

Fig. 10*a–c*. *Loriolithyris melaitensis* sp. nov. Plaster cast of specimen sectioned (see text-fig. 12), S.556/1, Gentil Coll., Hauterivian, Tizi Ouarioum.

Figs. 11*a–d*. *Loriolithyris melaitensis* sp. nov. Holotype, S.556/2, Gentil Coll., Barremian, Ait Ben Melait, Ida ou Guelluill.

All natural size.

MIDDLEMISS, Cretaceous Terebratulidae

Loriolithyris russillensis (de Loriol)

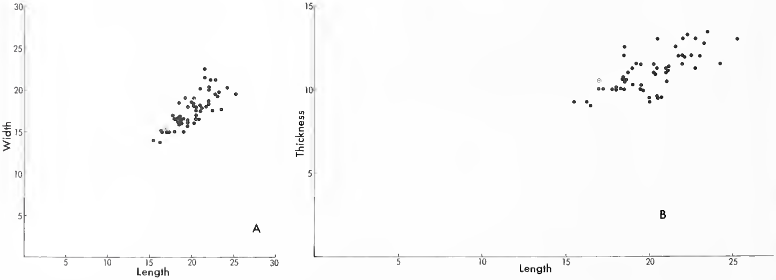
Plate 55, figs. 1–4; text-figs. 3–7

*1866	*Terebratula russillensis* de Loriol, p. 88, pl. E, figs. 12–15.
1867	*Terebratula russillensis* de Loriol, p. 393, pl. C, figs. 28–31.
1869	*Terebratula russillensis* de Loriol, p. 28, pl. 4, fig. 1.
v1872	*Terebratula russillensis* de Loriol; Pictet, p. 68, pl. 202, figs. 1–8.
v1872	*Terebratula latifrons* Pictet, p. 67, pl. 201, figs. 16–17.
?1964	*Sellithyris* (?)*russillensis* (de Loriol); Ager, p. 340.
non 1966	*Sellithyris russillensis* (de Loriol); Bogdanova and Lobacheva, p. 53, pl. 5, figs. 5–6.
v1968	*Loriolithyris russillensis* (de Loriol); Middlemiss, p. 176, pl. A, figs. 1–4.

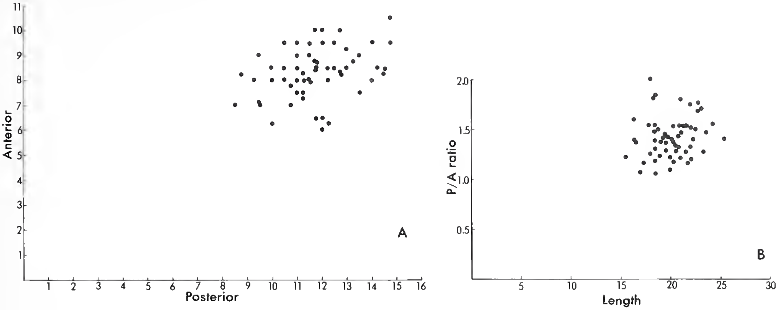
Lectotype. Muséum d'Histoire Naturelle, Geneva (Pictet Collection), no. CB 1520. Designated Middlemiss 1968. Fig. Pictet and de Loriol 1872, pl. 202, fig. 4; from the urgonian of La Russille, Vaud, Switzerland.

Material. Fifty-seven specimens from the Whitaker Collection. About fifty-five specimens in the Gentil Collection.

Remarks. Specimens from Morocco tend to be wider and thinner, in relation to length, than the typical members of the species from La Russille and Orgon and many have the characters of the form described by Pictet (1872) as *Terebratula latifrons*. I have previously (Middlemiss 1968*a*) believed the latter form to be a variety of *Loriolithyris russillensis* and experience of the Moroccan fauna has reinforced this belief. Forms from the Jura region which Pictet recognized as *T. latifrons* (Geneva Museum) are distinct because of their decidedly small umbones and foramina, not because of their wide depressed shape. They usually display well-developed *russillensis*-like folding of the shell and as regards shape there seems to be a complete gradation between the two species. In both south-west France and south-west Morocco forms apparently referable to *L. russillensis* show continuous variation, in the same assemblages, into other forms with the same characters except for the proportions of shell shape, which are those of *T. latifrons*. The forms with decidedly small umbones and foramina do not occur in these regions. The internal skeletal arrangements revealed by serial sectioning are the same in all these forms: the concave piped hinge plates, situated close to the floor of the brachial valve, and the sigmoid passage from inner socket ridge to hinge plate, are unmistakeable. Pictet records his typical *T. latifrons* forms only from the Upper Valanginian of Villers-le-Lac and Vesency. *L. russillensis* was apparently a species-group very variable in proportions of length, width, and thickness, some members of which, in part of the Jura region and for a short time in the Upper Valanginian, became locally sufficiently differentiated to deserve recognition as a subspecies '*latifrons*'.

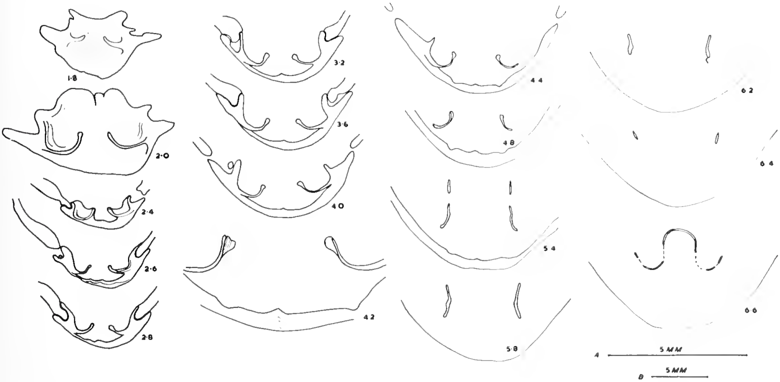


TEXT-FIG. 3. Scatter diagrams of relationships of width to length and thickness to length in *Loriolithyris russillensis* from the Whitaker Collection.



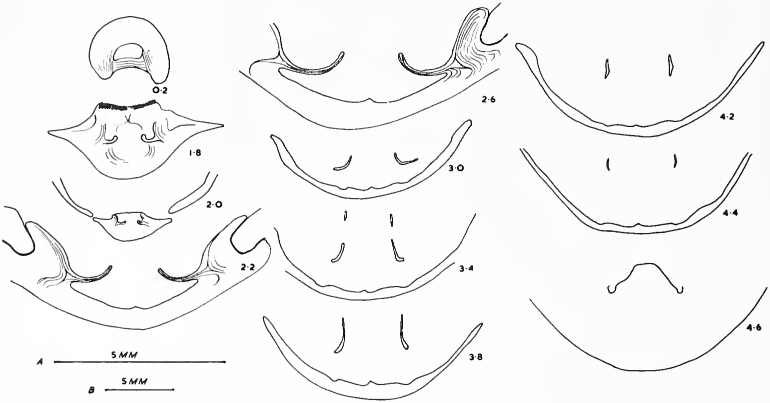
TEXT-FIG. 4. Scatter diagrams of the posterior/anterior ratio in *Loriolithyris russillensis* from the Whitaker Coll.

The main differences between this species and *L. valdensis* are that *L. valdensis* is longer is relation to both width and thickness and has a higher P/A ratio than *L. russillensis*. These points are graphically illustrated, as far as the Moroccan specimens are concerned, in text-figs. 3, 4, 8, 9, and 10. Internally, a point of distinction is that in *L. russillensis* the hinge plates are close to, or even in part in contact with, the floor of the brachial valve, whereas in *L. valdensis* they are raised clearly above the floor of the valve for their whole width. It can be added that, internally, *L. russillensis* has a very short loop, little more than 1 mm from the crural processes to the transverse band in adult shells. Unfortunately it is characteristic of species of *Loriolithyris* that the transverse band is delicate and seldom preserved and I have never yet seen this structure in *L. valdensis*.



TEXT-FIG. 5. Transverse sections through a small, strongly folded specimen of *Loriolithyris russillensis*. Sections 1.8 and 2.0 are enlarged in order to show the shape of the juvenile hinge plates enclosed within the cardinal process (punctate tissue is stippled in section 1.8). Section 4.2 is enlarged in order to show the structure of the piped hinge plates. BM BB 76544, Whitaker Coll. A—scale for sections, 1.8, 2.0 and 4.2. B—scale for the remaining sections.

Distribution. Ager (1964) claims this species in the Berriasian of the southern Jura and Pictet (1872) notes it in the Valanginian of Sainte-Croix (Vaud). It certainly occurs in the Hauterivian of Vaud, Doubs, Haute-Marne, and Yonne and of Les Corbières (Aude). It is at its most abundant, however, in the Barremian of Vaud, Jura, the south-east Paris Basin, Bouches-du-Rhône, Gard, Aude, eastern Spain, and Ibiza. It occurs very rarely in the Aptian of Aude. In south-west Morocco it ranges from the Hauterivian to Aptian inclusive.



TEXT-FIG. 6. Transverse sections through a small, strongly folded specimen of *Loriolithyris russillensis* to show the short loop. Section 1.8 is enlarged in order to show the shape of the juvenile hinge plates enclosed in the cardinal process. Sections 2.2 and 2.6 are enlarged in order to show the primary hinge plates (stippled). The maximum height of the crural processes is seen in section 3.4. BM BB 76543, Whitaker Coll. A—scale for sections 1.8, 2.2, and 2.6. B—scale for the remaining sections.

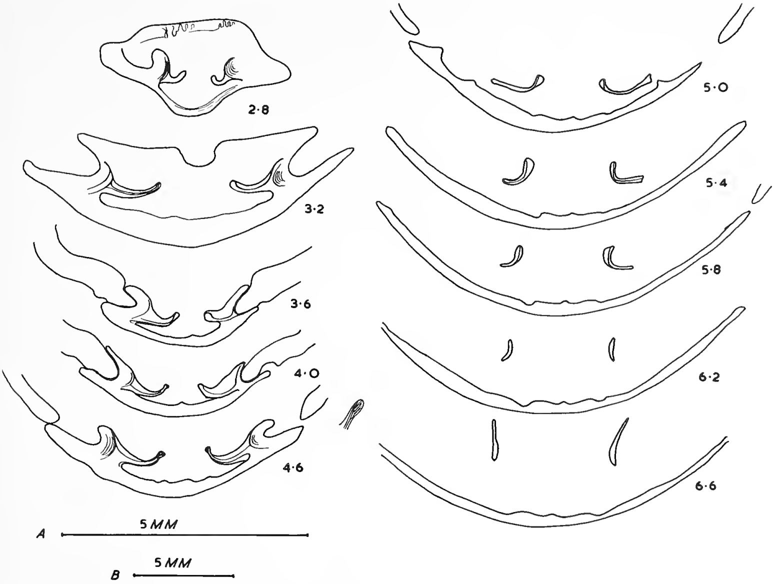
Loriolithyris valdensis (de Loriol)

Plate 55, figs. 5–9; text-figs. 8–11

v*1868 *Terebratula valdensis* de Loriol, p. 52, pl. 4, figs. 9–12.
v1872 *Terebratula valdensis* de Loriol; Pictet, p. 66, pl. 201, figs. 11–15.
non 1939 *Terebratula valdensis* var. *kentugajensis* Moisseev, p. 200, pl. 2, fig. 6.
1960 '*Terebratula*' *valdensis* de Loriol; Smirnova, p. 374, pl. 1, fig. 1.
pars 1966 *Sellithyris valdensis* (de Loriol); Bogdanova and Lobacheva, p. 55, pl. 5, fig. 7 (*non* pl. 7, fig. 11).
v1968 *Loriolithyris valdensis* (de Loriol); Middlemiss, p. 182, pl. A, fig. 5.
1972 *Sellithyris valdensis* (de Loriol); Smirnova, p. 81, pl. 7, fig. 5.
v1975 *Loriolithyris valdensis* (de Loriol); Dieni and Middlemiss, p. 182, pl. 36, figs. 9–10.

Lectotype. Muséum d'Histoire Naturelle, Geneva (Arzier Collection), no. CB 1505. Designated Middlemiss 1968. Fig. de Loriol 1868, pl. 4, figs. 9*a–d*, from Bed B, Valanginian, Arzier Quarry, Vaud, Switzerland.

Material. Thirty-nine specimens in the Whitaker Collection. About 200 specimens in the Gentil Collection. Eight specimens from Barremian or Aptian, Tizi ou Elma, Agadir (D.V. Ager Collection).

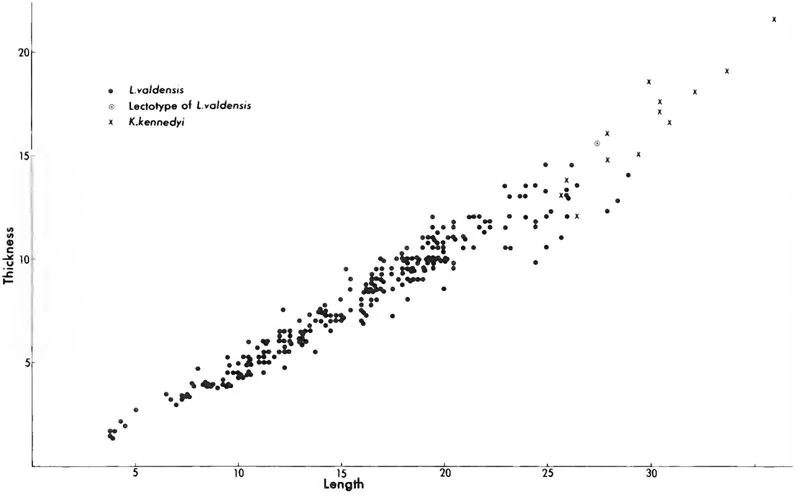


TEXT-FIG. 7. Transverse sections through a broad, *latifrons*-like specimen of *Loriolithyris russillensis*. Sections 2.8 and 3.2 are enlarged in order to show the shape of the juvenile hinge plates. The structure of the piped inner margin of the hinge plate is enlarged at section 4.6 (see plate 60, fig. 5). The transverse band was not preserved in this specimen. BM BB 76552, Whitaker Coll. A—scale for sections 2.8, 3.2, and 4.6 (inset). B—scale for the remaining sections.

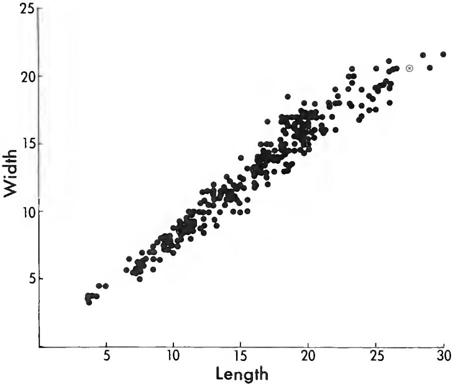
Description. Text-figs. 8 and 9 compare the thirty-nine specimens in the Whitaker Collection with a collection of 227 specimens made at the type locality of Arzier by Monsieur Roessinger and preserved at the Geneva Natural History Museum. The isometric development of length and width is well shown in text-fig. 9. Thickness in relation to length develops allometrically, although with a very small differential growth ratio (text-fig. 8). Text-fig. 10 shows that the P/A ratio develops allometrically with a very wide range of variation (about double the width of that shown by *Sellithyris sella* from the Isle of Wight Aptian (Middlemiss 1968*b*, fig. 9)). The smallest shells, less than 5 mm in length, are subcircular in ventral profile but posterior length increases allometrically with growth, at the expense of anterior length. There is a marked tendency for Moroccan specimens to have a lower P/A ratio, i.e. to have a relatively greater anterior length than those from the type area; in this respect the lectotype has an anomalous position.

The anterior commissure remains rectimarginate until the shell is about 12 mm in length. It then passes through a well-marked uniplicate stage until the shell reaches a length of about 16 mm, after which plicae and sinuses are rapidly developed, shells from 17 mm upwards being normally sulciplicate. The episulcate stage is occasionally seen at Arzier but is very rare in Morocco.

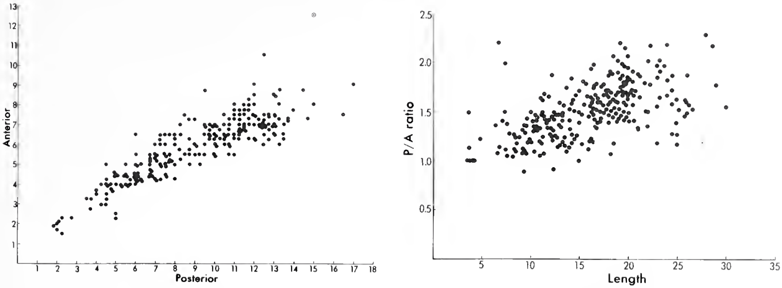
Remarks. Differences between this species and *L. russillensis* were discussed above. Roch remarks on the abundance of this species in the Valanginian and Barremian of south-west Morocco, especially in the Barremian of Jebel Graa and Aghbalou.



TEXT-FIG. 8. Scatter diagrams of the relationship of thickness to length in *Loriolithyris valdensis* (Arzier and Whitaker Colls.) and *Kutchithyris kennedyi* (all available specimens).

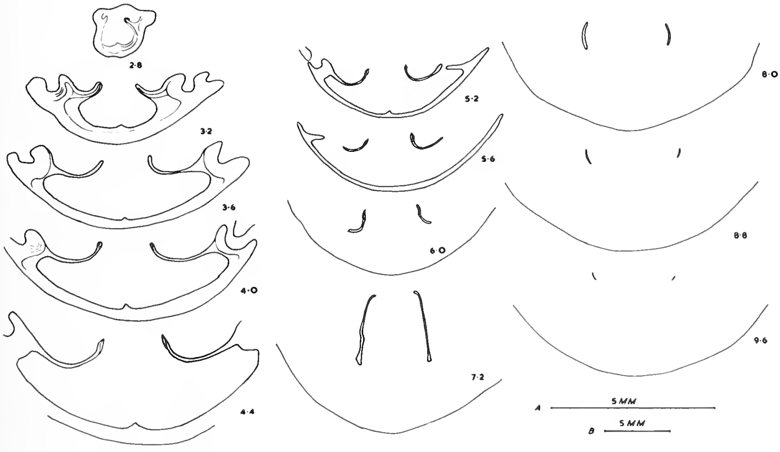


TEXT-FIG. 9. Scatter diagram of the relationship of width to length in *Loriolithyris valdensis* (Arzier and Whitaker Colls.).



TEXT-FIG. 10. Scatter diagrams of the posterior/anterior ratio in *Loriolithyris valdensis* from Arzier.

Distribution. Berriasian and Valanginian of Vaud and Haute-Savoie; Valanginian and Hauterivian of the south-east Paris Basin; Valanginian of Georgia and Hauterivian of the northern Caucasus (Smirnova 1972); Neocomian of the Kopet Daga (Bogdanova and Lobacheva 1966); Hauterivian of north-east Bulgaria. Valanginian and Hauterivian of eastern Spain; Barremian of Basses-Alpes and Alpes-Maritimes. Aptian of La Presta (Neuchâtel). In south-west Morocco the range is Valanginian to Aptian inclusive.



TEXT-FIG. 11. Transverse sections through *Loriolithyris valdensis*. Sections 2.8–4.4 are enlarged in order to show the shape of the juvenile hinge plates enclosed within the cardinal process and the structure of the crural bases within the piped inner margins of the hinge plates. Maximum development of the crural processes is seen in section 7.2. The transverse band was not preserved in this specimen. BM BB 76545, Whitaker Coll. A—scale for sections 2.8–4.4. B—scale for the remaining sections.

Loriolithyris melaitensis sp. nov.

Plate 55, figs. 10, 11; text-fig. 12

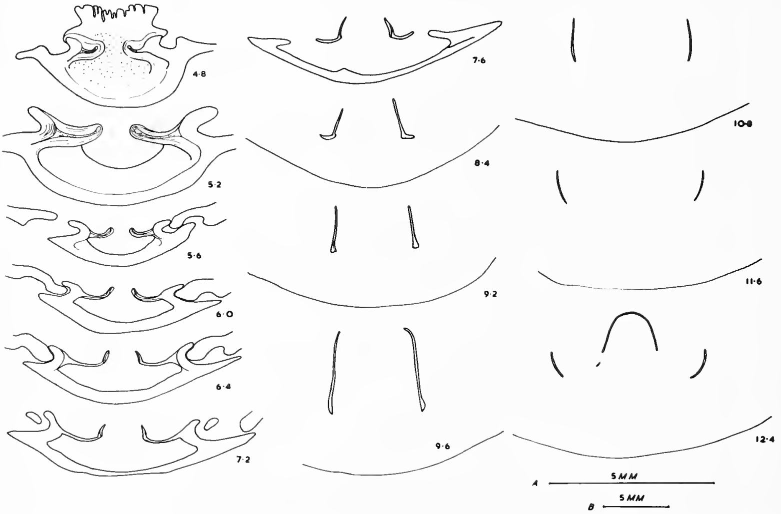
v1951 *Terebratula salevensis* de Loriol; Gigout, p. 360, pl. 9, figs. 15–18.

Types. Holotype, Gentil Collection specimen no. S.556/2, from the Barremian of Ait Ben Melait. Dimensions: L 31, W 28·5, T 18·5. Paratype, Gentil Collection specimen no. S.556/1 (locality as holotype).

Material. Ten specimens in the Gentil Collection; nine from the Hauterivian of Tizi Ouarioum, one from the Barremian of Ait Ben Melait, Ida ou Guelluill.

Diagnosis. Loriolithyris of elongate oval ventral profile, becoming thick in adult stage (thickness nearly equal to width); P/A ratio slightly more than 1. Valves equally convex. Umbo suberect. Foramen mesothyrid, attrite, slightly labiate. Beak ridges rounded. Symphytium very short, but visible. Lateral commissure strongly arched; anterior commissure sulciplicate. Shell not folded except at extreme anterior. Small pedicle collar present. Hinge plates concave, piped. Crural bases well developed. Crural processes slightly incurved. Transverse band high-arched, rounded.

Remarks. The thick, well-filled appearance of the shell, the arched lateral commissure, and the relative lack of folding give this species a superficial resemblance to *Tropeothyris salevensis* (de Loriol) and it is likely that Ambroggi's (1963) record of *T. salevensis* in both Lower and Upper Barremian of south-west Morocco refers to this species.



TEXT-FIG. 12. Transverse sections through *Loriolithyris melaitensis*. Section 4.8 is enlarged in order to show the shape of the juvenile hinge plates enclosed within the cardinal process and the boundary between punctate tissue (stippled) and impunctate laminated tissue. Section 5.2 is enlarged in order to show the primary hinge plates (stippled). The crural bases, unusually large for *Loriolithyris*, are well shown in sections 6.4–7.6. Section 9.6 shows the maximum development of the crural processes. S.556/1, Gentil Coll., Hauterivian, Tizi Ouarioum. A—scale for sections 4.8 and 5.2. B—scale for the remaining sections.

It is distinguished from other species of *Loriolithyris* especially by the unusually large size of the crural bases attached to the inner edges of the hinge plates (text-fig. 12), but also by its external appearance.

Distribution. Hauterivian and Barremian of south-west Morocco.

Loriolithyris marocensis sp. nov.

Plate 56, figs. 1, 2; text-fig. 13

Types. Holotype, Gentil Collection specimen no. S.547/2; age given as Upper Hauterivian (locality unknown). Dimensions: L 49·75, W 32, T 26·25. Paratype, Gentil Collection specimen no. S.547/1.

Material. Sixteen specimens in the Gentil Collection: four from the Hauterivian (including Oued Tidzi), two from the Barremian, Chaine d'Azour, ten from the Barremian of Oued Aghbalou.

Diagnosis. Elongate *Loriolithyris*, attaining large size; P/A ratio slightly more than 1. Valves equally convex. Umbo erect. Foramen mesothyrid, labiate. Beak ridges rounded. Symphytium hidden in adult stage. Lateral commissure very strongly arched. Anterior commissure sulciplicate with shallow median sinus, rarely episulcate. Shell folded only at extreme anterior, marked by strong concentric growth ridges. Small pedicle collar present.

TEXT-FIG. 13. Transverse sections through *Loriolithyris marocensis*. Sections 5.6 and 6.0 are enlarged in order to show the detailed structure of the cardinal process, with juvenile primary hinge plates (fine stipple) surrounded by laminated thickening and the body of the cardinal process infilled with punctate skeletal tissue (coarse stipple). Section 6.4 is enlarged to show the primary hinge plates (stippled). Maximum development of the crural processes is seen in section 11.2. Note the height of the transverse band above the floor of the valve in section 14.4. S.547/1, Gentil Coll., Hauterivian, locality unknown. A—scale for sections 5.6, 6.0, and 6.4. B—scale for the remaining sections.

Hinge plates initially concave, becoming rounded L-shaped, piped. Cardinal process extends along the hinge plates, leaving small dorsal umbonal cavity. Transverse band high-arched, with somewhat pointed crest, high above floor of valve.

Remarks. As all the specimens available are fully adult or gerontic little can be said about the ontogeny, except that biplication of the anterior commissure and folding of the shell appear to develop very late. *L. marocensis* differs from most species of the genus in the large size attained when adult and the massive, little-folded form of the shell; in those respects it is nearest to *L. melaitensis* but differs markedly from that species in its internal structures: *L. melaitensis* is distinguished by the large size of its crural bases whereas in *L. marocensis* the crural bases are small and enclosed within the piped edge of the hinge plate as usual in *Loriolithyris*. *L. marocensis* is also distinct from other species of the genus in the L-shape developed by the hinge plates as seen in transverse section (text-fig. 13). Another Moroccan Lower Cretaceous species which closely resembles *L. marocensis* is *Cyrtothyris middlemissi*; the latter is broader in relation to length, and has a less erect umbo, and lacks the loriolithyrid boldly arched lateral commissure of *L. marocensis*, besides the internal differences.

Distribution. Hauterivian and Barremian of south-west Morocco.

Genus BOUBEITHYRIS Cox and Middlemiss, 1978

Type species. *Terebratula boubei* d'Archiac, 1847.

Species included. *T. boubei* d'Arch. *Boubeithyris buzzardensis* Cox and Middlemiss, *B. tibourrensis* nov., *B. pleta* nov. Range: Hauterivian?, Barremian to Cenomanian.

Boubeithyris tibourrensis sp. nov.

Plate 56, figs. 3, 4; text-fig. 14

Types. Holotype, Gentil Collection specimen no. S.548/2/1, from Butte de Tibourr'm; labelled Aptian (more likely Barremian). Dimensions: L 20·5, W 16·25, T 12·5. Paratype, Gentil Collection specimen no. S.552/3/1, Barremian, Tibourr'm.

Material. Two specimens in the Gentil Collection from Butte de Tibourr'm, one labelled Aptian, the other Barremian.

Diagnosis. *Boubeithyris* regularly oval as seen in ventral profile, apart from short straight anterior (between the lateral plicae). Valves equally convex. P/A ratio slightly greater than 1. Umbo suberect; beak ridges moderately well defined. Foramen mesothyrid, marginate, slightly telate. Lateral commissure arched. Anterior commissure sulciplicate; lateral plicae close together; median sinus narrow. Plication reflected by small folds and sulci in extreme anterior part of brachial valve only. Hinge plates thin, concave, piped to strongly corniced. Inner socket

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EXPLANATION OF PLATE 56

Figs. 1, 2. *Loriolithyris marocensis* sp. nov. 1*a–d*, holotype, S.547/2 Gentil Coll., Upper Hauterivian, loc. unknown. 2*a–c*, plaster cast of specimen sectioned (see text-fig. 13), S.547/1, Gentil Coll., Upper Hauterivian, loc. unknown.

Figs. 3, 4. *Boubeithyris tibourrensis* sp. nov. 3*a–d*, holotype, S.548/2/1, Gentil Coll., Barremian or Aptian, Butte de Tibourr'm. 4*a–c*, plaster cast of specimen sectioned (see text-fig. 14), S.522/2/1, Gentil Coll., Barremian, Tibourr'm.

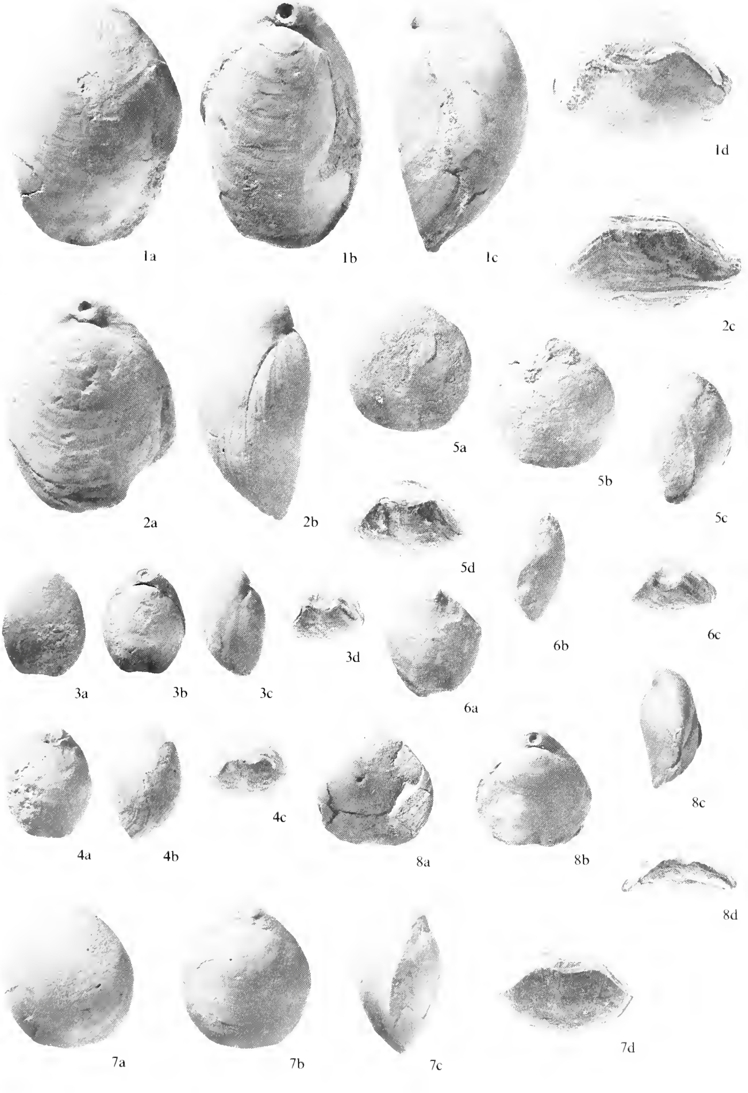
Figs. 5, 6. *Boubeithyris pleta* sp. nov. 5*a–d*, holotype, S.553/3, Gentil Coll., Barremian, Sidi Bou Rjaa. 6*a–c*, plaster cast of specimen sectioned (see text-fig. 15), S.553/1, Gentil Coll., Barremian, Sidi Bou Rjaa.

Fig. 7*a–d*. *Boubeithyris pleta* sp. nov. Large typical specimen, S.557/6, Gentil Coll., Barremian, Igueni Ouram.

Fig. 8. *Paraboubeithyris plicae* gen. et sp. nov. 8*a–d*, holotype, S.548/1/3, Gentil Coll., Barremian, Vallee Asif Ait Ameur.

All natural size.

PLATE 56


1a 1b 1c 1d

2a 2b 2c

3a 3b 3c 3d

4a 4b 4c

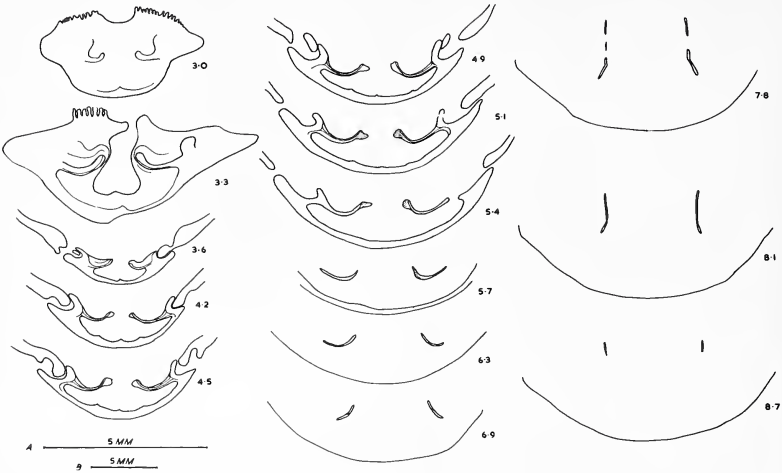
5a 5b 5c 5d

6a 6b 6c

7a 7b 7c 7d

8a 8b 8c 8d

MIDDLEMISS, Cretaceous Terebratulidae



TEXT-FIG. 14. Transverse sections through *Boubeithyris tibourrensis*. Sections 3.0 and 3.3 are enlarged to show the initial shape of the juvenile hinge plates within the cardinal process. Cornicing of the hinge plates is best seen in sections 4.2–5.4. Section 7.8 shows the maximum development of the crural processes. The transverse band was not preserved in this specimen. S.552/2/1, Gentil Coll., Barremian, Tibourr’m. A—scale for sections 3.0 and 3.3 B—scale for the remaining sections.

ridges narrow. Accessory articulation slightly developed. Euseptoidum short, confined to posterior part of hinge plates, flanked by lateral ridges.

Remarks. This species closely resembles the type species in general shape, the close-set lateral plicae being particularly characteristic of both species. *B. tibourrensis* differs from *B. boubei* in being more oval, less pentagonal, in ventral profile and somewhat more convex in lateral profile. Like *B. boubei*, it differs from *B. buzzardensis* in being narrower and thicker, having a higher P/A ratio and folding almost confined to the brachial valve. Internally the hinge plates are more deeply concave and the cornice-structure better developed than in either *B. boubei* or *B. buzzardensis*. A species of *Boubeithyris* which occurs in the Aptian of the Jura region, so far undescribed, differs from *B. tibourrensis* in being still more convex and in having a lateral commissure still more strongly arched, lateral plicae even closer together, and a longer symphytium. Although only two specimens are available, this species is important because it extends back to the Barremian the time-range of the typical oval form of *Boubeithyris*, which can thence be traced through the undescribed Aptian species from the Jura to *B. boubei* itself in the Albian and Cenomanian.

Distribution. Barremian of south-west Morocco.

Boubeithyris pleta sp. nov.

Plate 56, figs. 5–7; text-fig. 15

Types. Holotype, Gentil Collection specimen no. S.553/3, from the Barremian of Sidi Bou Rjaa, Oued Tidzi. Dimensions: L 25·5, W 23·75, T 15. Paratypes, Gentil Collection specimens S.553/1 (age and locality as holotype) and S.557/6, Barremian, Igueni Ouram.

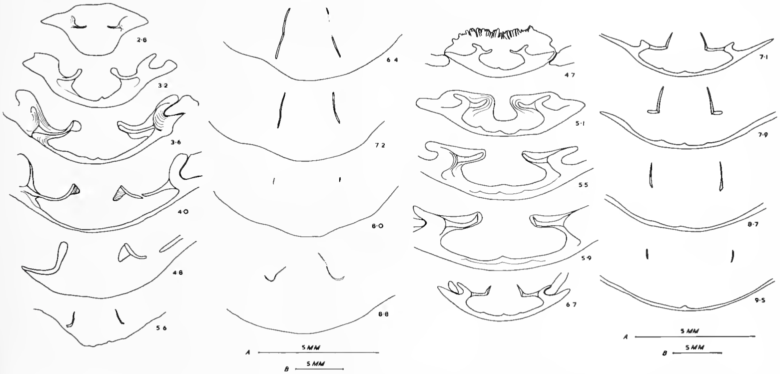
Material. Twenty-one specimens in the Gentil Collection.

Name. Latin *pleta*, 'filled', from the well-filled appearance of the shell.

Diagnosis. Boubeithyris almost as broad as long, with thickness less than two-thirds of width. Subcircular in ventral profile. Valves equally convex. P/A ratio about 1. Umbo short, suberect. Beak ridges rounded. Foramen mesothyrid, attrite. Lateral commissure arched. Anterior commissure sulciplicate; median sinus low. Shell little folded. Hinge plates concave, piped to strongly corniced. Euseptoidum short and weak. Transverse band moderately high.

Remarks. In external appearance this species could be taken for a sulciplicate species of *Sellithyris* but the extremely gentle folding imparts to the shell a tumid or 'well-filled' appearance which is distinctive; also the ventral profile is less pentagonal than in most species of *Sellithyris*, even *S. deningeri* which is a particularly rounded species of that genus. It differs from other species of *Boubeithyris* mainly in being relatively wide and flat in comparison with its length and in the wider spacing of the plicae of the anterior commissure.

Distribution. Hauterivian(?) and Barremian of south-west Morocco.



TEXT-FIG. 15. Transverse sections through *Boubeithyris pleta.* Sections 2.8–4.8 are enlarged to show details of the structure of the hinge plates and of the cornicing. Maximum height of the crural processes is seen in section 6.4. S.553/1, Gentil Coll., Barremian, Sidi Bou Rjaa. A—scale for sections 2.8–4.8. B—scale for the remaining sections.

Genus PARABOUBEITHYRIS gen. nov.

Type species. Paraboubeithyris plicae sp. nov.

Diagnosis. Ventral profile rounded pentagonal, as wide as, or wider than, long. Depressed. P/A ratio slightly more than 1. Umbo suberect to erect. Beak ridges rounded. Foramen mesothyrid, marginate, becoming labiate. Lateral commissure strongly arched. Anterior commissure deeply uniplicate, or sulciplicate with very small median sinus. Brachial valve has a strong median fold extending from the umbonal region to the anterior; corresponding to a deep, wide sulcus in the anterior half of the pedicle valve. Hinge plates concave, thin, sharply differentiated from the inner socket ridges; piped to strongly corniced. Transverse band high-arched. Euseptoidum weak, flanked by two low lateral ridges.

Paraboubeithyris plicae sp. nov.

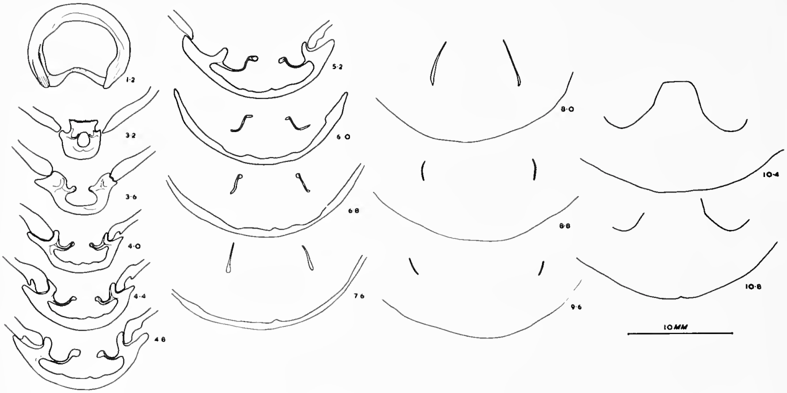
Plate 56, fig. 8; Plate 57, figs. 1–3; text-fig. 16

Types. Holotype, Gentil Collection specimen no. S.548/1/3, from the Barremian of the Vallée Asif Ait Ameur. Dimensions: L 22, W 22·5, T 10. Paratypes, Gentil Collection specimens S.546/1/1, S.546/1/2, and S.546/1/3; age given as Upper Hauterivian (locality unknown).

Name. Genitive of Latin *plica*, 'a fold'.

Material. Thirty-three specimens in the Gentil Collection, of which ten are from the Barremian of Vallée Asif Ait Ameur and twelve from the Barremian of Ida ou Tanan, the remainder being unlocated.

Description. This species has a deep and dramatic uniplication, especially in the more gerontic specimens. Some of the smaller specimens have a very small median sinus, so that the anterior commissure is strictly sulciplicate, but the sinus is always extremely small and usually *asymmetrically* placed. We lack juvenile representatives of the



TEXT-FIG. 16. Transverse sections through *Paraboubeithyris plicae*. Section 1.2 shows the pedicle collar (stippled). Section 3.2 shows a dorsal umbonal cavity. The corniced hinge plates are well seen in sections 4.8 and 5.2. S.546/1/1, Gentil Coll., Hauterivian, locality unknown.

EXPLANATION OF PLATE 57

Figs. 1–3. *Paraboubeithyris plicae* gen. et sp. nov. 1*a–c*, plaster cast of specimen sectioned (see text-fig. 16), S.546/1/1, Gentil Coll., Upper Hauterivian, loc. unknown. 2*a–d*, adult but uniplicate form, S.546/1/2, Gentil Coll., Upper Hauterivian, loc. unknown. 3*a–d*, elongate form showing incipient biplication, S.546/1/3, Gentil Coll., Upper Hauterivian, loc. unknown.

Fig. 4*a–c*. *Cyrtothyris middlemissi* (Calzada), plaster cast of specimen sectioned (see text-fig. 18), BM BB 76564, D.V. Ager Coll., Aptian, Ait Abaid, Agadir.

Figs. 5, 6. *Cyrtothyris middlemissi* (Calzada). 5*a–c*, plaster cast of specimen sectioned (see text-fig. 17), BM BB 76565, Calzada Coll., Aptian, La Roqueta, Spain. 6*a–c*, BM BB 76566, Calzada Coll., Albian, Peracals, Spain.

All natural size.

PLATE 57

MIDDLEMISS, Cretaceous Terebratulidae

species but specimens in the Gentil Collection indicate that the sinus appears late, following juvenile rectimarginate and uniplicate stages, when the shell has attained a length of about 15 mm, and is then lost again in the gerontic stage. Some individuals show no sign of biplication, however.

Remarks. This species is almost certainly the form that both Roch and Ambroggi identified as *Terebratula collinaria* d'Orbigny, which it resembles in general shape. The principal differences between these two species are (*a*) *T. collinaria* is always uniplicate, never biplicate; (*b*) the cardinal slopes of *T. collinaria* tend to be concave in dorsal profile, with a sharply produced umbo, those of *P. plicae* are convex, with an umbo which does not protrude beyond the curve of the cardinal slopes; (*c*) *T. collinaria* has relatively flat hinge plates with no trace of the corniced structure characteristic of *Paraboubeithyris*.

Distribution. Barremian of south-west Morocco.

Subfamily RECTITHYRIDINAE Muir-Wood, 1965
Genus CYRTOTHYRIS Middlemiss, 1959

Type species. Terebratula depressa var. *cyrta* Walker, 1868.

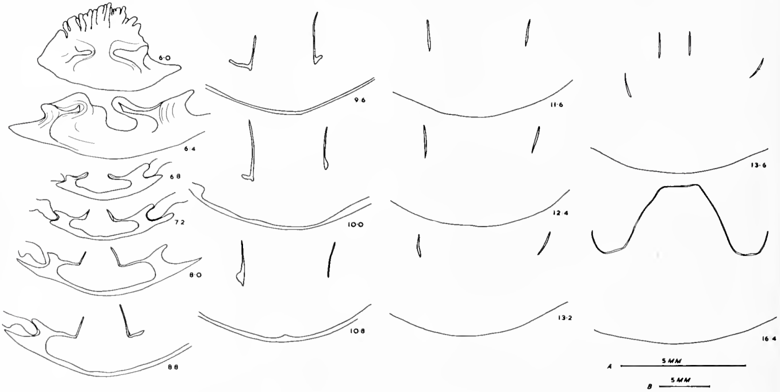
Species included. T. depressa var. *cyrta* Walker, *T. depressa* var. *uniplicata* Walker, *T. depressa* var. *cantabridgiensis* Walker, *T. seeleyi* Walker, *T. dallasi* Walker, *Cyrtothyris middlemissi* Calzada, *C. cyrta arminiae* Middlemiss, '*Cyrtothyris*' *maynci* Owen. Range: Valanginian to Albian.

Cyrtothyris middlemissi Calzada

Plate 57, figs. 4–6; text-figs. 17, 18

*1972 *Cyrtothyris middlemissi* Calzada, p. 66, fig. 1.

Holotype. Geological Museum of the Seminario de Barcelona, specimen no. 23.346, from the Aptian of La Roqueta, Garraf, Barcelona.



TEXT-FIG. 17. Transverse sections through *Cyrtothyris middlemissi.* Sections 6.0 and 6.4 are enlarged to show the initial horizontal cuneate shape of the hinge plates. BM BB 76565, Coll. S. Calzada, Aptian, La Roqueta, Spain. A – scale for sections 6.0 and 6.4. B—scale for the remaining sections.

TEXT-FIG. 18. Transverse sections through *Cyrtothyris middlemissi*. Maximum height of the crural processes is seen at 16.4. BM BB 76564, Coll. D. V. Ager, Aptian, Ait Abaid, Agadir, Morocco.

Material. Nineteen specimens in the Gentil Collection (seventeen from the Clansayesian of Sidi Bou Rjaa, one from the Clansayesian of Imi ou Tanant, one from the Aptian of Ait Moujjout). Three specimens from probable Aptian, Ait Abaid, north-east of Agadir (Ager Collection). Also nineteen other specimens: three from the Aptian of La Roqueta (Calzada Collection); four from the Upper Aptian, Plan de Coloubret, Taura, Aude (Charrière Collection); six from the Aptian of Combe Longue, Taura, Aude; two from the Albian of Peracals, Lerida, Spain (Calzada Collection); four from the Albian of Pic du Seigneur, Tuchan, Aude (Debuyser Collection).

Original diagnosis (after Calzada 1972). Large forms (maximum L 53, W 36, T 24; L/W ratio 1·1–1·6; L/T ratio 1·7–2·1) of subpentagonal to oval ventral profile. Maximum width and thickness in middle of length. Valves convex, pedicle valve much more so than brachial valve. Valves may show folding (but this character is very variable). Lateral commissure inclined ventralwards at about 20° and arched. Anterior commissure uniplicate to slightly sulciplicate. Umbo wide, massive, suberect to erect. Foramen wide, labiate, circular, mesothyrid. Interareas somewhat concave; beak ridges moderately rounded. Deltidial plates small but visible, fused into a symphytium. Growth lines visible. Hinge plates concave, somewhat clubbed, becoming anteriorly persistently virgate or even V-shaped. Angle between the crural bases and the crural rami 70°–100°. Loop strongly recurved in a posterior direction so that no one serial section includes the whole of the arch of the transverse band.

Remarks. Specimens from Morocco and from the Albian of north-east Spain exceed Calzada's stated maximum width (up to 43 mm); nevertheless all specimens available fall into the range of L/W ratios given in his diagnosis. On the other hand specimens from both areas, and including the type locality, fall outside the range of L/T ratios given (extremes are specimen MDA 2/1, from Morocco, 1·57 and CaP2, from the Albian of Peracals, 2·12). Calzada understates the plication of the anterior commissure, which is normally gently sulciplicate in the adult stage. The foramen should be described as strongly marginate, labiate in the adult stage. The wide triangular shape of the loop and the strong recurvature of the transverse band are generic features in *Cyrtothyris* (Middlemiss 1976).

Distribution. Aptian of Aude and north-eastern Spain; Aptian (including Clansayesian) of south-western Morocco; Albian of Aude and north-eastern Spain.

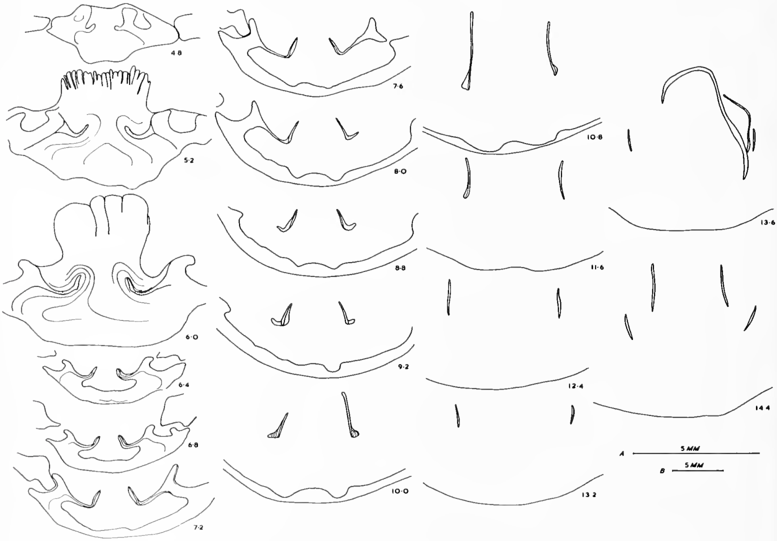
Subfamily uncertain

Genus KUTCHITHYRIS Buckman, 1918

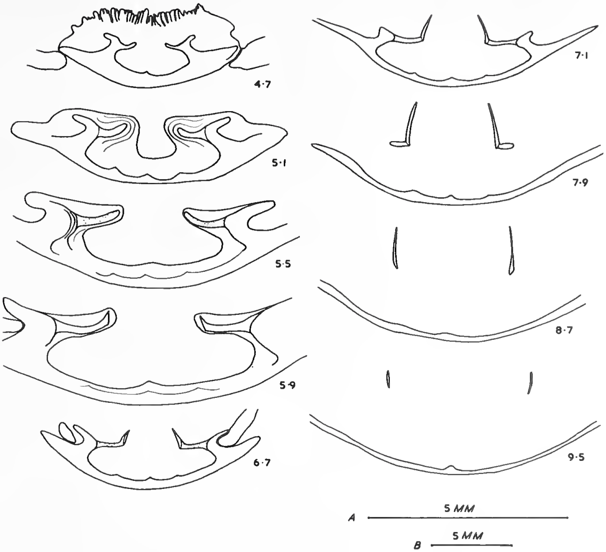
Type species. *Terebratula acutiplicata* Kitchin, 1900.

Original definition (Buckman 1918). 'Permesothyrid (beak stout, broad, quite short, thickened with callus, obliquely truncate, foramen large, circular, attrite, close to umbo, symphytium very short); morphogeny, biconvex to strongly sulciplicate; muscle-tracks obliterated posteriorly, not reaching far down valves, rather sharply divergent, starting not from the umbo but from about midway of the posterior half of the shell, showing little more than scars; dorsal septum feeble—ovarian areas large, mammillate on cast. The muscle scars posteriorly obliterated and diverging from a point well removed from the umbo, the short beak with little exposure of symphytium: these characters at once distinguish the genus.'

Diagnosis. Umbo suberect to incurved. Foramen mesothyrid to epithyrid; may be slightly labiate. Development of anterior commissure uniplicate to sulciplicate, more rarely to episulcate. Hinge plates wide, concave, flattening anteriorly, very little differentiated from the laterally deflected inner socket ridges. Crural bases low where attached to hinge plates, rapidly elongating anteriorly and passing into high, thin, slightly flanged crural



TEXT-FIG. 19. Transverse sections through *Kutchithyris acutiplicata* (type species of the genus). Sections 4.8–6.0 are enlarged in order to show details of the structure of the cardinal process. The crural bases first appear at 6.0. The transverse band at 13.6 is broken and partially displaced. BM 52420, Putchum Group (Upper Jurassic), Jumara, Kutch, India. A—scale for sections 4.8–6.0. B—scale for the remaining sections.

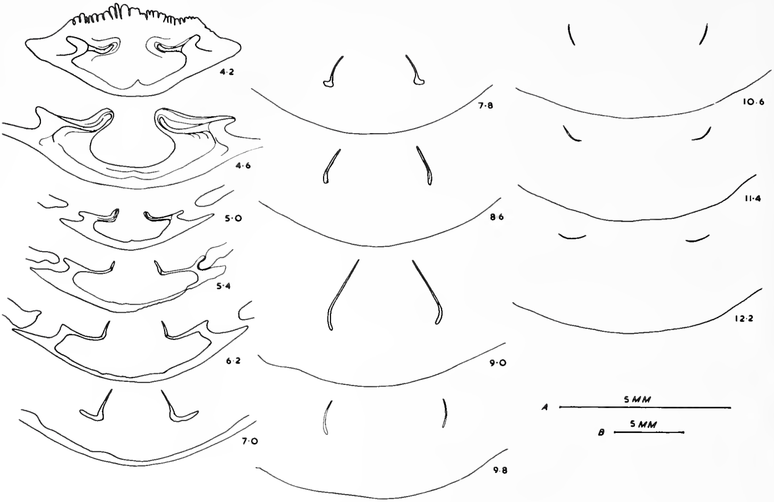


TEXT-FIG. 20. Transverse sections through *Kutchithyris subsella*. Sections 4.7–5.9 are enlarged to show the initial shape of the hinge plates at 4.7 and 5.1, the primary hinge plates (stippled) at 5.5, and the first appearance of the crural bases at 5.9. Maximum height of the crural processes is seen at 7.9. The transverse band was not preserved in this specimen. BM BB 76555, Kimeridgian, Le Havre, France. A—scale for sections 4.7–5.9. B—scale for the remaining sections.

processes. Hinge plates and crural processes usually clubbed. Descending lamellae thin. Transverse band high-arched, ogival. Euseptoidum present but usually weak; may be bounded by two low euseptoidum-like ridges bounding the adductor impressions.

Remarks. The species here ascribed to this genus differ one from another considerably in external proportions, from the highly convex globular form of *Kutchithyris brivesi*, through the pentagonal ventral profile of *K. acutiplicata* and *K. subsella* to the elongate form of *K. kennedyi*. They are linked, however, by close similarity in the internal characters, especially those of the hinge plates, inner socket ridges, and crural bases. Buckman erected the genus *Kutchithyris* mainly to accommodate six species from the Bathonian and Callovian of India previously established by Kitchin but he also included two European species of Deslongchamps and two newly established species of his own from the English Great Oolite (Bathonian) of Bradford-on-Avon, *K. fulva* and *K. egregia*.

I here refer to *Kutchithyris* the species *T. subsella* Leymerie, a familiar Upper Jurassic species in Europe, which has been previously referred to *Sellithyris* by Barczyk (1969). I exclude it from *Sellithyris* mainly because of the lack of differentiation between hinge plates and inner socket ridges, the detailed form of the hinge plates (as seen in transverse section they are like hockey sticks), and the form of the crural processes; these are features which it shares with other species of *Kutchithyris*. *K. subsella* survived into the Lower Cretaceous and occurs in the Upper Valanginian of La Querola



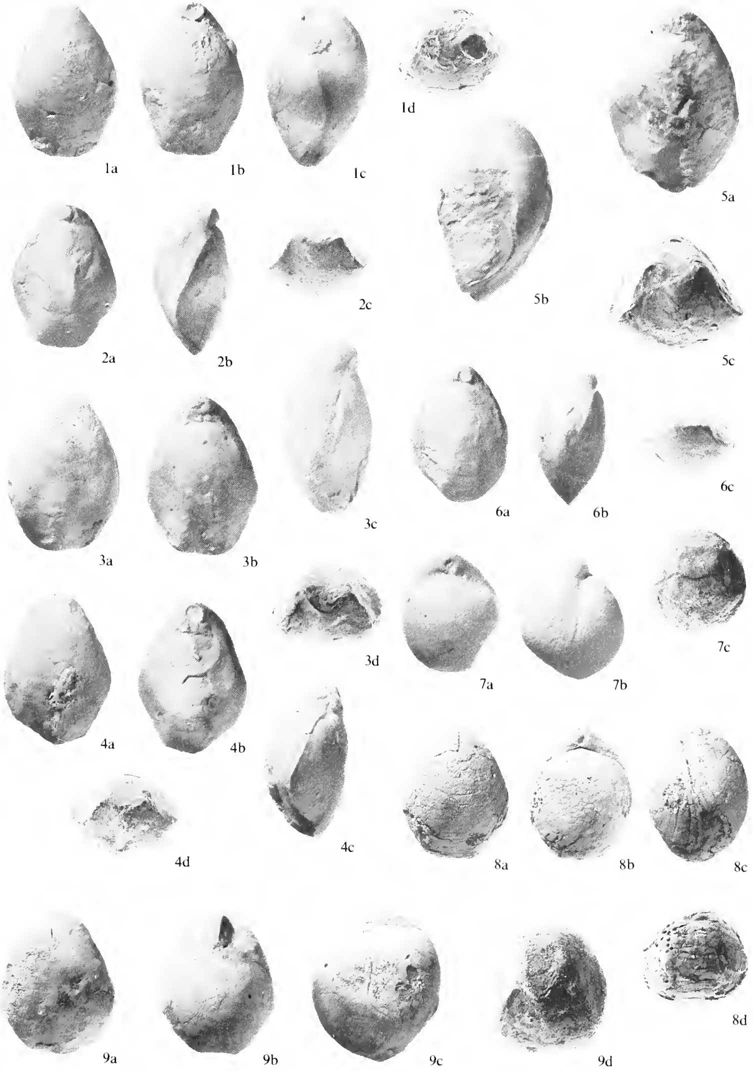
TEXT-FIG. 21. Transverse sections through *Kutchithyris subsella*. Sections 4.2 and 4.6 are enlarged to show detail of the primary hinge plates. The crural bases are first seen at 5.0. The crural processes are at their maximum height at 9.0. The transverse band was not preserved in this specimen. BM BB 76558, Coll. M. Durand Delga, Niveau 14A, Valanginian, La Querola, Spain. A—scale for sections 4.2 and 4.6. B—scale for the remaining sections.

EXPLANATION OF PLATE 58

Figs. 1–6. *Kutchithyris kennedyi* sp. nov. 1*a–d*, holotype, BM BB 76556, Y. Champetier Coll., Hauterivian or Barremian, Oliva, Valencia, Spain. 2*a–c*, plaster cast of specimen sectioned (see text-fig. 23), BM BB 76557, Y. Champetier Coll., Hauterivian or Barremian, Oliva, Valencia, Spain. 3*a–d*, BM BB 76559, Durand Delga Coll., Valanginian, La Querola, Alicante, Spain. 4*a–c*, typical specimen, BM BB 76562, W. J. Kennedy Coll., Lower Barremian, Les Moulins, Mont Chauve, Nice, France. 5*a–c*, large adult specimen, plaster cast of specimen sectioned (see text-fig. 24), BM BB 76561, Y. Rangheard Coll., ?Hauterivian, Punta Torreta, Ibiza. 6*a–c*, plaster cast of specimen sectioned (see text-fig. 22), S.552/1/1, Gentil Coll., Hauterivian, Ifrech-Oued-Igouzoulen.

Figs. 7–9. *Kutchithyris brivesi* (Roch). 7*a–c*, plaster cast of specimen sectioned (see text-fig. 26), S.549/2, Gentil Coll., Hauterivian, Ifrech-Oued-Igouzoulen. 8*a–d*, uniplicate specimen, S.549/3, Gentil Coll., Hauterivian, Ifrech-Oued-Igouzoulen. 9*a–d*, gerontic episulcate specimen, S.549/4, Gentil Coll., Hauterivian, Ifrech-Oued-Igouzoulen.

All natural size.



MIDDLEMISS, Cretaceous Terebratulidae

north of Alcoy, Alicante, Spain (Durand Delga Collection). The other Cretaceous species of the genus, which are described here, are new.

Species included. Bathonian: *T. hypsogonia* Kitchin, *T. acutiplicata* Kitchin, *T. propinqua* Kitchin, *T. circumdata* Deslongchamps, ?*K. fulva* Buckman, ?*K. egregia* Buckman. Callovian: *T. aurata* Kitchin, *T. jooraensis* Kitchin, ?*T. longicarinata* Kitchin, *T. subcanaliculata* Deslongchamps. Oxfordian to Valanginian: *T. subsella* Leymerie. Valanginian to Barremian: *K. kennedyi* nov., *K. brivesi* (Roch).

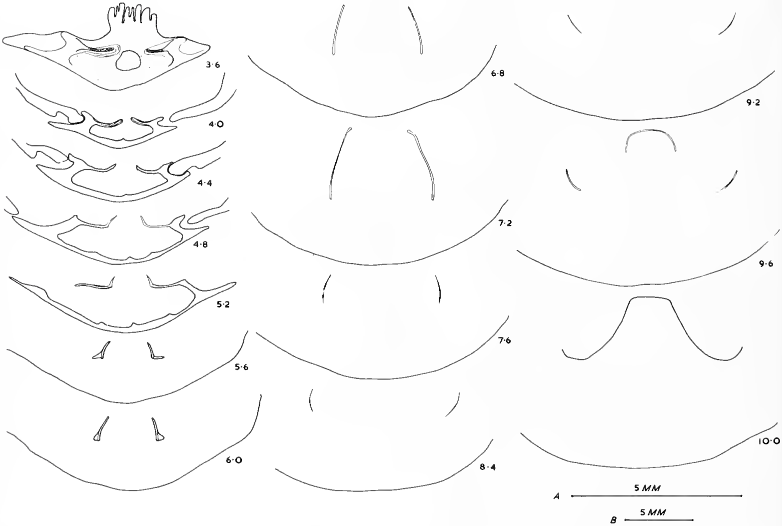
Range of the genus. Bathonian to Barremian.

Kutchithyris kennedyi sp. nov.

Plate 58, figs. 1–6; text-figs. 22–24

Types. Holotype, BM BB 76556, from Oliva, Valencia, Spain (Champetier Collection). The horizon is dubious but is probably Hauterivian or Barremian. Dimensions: L 30, W 20, T 18·5. Paratypes. BM BB 76557, Oliva, Valencia, Spain; BM BB 76559, Upper Valanginian, La Querola, Alicante, Spain; BM BB 76561, Punta Torreta, Ibiza; BM BB 76562 and 76563, Lower Barremian, Mont Chauve, Alpes Maritimes, France; Gentil Collection S.552/1/1, Hauterivian, Ifrech Oued Igouzoulen, Morocco.

Material. Three specimens from Oliva, Valencia, Spain (Champetier Collection, horizon uncertain). Five specimens from niveau 14A at La Querola, north of Alcoy, Alicante, Spain (Busnardo and Durand Delga 1960)



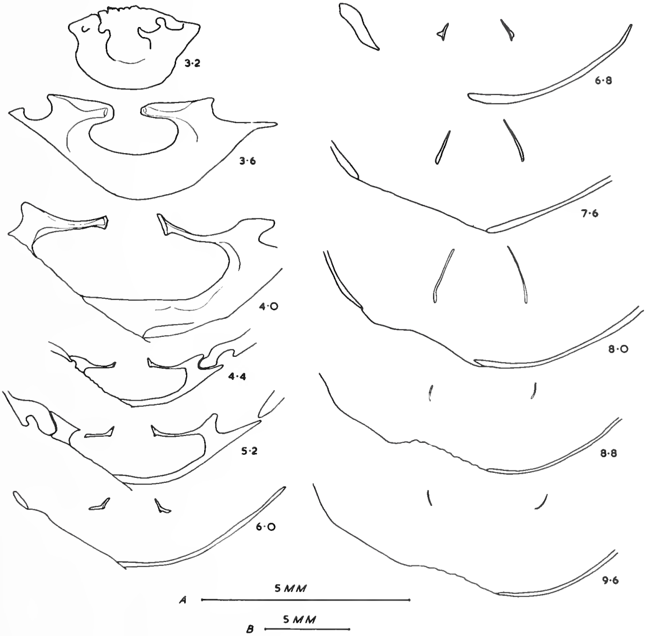
TEXT-FIG. 22. Transverse sections through *Kutchithyris kennedyi*. Section 3.6 is enlarged to show the juvenile primary hinge plates within the cardinal process. The crural bases are first seen at 4.4 and maximum development of the crural processes at 7.2. Sections 3.6–6.0 S.552/1/1; sections 6.8–10.0 S.552/1/2. Both specimens Gentil Coll., Hauterivian, Ifrech-Oued-Igouzoulen. A—scale for section 3.6. B—scale for the remaining sections.

(Durand Delga Collection, probably Valanginian). Two specimens from the Lower Barremian of a stream section 800 m north of Les Moulins, east of Mont Chauve, north of Nice, Alpes Maritimes (Kennedy Collection). One specimen from Ecru, Morocco (Whitaker Collection). One specimen from Punta Torreta, Ibiza (Rangheard Collection, probably Hauterivian). Four specimens in the Gentil Collection (three from the Hauterivian of Ifrech Oued Igouzoulen, one from the Barremian of Asif Ait Ameur).

Name. Named after Dr. W. J. Kennedy, who supplied some of the specimens.

Diagnosis. *Kutchithyris* of elongate oval ventral profile (width about 0·7 length); thickness more than half length. P/A ratio 1·3–1·6. Umbo suberect to erect in adults. Symphytium very short or invisible. Foramen mesothyrid, labiate. Beak ridges rounded. Anterior commissure sulciplicate to episulcate. Folding of the shell, corresponding to the plicae and sinuses of the commissure, weak and confined to the anterior third of the shell except in gerontic stage.

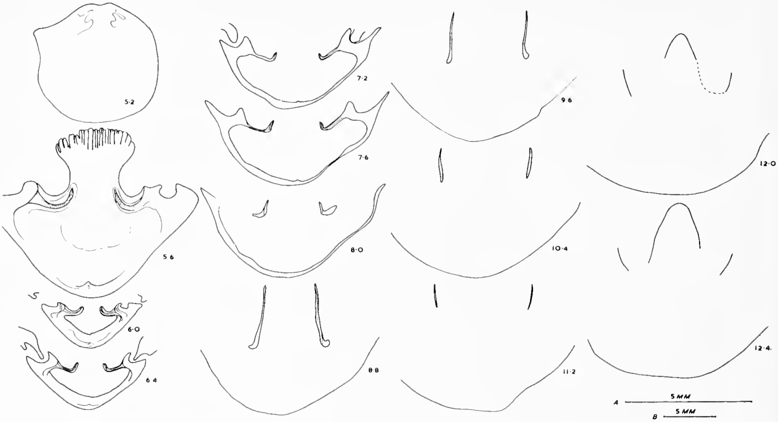
Description. Because of the few specimens available little can be said about the ontogeny of this species except that the width/length ratio appears to be isometric and to remain constant during growth at a little less than 0·7, whereas the thickness/length ratio is allometric.



TEXT-FIG. 23. Transverse sections through *Kutchithyris kennedyi*. Sections 3.2–4.0 are enlarged in order to show the juvenile hinge plates within the cardinal process (at 3.2) and the crural bases (at 3.6 and 4.0). Maximum height of the crural processes is seen at 8.0. The transverse band was not preserved in this specimen. BM BB 76557, Coll. Y. Champetier, Oliva, Spain. A—scale for sections 3.2–4.0. B—scale for the remaining sections.

Remarks. This species is easily distinguished from other members of *Kutchithyris* by its elongate form. The species with which it is most likely to be confused is *Loriolithyris valdensis*. *K. kennedyi* is thicker in relation to its length than *L. valdensis*, because the differential growth ratio of this character is slightly bigger, giving the allometric distribution a slightly steeper slope (fig. 8). In addition, the brachial valve of *K. kennedyi* is slightly concave in anterior third, that of *L. valdensis* uniformly convex in lateral view. Internally the characters of the hinge plates, inner socket ridges, and crural bases are all quite different in the two species.

Distribution. ?Valanginian of south-east Spain; Hauterivian and Barremian of south-west Morocco; ?Hauterivian of Ibiza; Lower Barremian of south-east France.



TEXT-FIG. 24. Transverse sections through a large, adult specimen of *Kutchithyris kennedyi*. Sections 5.2 and 5.6 are enlarged to show the juvenile hinge plates (at 5.2) and the primary hinge plates (stippled at 5.6). The crural bases are already visible at 5.6. BM BB 76561, Coll. Y. Rangheard, Punta Torreta, Ibiza. A—scale for sections 5.2 and 5.6. B—scale for the remaining sections.

Kutchithyris brivesi (Roch)

Plate 59, figs. 1, 2; text-figs. 25, 26

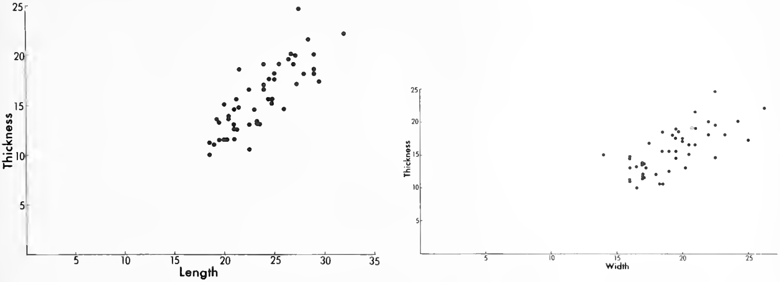
v*1930 *Terebratula brivesi* Roch, p. 259, pl. 22, figs. 12–13.
v1951 *Terebratula brivesi* Roch; Gigout, p. 361, pl. 9, figs. 27–34.

Lectotype. Roch figured two specimens but there is confusion in the numbering of the figures; figs. 12*a* and 13*b* represent one specimen, figs. 12*b* and 13*a* the other. The specimen represented by figs. 12*a* and 13*b* is here chosen as lectotype. It is in the collection of the Service de la Carte Géologique du Maroc at Rabat, bearing the number Ci 55, and is from the Valanginian of Zauouia Embarek des Ida ou Troumma. The label describes it as 'Coll. E. Roch' but Roch in his caption gives it as 'Brives Coll.'.

Paratypes. The specimen figured by Roch as figs. 12*b* and 13*a* (at Rabat, bearing the same number as the lectotype and from the same horizon and locality). A specimen in the Roch Collection at Rabat bearing number P 62 and coming from the Berriasian of Dar Caid Tigzirin. Six specimens in the Roch Collection at Rabat bearing the number P 50 and coming from the Valanginian of Oued Igoulouzen. The following specimens in the Gentil Collection: S.549/1, S.549/2, S.549/3, S.549/4, S.549/5, S.559/1, all labelled Hauterivian, Ifrech-Oued-Igoulouzen. The two specimens figured by Gigout (both numbered 720 in the Gigout Collection, Université Mohamed V, Rabat).

Material. Nine specimens from the Roch Collection (detailed above). Forty-eight specimens from the Gentil Collection (forty-five labelled Hauterivian of Ifrech-Oued-Igoulouzen; three labelled Barremian, Chaine d'Azour).

Diagnosis. *Kutchithyris* highly obese in lateral profile, oval in ventral profile. P/A ratio slightly more than 1. Brachial valve more convex than pedicle valve. Umbo erect to incurved. Symphytium very short to invisible. Foramen mesothyrid, labiate in older individuals. Beak ridges rounded. Lateral commissure arched. Anterior commissure rectimarginate to sulciplicate or episulcate. Shell tumid and little folded, or not folded. Euseptoidum well developed in the region of the hinge plates and flanked by two lateral ridges.

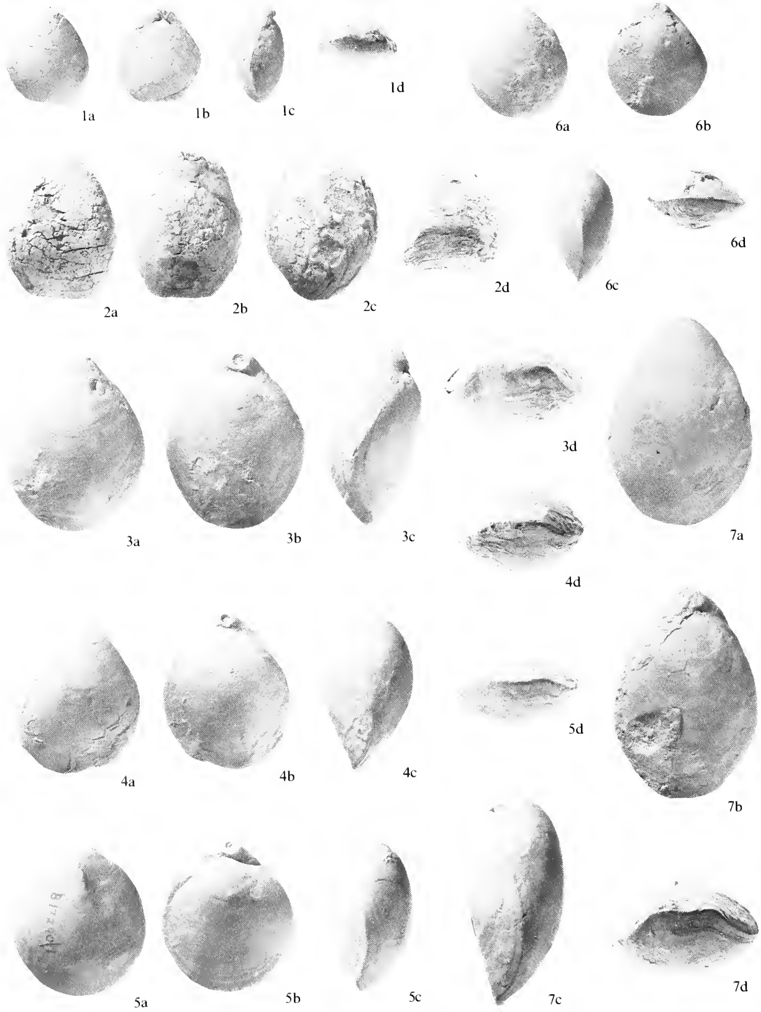


TEXT-FIG. 25. Scatter diagrams of the relationships of thickness to length and thickness to width in *Kutchithyris brivesi* (Gentil Coll.).

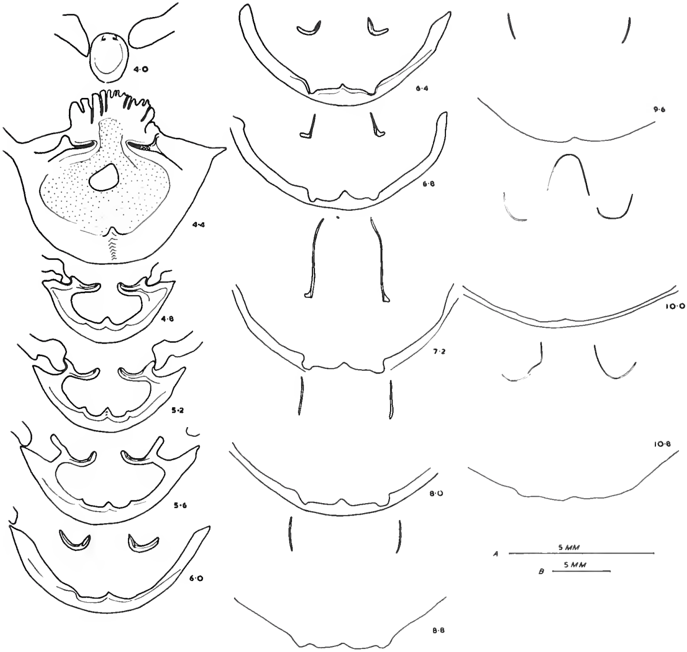
Description. The growth of this species is accompanied by rapid increase in the thickness/length ratio. In the most adult individuals thickness can exceed width. The smallest specimens available (L 18·5) are either rectimarginate or gently uniplicate but the later development of the commissure is the most variable character of the species. Some specimens of 29 mm in length are clearly and deeply uniplicate, while other specimens of similar size are sulciplicate or, rarely, episulcate. In other specimens again a clearly episulcate commissure is developed at a shell length of as little as 19·5 mm.

Remarks. This species is distinguishable at once from other species of *Kutchithyris* and from all the other species considered here by its globular form and the tumid appearance of both valves. Internally it differs from other species of *Kutchithyris* in having a well-developed, although short, euseptoidum. Both Roch and Gigout underestimate the plication which the anterior commissure may show in this species. Roch states: 'La commissure frontale est pratiquement droite, sauf deux petits plis à peine marqués.' According to Gigout: 'Commissure frontale droite ou très légèrement convexe vers la petite valve.' The larger specimens (L 25·5) in Roch's own collection, however, are strongly uniplicate. The form of the anterior commissure of the larger specimens in the Gentil Collection is very variable, suggesting that Roch and Gigout may have seen only small, relatively juvenile specimens such as the lectotype. Roch, Gigout, and Ambroggi all give the main occurrence of this species as of Valanginian age, Roch and Ambroggi recording some also from the Berriasian, whereas the great majority of the Gentil Collection specimens are labelled Hauterivian, with a few labelled Barremian. It is possible that strong sulciplication or episulcation was developed in this species only after the Valanginian. The unity of the species is demonstrated by the remaining

PLATE 59



MIDDLEMISS, Cretaceous Terebratulidae



TEXT-FIG. 26. Transverse sections through *Kutchithyris brivesi*. Section 4.4 is enlarged to show detail of the structure of the cardinal process. The crural bases are first seen at 4.8. The crural processes are at their maximum height at 7.2. S.549/2, Gentil Coll., Hauterivian, Ifrech-Oued-Igouzoulen. A—scale for section 4.4. B—scale for the remaining sections.

EXPLANATION OF PLATE 59

Figs. 1, 2. *Kutchithyris brivesi* (Roch). 1*a*–*d*, juvenile but incipiently biplicate specimen, S.549/5, Gentil Coll., Hauterivian, Ifrech-Oued-Igouzoulen. 2*a*–*d*, adult but uniplicate specimen, S.559/1, Gentil Coll., Hauterivian, Ifrech-Oued-Igouzoulen.

Figs. 3–7. *Juralina ecruensis* sp. nov. 3*a*–*d*, holotype, BM BB 76547, Whitaker Coll. 4*a*–*d*, typical uniplicate form, BM BB 76548. 5*a*–*d*, plaster cast of specimen sectioned (see text-fig. 28), BM BB 76550. 6*a*–*d*, juvenile specimen, BM BB 76551. 7*a*–*d*, elongate adult form, BM BB 76553.

All natural size.

characters both external and internal. A specimen from Roch's collection (from the Valanginian of Oued Igouzoulen) was serially sectioned and differed slightly from the Gentil specimen shown in text-fig. 26 in having hinge plates less concave in their earlier stages, a less developed euseptoidum, and in lacking any clubbed thickening of the hinge plates and crural processes. These are signs of immaturity, confirming that the specimens described by Roch were comparatively juvenile.

Distribution. Berriasian to Barremian of south-west Morocco.

Genus JURALINA Kyansep, 1961

Type species. Juralina procerus Kyansep.

Original diagnosis (from Kyansep 1961). 'Shell plano-convex to biconvex. Anterior commissure rectimarginate to uniplicate. Umbo massive, straight to erect. Deltidium high. Socket ridges high. Cardinal process well developed and separated from the floor of the dorsal valve. Hinge plates divided, very narrow, in close proximity to the socket ridges. Crural bases given off ventrally from the hinge plates. Crura narrow, with well-developed, sharp-pointed crural processes. Loop about one-third of the length of the dorsal valve, triangular, with arched transverse band. Pedicle collar shaped like a ring valve. Hinge teeth massive, without denticulae. Adductor muscle impressions oval triangular, narrowing to fine lines posteriorly. Euseptoidum small. Shell smooth, punctate.'

Emended diagnosis. Shell plano-convex to biconvex, depressed (thickness/length ratio low), subcircular in ventral profile. Umbo straight to erect. Foramen mesothyrid, slightly labiate. Lateral commissure oblique to arched; anterior commissure rectimarginate to squarely uniplicate or slightly sulciplicate. Cardinal process well developed. Hinge plates rectangularly virgate (that is, L-shaped in cross-section with an inner lamina at right angles to the outer lamina); clubbed. Crural bases given off from the anterior ventral extremities of the hinge plates. Crural processes high, sharp-pointed, incurved at their extremities. Loop broad; transverse band high-arched, arcuate to trapezoidal.

Remarks. Kyansep considered that his new genus strongly resembled *Lobothyris* Buckman but *Juralina* differed in having very narrow hinge plates, high socket ridges, and well-developed crural processes, in lacking a septum to its pedicle collar, and in the elliptical shape of its ventral umbonal cavity. Boullier (1976) has, however, pointed out several additional differences. Kyansep also correctly pointed to a marked external resemblance, but equally marked internal differences, between *Juralina* and *Rectithyris* Sahni. In addition to his new species, Kyansep included in *Juralina* several species from the Jurassic of Europe: *Terebratula rauraca* Rollier, *T. repelliniana* D'Orbigny, *T. censoriensis* Rollier, *T. bullingdonensis* Rollier, *T. cotteaui* Douvillé, and *T. moravica* Glocker. Of these, *T. moravica* was referred to a new genus *Weberithyris* by Smirnova (1969). In her discussion of the genus Boullier (1976) rejects affinities with *Lobothyris*, *Weberithyris*, *Tropeothyris* Smirnova, and *Postepithyris* Makridin but finds considerable resemblance to *Cyrtothyris* Middlemiss. Boullier added three more previously established species—*T. bauhini*, *T. valfinensis*, and *T. subformosa*.

Barczyk (1969) added the following species from Upper Jurassic rocks of the Holy Cross Mountains of Poland to *Juralina*: *T. insignis insignis* Schübler, 1830, *T. insignis maltonensis* Oppel, 1858, *T. immanis immanis* Zejszner, 1856, *T. immanis speciosa* Schlosser, 1882. Of these, Boullier (1976) has since referred *T. insignis* var. *maltonensis* Oppel to the genus *Galliennithyris* as *G. maltonensis*.

I introduced the terms inner and outer lamina in 1959 and defined them as follows: 'A virgate hinge plate is divisible into two parts, the outer lamina from the socket ridge to the virgation and the inner lamina on the inner (median) side of the virgation.' The accompanying figure (Middlemiss 1959, text-fig. 1J), however, showed cuneate hinge plates with large crural bases. Because of this confusion I later withdrew the terms inner lamina and outer lamina (Dieni *et al.* 1975; Middlemiss 1976). Now that more is known about the detailed structure of terebratulid hinge plates (Cox and Middlemiss 1978) the terms are seen to be useful in their original sense and I use them here.

Species included. J. procerus Kyansep, ?*Terebratula rauraca* Rollier, ?*T. repelliniana* d'Orbigny, *J. graciosa* Kyansep, ?*T. censoriensis* Rollier, *T. bullingdonensis* Rollier, *J. naklivkini* Kyansep, *T. cotteaui* Douvillé, *J. babugani* Kyansep, *J. carus* Kyansep, *T. bauhini* Etallon, *T. valfinensis* de Loriol, *T. subformosa* Rollier, *J. ecruensis* nov.

Range of the genus. Middle Oxfordian to Barremian.

Juralina ecruensis sp. nov.

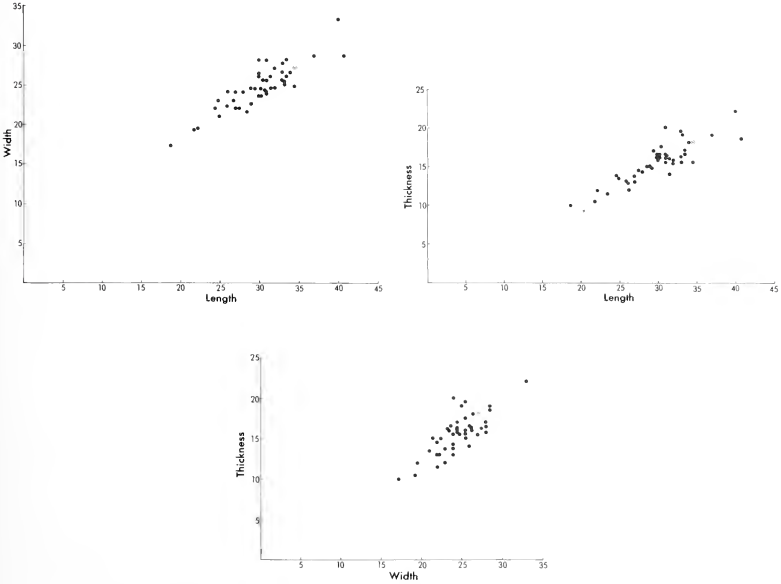
Plate 59, figs. 3–7; text-figs. 27, 28

Types. Holotype, BM BB 76547, Whitaker Collection. Dimensions: L 34·5, W 27, T 18. Paratypes: Whitaker Collection specimens BM B 17273, B 17277, BB 76548, BB 76550, BB 76551, BB 76553.

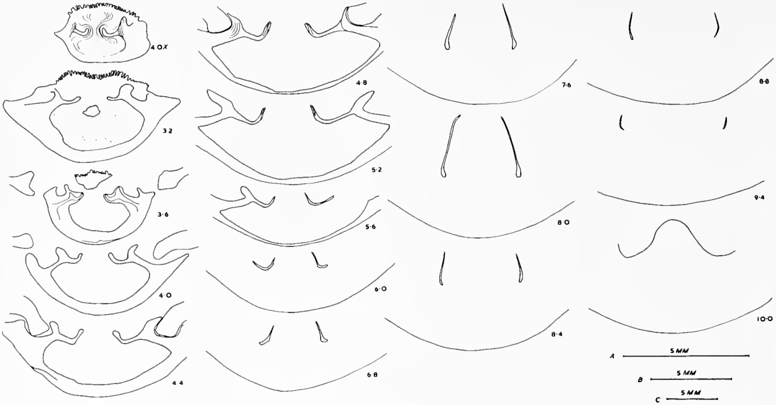
Material. Forty-six specimens in the Whitaker Collection. Forty-two specimens in the Gentil Collection (twenty-five from the Berriasian or Valanginian of Tinirt Ait Ameur, two from the Hauterivian of an unnamed locality, three from the Barremian of Igueni Ouram, twelve from the probable Barremian of Oued Aghbalou).

Diagnosis. Juralina of subcircular to oval ventral profile; maximum width about the mid-line; valves equally convex. Umbo erect. Foramen mesothyrid, marginate, becoming labiate. Beak ridges rounded. Symphytium short, hidden in adult stage. Shell smooth, with faint growth lines. Lateral commissure oblique to arched. Anterior commissure rectimarginate to squarely uniplicate or slightly sulciplicate. Euseptoidum absent or negligible. Transverse band high-arched, rounded.

Description. Juvenile specimens resemble the adults except in being rectimarginate. At a length of about 22 mm the characteristic adult uniplicate commissure begins to develop. In adults over about 30 mm in length the



TEXT-FIG. 27. Scatter diagrams of the relationships of simple dimensions in *Juralina ecruensis* (Whitaker Coll.).



TEXT-FIG. 28. Transverse sections through *Juralina ecruensis*. The first two sections (upper left) are enlarged in order to show detail of the structure of the cardinal process. Sections 3.6–5.2 are enlarged to show the form of the hinge plates and of the crural bases. Maximum height of the crural processes is seen at 8.0. BM BB 76550 except that 4.0x is from BM B 17273 and 3.2 from BM B 17277 as these showed better the details of the cardinal process (Whitaker Coll.). A—scale for sections 3.2 and 4.0x. B—scale for sections 3.6–5.2. C—scale for the remaining sections.

uniplica may be angular, the commissure horizontal in the centre; or it may develop a gentle sinus in the centre, giving a slightly sulciplicate stage. The other main gerontic development is that the foramen becomes labiate in specimens over about 30 mm in length. Text-fig. 27 shows that there are a few long, narrow variants and others that are exceptionally thick.

Remarks. This species is referred to *Juralina* because of (*a*) its external appearance, the distinctive elements of which are the biconvex but moderately depressed form and the erect umbo; (*b*) the internal characters, especially the L-shaped form of the hinge plates in transverse section, with the crural bases developed in the extreme ventral tips of the inner laminae in the anterior parts of the hinge plates only. All these characters appear closely comparable to those described and figured by Kyansep (1961), Barczyk (1969), and Boullier (1976).

Distribution. Valanginian to Barremian of south-west Morocco.

EXPLANATION OF PLATE 60

Fig. 1. *Loriolithyris melaitensis* sp. nov. Section 4.8 of text-fig. 12 photographed to show the shape of the juvenile hinge plates and the distinction between punctate and inpunctate skeletal tissue within the cardinal process.

Fig. 2. *Loriolithyris marocensis* sp. nov. Part of section 6.0 of text-fig. 13 photographed to show the primary piped hinge plate with its secondary clubbed thickening and the structure of the cardinal process.

Fig. 3. *Boubeithyris pleta* sp. nov. Part of section 4.0 of text-fig. 15 enlarged to show the detailed structure of the junction between hinge plate and inner socket ridge.

Fig. 4. *Kutchithyris acutiplicata* (Kitchin). Part of section 6.0 of text-fig. 19 enlarged to show the primary hinge plate with its clubbed thickening and the incipient crural base, all enclosed within the cardinal process.

Linear scale = 2 mm.

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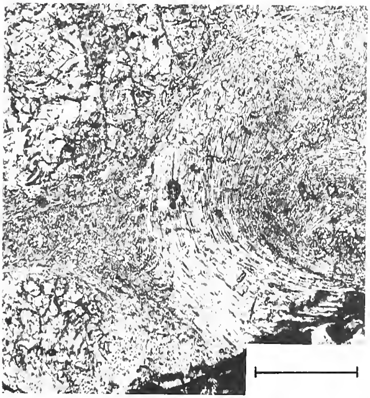

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4

TEREBRATULID SPECIES OF MORE DOUBTFUL OCCURRENCE IN THE LOWER CRETACEOUS OF SOUTH-WEST MOROCCO

Terebratula sueuri Pictet is recorded by Gigout from the Valanginian and Hauterivian at Safi and by both Roch and Ambroggi from the Barremian. *T. sueuri* is a Jura species which is also found rarely in the Hauterivian of the Lower Saxon Basin. Three specimens in the Gentil Collection, S.544/1 (from Safi), S.547/2/1, and S.547/2/2 (both from the Barremian of Ait el Faci) have a close external resemblance to this species and probably represent the form to which the name was applied by previous authors. Serial sectioning proved these to be an undescribed species of terebratellidine, which also occurs in the Jura region (Collections of the Institut de Géologie, Neuchâtel). Gigout's figured specimen (Gigout 1951, pl. 9, figs. 19–22) has a well-developed dorsal median septum and is almost certainly the same terebratellidine species. The occurrence of these two externally similar but quite unrelated species together in the Jura region is a good example of homochronous homoeomorphy.

Terebratula collinaria d'Orbigny is recorded by both Roch and Ambroggi from the Hauterivian and Barremian and by Roch from the Valanginian also. The records probably refer to *Paraboubeithyris plicae*, although the Gentil Collection contains specimens of this species only from the Barremian.

Tropeothyris salevensis (de Loriol). This is recorded by Gigout from the Valanginian of the environs of Safi and by Ambroggi from the Barremian of his area. On first viewing the collections I referred to *T. salevensis* the specimens which I have here named *Loriolithyris melaitensis*; Gigout's figured specimen (Gigout 1951, pl. 9, figs. 15–18) is apparently similar to these externally except that it is a gerontic specimen. The records probably refer to *L. melaitensis*.

Moutonithyris moutoniana (d'Orbigny) is recorded by Roch from the Barremian and by Gigout from the 'Neocomian' and Aptian of Safi and Sidi Bou Zid. Although Gigout gives in synonymy Pictet's (1872) figure of the species, not d'Orbigny's original, his own figured specimen looks reasonably convincing (Gigout 1951, pl. 9, figs. 23–26). In the Gentil Collection are four specimens from the Hauterivian of Oued Tidzi, one from the Hauterivian of Ifrech Oued Igoulouzen, four from the Barremian of Ait el Faci, and seven from the Barremian of Asif Ait Ameur which are probably this species. *M. moutoniana* is a sub-Tethyan species of very widespread occurrence throughout the Lower Cretaceous (see Middlemiss 1976, 1979) and it would indeed be surprising if some specimens were not to be found in south-west Morocco.

EXPLANATION OF PLATE 61

Fig. 1. *Loriolithyris melaitensis* sp. nov. Section 6.8 of specimen S.556/1 (not included in text-fig. 12) enlarged to show the development of the crural base with secondary clubbing. The primary hinge plate has a cuneate relationship to the crural base.

Fig. 2. *Loriolithyris melaitensis* sp. nov. Section 4.8 of text-fig. 12 photographed to show the internal structure of the cardinal process, especially the distribution of punctate and impunctate skeletal tissue. The juvenile primary hinge plates have a secondary clubbed thickening which was deposited prior to the incorporation of the hinge plates into the cardinal process.

Fig. 3. *Loriolithyris melaitensis* sp. nov. Section 5.2 of text-fig. 12 enlarged to show the primary hinge plate surrounded by secondary tissue and the first sign of development of the crural base within the piped inner margin of the hinge plate.

Fig. 4. *Loriolithyris russillensis* (de Loriol). Section 4.6 of text-fig. 7 enlarged to show the structure of the piped inner margin of the hinge plate.

Fig. 5. *Paraboubeithyris plicae* gen. et sp. nov. Part of section 4.8 of text-fig. 16 enlarged to show the structure of the corniced inner margin of the hinge plate.

Linear scale = 2 mm.

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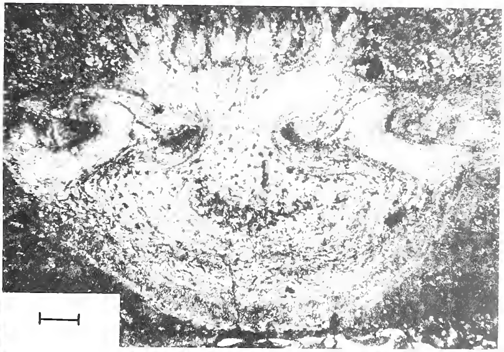

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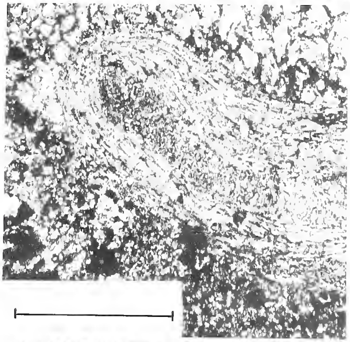

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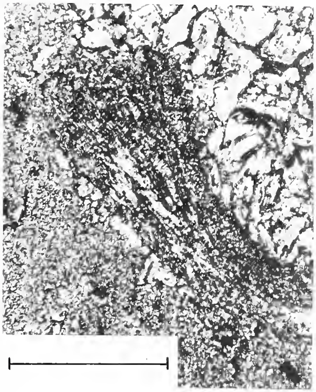

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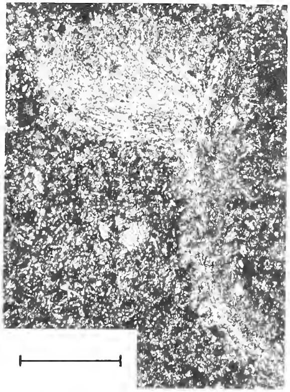

5

MIDDLEMISS, Cretaceous Terebratulidae

Sellithyris carteroniana (d'Orbigny) is recorded by Roch from the Berriasian and the Barremian, by Gigout from the Valanginian (of Safi) and by Ambroggi from the Hauterivian. In the Gentil Collection there is one specimen from Tinirt Ait Ameur (probably Hauterivian) which has some resemblance to *S. carteroniana* in being obese, equidimensional, and strongly episulcate but the resemblance is closer, in fact, to the Algerian variety or subspecies of *S. sella* (see below). The same can be said of Gigout's figured specimen (Gigout 1951, pl. 9, figs. 11–14). *S. carteroniana* is an interesting species from the palaeobiogeographical point of view as (*a*) it is a characteristic member of the Jura fauna which is also found in north Germany during the time of the Valanginian–Hauterivian transgression (Middlemiss 1976, 1979) and (*b*) *Terebratula coahuilensis* of the Neocomian of northern Mexico is probably synonymous with it. In view of my thesis of the Jura affinities of the south-west Moroccan fauna the occurrence of this species would be significant. Unfortunately there is no evidence that all the records do not refer to *S. sella*, although some may refer to *Boubeithyris pleta*.

Sellithyris sella (J. de C. Sow) is recorded by both Roch and Ambroggi from the Barremian and Gargasian and by Roch from the Bedoulian also. This almost ubiquitous Lower Cretaceous species would be expected to occur in south-west Morocco, especially as an undescribed form of it is certainly known from the Lower Cretaceous of the High Plateaux region of Algeria. In the Gentil Collection are twenty-three specimens from Tinirt Ait Ameur (labelled Berrisian–Valanginian but more likely Hauterivian) which appear to be this obese Algerian variety of the species. There is also one specimen from the Hauterivian of Oued Tidzi, one from the Barremian of Ida ou Troumma, and two from the Barremian of Tibourr'm; these resemble the more normal somewhat depressed Neocomian form of the species.

Moutonithyris dutempleana (d'Orbigny). This almost ubiquitous Albian species is recorded by both Roch and Ambroggi from both the Clansayesian and the Albian. Its occurrence in the Albian would not be surprising. Doubts are raised, however, by two circumstances: (*a*) *M. dutempleana* is very rare in the Clansayesian and known certainly from that stage only in Sardinia (Dieni *et al.* 1975). On the other hand if, as is likely, the species spread from south to north, it could well occur in the Clansayesian of Morocco. (*b*) *Cyrtothyris middlemissi* certainly occurs in both Clansayesian and Albian and is easily mistaken for *M. dutempleana* (Calzada 1972, p. 66). The specimen figured by Gigout (1951, pl. 13, figs. 5–8) as *T. biplicata* is a *Concinnithyris* cf. *obesa.*

To summarize: *T. sueuri*, *T. collinaria*, *T. salevensis*, *T. carteroniana*, and *M. dutempleana* have probably been misidentified by previous authors. *M. moutoniana* and *S. sella* probably do occur rarely in south-west Morocco.

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COLLIGNONICERATID AMMONITES FROM THE MID-TURONIAN OF ENGLAND AND NORTHERN FRANCE

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ABSTRACT. *Collignoniceras* Breistroffer, 1947 is represented by five species in the mid-Turonian of England and Touraine (the type area of the Turonian stage) in northern France. The cosmopolitan and highly variable type species *C. woollgari* (Mantell) is shown to be a senior synonym of *C. schlueterianum* (Laube and Bruder) and *C. mexicanum* (Böse) amongst others, and shows features indicating that *Selwynoceras* Warren and Stelck, 1940 (the type species of which *S. boreale* (Warren), is also redescribed) is a synonym of *Collignoniceras* sensu stricto. Other species referred to the genus are *C. carolinum* (d'Orbigny), *C. papale* (d'Orbigny), *C. canthus* (Sornay) and *C. turoniense* (Sornay). *Ammonites fleuriausianus* d'Orbigny, 1841 is a senior synonym of *A. vielbancii* d'Orbigny, 1850 and is made the type species of *Lecointriceras* gen. nov., to which two further species, *L. carinatum* sp. nov. and *L. costatum* sp. nov. are also referred.

Collignoniceras woollgari (Mantell) is one of the most widely cited mid-Cretaceous ammonite species, giving its name to the middle zone of the Turonian standard sequence (Wright in Arkell *et al.* 1957; Rawson *et al.* 1978). As with other classic species, the type material has never been adequately figured and is of uncertain horizon, although it has at least survived the vicissitudes of a century and a half since its original description (Mantell 1822, p. 197; pl. 21, fig. 16; pl. 22, fig. 7). In England, where it was first described, the species is rare and the lectotype remains the only good adult specimen known. Elsewhere, however, it is recorded abundantly, especially in the U.S. Western Interior region, where it formed the basis of one of the early accounts of intraspecific variability in Cretaceous ammonites (Haas 1946), although as Haas and Meek before him (1876, p. 455) noted, authors have questioned whether the great majority of specimens referred to this cosmopolitan species are indeed conspecific with Mantell's types.

We have studied hundreds of European, American and Japanese *Collignoniceras* in connection with this project, and encountered an initially bewildering range of variation, both in adult ornament and the size at which ontogenetic changes occur. We have relatively few juveniles from Europe but many from the U.S.A.; conversely, large complete adults are common in European collections, but those from the U.S. are usually fragmentary. Whilst it would be possible to select individuals with differences that could be framed into diagnostic features for specific or subspecific separation, this would be misleading and conceal the over-all common features of the species recognized below. In *C. woollgari* in particular we have no doubt that a series of local races of the species existed over its wide spread, but to separate formally the successive or local populations, differing in the extent of morphological variation but overlapping, would serve no useful purpose. The broad, variable species described below not only represent reality but are adequate for detailed correlation and discussion of the evolution of the genus.

SYSTEMATIC DESCRIPTIONS

Location of specimens. The following abbreviations are used to indicate the repositories of specimens studied:

AM	Muséum de Paléontologie d'Angers.
BMNH	British Museum (Natural History), London.
CS	Château de Saumur
EMP	École des Mines, Paris (now housed at the Université Claude Bernard, Lyon).

[Palaeontology, Vol. 23, Part 3, 1980, pp. 557–603, pls. 62–77.]

FSM	Faculté des Sciences, Le Mans; chiefly collections formerly housed in the Musée de Tessé, Le Mans.
FSR	Institut de Géologie, Université de Rennes.
GK	Department of Geology, Kyushu University, Fukuoka.
MNHP	Muséum National d'Histoire Naturelle, Paris.
OUM	University Museum, Oxford; unless stated otherwise, these are collections made by Hancock and Kennedy.
SP	Collections of the Sorbonne, now Université de Paris VI.
WW	C. W. and E. V. Wright collection.

Dimensions. All dimensions are given in millimetres; figures in parentheses are the dimensions as a percentage of the total diameter. D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus; Ic = intercostal; c = costal; R = number of ribs per whorl.

Suture terminology. The suture terminology of Wedekind (1916; see Kullman and Wiedmann 1970 for a recent review) is followed here: I = Internal lobe, U = Umbilical lobe, L = Lateral lobe, E = External lobe.

Suborder AMMONITINA Hyatt, 1889
Superfamily ACANTHOCERATACEAE de Grossouvre, 1894
[*nom transl. et correct.* Hyatt 1900, *ex* Acanthoceratidés de Grossouvre, 1894]
Family COLLIGNONICERATIDAE Wright and Wright, 1951
Subfamily COLLIGNONICERATINAE Wright and Wright, 1951
Genus COLLIGNONICERAS Breistroffer, 1947
(*non* Van Hoepen, 1955)

Type species. *Ammonites woollgari* Mantell, 1822 by the original designation of Meek (1876) as type species of *Prionotropis* Meek, 1876 (*non* Fieber, 1853), for which Breistroffer (1947) proposed *Collignoniceras* as *nomen novum*.

Diagnosis. Medium to large, moderately involute to evolute ammonites. Early whorls compressed, parallel sided, ornamented by crowded or sparse, prorsiradiate, straight or flexuous ribs, mostly long, with weak to strong umbilical bullae. All ribs bear in the early stages outer ventrolateral tubercles in addition to siphonal clavi.

This style of ornament is, in some species, retained to maturity. In most, however, the ribs coarsen, become widely spaced, with strong to weak umbilical tubercles (which migrate progressively outwards from the umbilical margin), prominent inner and outer ventrolateral tubercles which may fuse into a massive horn or flared rib, from which commonly arise pairs of low ribs, joining siphonal clavi more numerous than the ventrolateral and linked into a more or less continuous keel. Rarely the ornament is greatly reduced on the body whorl.

The sutures are little incised, with massive saddles.

Discussion. The diagnosis given above summarizes the rather wide variation seen in species referred to this genus, which include *C. boreale* (Warren), *C. papale* (d'Orbigny), *C. canthus* (Sornay), *C. turoniense* (Sornay) and *C. carolinum* (d'Orbigny). The nomenclatorial history of the genus is somewhat complex. Meek introduced a subgenus *Prionotropis* in 1876, with *Ammonites woollgari* Mantell as type species. Breistroffer (1947) pointed out the prior usage of *Prionotropis* by Fieber (1853) and proposed *Collignoniceras* as *nomen novum*. Meanwhile Warren and Stelck (1940) had proposed the genus *Selwynoceras* with *P. borealis* Warren, 1930 as type species, distinguishing it from Meek's *Prionotropis* by the presence of a row of nodes instead of a keel on the inner whorls and the marked alternation in length and strength of the ribs. Wright (in Arkell *et al.* 1957, p. L426) regarded *Selwynoceras* as a subgenus of *Collignoniceras*, whilst Powell (1963, p. 1223) considered the two synonymous. Following an application by Matsumoto and Wright in 1966, the International Commission on Zoological Nomenclature ruled in 1968 (Opinion 861) that *Collignoniceras* Breistroffer, 1947, should be given priority over *Selwynoceras* Warren and Stelck, 1940, by those who regard the two as synonyms.

From a comparison of the types and other specimens of *C. woollgari* and *S. boreale*, we would agree with Powell that the two do not bear even subgeneric separation: *boreale* is simply a small species of *Collignoniceras* in which the flared ribs appear at a relatively early stage. The ventral tuberculation visible on the outer whorl of the lectotype (here designated), which is refigured here as Pl. 70, figs. 1–2, is on exactly the same plan as in English *woollgari*, whilst, as Haas (1946), Powell (1963) and Matsumoto (1965) have shown, the style of ribbing of juvenile *Collignoniceras* is very variable.

Collignoniceras differs from *Prionocyclus* Meek, 1876 (type species *P. wyomingensis* Meek) in that the latter has very fine dense irregular ribs through most or all of its ontogeny and a broader venter with an entire or serrated keel. *C. woollgari* and *P. hyatti* (Stanton) overlap in time in the southern U.S. and some late *C. woollgari* there and also in Europe show a low siphonal keel at maturity, emphasizing the intimate relationship between the two. Ribbing is usually dominant over tuberculation in *Prionocyclus*, although some species bear finger-like ventrolateral spines, foreshadowing the development seen in the later *Prionocycloceras* (Young 1963, pl. 23, figs. 1–6; pl. 27, figs. 2–4). Matsumoto (1965, p. 19) discusses other differences between these two genera.

Subprionocyclus Shimizu, 1932 was originally separated from *Collignoniceras* [*Prionotropis*] on the basis of minor differences between the internal sutures. As Matsumoto (1959, p. 109) notes, however, distinguishing features also include the paired or alternately long and short sigmoidal ribs of *Subprionocyclus* which may flatten on the outer whorl, greater persistence of outer ventrolateral tubercles and absence of massive horns. Like *Prionocyclus*, *Subprionocyclus* has a continuous persistent keel which varies with the density of the ribbing from finely to coarsely serrate.

Germariceras Breistroffer, 1947 is perhaps only doubtfully separable from *Prionocyclus*; known only from juveniles, it may be separated from *Collignoniceras* by the possession of fine dense narrow ribs with small sharp umbilical, inner and outer ventrolateral tubercles and a finely serrated continuous keel with more serrations than the number of ventrolateral tubercles.

Reesidites Wright and Matsumoto, 1964, which should perhaps be placed in Barroisiceratinae, is compressed and involute, high whorled, with a fastigiate venter; sinuous ribs branch in groups of two or three from small umbilical bullae, with single ventrolateral and siphonal clavi only. The largest individuals barely exceed 100 mm diameter (Matsumoto 1965).

Subprionotropis Basse, 1950, known only from specimens a few centimetres in diameter, differs from *Collignoniceras* in being involute with compressed whorls, with ribs arising in pairs from umbilical bullae (with additional intercalated ribs) bearing only ventrolateral and siphonal clavi and forming strong chevrons on the fastigiate venter. At the end of the body chamber, ribs and tubercles weaken and the venter becomes rounded.

Lymaniceras Matsumoto, 1965 and *Niceforoceras* Basse, 1948 are both compressed and involute, with weak, dense flexuous ribs or striae, a single ventrolateral tubercle and a finely serrated keel.

Collignoniceras is the earliest genus of Collignoniceratidae to appear in the Turonian, and, as Matsumoto (1965) has noted, some individuals in variable United States Western Interior populations show early whorls which foreshadow *Prionocyclus*, *Subprionocyclus* and thence the remaining late members of the group.

With respect to the evolutionary origins of the genus, Wright (in Arkell *et al.* 1957, p. L426) and Matsumoto (1965, p. 10) have suggested that the diminutive late Cenomanian acanthoceratinid *Protacanthoceras* Spath, 1923 might be the ultimate ancestor, with *Neocardioceras* Spath, 1926 as an intermediate. Recent collecting from the latest Cenomanian/early Turonian faunas of the condensed *Neocardioceras* Pebble Bed of Devon (see Hancock, Kennedy and Wright 1977, fig. 2 for details) has now produced a range of specimens that provisionally we refer to *Thomelites* Wright and Kennedy, 1973, among which are individuals with siphonal clavi tending to form a continuous serrated keel. In addition, a few poorly preserved fragments seem already to have reached the stage of *Collignoniceras* in some features of decoration. There remains, however, a gap in the European successions, corresponding to most of the *Mammites nodosoides* assemblage Zone, in which the genus is absent apart from a single possible example in the collection of Colonel O. H. Bayliss, from Shapwick, Devon; W. A. Cobban (*in litt.*, 1978) tells us that *Collignoniceras* appears at the top of the North American correlatives of this zone.

Occurrence. Collignoniceras is widespread in the middle of the Turonian stage, the classic *woollgari* Zone. There are records from England, France, Germany, Czechoslovakia, Poland, Rumania, Turkestan, Japan, California, Texas, the U.S. and Canadian Interiors, Greenland, north Africa, Colombia, and northern Australia.

Collignoniceras woollgari (Mantell)

Plates 62–67; Plate 69, figs. 3–4; Plate 71, figs. 1–3; text-figs. 1A, 2–4

1822 *Ammonites Woollgari* Mantell, p. 197, pl. 21, fig. 16; pl. 22, fig. 7.
non 1841 *Ammonites Woollgari* Mantell; d'Orbigny, p. 352, pl. 108, figs. 1–3.
1850 *Ammonites Woolgarii* d'Orbigny, p. 189 (*pars*).
1855 *Ammonites Woollgari* Mantell; Sharpe, p. 27, pl. 11, figs. 1, 2.
1860 *Ammonites carolinus* (d'Orbigny); Courtiller, p. 251, pl. 3, fig. 2.
1867 *Ammonites Woolgarii* Mantell; Courtiller, p. 7, pl. 8, figs. 1–4.
1872 *Ammonites Woolgari* Mantell; Schlüter, p. 25, pl. 9, figs. 1–5; *non* pl. 12, figs. 5, 6.
1872 *Ammonites Woollgari* Mantell; Geinitz, p. 184, pl. 33, figs. 1, 2 (?), *non* 4–5.
1872 *Ammonites Woolgari* Fritsch, p. 30 (*pars*), pl. 3, figs. 1–3; pl. 4, figs. 1–2; pl. 14, fig. 6; *non* pl. 2, figs. 1–2; pl. 15, fig. 6.
1887 *Acanthoceras Woollgari* (Mantell); Laube and Bruder, p. 235, text-fig.
1887 *Acanthoceras Schlüterianum* Laube and Bruder, p. 236, pl. 29, figs. 2–3.
1902 *Acanthoceras Woollgari* (Mantell); Petrascheck, p. 149, text-figs. 7–8.
1902 *Acanthoceras* cfr. *Woollgari* (Mantell); Petrascheck, p. 148, pl. 12, figs. 2–3.
1902 *Acanthoceras Schlüterianum* Laube and Bruder; Petrascheck, p. 150, pl. 10, fig. 3; pl. 11, fig. 3; pl. 12, fig. 1.
1907 *Prionotropis Schlüterianum* Laube and Bruder; Pervinquière, p. 275.
1925 *Prionotropis Schlüteriana* Laube and Bruder; Diener, p. 156.
1928 *Prionotropis woollgari* Mantell var. *mexicana* Böse, p. 262, pl. 11, figs. 11, 12.
1931 *Pseudaspidoceras*(?) *chispaense* Adkins, p. 51, pl. 3, figs. 1–2.
1931 *Pseudaspidoceras*? sp. Adkins, p. 53, pl. 2, fig. 2.
1931 *Pseudaspidoceras*(?) n.sp. A; Adkins, p. 53, pl. 3, figs. 3–4.
1946 *Prionotropis woollgari* Meek (? *non* Mantell); Haas, p. 150, pls. 11, 12; pl. 13, figs. 1–3, 5–18; pl. 14, figs. 1–10, 12–16; pl. 15, figs. 1–6, 9, 10; pls. 16, 17; pl. 18, figs. 1–2, 7–9; text-figs. 1–91.
1963 *Selwynoceras mexicanum* (Böse); Powell, p. 1225, pl. 166, figs. 2–7; pl. 167, figs. 1, 3–8; pl. 168, fig. 4; text-figs. 2–4.
1971 *Collignoniceras woollgari* (Mantell); Matsumoto, p. 130, pl. 21, fig. 4, text-fig. 1.
1972 *Collignoniceras woollgari* (Mantell); Cobban and Scott, p. 94, pl. 14, fig. 5; pl. 30, fig. 1; pl. 37, figs. 9–10 (with additional synonymy).
1975 *Collignoniceras woollgari* (Mantell); Hattin, pl. 10, figs. N, P, Q, R.
1977 *Collignoniceras* (*Selwynoceras*) *schlueterianum* (Laube and Bruder); Hancock, Kennedy and Wright, p. 156.
1977 *Collignoniceras* (*Collignoniceras*) cf. *C. woollgari sensu* Matsumoto, 1965, group E; Hancock, Kennedy and Wright, p. 156.

Types. The lectotype, designated by Wright and Wright (1951, p. 35), is BMNH 5682, from the Middle Chalk of Lewes, Sussex, refigured here as Plate 62, figs. 1–2; Plate 63, fig. 9. Two additional specimens from Mantell's collection, BMNH C5742 a–b (Plate 69, figs. 3, 4), are presumed to be paralectotypes.

Other specimens studied. These include: BMNH 4863 a–b, from the Middle Chalk 'near Lewes, Sussex'; BMNH 43963 'Lower Chalk, near Lewes' (J. de C. Sowerby Collection); BMNH C30394 'Turonian Mount Caburn Pit, near Glynde, Sussex' (labelled aff. *woollgari* by L. F. Spath); BMNH C40152 from the Middle Chalk, *Terebratulina lata* Zone, Mickleham Bypass, Surrey (C. W. and E. V. Wright Collection); WW 16682, 14792–4, from the Middle Chalk, top of the *T. lata* Zone Middle Chalk, Mickleham Bypass, Surrey; WW 22925–7, Middle

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EXPLANATION OF PLATE 62

Figs. 1–2. *Collignoniceras woollgari* (Mantell). The lectotype, BMNH 5682, from the Middle Chalk of Lewes, Sussex.

2

1

KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

Chalk, Lewknor Crossroads, Lewknor, Oxon. (ex R. E. H. Reid Collection); OUM K 10273, K 10275–76 from no more than 5 m below the top of the Chalk Rock at Fognam Barn, Berkshire, 3 km WNW of Lambourn. BMNH 88988 b, 88989 a–c from the Turonian of the White Mountain, near Prague, Czechoslovakia.

French specimens include the following: OUM KZ 741, 743–4, 746, 748–9, 753, from the St. Cyr-en-Bourg Fossil Bed, Champignonnière Les Rochains, 7 km south of Saumur and north-east of Montreuil-Bellay, Maine-et-Loire, and numerous specimens in the Muséum de Paléontologie, Angers, from this bed and adjacent levels in the Tuffeau Blanc (Couffon Collection etc.) variously labelled Saumoussay, St. Cyr-en-Bourg, Saumur, and elsewhere, including AM 57, AM 59, AM 116.

There are numerous specimens from Poncé, Sarthe, and others from Bourré in the Cher Valley, Loir-et-Cher, including BMNH C74803.

Dimensions

	D	*Wb*	*Wh*	*Wb*: *Wh*	*U*	*Ribs*
Lectotype	130 (100)	40 (31)	40 (31)	1	50 (38)	13
FSR, C273	67·3 (100)	20·4 (30)	25·0 (37)	0·81	23·9 (36)	24
MNHP W7	58·5 (100)	21·0 (36)	— (—)	—	22·8 (39)	19
MNHP W18	61·0 (100)	24·0 (39)	23·7 (39)	1·01	22·0 (36)	22
MNHP 'X'	86·0 (100)	29·0 (34)	34·9 (41)	0·83	29·5 (34)	~20
MNHP W15	81·0 (100)	32·0 (40)	32·0 (40)	1·0	27·8 (34)	19
MNHP Ic	141·0 (100)	52·0 (37)	49·5 (35)	1·05	55 (39)	—
Ic		41·5 (29)	49·5 (35)	0·83	44·5 (33)	18
MNHP 6778	133·0 (100)	45·0 (34)	50·0 (38)	0·9		
MNHP W20						
Ic	162·0 (100)	55·0 (34)	52·0 (32)	1·05	67 (41)	—
MNHP W4 c	137·0 (100)	60·0 (43)	51·0 (37)	1·18	— (—)	15/16
Ic		39·5 (29)	39·5 (29)	1·0		
MNHP W10	109.0 (100)	47·5 (44)	42·0 (39)	1·13	37·0 (34)	—
		33·5 (31)	38·8 (36)	0·86		
MNHP W19	175·0 (100)	74·8 (43)	65·0 (37)	1·15	65·0 (37)	15

Description. The inner whorls of our smallest specimens show coiling to have been moderately evolute, with compressed whorls and a shallow umbilicus. At about 10–15 mm diameter, there are 27–32 ribs per whorl; the density decreases with increasing size. The ribs are even, bar-like, prorsiradiate, straight and clearly demarcated from the flat interspaces. As size increases, ribs become much more widely spaced; at 40–50 mm diameter there are only 17–24 ribs per whorl. They are of variable strength, arise from weak to strong umbilical bullae and are narrow, high and separated by wide, flat interspaces; they are markedly prorsiradiate and straight to concave on the flanks, always single, with no intercalated ribs. At the ventrolateral shoulder they bear conical to feebly clavate inner ventrolateral tubercles. From these the ribs are either weakly or strongly projected forwards to elongate outer ventrolateral clavi. A broadened swelling connects these in turn to a sharp, continuous siphonal keel, strengthened into sharp high clavi at the peak of the variably angled ventral chevron formed by the termination of the ribs.

This type of ornament may extend to diameters of 100 mm, but typically, as size increases, a series of changes in ornament occur, more or less independently of each other. The umbilical bullae move outwards and come to occupy a lower flank position, whilst the ribs are differentiated into long bullate ones and (in most specimens) from one to four shorter ribs, restricted to the outer flank and venter and sometimes lacking ventrolateral tubercles. The inner ventrolateral tubercles may at this stage develop into a distinctive conical horn which supports, on the outer flank of its base, the outer ventrolateral clavus; some specimens present a ventral aspect in

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EXPLANATION OF PLATE 63

Figs. 1–12. *Collignoniceras woollgari* (Mantell). 1–4, OUM KZ 746; 11–12, OUM KZ 748, from the St. Cyr-en-Bourg Fossil Bed, Champignonnière les Rochains, south of Saumur and north-east of Montreuil-Bellay, Maine-et-Loire. 5–6, MNHP 6778 (d'Orbigny Collection), Poncé, Sarthe; 7–8, OUM KT 1160, from the Ojinaga Formation at Cannonball Hill, northern Chihuahua, Mexico. 9, Apertural view of the lectotype, BMNH 5682; see explanation of Plate 62 for details. 10, MNHP W1, 'Le Mans, Sarthe' (from Poncé?). Figures 1–2 are × 2; the remainder are × 1.


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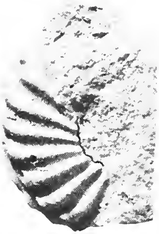
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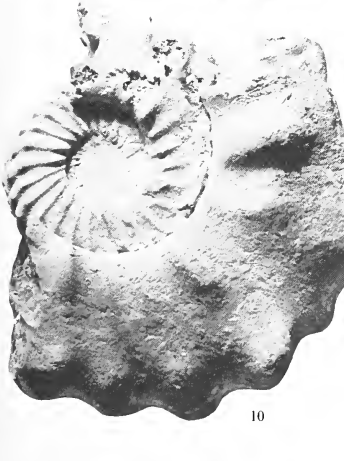
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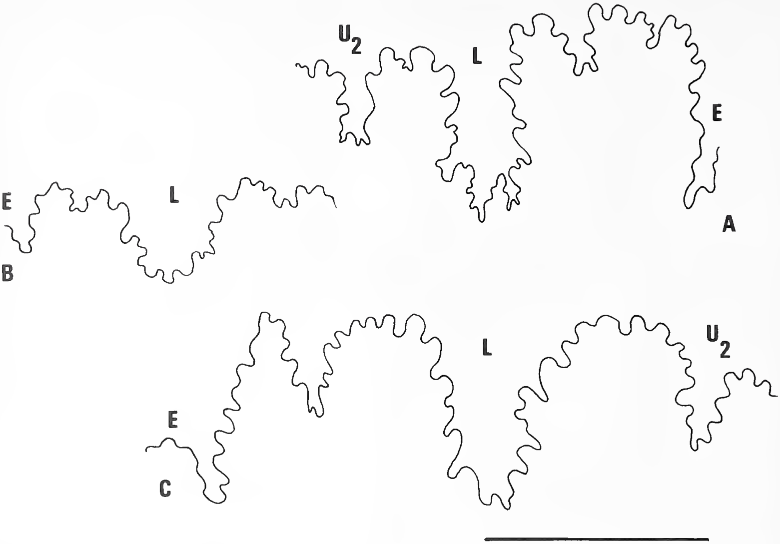
KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites



TEXT-FIG. 1. Sutures of *Collignoniceras* species. A, *C. woollgari* (Mantell), from BMNH C74803; B, *C. carolinum* (d'Orbigny), from the Sorbonne specimen (de Grossouvre Collection); C, *C. papale* (d'Orbigny), from a Sorbonne specimen (de Grossouvre Collection). Bar scale is 2 cm.

which siphonal tubercles greatly outnumber ventrolateral, whilst others show a more or less equal number; no two specimens agree in details of ornament.

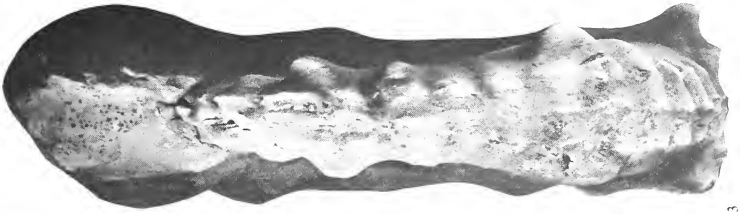
Mature specimens show two broad types of decoration, but again no two specimens agree in detail. In the first group the umbilical bullae move outwards and fuse with the inner ventrolateral tubercles to form a strong to massive horn (if broad) or flange (if narrow). This supports a long, low, narrow outer ventrolateral clavus, and the front and rear of the horn strengthens into a pair of ribs which loop to the pair of siphonal clavi corresponding to each horn. Some specimens may develop a low siphonal horn at this stage and at the adult aperture up to three ventral ribs may appear between the primary ribs, although in other specimens these may be absent, the spaces between the major ribs being smooth. The second type is a more evolute form, retaining long, straight, distant flank ribs with bullae of variable strength, connected by weak or almost effaced ribs to strong conical ventrolateral horns which bear the outer ventrolateral clavus. A low siphonal ridge is present and there are pairs of clavi corresponding to the horns as well as additional clavi in the interspaces. This form differs most obviously from the first in the retention of bullae and in being somewhat larger.

The suture line is simple, with a massive, slightly incised, asymmetrically bifid E/L, narrow L and narrow, bifid L/U_2.

EXPLANATION OF PLATE 64

Figs. 1–3. *Collignoniceras woollgari* (Mantell). The lectotype of *Acanthoceras schlueterianum* (Laube and Bruder), from the Turonian of the White Mountain near Prague, Czechoslovakia. Pictures supplied through the courtesy of Dr. V. Houša (Prague).

PLATE 64



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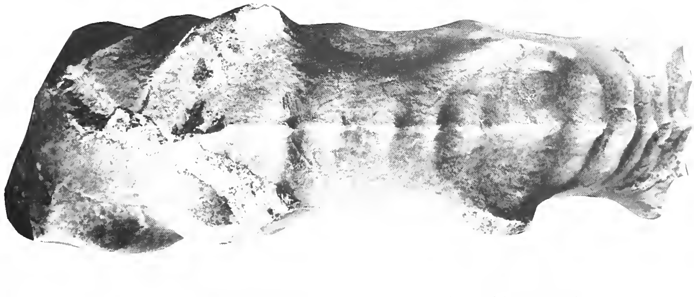
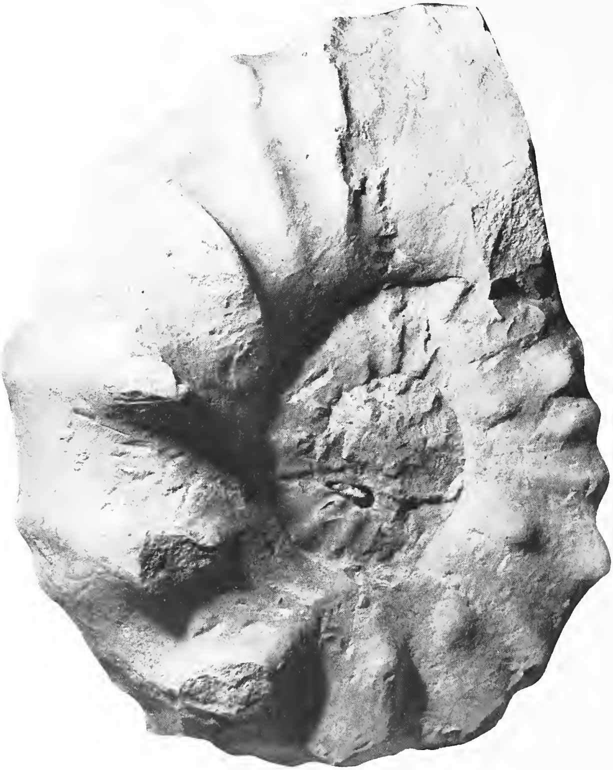


1

KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

Discussion. The above description is based upon the available English material, the large suite of specimens from Touraine and a few Czechoslovakian specimens before us. It must be stressed that no two specimens are alike and that description is inevitably generalized. Mantell's original figures of *Ammonites woollgari* give a clear and accurate representation of the juvenile form, but only suggest the very different adult form in general terms, better shown in Sowerby's (1828, p. 165; pl. 587, fig. 1) beautiful water colour and Sharpe's (1855, p. 27; pl. 11, figs. 1a–b) slightly inaccurate reconstruction.

The lectotype is, in fact, a moderately distorted composite internal mould only 130 mm in diameter, as can be seen from our photographs (Pl. 62, figs. 1–2; Pl. 63, fig. 9), showing no trace of sutures or any indications of how much is body chamber. In terms of the description given above, it falls into the first group of specimens. It is distinctive in the small size at which the massive horns are developed and the brevity of the stage with intercalated ribs.



TEXT-FIG. 2. *Collignoniceras woollgari* (Mantell) BMNH 88989a, a crushed specimen from the Turonian of the White Mountain, near Prague, Czechoslovakia.

TEXT-FIG. 3. *Collignoniceras woollgari* (Mantell) A, B, MNHP W14, 6778 (d'Orbigny Collection), from Poncé, Sarthe. A. tuffeau specimen agreeing closely with the type. Reduced × 0·5 approx. C. D. MNHP 1946–19, from St. Maure de Touraine. A hypernodose adult of the first type. Reduced × 0·4 approx.

At the beginning of the outer whorl the ribs bear strong umbilical bullae, strong conical inner ventrolateral and long, low, clavate outer ventrolateral tubercles and a strong elongate siphonal clavus. Between these long primary ribs are one or two shorter intercalated ribs which extend across the venter and bear small siphonal clavi. By 90 mm diameter these are lost and the ornament consists of an umbilical bulla which moves out progressively to occupy a mid-lateral position, linked by a broad rib to a massive inner ventrolateral horn which bears, at its base, the outer ventrolateral clavus. From this clavus two poorly defined, low, rounded ribs link to two ventral clavi.

The best-preserved horn on the lectotype is at 120 mm diameter, and here the bulla on the flank and the inner ventrolateral horn have merged into a massive horn bearing a much weakened outer ventrolateral clavus and subdued weakened ribs.

D'Orbigny (1841, p. 352, pl. 108, figs. 1-3) figured under the name *A. woollgari* a distinctive form which he subsequently (1850) named *A. vielbancii*; it is redescribed below as a junior subjective synonym of *Lecointriceras fleuriausianum* (d'Orbigny). D'Orbigny also described in *Paléontologie Française* a related form, *A. carolinus* (1841, p. 310, pl. 91, figs. 5-6), which he subsequently (1850) regarded as a synonym of *A. woollgari*, a view followed by most later authors. Sharpe (1855, p. 27, pl. 11, figs. 1a-b, 2a-b) clearly recognized the differences between young *woollgari* and *carolinum* ('. . . the French shell has twice as many ribs, is less compressed, and has the keel more completely separated from the ribs by two regular channels, than in our species'), and, as we describe below, the two are indeed specifically distinct.

Fritsch (1872) provided a very clear discussion of Mantell's species, and recognized three variants; his descriptions are loosely translated as follows:

(*a*) Typical form, which agrees exactly with the illustrations of Mantell and Sharpe. It has very strong tubercles on the siphonal side (pl. 4, figs. 1, 2).

(*b*) Form with slender ribs and weaker tubercles (pl. 3, fig. 2).

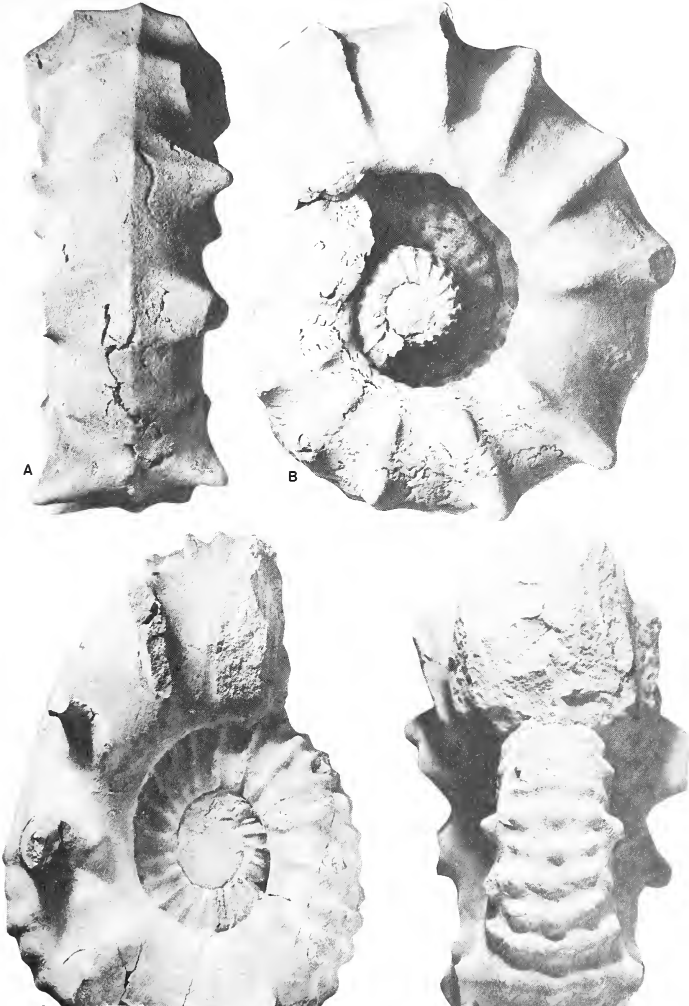
(*c*) More involute form with an inverse egg-shaped mouth opening. There are tubercles close to the umbilical seam, which remain there for a long period, and are stronger and more widely separated than in the typical form; there are only six, even on the inner whorl (pl. 3, fig. 1).

He also described a variety *lupulina* from Měcholup [Michelob] near Saatz, close to Prague (1872, p. 31, pl. 2, figs. 1, 2; pl. 15, fig. 6), which was said to be very similar to *woollgari* when young, but when old, has a different venter, large sparse tubercles and an almost square cross-section. It is, in fact, a *Mammites nodosoides* (Schlüter).

Schlüter (1872) figured a similar range of variants; his pl. 9, figs. 1-3 correspond to Fritsch's form c and his pl. 9, figs. 4-5 to the typical form. His variety (pl. 12, figs. 5-6) is, as he suggested, close to the *papale* group in many respects and it could well be referred to as *Collignoniceras* aff. *canthus* (Sornay).

Laube and Bruder (1887) reviewed a similar range of central European specimens but referred Fritsch's typical form (var. a) to a new species, *Acanthoceras schlueterianum*; they regarded the involute form (var. c) as typical *C. woollgari* and var. *lupulina* as a *Mammites*, which they renamed *Mammites michelobensis*. Petrascheck (1902) followed Laube and Bruder and described forms he called *woollgari*, *schlueterianum*, and aff. *woollgari*.

From our study of the type material and the Touraine populations, it is quite clear that no two adult *Collignoniceras* of these types are the same. The lectotype of *C. woollgari*, showing as it does an early loss of umbilical bullae, which move out to mid flank, fuse into ventrolateral horns, with much elongated outer ventrolateral clavi and subdued ribs looping to low siphonal clavi is clearly of the same general morphology as Fritsch's typical form (e.g. 1872, pl. 4, figs. 1-2) and the lectotype (here designated) of *Acanthoceras schlueterianum* (Laube and Bruder 1887, pl. 29, figs. 2a-b) (Pl. 64). It differs, however, in showing a decline in ventral ribs and clavi at only 90 mm diameter, whereas the Czechoslovakian examples retain umbilical bullae and intercalated ribs (particularly on the venter) to a much greater size and in consequence have a longer middle growth stage with umbilical bullae, conical inner ventrolateral and outer ventrolateral and siphonal clavi, like the specimen illustrated here (text-fig. 4 C-D), Fritsch's pl. 14, fig. 6 and Laube and Bruder's smaller paralectotype (1887, pl. 29, fig. 3). This stage is virtually suppressed in the lectotype of *C. woollgari*, which in these respects



TEXT-FIG. 4. *Collignoniceras woollgari* (Mantell) A, B. MNHP W22, 6778 (d'Orbigny Collection), from Poncé, Sarthe. An adult of the second type, retaining long ribs and moderately evolute coiling. Reduced ×0·4 approx. C, D. BMNH 88988b, from the Turonian of the White Mountain, near Prague. Reduced ×0·5 approx.

is atypical. Other specimens show that the intercalated ventral ribs are accompanied by weak flank ribs in middle growth but that there is great variation at this stage. The Touraine populations, which yield specimens that both match the lectotype of *C. woollgari* (text-fig. 3 A–B) and show every gradation to the other forms (Pl. 66, figs. 1–3; text-fig. 3 C–D) with strong intercalated ribs and tubercles, show that *C. woollgari* and *C. schlueterianum* should be treated as synonyms. Indeed, a specimen from Fritsch's own collection, now in the British Museum (Natural History) (no. 88989a) and labelled in his own hand 'Weisser Berg', the type locality of *C. schlueterianum* (text-fig. 2), exhibits the fusion of umbilical bullae with strong horns seen in the lectotype of *woollgari* but with more persistent intercalated ribs on the venter of the last whorl. The specimen is, furthermore, adult at only 150 mm, showing a rapid decline in ornament and loss of horns on the outer whorl.

In Germany (?), Czechoslovakia and Touraine (but not England where only one adult is known) this hypernodose, horned form, enormously variable in its adult ornament, is accompanied by the evolute, square-whorled forms which correspond to Fritsch's form C, to Laube and Bruder's 'typical form' and Petrascheck's *A. woollgari* + *A.* cfr. *woollgari.* Inner whorls of this type are inseparable from typical juvenile English *C. woollgari*, but again the variable adult whorls are quite distinctive, as Fritsch described, and as outlined above in our description; we conclude that these are probably sexual dimorphs.

C. woollgari var. *mexicana* (Böse) (1928, p. 262, pl. 11, figs. 11, 12) was originally described on the basis of a single, crushed specimen from the Turonian Ojinaga Formation equivalent, near Jimenez, Coahuila, Mexico, reillustrated here as Plate 65, figs. 1–3. Powell (1963) has redescribed this form (as *Selwynoceras mexicanum*) and discussed the intraspecific variation on the basis of large collections of fragmentary material. From large additional collections from the same area (OUM KT 1160–1183, 1200–1222, 1264–1313) and Chispa Summit, Jeff Davis County, Texas and specimens in the Adkins Collection (preserved in the Texas Memorial Museum) we conclude that it too is a synonym of *C. woollgari.* Juveniles, as Powell himself noted (op. cit., p. 1225), include individuals which cannot be separated from the English *C. woollgari* (Pl. 63, figs. 7–8), in addition to those which are more compressed, finely and densely ribbed.

Powell (1963, pl. 168, fig. 4) has figured a specimen in middle growth, showing the irregularly ribbed stage with development of inner ventrolateral horns as seen in Bohemian and Touraine specimens and we have other slender fragments which match Petrascheck's (1902, pl. 10, figs. 3a–b) juvenile *A. schlüterianum.* Larger fragments show a wide range of variation, from robust fragments having essentially equal numbers of inner and outer ventrolateral and siphonal tubercles to those with multiple ventral tuberculation. Adult body chambers show clear dimorphism, as in European material, the one form with flanges or flared horns produced by amalgamation of umbilical and ventrolateral tubercles, the other more quadrate, retaining to maturity umbilical bullae and distant ribs of variable strength. As can be seen from our and Powell's figures, distinction on the basis of the nature of the less complex suture, the finer ribbed juveniles and the coarse ornament of adults, by which Powell separated it from *C. schlueterianum*, cannot be upheld in the light of the variation seen in European specimens (not known to Powell); there is a clear overlap. We note the relatively frequent occurrence of individuals with flares and a compressed whorl, rarely seen in Europe, suggesting the Texas/Mexico material belongs to a local population more variable than their old world contemporaries.

EXPLANATION OF PLATE 65

Figs. 1–8. *Collignoniceras woollgari* (Mantell). 1–3, the holotype of *Prionotropis woollgari* (Mantell) var. *mexicana* Böse, from near Jimenez, Coahuila, Mexico. University of California, Berkeley, Collections. 4–6, BMNH 4863a, from the Middle Chalk near Lewes, Sussex. 7–8, a juvenile U.S. Western Interior specimen in the U.S. Geological Survey Collections, Denver, from USGS Mesozoic locality 21792, the mid-Turonian Carlile Shale of the Black Hills.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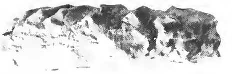
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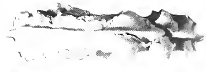
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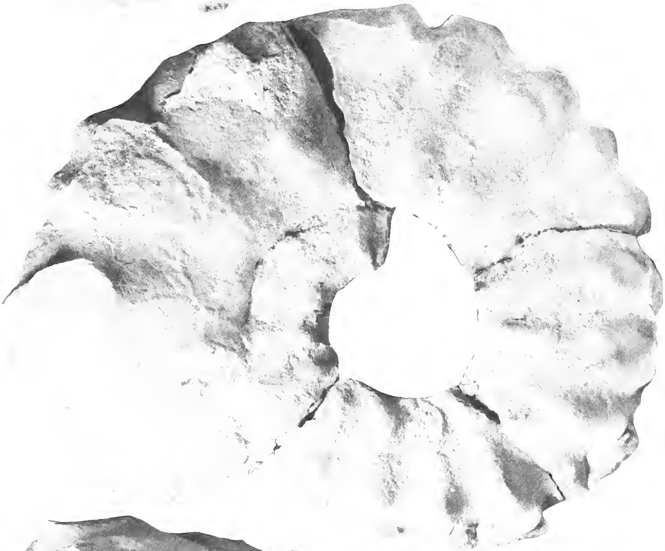
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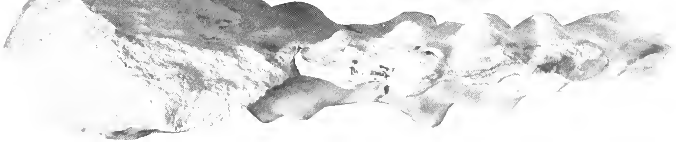
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KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

The relationship of European specimens to the widely documented U.S. Western Interior material referred to *C. woollgari* has been complicated by the relatively few illustrations of English juveniles. Adults such as Meek's specimen (1876, pl. 7, fig. 1g) from the Black Hills, Dakota, would certainly fall within the concept of *C. woollgari* outlined here, although differing from the lectotype most obviously in the retention of umbilical bullae to a greater diameter. Dr. W. A. Cobban (Denver) has also shown us medium-sized specimens in which all ribs are long and the ventrolateral and siphonal clavi are equal in number, a feature uncommon in European material. American juveniles, described by Haas (1946) and Matsumoto (1965) amongst others, show a much wider range of variation than European material. This may be merely a consequence of the small number of juveniles known from Europe: indeed, the latter fall closest to Matsumoto's group E, one of the commonest forms in the Western Interior. Nevertheless, there is a clear overlap with European *C. woollgari*. The presence of similar individuals would also seem to preclude subspecific separation and we regard them as conspecific, but with a different population structure. Specific differentiation of the American fauna from their European contemporaries occurred later, with the evolution of the early members of the *Prionocyclus hyatti* group.

W. A. Cobban (*in litt.*) has suggested to us that forms with more siphonal than ventral nodes predate those in which the numbers are equal in the U.S. Western Interior, but, as we do not know the precise horizon of the holotype of *woollgari* in relation to these, we prefer to unite them here, leaving revision of these faunas to Dr. Cobban.

According to Matsumoto (1959, p. 107; 1965, p. 16, pl. 3, figs. 3–4) *C. woollgari bakeri* Anderson is a subgroup of *C. woollgari* that characterizes the north Pacific region. All described specimens are small, compressed, evolute *Subprionocylus*-like densely ribbed shells, close to subgroup D of *C. woollgari* of Matsumoto (1965) from the U.S. western Interior, but more evolute and with less prorsiradiate ribs. These differences probably do not merit separation, but without more and adult specimens further comment is inadvisable.

C. woollgari is easily separated from the remaining species of the genus. *C. carolinum* (d'Orbigny) (p. 574) is usually more densely ribbed and even in sparsely ribbed juveniles (Pl. 68, fig. 11) the ribs are low and subdued rather than bar-like. Adults are quite distinct; *C. carolinum* reaches maturity at only 100–120 mm diameter, never develops the coarse umbilical bullae, ribs, and horns of *woollgari*, nor the complex looped ventral ornament. Instead, it remains compressed and flat sided, with weak ribs and tubercles and a persistent, crenulated siphonal ridge. *C. canthus* (Sornay) (p. 582) has coarsely and sparsely ribbed and tuberculate inner whorls but a virtually smooth body chamber with only faint ribs and many tiny siphonal tubercles. *C. turoniense* (Sornay) (p. 584) has similarly coarsely ornamented early whorls, is adult at a much smaller size with more massive whorls, coarse sparse bullae, weak ribs and ventrolateral horns and the inner ventrolateral tubercles disappear at an early stage.

There is a closer resemblance to *C. papale* (d'Orbigny) (p. 578) but here juveniles have fewer, coarser ribs with strong bullae displaced well out from the umbilical shoulder, with much more prominent inner ventrolateral tubercles. In middle growth *C. papale* lacks the prominent ventrolateral horns of many *C. woollgari* and the inner and outer ventrolateral tubercles merge into a pinched clavus, retained to much greater diameters in *C. woollgari*. Other differences are noted on p. 582.

C. boreale (p. 586) is a genuinely small form, showing adult features at only 100 mm diameter in the holotype. It has narrow, distant ribs and retains umbilical bullae to the end of the phragmocone, showing early development of flared ventrolateral flanges and traces of looped ventral ribs.

EXPLANATION OF PLATE 66

Figs. 1–3. *Collignoniceras woollgari* (Mantell). Adult phragmocone showing intercalation of flank and ventral ribbing, multiple ventral tuberculation and early stages of horn development. MNHP W10, from either Poncé (Sarthe) or Bourré (Loir-et-Cher).

PLATE 66

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1

KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

Occurrence. Few *C. woollgari* from England are well dated. Through the courtesy of the Director of the Institute of Geological Sciences and Mr. C. J. Wood we have been able to examine the precisely positioned material from the Leatherhead (Fetcham Mill), Surrey, Borehole (Gray 1965). Here *C.* cf. *woollgari* occurs at a depth of 570′ 6″ (GSM.WN 1979–80, 1982–3), 73′ 1″ (22·28 m) above the base of the Melbourn Rock and 17′ 6″ (5·33 m) above a specimen of ?*Mytiloides hercynicus*; at 535′ 10″ (GSM.WN 1942), 12′ (3·66 m) above the level of large *Inoceramus* of *inequivalvis* type, and at 518′ 9″ (GSM.WN 1900, 1901), 26′ 9″(8·15 m) below specimens of *Mytiloides* sp. and *I.* cf. *apicalis* (inoceramids determined by Mr. P. Woodroof). This range, through 51′ 9″ (15·8 m) of section, includes the top of the *Inoceramus labiatus*/*Orbirhynchia cuvieri* and the lower part of the *Terebratulina lata* Zones. Other English specimens have been recorded from both *labiatus* and *lata* Zones. Specimens from Sussex, the type area, come mostly from the Lewes region. One specimen (BMNH C30394) is said to be from Mount Caburn; unfortunately the classic pit here extends from the Melbourn Rock to basal Upper Chalk (*labiatus–planus* Zones).

Specimens from the upper part of the *lata* Zone of Surrey (e.g. WW 14792–4, 16682), and OUM K 10273, K10275–6 from no more than 5 m below the top of the Chalk Rock at Fognam, Berkshire, indicate the upper limit of its relatively long range. This is confirmed by occurrences in Sarthe and Touraine through the middle and upper part of the Tuffeau Blanc, in the St. Cyr-en-Bourg Fossil Bed, Bourré and Poncé faunas. In the United States the species occurs rarely in the top of Cobban and Scott's (1972) *Mammites nodosoides* Zone (Cobban *in litt.*) and overlaps with the succeeding *Prionocyclus hyatti* (Powell, 1963).

Elsewhere the species is known to occur widely in Europe, the U.S.S.R. west to Transcaspia, Japan, California and Oregon, Texas, Mexico, the U.S. Western Interior and northern Australia.

Collignoniceras carolinum (d'Orbigny)

Plate 68, figs. 1–11; Plate 76, figs. 1–2; text-figs. 1b, 5

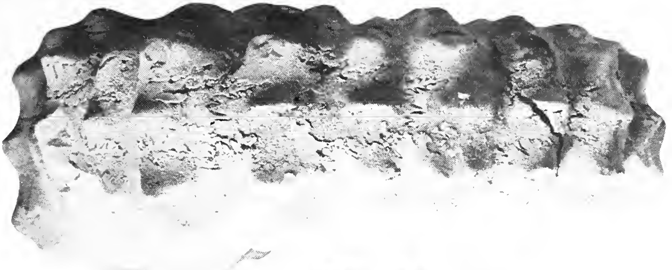
1841 *Ammonites Carolinus* d'Orbigny, p. 310, pl. 91, figs. 5–6.
1850 *Ammonites Woolgarii* Mantell; d'Orbigny, p. 189 (*pars*).
1860 *Ammonites Carolinus* d'Orbigny; Pictet and Campiche, p. 316.
1872 *Ammonites carolinus* d'Orbigny; Schlüter, p. 27, pl. 9, fig. 6.
1881 *Ammonites Carolinus* d'Orbigny; Windmöller, p. 33.
?1887 *Acanthoceras Carolinum* d'Orbigny; Laube and Bruder, p. 232, pl. 27, fig. 1.
1902 *Prionotropis carolinus* d'Orbigny; Petrascheck, p. 152.
?1912 *Prionotropis woolgari* var. *Carolinus* (d'Orbigny); Arkhanguelsky, p. 72, pl. 3, figs. 20–22 (*fide* Arkhanguelsky, 1916).
1925 *Prionotropis carolina* (d'Orbigny); Diener, p. 156 (*pars*).
1977 *Collignoniceras* (*Collignoniceras*) *carolinum* (d'Orbigny); Hancock, Kennedy and Wright, p. 156.

Types. D'Orbigny's original account of this species is as follows: 'Je l'ai recueillie en place aux Martrous, près de Rochefort (Charente-Inférieure), dans la craie que je rapporte aux grès verts supérieurs ou aux craies chloritées. Elle y est rare à l'état de moule. M. d'Archiac l'à aussi rencontrée à Sainte-Maure (Indre-et-Loire), dans le même couche.' By 1850 d'Orbigny had concluded that *carolinus* was a synonym of *woollgari* (*Prodrome*, p. 189), and in consequence no specimens are represented in his collections under the name *carolinus*. Under *Ammonites woollgari*, however, there is a specimen from Martrous with the label 6778a which is clearly the basis of the original figure (Pl. 68, figs. 4–8), and this is here designated lectotype of the species.

Other specimens studied. OUM KZ 747, from the St. Cyr-en-Bourg Fossil Bed, Champignonnière les Rochains, 7 km south of Saumur and north-east of Montreuil-Bellay, Maine-et-Loire. An unregistered specimen in de Grossouvre's collection (Sorbonne, Paris) from either Poncé (Sarthe) or Bourré (Loir et Cher). MNHP W8, from an unknown locality in the Tuffeau. WW 14791 from the *Terebratulina lata* Zone, Mickleham Bypass, Surrey.

EXPLANATION OF PLATE 67

Figs. 1–3. *Collignoniceras woollgari* (Mantell). Adult phragmocone of sparsely and robustly ribbed variant with equal numbers of umbilical, ventrolateral and siphonal tubercles. MNHP W2. 1904–32. 'Le Mans, Sarthe'.



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KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

Dimensions

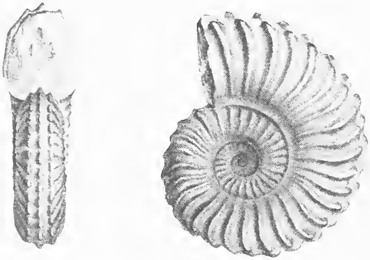
	D	*Wb*	*Wh*	*Wb:Wh*	*U*
Lectotype MNHP 6778a	46·0 (100)	14·0 (30)	15·0 (33)	0·93	16·7 (36)
Sorbonne spec.	108·5 (100)	28·2 (26)	37·5 (35)	0·75	34·3 (32)

Description. The lectotype from Martrous (Charente-Maritime) is a fragment with juvenile body chamber preserved in calcarenite typical of the Calcaires à Céphalopodes of the Rochefort area. Coiling is relatively evolute, with a broad, shallow umbilicus (36% of the diameter). The umbilical wall is low and rounded. The whorl section is compressed (whorl breadth to height ratio is approximately 0·93), with flattened, convergent sides, the maximum breadth close to the umbilical shoulder and the venter fastigiate. Ornament consists of strong, dense, narrow ribs (nineteen on last half-whorl), arising at the umbilical shoulder without clear bullae after the first two visible ribs. They are straight or slightly flexed and prorsiradiate on the inner flank, curving strongly forwards across the ventrolateral shoulders and venter. Single, shorter intercalated ribs occur commonly on the early part of the specimen but there are only two in the last half-whorl. The ribs are strengthened into distinct if small inner ventrolateral tubercles at the beginning of the body chamber, but these are lost beyond a diameter of about 34 mm. There are well-marked outer ventrolateral clavi, connected by forwards-directed weak ribs to elongate siphonal clavi borne on a low, rounded keel. Other specimens show both denser and sparser ribbing of the same style, as in other *Collignoniceras* juveniles (Pl. 68, figs. 10, 11).

Body chambers show the species to have been adult at small diameters (100–120 mm). The adult whorls are compressed (whorl breadth to height ratio as little as 0·75) with gently inflated inner, and flattened outer flanks, with a fastigiate venter. Ornament consists of numerous (about thirty) rather low, rounded, prorsiradiate ribs, arising at the umbilical shoulder without bullae and flexed strongly forwards, concave on the outer flank and ventrolateral shoulder, where they bear blunt, clavate tubercles. The ribs are narrow as they sweep forwards from these to long siphonal clavi. Rarely ribs branch from the umbilical seam or are intercalated, so that there are more siphonal clavi than long ribs.

The sutures are indifferently exposed (text-fig. 1B), but are typically collignoniceratid, with broad, simple, bifid elements.

Discussion. D'Orbigny's figure is partly idealized: in addition the figure lacks the abrupt start of the ribs at the umbilical shoulder, shows too many short ribs and makes the species appear too inflated (text-fig. 5). Pictet and Campiche (1860, p. 316) and de Grossouvre (1894, p. 75) regarded this species as a juvenile *C. woollgari*, but Sharpe (1855, p. 27) had already noted that 'the French shell has twice



TEXT-FIG. 5. *Collignoniceras carolinum* (d'Orbigny). Copies of d'Orbigny's original figures (1841, pl. 91, figs. 5–6).

EXPLANATION OF PLATE 68

Figs. 1–11. *Collignoniceras carolinum* (d'Orbigny). 1–3, SP, de Grossouvre Collection, probably from Bourré (Loir-et-Cher). 4–8, the lectotype, MNHP 6778a, from the Calcaire à Céphalopodes of Martrous, near Rochefort (Charente-Maritime). 9–10, OUM KZ 747, from the St. Cyr-en-Bourg Fossil Bed, Champignonnière les Rochains, south of Saumur and east of Montreuil-Bellay (Maine-et-Loire). 11, MNHP, from an unknown locality in the Tuffeau Blanc de Touraine.

PLATE 68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KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

as many ribs, is less compressed, and has the keel more completely separated from the ribs by two regular channels'. Schlüter (1872, p. 27) maintained the species, as did Laube and Bruder (1887, p. 232), although their specimen is only doubtfully referable to it. Meek (1876, p. 457) regarded d'Orbigny's *Ammonites bravaisianus* as the juvenile of *carolinum*, which he in turn treated as a synonym of *woollgari*.

In the last 50 years the name has dropped out of currency. The most recent reference was by Matsumoto (1971, p. 131) who upheld the view that it was possibly an immature example of *C. woollgari* in which the appearance of strong distant ribs was delayed, in this respect being intermediate between *C. woollgari woollgari* and *C. woollgari bakeri*.

C. carolinum is in fact quite distinct from *C. woollgari*. As early authors noted, the type of the species is consistently more finely and densely ribbed than European *C. woollgari* and at comparable diameters the ribbing is much more subdued and the ventral tuberculation finer. Other examples before us show much sparser ribbing (Pl. 68, fig. 11), but even here the ribbing is more subdued. When adult the species are very distinct; *C. carolinum* reaches maturity at only 100–120 mm and never develops the coarse umbilical bullae and ribs, the massive ventrolateral horns or the complex looped ventral ribbing and tubercles of *C. woollgari*.

The delicately ribbed inner whorls immediately distinguish the species from the grossly tuberculate young of *C. canthus*, *C. turoniense* and *C. papale*. Adult *C. canthus* are broader whorled and retain massive bullae and ribs, whilst *C. papale* has strong ribs with conspicuous looping as well as being more inflated. The feebly ornamented body chamber of *C. turoniense* is superficially similar, but is much broader, virtually lacks ribs but has a row of small siphonal tubercles.

C. boreale, although adult at a similarly small diameter, has much coarser ribbing when young, and develops distant coarse flared ribs when adult.

The confusion of *C. carolinum* with *C. woollgari* stems from the similarity of the former to finely ribbed forms of the latter known from Japan and the United States. These have been described by Haas (1946) as *Prionotropis woollgari* vars. *regularis* and *tenuicostata*, and by Matsumoto (1965) as his Group B of *C. woollgari*. These finely ribbed forms are distinguished from the type of *C. carolinum* in always developing relatively coarse ribs at a diameter of 20 mm or less and by ribs that are sharp rather than subdued, straight rather than flexuous.

Occurrence. This is a rare species. Apart from the Touraine records above, it is known in France from the environs of La Rochelle in Charente; in England from the *Terebratulina lata* Zone of Surrey; in north Germany, Bohemia and Turkestan.

Collignoniceras papale (d'Orbigny)

Plate 69, figs. 1, 2; Plate 70, figs. 3–5; text-figs. 1c, 6–7

1841 *Ammonites Papalis* d'Orbigny, p. 354, pl. 109, figs. 1–3.
1850 *Ammonites papalis* d'Orbigny, p. 189.
1887 *Acanthoceras papaliforme* Laube and Bruder, p. 237, pl. 27, figs. 3–4.
1925 *Prionotropis papalis* d'Orbigny; Diener, p. 156.
1925 *Prionotropis papaliformis* Laube and Bruder; Diener, p. 156.
1977 *Collignoniceras* (*Selwynoceras*) aff. *papale* (d'Orbigny); Hancock, Kennedy and Wright, p. 156.
1977 *Collignoniceras* (*Selwynoceras*) gr. *papale* (d'Orbigny); Hancock, Kennedy and Wright, p. 156.

Holotype. By monotypy the specimen in the Requien Collection (Musée d'Avignon), presumed to come from the 'craie tuffeau ou chloritée du département de Vaucluse' (d'Orbigny 1841, p. 356). We have not seen the holotype, but d'Orbigny's figure (text-fig. 6) is little more than two-thirds natural size.

Specimens studied. There is a series of specimens in the Muséum d'Histoire Naturelle, Paris; five recorded in the d'Orbigny Collection as coming from Montrichard (Loir-et-Cher), reg. no. 6780; MNHP W.9, unlabelled but probably from Bourré; MNHP '3', from Montrichard; MNHP 'A' 'B' 'D'–'E' from Bourré. MNHP 'F' unlocalized but from the Tuffeau de Touraine.

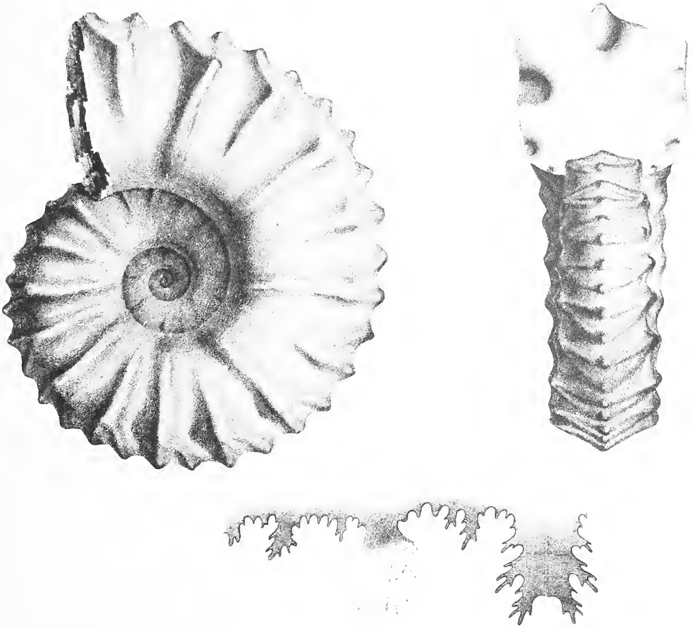
There are several unregistered specimens in the de Grossouvre Collection, housed in the Sorbonne, from either Bourré or Poncé; a specimen labelled Bourré showing the inner whorls; and a small body chamber, also unregistered, is labelled Bourré.

OUM KZ 738 and 745 are from the St. Cyr-en-Bourg Fossil Bed, Champignonnière les Rochains, 7 km south of Saumur and north-east of Montreuil-Bellay, Maine-et-Loire.

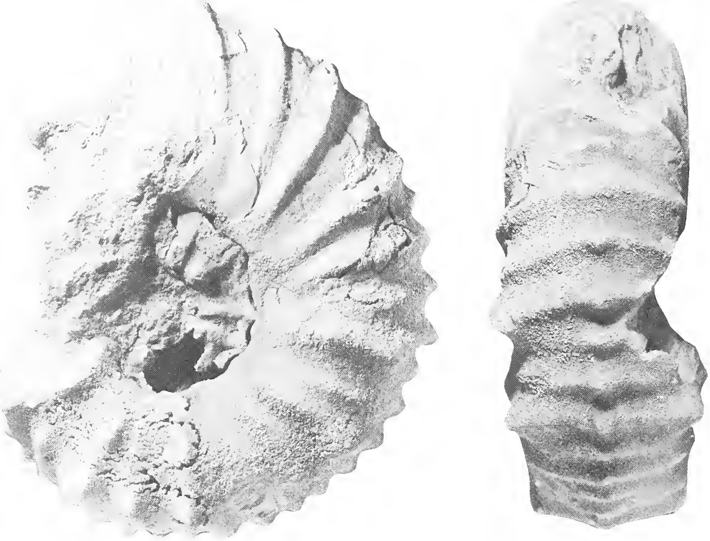
Dimensions

	D	*Wb*	*Wh*	*Wb:Wh*	*U*
MNHP W '9'	112·3 (100)	36·4 (32)	41·8 (37)	0·87	— (—)
MNHP 'B'	111·7 (100)	— (—)	41·0 (37)	—	39 (35)
SP, de Grossouvre	160·0 (100)	51·0 (32)	60·0 (37)	0·85	53·0 (33)
Collection	at 135·0 (100)	54·5 (40)	58·0 (43)	0·94	44·5 (33)
SP, Bourré	120·0 (100)	40 (33)	46·0 (38)	0·87	38·8 (32)

Description. The inner whorls of this species are best displayed by the specimen from Bourré in the Sorbonne Collections illustrated as Plate 70, figs. 3–5. Up to a diameter of 55 mm the coiling is relatively evolute, with a medium-sized umbilicus (30% of diameter), quite shallow, showing on the mould a rounded and undercut wall.



TEXT-FIG. 6. *Collignoniceras papale* (d'Orbigny). Copies of d'Orbigny's original figures (1841, pl. 109, figs. 1–3) of the holotype from the 'Craie Chloritée ou Craie Tuffeau du département de Vaucluse'. The specimen is said to be 120 mm in diameter.



TEXT-FIG. 7. *Collignoniceras papale* (d'Orbigny). Adult specimen in the Sorbonne Collections (de Grossouvre Collection), from either Poncé or Bourré. Reduced × 0·6.

The intercostal whorl section is slightly compressed (Wb:Wh is 0·9), with convergent flanks, broadly rounded ventrolateral shoulders and a flattened venter. The costal section is polygonal, with the greatest breadth at the umbilical bulla. There are thirteen umbilical bullae per whorl. At the smallest diameter visible, they are very elongate and lie close to the shoulder. With growth the maximum development migrates outwards leaving a weak development only at the umbilicus, with the main bulla low on the flank. Broad, strong, straight, slightly prorsiradiate ribs arise from the bullae, cross the flanks and connect to strong, conical inner ventrolateral tubercles, from which a broad, strong rib sweeps forwards to strong outer ventrolateral clavi. These are in turn connected to elongate siphonal clavi by a broad, low, forwardly directed rib. Between long ribs there are some four intercalatories, usually with outer ventrolateral and siphonal clavi only.

From 50 mm onwards the ribs connecting the inner and outer ventrolateral tubercles strengthen and at 55 mm they have fused into blunt, oblique clavi.

During middle growth, ornament consists of distant, weak to strong umbilical bullae, displaced progressively outwards to a low or even mid flank position (not shown on d'Orbigny's figure), which give rise to one or rarely a

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EXPLANATION OF PLATE 69

Figs. 1–2. *Collignoniceras papale* (d'Orbigny). SP, from Bourré (Loir-et-Cher) (Saemann Collection).
Figs. 3–4. *Collignoniceras woollgari* (Mantell); BMNH 5742a–b, paralectotypes from the Middle Chalk near Lewes, Sussex.

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KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

pair of narrow, straight, prorsiradiate ribs, whilst single intercalated ribs arise at varying levels on the flank. All ribs bear a pinched ventrolateral bulla (if weak) or horn (if strong). These are commonly limited before and behind by narrow ribs, which loop across the venter, although the extent of this looping varies widely from specimens in which it predominates (Pl. 70, fig. 4) to those where it is simple (Pl. 69, fig. 1).

Over the last half whorl of adult body chamber the tubercles decline markedly, leaving rather weak, relatively crowded ribs without umbilical bullae, a weak, oblique to radially elongate ventrolateral tubercle (which may disappear several ribs before the aperture) and a small blunt siphonal tubercle (text-fig. 7).

The suture is rather simple, with a broad E which tapers apically; broad, rather simply incised and asymmetrically bifid E/L, narrow L and smaller, bifid L/U_2. U_2 is small (text-fig. 1c).

Discussion. The material before us shows considerable variation in the relative strength of umbilical bullae and ribs, as well as being adult (and showing typical decline in ornament) over a range of 120–180 mm diameter. Nevertheless, it forms a compact species group.

Collignoniceras canthus is immediately distinguishable on the basis of its massively tuberculate inner whorls and feebly ribbed, almost smooth body chamber with many fine ventral clavi, as discussed on p. 584. There are closer similarities to *C. turoniense*, but here the massive bullae of the inner whorls and general dominance of tuberculation over ribbing is diagnostic, as discussed on p. 586.

There are also similarities between juveniles of *C. papale* and *C. woollgari*, but *papale* have fewer, coarser ribs (compare Pl. 69, figs. 3–4 and Pl. 70, fig. 3), with strong bullae displaced well out from the umbilical shoulder and much more prominent inner ventrolateral tubercles. *C. papale* in middle growth is more sharply and distantly ribbed and does not have the prominent ventrolateral horn of many *woollgari*. The inner and outer ventrolateral tubercles merge into pinched, radially elongated clavi during middle growth in *papale*; in *woollgari* they are distinct to a much greater size. The venter of *C. papale* may bear strong narrow looped ribs at a much earlier stage than *woollgari* and is mature at a much smaller diameter, never developing the spectacular distantly ribbed, hypernodose body chamber of the latter.

C. carolinum has some common features, particularly its rather small adult size. It differs in having densely and evenly ribbed inner whorls without strong bullae, and a compressed flat-sided body chamber without the umbilical bullae, strong ventral tubercles and broad venter with looped ribbing of *papale*.

C. papaliforme (Laube and Bruder) (1887, p. 237; pl. 27, figs. 3–4), from the Turonian Greensand of the White Mountain, near Prague, is no more than a deformed *C. papale*.

Occurrence. This is a relatively long-ranging species in the Tuffeau Blanc of Touraine, first appearing in the St. Cyr-en-Bourg Fossil Bed of the Saumur region, and also occurring at Montrichard, Bourré, and Tourtenay (Deux Sèvres). Elsewhere in France there are records from Uchaux (Vaucluse). The species also occurs in the Turonian of Czechoslovakia.

Collignoniceras canthus (Sornay)

Plate 73, figs. 1–4

1951 *Ammonites canthus* d'Orbigny *in litt.*; Sornay, p. 629, text-figs. 1e, 2.
1955 *Ammonites* (*Selwynoceras*) *canthus* d'Orbigny ms; Sornay, fiche 8, figs. 1–2.
1977 *Collignoniceras* (*Selwynoceras*) *canthus* (Sornay *ex* d'Orbigny ms); Hancock, Kennedy and Wright, p. 156.

EXPLANATION OF PLATE 70

Figs. 1–2. *Collignoniceras boreale* (Warren). Cast of the holotype, Alberta Museum Collections no. CT 468, from the basal beds of the Smoky River Shale, Grimshaw, near Peace River, Alberta.

Figs. 3–5. *Collignoniceras papale* (d'Orbigny), nucleus, showing coarse juvenile ornament; SP, from Bourré (Loir-et-Cher).


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KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

Holotype. By monotypy the original of Sornay's (1951), text-figs. 1e, 2, from the Tuffeau Blanc de Touraine of Bourré (Loir-et-Cher), Muséum d'Histoire Naturelle, Paris, no. 6793.

Dimensions	*D*	*Wb*	*Wh*	*Wb:Wh*	*U*
Holotype MNHP 6793	126 (100)	40·8 (32)	49·5 (39)	0·82	48·6 (39)

Description. The holotype and only known specimen consists of the internal mould of a body chamber 126 mm in diameter and an external mould of the umbilicus of the inner whorls. The umbilical mould shows that the species bore seven massive conical umbilical bullae at the smallest diameter visible (Pl. 73, fig. 3) and a similar number on the following whorl, supplemented by three ribs lacking bullae but extending to the umbilicus. From the bullae arose rather strong ribs, usually in pairs, with occasional shorter intercalated ribs. The external mould of the dorsum of the last part of the phragmocone shows each of these ribs to have borne a conical ventral tubercle whence arose a pair of feeble ribs, connecting to feeble siphonal tubercles in the same looped style seen in *Collignoniceras papale* (d'Orbigny).

The body chamber shows coiling to have been moderately evolute, with a small umbilicus comprising 39% of the diameter. The umbilical wall is low and rounded, the flanks flattened and convergent, with a low fastigiate venter which tends to become rounded towards the aperture. The maximum whorl breadth is low on the flanks, close to the umbilical shoulder.

On the early part of the body chamber there are weak umbilical bullae, which give rise to pairs of low, broad, radial ribs, almost insensible save to touch, as are occasional shorter, intercalated ribs. The ribs become progressively finer, denser and more subdued towards the mature aperture, and are gently flexed.

All ribs bear faint, low, rounded ventrolateral clavi which give rise to pairs of low ribs which loop forwards and across the venter to low siphonal clavi linked into a semi-continuous serrated ridge.

The rather poorly preserved sutures of the holotype are approximated, confirming it as an adult.

Discussion. The strongly ornamented inner whorls of *C. canthus* place it in the same group as *C. papale* and *C. turoniense*. It differs from both of these in the marked decline and virtual disappearance of ornament on the outer whorl. We have seen no intermediate forms. *C. carolinum* (d'Orbigny) has delicately and densely ribbed, rather than coarsely bullate inner whorls. The body chambers of the two are more similar, especially in the marked decline in ornament, but *carolinum* is much more compressed and flat-sided, the ribs are stronger, with quite thick ventral development, and stronger siphonal clavi.

Occurrence. *C. canthus* is known only from the Tuffeau Blanc de Touraine of Bourré.

Collignoniceras turoniense (Sornay)

Plate 71, figs. 4–5; Plate 72, figs. 1–3

1951 *Prionotropis turoniense* Sornay, p. 630; pl. 21, figs. 1–3.
1977 *Collignoniceras* (*Selwynoceras*) *turoniense* (Sornay); Hancock, Kennedy and Wright, p. 156.

Holotype. MNHP unregistered, Peron Collection, from Bourré (Loir-et-Cher), by monotypy.

Other specimens studied. MNHP 'A', from Bourré, and two unregistered specimens in the de Grossouvre Collection (Sorbonne, Paris), probably from Bourré.

Dimensions	*D*	*Wb*	*Wh*	*Wb: Wh*	*U*
Holotype	120 (100)	48 (40)	48·3 (40)	1·0	— (—)
MNHP 'A'	107 (100)	52 (49)	44 (41)	1·18	34·5 (32)
Sorbonne, 1	125 (100)	43·5 (35)	48·5 (39)	0·9	34·5 (28)
	at 107·5 (100)	52·5 (49)	43·5 (43)	1·2	23·0 (21)

EXPLANATION OF PLATE 71

Figs. 1–3. *Collignoniceras woollgari* (Mantell) FSR C273, from Poncé, Sarthe.

Figs. 4–5. *Collignoniceras turoniense* (Sornay), the holotype, MNHP, Peron Collection, from Bourré (Loir-et-Cher).

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KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

Description. All known specimens are adults, with two-thirds of the last whorl being body chamber, and none show the early whorls. Coiling is involute on the phragmocone, becoming relatively evolute at maturity, with a deep umbilicus. On the phragmocone the whorl section is depressed, with convergent flanks and a fastigiate venter intercostally. The costal section is even more depressed, the greatest breadth being at the umbilical bullae, and subcarinate. There are five massive blunt conical umbilical nodes per whorl. These give rise to groups of two or three broad, low ribs, with additional ribs intercalated low on the flank between the groups. At the smallest diameters visible these bear blunt conical inner ventrolateral tubercles and small clavate outer ventrolaterals, with a broad low rib connecting them to stronger siphonal clavi borne on a blunt keel. On the last part of the body chamber the intercalated ribs decline, the inner and outer ventrolateral tubercles combine into a blunt transversely elongate tubercle, which gives rise to pairs of ribs which loop to strong siphonal clavi, which become first rounded, then transversely elongate. Some short ventral ribs with a siphonal tubercle are intercalated, to give a serrated blunt keel; there are three to five siphonal nodes to each pair of umbilicals.

On the body chamber the umbilical nodes decline in strength and disappear towards the aperture; intercalated ribs are lost and the primary ribs weaken and become irregular and closely spaced. There are irregularly spaced, clavate ventrolateral nodes, which also decline towards the aperture, with many more ventral ribs and siphonal tubercles than ventrolateral.

The body chamber uncoils markedly and the shell becomes much more evolute as a result. Whorl height: breadth ratio decreases, so that the aperture appears relatively constricted.

None of the specimens shows the suture well but they appear to have comprised broad, plump, rather simple bifid lobes and saddles.

Discussion. The inner whorls of *Collignoniceras turoniense* are easily distinguished from those of *C. woollgari* and *C. carolinum*, which are densely and evenly ribbed by comparison, lacking massive bullae. In middle growth, *C. turoniense* has a much more massive whorl, broad and low rather than narrow ribs and stronger ventrolateral than umbilical nodes. The adults are quite distinct (compare Pl. 62, figs. 1–2 and Pl. 71, figs. 4–5).

C. canthus has similar inner whorls, but becomes virtually smooth in middle and later growth, lacking massive umbilical bullae and strong ventrolateral tubercles.

C. papale juveniles (Pl. 70, figs. 3–5) have many more (typically 9–11) and smaller umbilical bullae, narrow and widely spaced ribs and more markedly clavate ventrolateral and siphonal tubercles. In middle and later growth the differences between the two lie in the predominance of tuberculation in *C. turoniense* and of ribbing in *C. papale*, the latter having the bullae displaced outwards to a lower flank position and strong, narrow, well-differentiated ventral ribs looping between the ventrolateral and siphonal tubercles with intercalatories.

C. carolinum is compressed, parallel-sided and feebly ribbed without strong bullae in middle and later growth.

Occurrence. C. turoniense is known only from the Tuffeau Blanc de Touraine of Bourré.

Collignoniceras boreale (Warren)

Plate 70, figs. 1–2

1930 *Prionotropis borealis* Warren, p. 25, pl. 3, figs. 1–4; pl. 4, fig. 1.
1940 *Selwynoceras borealis* Warren; Warren and Stelck, p. 151.

Types. The holotype is the original of Warren 1930, pl. 3, fig. 1, University of Alberta Museum Collections no. CT 468. Paratypes are CT 469–76, all from the basal beds of the Smoky River Shale, Grimshaw, near Peace River, Alberta.

EXPLANATION OF PLATE 72

Figs. 1–3. *Collignoniceras turoniense* (Sornay) SP, de Grossouvre Collection, probably from Bourré (Loir-et-Cher).

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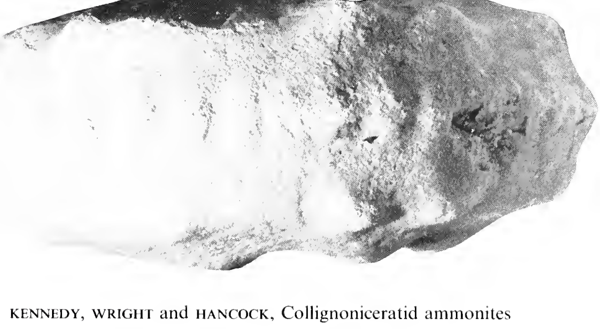

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KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

Description. The holotype, a cast of which is before us, is a slightly distorted mould retaining traces of shell and consists of half a whorl of body chamber and one quarter of a whorl of phragmocone with the following dimensions:

	D	*Wb*	*Wh*	*Wb:Wh*	*U*
costal	92·5 (100)	40 (43)	33·5 (36)	1·19	35·2 (38)
intercostal	90·2 (100)	29·5 (33)	31 (34)	0·98	35·2 (39)

Coiling is moderately evolute, the umbilicus comprising 38% of the diameter, broad and rather shallow. The umbilical wall slopes gently outwards and the whorl section is a compressed oval (whorl breadth to height ratio is 0·98) with flattened flanks. The phragmocone bears three long, straight, prorsiradiate distant ribs. These arise from small umbilical bullae and also bear conical inner and clavate outer ventrolateral tubercles; there is a siphonal row of distant clavi corresponding in position to the ventrolateral tubercles. Two shorter, intercalated ribs are also present, bearing outer ventrolateral and siphonal clavi only. This same style of ventral ornament is shown on the penultimate whorl, preserved in the dorsum of the body chamber, and in two of the paratypes (Warren 1930, pl. 3, figs. 2–3).

On the body chamber the umbilical bullae decline and the ribs become high, distant, and flared into a ventrolateral horn which supports the outer ventrolateral clavus. There is a poorly defined siphonal ridge, accentuated into siphonal clavi, and the upper ventrolateral and siphonal clavi are linked by broad transverse ribs which show incipient doubling with a riblet developing at both front and rear.

The suture is simple and little incised, with broad bifid saddles.

Discussion. Small size and even ventral tuberculation are the features by which Warren's species is most easily distinguished from *C. woollgari*; other differences are noted on p. 572. There are no other species with which it is likely to be confused. Of interest, however, is the striking resemblance of the holotype to specimens of *C. woollgari* from the Black Hills area of the U.S. Western Interior, which also show a very even and equal number of upper ventrolateral and siphonal clavi, never, apparently developing the intercalated ribs and tubercles of what we take as typical *woollgari*. These specimens (so far as we have seen) are much larger when adult and have horns with a triangular outline in ventral view rather than flares. These Interior examples are obviously close relatives of the Canadian form, although their precise relative ages are not known.

Occurrence. As for types.

Genus LECOINTRICERAS gen. nov.

Type species. Ammonites fleuriausianus d'Orbigny, 1841, p. 350.

Diagnosis. Medium-sized, involute during early and middle growth, becoming evolute at maturity. Whorls trapezoidal when young, with sparse conical umbilical tubercles giving rise to pairs of low broad ribs, with occasional intercalatories. All ribs bear outer ventrolateral and siphonal clavi on a fastigiate venter, but the appearance and persistence of inner ventrolateral tubercles is variable. In middle growth the venter often broadens and flattens, the ventrolateral tubercles fuse into a blunt horn and there is a low continuous undulant siphonal ridge, strengthened between horns. The last part of the adult body chamber is contracted, tubular and unornamented except for growth lines, and the aperture is simple.

The suture is simple with broad, asymmetrically bifid E/L, narrower L and smaller bifid L/U_2.

Discussion. The whorl section, massive umbilical tubercles and sparse low ribs of early middle growth, the blunt horns and the tubular body chamber distinguish *Lecointriceras* from all other collignoniceratids and the persistence of short ribs on the sides from contemporaneous *Collignoniceras*. Some *C. woollgari* develop a short, smooth terminal portion to the body chamber but their

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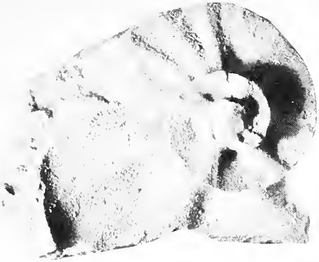
EXPLANATION OF PLATE 73

Figs. 1–4. *Collignoniceras canthus* (Sornay). The holotype, SP 6793, from Bourré (Loir-et-Cher). 3 is the external mould of the nucleus; 4 shows the decline in ornament over the last part of the body chamber.



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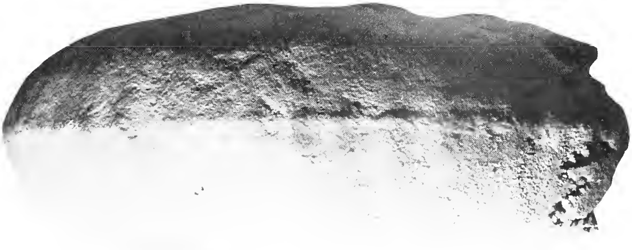

1

KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

compressed, finely ribbed inner and middle growth stages, much narrower flank ribs, retention of multiple siphonal ribs and clavi is distinctive. This ventral ribbing and retention of clavi also distinguish *C. canthus* and *C. papale*; *C. turoniense* has a smooth body chamber, but lacks the massive umbilical tubercles and ventral horns in middle growth and on the first part of the body chamber. The phragmocone of some *Lecointriceras* and the adult shell of *C. boreale* are superficially similar, but Warren's species has compressed finely ribbed inner whorls and on the outer whorl, which is slender and rounded intercostally, the ribs lack a massive bulla, are narrower and produced into a narrow flared bituberculate horn rather than the single broad protuberance seen in *Lecointriceras*.

As is discussed below, *Ammonites vielbancii* d'Orbigny, 1850 is a synonym of *A. fleuriausianus*. Schlüter (1871, pp. 21-22) believed the former might be a synonym of *Mammites nodosoides* (Schlüter), and Collignon (1939) and Wiedmann (1960, 1964) referred it to *Mammites*. As Pervinquière (1907, p. 311) noted, the siphonal tubercles are quite distinctive.

In Europe *Lecointriceras* first appears in the mid-Turonian St. Cyr-en-Bourg Fossil Bed, accompanying typical *Collignoniceras*. Its origins may lie in one of the undescribed *Thomelites*-like forms occurring in the earliest English Turonian.

Occurrence. Widespread in the French Turonian (Touraine and Aquitaine); also occurring in northern Spain, Czechoslovakia, north Germany and southern England.

Lecointriceras fleuriausianum (d'Orbigny)

Plate 74, figs. 1-10; Plate 75, figs. 1-5; text-figs. 8, 9

1841 *Ammonites Fleuriausianus* d'Orbigny, p. 350, pl. 107, figs. 1-3.
1841 *Ammonites Woollgari* d'Orbigny, p. 352 (*pars*), pl. 108, figs. 1-3.
1850 *Ammonites Vielbancii* d'Orbigny, p. 189.
1860 *Ammonites Fleuriausianus* (d'Orbigny); Courtiller, p. 250, pl. 3, fig. 1.
1867 *Ammonites Fleuriausianus* d'Orbigny; Courtiller, p. 7, pl. 7, figs. 1-4.
non 1869 *Ammonites Fleuriauanus* d'Orbigny; Schloenbach, p. 291.
1871 *Ammonites Vielbancii* d'Orbigny; Schlüter, p. 19 et seq.
?1872 *Ammonites Fleuriausianus* d'Orbigny; Schlüter, p. 28, pl. 10, figs. 1-3.
1887 *Acanthoceras Fleuriausianum* d'Orbigny; Laube and Bruder, p. 234.
non 1902 *Acanthoceras Fleuriausianum* d'Orbigny; Petrascheck, p. 147, pl. 11, figs. 1a-b, 2.
1907 *Ammonites Vielbancii* d'Orbigny; Pervinquière, p. 311.
1939 *Mammites Vielbancii* d'Orbigny; Collignon, p. 81, pl. 11, figs. 1, 2.
1946 *Ammonites vielbancii* d'Orbigny; Sornay, p. 213.
1946 *Ammonites fleuriausianus* d'Orbigny; Sornay, p. 214.
1960 *Mammites vielbanci* (d'Orbigny); Wiedmann, p. 721.
1977 *Collignoniceras* (*Selwynoceras*) *fleuriausianum* (d'Orbigny); Hancock, Kennedy and Wright, p. 156.

Type series. *Ammonites fleuriausianus* has been a poorly understood species, although the type figure (if taken to be natural size) is an accurate representation of the middle growth stages and the type series survives. In his original description d'Orbigny recorded the species 'en place dans la craie chloritée ou craie tufau des Martrous,

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EXPLANATION OF PLATE 74

Figs. 1-10. *Lecointriceras fleuriausianum* (d'Orbigny). 1-2, the lectotype of '*Mammites*' *vielbancii* (d'Orbigny), MNHP 6779, (d'Orbigny Collection) from Saumur (Maine-et-Loire). 3-5, CS 629b, from the environs of Saumur (Maine-et-Loire), a juvenile of moderate inflation. 6-7, the lectotype, MNHP 6777b (d'Orbigny Collection) from the Calcaire à Céphalopodes of Rochefort (Charente-Maritime). 8-10, FSM 125, from Poncé, Sarthe, a hypernodose juvenile.

PLATE 74


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KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

près de Rochefort (Charente-Inférieur); M. Dufrenoy l'a aussi du même lieu; M. d'Archiac l'à observée à Gourdon (Lot); MM. Dufrenoy et Graves l'ont trouvée, aux environs de Saumur' (d'Orbigny 1841, p. 352). In the posthumous catalogue of his collection (dating from 1858–60) the following are recorded:

6777 Saumur, Maine-et-Loire, 3 specimens (4 are present).
6777a Martrous, 1 specimen (missing).
6777b Rochefort, Charente-Inférieur, 2 specimens (3 are present).
6777c Chatellerault, Vienne, 2 specimens (1 missing).

The Saumur specimens belong to at least two species. The first, 34·5 mm in diameter, is a crushed tuffeau specimen, and is labelled [La] Flèche. It has rather flattened flanks, with umbilical bullae giving rise to 2–3 flexuous ribs with some intercalatories, giving a total of sixteen ribs per whorl. There are distinct conical inner ventrolateral tubercles and subequal outer ventrolateral and siphonal clavi, which show it to be a *fleuriausianum*, as is a second individual with an estimated diameter of 55 mm, but having little indication of inner ventrolateral tubercles and weak siphonal clavi.

A third specimen, 71 mm in diameter, and labelled Saumur, is a worn, wholly septate *Jeanrogericeras reveliereanus*. The final specimen has 'Rochefort' written on it in pencil and is also a *J. reveliereanus*, with a diameter of 104 mm. Superficially it could be the basis of d'Orbigny's side view but it lacks all signs of a siphonal clavus.

Two specimens from Rochefort are associated with a plaque labelled 6777b. Both are well preserved on one side, the larger 55 mm in diameter, the smaller 35 mm, and appear to be part of d'Orbigny's original suite. The larger of these, the most typical in the series, is here designated lectotype.

The single specimen to survive of those originally labelled 6777c is a very battered, crushed, distorted specimen in yellow tuffeau. Umbilical bullae give rise to pairs of ribs, terminating in rounded ventral clavi, with no sign of siphonal nodes, suggesting it to be a mammitid or *Jeanrogericeras*. Chatellerault was not mentioned as a locality by d'Orbigny in his original description and thus this specimen is not a syntype.

The types of *A. vielbancii*, herein regarded as a synonym, also present a confused situation. It is a *Prodrome* species introduced (d'Orbigny 1850, p. 189, no. 11) as follows: '*Vielbancii*, d'Orb., Paléont., 1, p. 352, pl. 108, figs. 1–3. Sous le faux nom de *Woolgarii*, Mantell. Martrous, Saumur, Tourtenay.'

In *Paléontologie Française* (1841, p. 354) he cites the species as occurring more widely, but we take these references (which include England) to be to the true *Collignoniceras woollgari*.

The d'Orbigny catalogue lists the following:

6779 Saumur, Maine-et-Loire, 3 (4 specimens).
6779a Bords de la Vienne, 2 (1 missing).
6770b Rochefort, (illegible) (missing).

whilst d'Orbigny notes that his lateral view (pl. 108, fig. 1) is of a specimen in his collection and the apertural view is of a specimen in the École des Mines.

Inspection shows that the d'Orbigny specimens have become mixed. The Rochefort specimen is present, but labelled 6779. It is poorly preserved, but may be the basis of d'Orbigny's side view. The specimen from the Bords de la Vienne is not a syntype; it is a large *Mammites nodosoides*. As Sornay has discussed (1946, p. 214), the specimen figured in side view by d'Orbigny does not look like any of the poor specimens which survive in his collections under the name *vielbancii*, and certainly there is little resemblance between d'Orbigny's figures and the specimen re-figured by Collignon as 'type'—which we take to be a valid lectotype designation. Even the specimen in the School of Mines upon which d'Orbigny (1841, p. 354) said his apertural view is based (no. A35.3, locality unknown: 'Bassin de la Loire, achête de Stur' reads the label) does not correspond to the figure (compare text-figs. 8 A–C and 9 A–B). We would suggest, in fact, that the illustrations are composite, the side view being based on the poor Rochefort specimen of appropriate size, combined with the ornament of the huge *Mammites* no. 6779a from the 'Bords de la Vienne', the apertural view being based on the School of Mines specimen plus the *Mammites*.

Description. The smallest individuals we have seen are approximately 30 mm in diameter. At this size the coiling is fairly involute (umbilicus = 25% or less of diameter) and the umbilicus quite deep, with a rounded wall. The

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EXPLANATION OF PLATE 75

Figs. 1–5. *Lecointriceras fleuriausianum* (d'Orbigny). 1–3, FSM 120, 4–5, FSM 121, compressed and inflated middle-aged individuals from the Turonian of Sarthe.

PLATE 75


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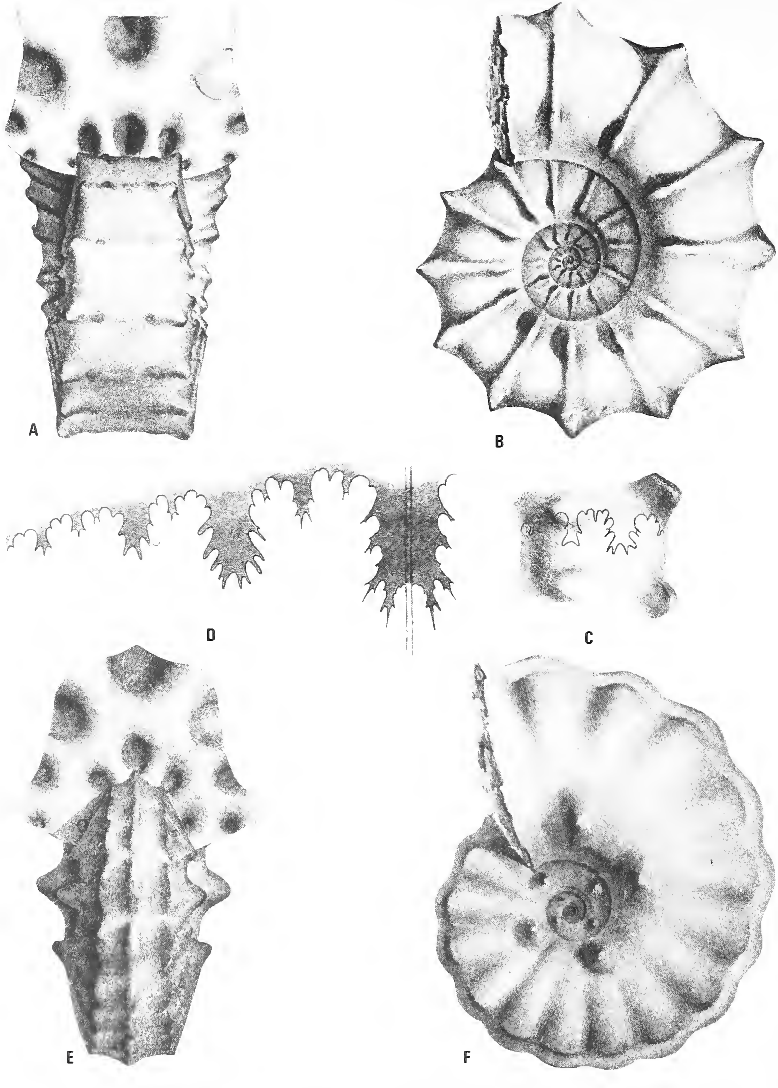
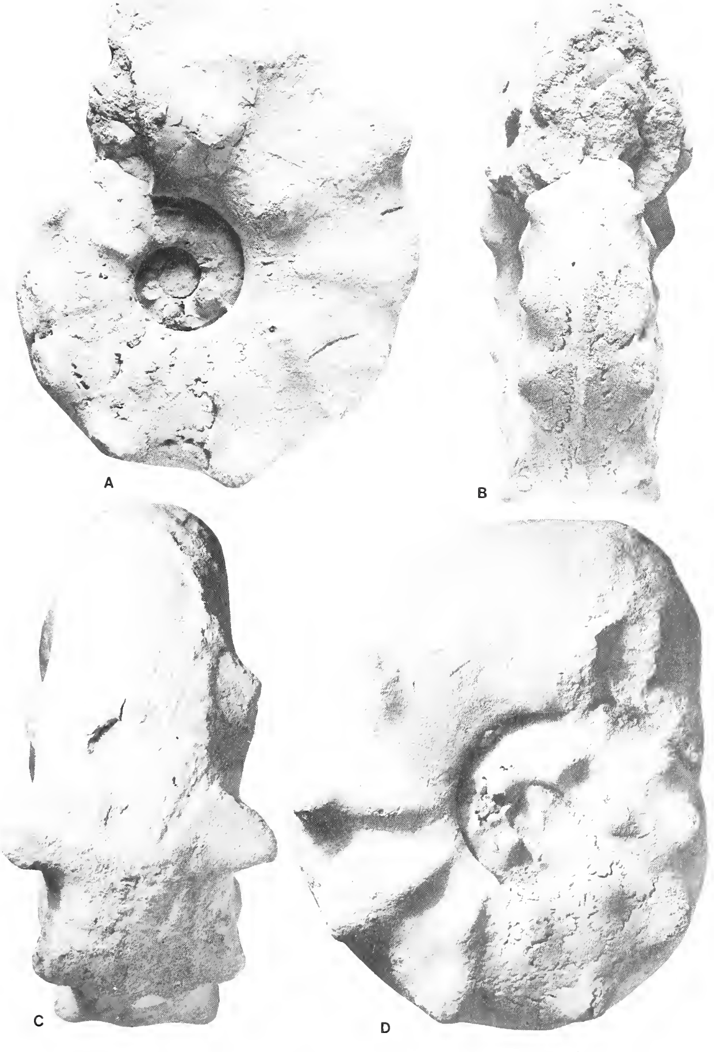
KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites



TEXT-FIG. 8. A–C, copies of d'Orbigny's original figures of '*Ammonites Woollgari* Mantell' (1841, pl. 108, figs. 1–3) = *Ammonites vielbancii* d'Orbigny, 1850. The illustration is said in the text to be reduced by a third and on the plate by a half. D–F, copies of d'Orbigny's original figures of *Ammonites fleuriausianus* (1841, pl. 107, figs. 1–3). The illustration is said to be reduced by a third.



TEXT-FIG. 9. *Lecointriceras fleuriausianum* (d'Orbigny) A, B, EMP A35.3, 'Bassin de la Loire, achête de Stur' — the original of d'Orbigny's (1841) pl. 108, fig. 2. Reduced ×0·66. C, D, FSM 119, an adult from Poncé, Sarthe(?) showing the smooth, tubular termination to the body chamber. Reduced ×0·6 approx.

intercostal whorl section is typically compressed, with the greatest breadth low on the convergent flank and with rounded shoulders and venter. In the costal section the greatest breadth is at the umbilical bulla and whorl breadth to height ratios vary greatly up to 1:2, with concave inner flanks and a fastigiate venter.

Ornament consists of weak to strong conical umbilical bullae, 7–9 per whorl, giving rise to pairs of low, broad straight ribs, with occasional intercalated ribs arising low on the flank. The ribs decline somewhat in strength on the mid-flank but then strengthen into rounded inner ventrolateral tubercles. These are connected by a strengthened rib to strong clavate outer ventral tubercles, from which a broad subdued rib sweeps forwards to a subequal clavate siphonal tubercle.

This general style of ornament varies from individual to individual, with slender, feebly bullate forms with weak ribs (Pl. 74, figs. 6–7) and strongly bullate inflated forms with strong ribs (Pl. 74, figs. 8–10). In many individuals, including the lectotype, there are no inner ventrolateral tubercles below diameters of 35–42 mm; occasionally they do not appear until 55 mm.

From 50 mm onwards there is usually a change in ornament; the bullate umbilical tubercles become more distant, the associated ribs lower and broader, effaced at mid-flank in some specimens. There are usually 7–9 bullae and 16–22 ribs per whorl. The outer ventral tubercles weaken rapidly and disappear; at the same stage the inner ventrolateral tubercles strengthen without joining the weakening ventral tubercles (Pl. 77, fig. 4). The former inner ventrolateral tubercles gradually develop into strong to massive horns on the shoulder, triangular when viewed ventrally and relatively narrow when viewed laterally, developed both upwards and outwards. At this, the '*vielbancii*' stage, the venter becomes relatively broad, with a continuous low undulant siphonal ridge, strengthened between horns at what corresponds to the site of the now coalesced siphonal clavi. The shell now closely resembles a *Mammites* in all but the siphonal ridge.

This style of ornament extends onto the first half of the adult body chamber, by which stage the siphonal ridge may become very reduced (text-fig. 9 C–D). On the last half of the body-chamber, extending for just over a quarter whorl, all ribs and tubercles are lost and there is a relatively smooth, compressed and constricted terminal portion with convergent sides, broadly rounded shoulders and a flattened venter, ornamented only by low, prorsiradiate growth striae. The aperture is simple and entire.

The suture line is relatively simple, with a broad medial element to E; broad, asymmetrically bifid E/L; narrow, symmetrically bifid L; smaller asymmetrically bifid L/U_2; and small and narrow U_2.

Discussion. D'Orbigny's original figure is idealized and bears little relationship to the surviving syntypes in his collection; in his explanation of the plate he says the figure is reduced by a third, so that the specimen is far larger than the proposed lectotype, being, presumably, the Martrous specimen which is now lost. The lectotype agrees well with the dimensions given by d'Orbigny for his smaller specimen (1841, p. 350). Juveniles of this species vary in the strength of the umbilical tubercles; the lectotype is worn but was probably a slender, weakly tuberculate variant. This variation continues into middle growth, where both slender and robust individuals are known (Pl. 74, figs. 3–10).

The striking contracted tubular termination of the body-chamber of adults of this species occurs at disparate sizes. Most specimens we have seen appear to be juveniles of individuals that would have been adult at approaching 150 mm diameter, but a specimen in the collections at Le Mans is complete at only 100 mm, with half a whorl of the body chamber so modified. Unfortunately our sample of adults is too small to show if the species shows a size dimorphism.

Some of the early references to this species are doubtful. Schloenbach's (1869) material probably belongs to *Barroisiceras*, whilst Schlüter's specimen (1872, p. 28; pl. 10, figs. 1–3), if indeed a true *L. fleuriausianum*, has suffered great *post-mortem* crushing to give a very compressed whorl section.

Lecointriceras carinatum sp. nov., described below, differs from *L. fleuriausianum* in its smaller adult size, early loss of umbilical tubercles and ribs, together with retention of a fastigiate venter on the adult body chamber, which bears an undulose siphonal and flanking, semi-continuous lateral

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EXPLANATION OF PLATE 76

Figs. 1–2. *Collignoniceras carolinum* (d'Orbigny), MNHP W8, an adult body-chamber from an unknown locality in the Tuffeau Blanc de Touraine.

Figs. 3–5. *Lecointriceras carinatum* sp. nov. The holotype, EMP, Poncé(?), Sarthe.

PLATE 76

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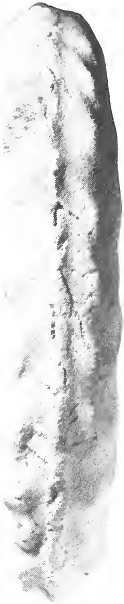

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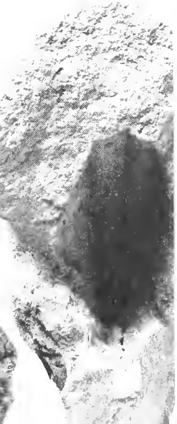

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KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

keels formed by coalescence of ventral and siphonal clavi. Differences from *L. costatum* sp. nov. are discussed below.

The combined features of *L. fleuriausianum* as here described are so distinctive that confusion with any other collignoniceratid is unlikely. Juveniles have a passing similarity to some Barroisiceratinae; species of *Barroisiceras* have less prominent umbilical tubercles and many strong, narrow ribs at a comparable size; whilst *Forresteria* and similar genera have an additional, lateral row of tubercles. In middle growth there is a superficial resemblance to *Mammites*, but that genus never develops a siphonal tubercle.

Occurrence. This species is common at the level of the mid-Turonian St. Cyr-en-Bourg Fossil Bed in the Saumur area in Touraine, occurs in northern Aquitaine, Vaucluse, Provence, northern Spain, north Germany(?), and Devon, England.

Lecointriceras carinatum sp. nov.

Plate 76, figs. 3–5

Holotype. A body-chamber in the Collections of the School of Mines, Paris, labelled Poncé(?) and in pencil "'*Choffaticeras*' typique; '*Thomasites*'". It is clearly from either Poncé or Bourré.

Description. The holotype and only known specimen is a half whorl, largely body-chamber and in typical rather coarse tuffeau preservation. Coiling is very involute with a tiny umbilicus (10% of diameter). The dorsum of the specimen (Pl. 76, figs. 3–5) shows the whorl section of the inner whorls to have been slightly depressed, with the greatest breadth at the umbilical shoulder, concave, convergent flanks and a fastigiate venter. There were sparse umbilical bullae giving rise to low, broad ribs which terminate at elongate ventrolateral clavi, with a sharp siphonal keel, accentuated into clavi which correspond to the ventrolaterals.

On the first part of the body chamber ornament is similar. There are low broad flank ribs which terminate in long clavi linked into undulant keels, flanking a similarly undulant keel in which clavi merge towards the aperture.

The poorly preserved suture shows a typical broad bifid E/L, narrow L, and broad L/U_2, all with only minor incisions.

Discussion. The single known individual is so distinctive that erection of a new species is justified. The inner whorls are typical of a *Lecointriceras*, differing from *L. fleuriausianum* in the sparse, low, broad ribs and presence of keels. Absence of a quadrate-whorled *vielbancii* stage makes the body chamber equally distinctive. There is a striking similarity to *Masiaposites* Collignon, 1965, a late Turonian form best known from Madagascar and currently regarded as a vascoceratid; however its siphonal keel is entire and its sutures are much more deeply incised, rather like that of *Neoptychites*, and the siphonal keel continuous throughout ontogeny.

Occurrence. The species is known only from the type occurrence at Poncé(?), Sarthe (mid-Turonian).

Lecointriceras costatum sp. nov.

Plate 77, figs. 1–3

1902 *Acanthoceras Fleuriausianum* d'Orbigny; Petrascheck, p. 147, pl. 11, figs. 1–2.

Holotype. AM 55 from the Tuffeau Blanc of Saumoussay, Maine-et-Loire, France.

Other specimens studied. AM 22 from Montsoreau, Maine-et-Loire; AM 53, 54, 60, 101, and 102 from Saumoussay, Maine-et-Loire, France.

EXPLANATION OF PLATE 77

Figs. 1–3. *Lecointriceras costatum* sp. nov. 1–2, the holotype, AM 55, from Saumoussay, Maine-et-Loire; 3, AM 53 from Saumoussay, Maine-et-Loire.

Fig. 4. *Lecointriceras fleuriausianum* (d'Orbigny). AM 36 from Saumoussay, Maine-et-Loire; oblique view to show the concurrent weakening of the outer and the strengthening of the inner ventrolateral clavi.

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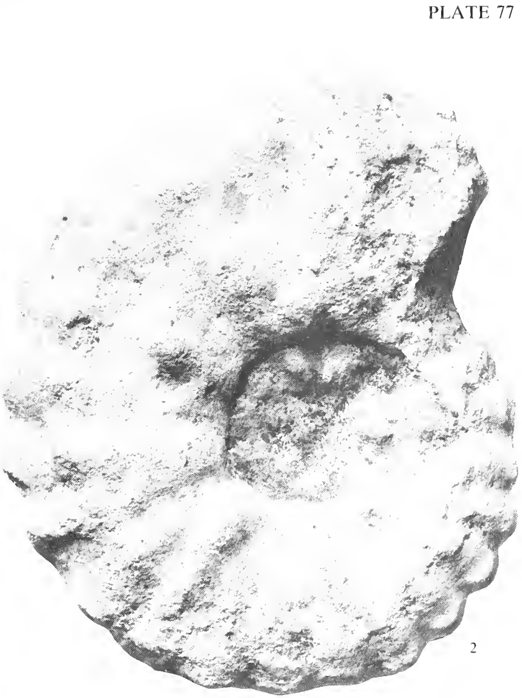

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KENNEDY, WRIGHT and HANCOCK, Collignoniceratid ammonites

Dimensions

	D	*Wb*	*Wh*	*Wb:Wh*	*U*	*R*
AM 55 (Holotype)	125·5 (100)	— (—)	53+		33	*c.* 21
AM 53	95 (100)	*c.* 36 ( )	*c.* 44·5	0·81		
AM 60	183 (100)	71	54	0·76		
AM 101	165 (100)					14
	at 129 (100)	50·5	56	0·90	35	17
AM 102	109 (100)	40	45	0.89	30	

Description. This is a moderately evolute and relatively compressed *Lecointriceras*, with the greatest whorl-breadth still at the umbilical tubercles in costal section. Of the fourteen to twenty-one ribs slightly less than half are long; the shorter ribs start about halfway up the sides. Each long rib bears an umbilical bulla, a clavus high on the sides rather than in the normal position of an inner ventrolateral, an outer ventrolateral clavus and a siphonal clavus. The siphonal clavi are elevated above the shoulder clavi and up to a diameter of 125 mm may form a nodose keel. During the earlier ontogeny the high lateral clavi are weaker than those on the shoulders, but at diameters which may be anything from 70–110 mm the upper lateral clavi strengthen and the shoulder clavi weaken; the upper lateral clavi eventually become ventrolateral horns on the body-chamber. Similarly the umbilical bullae become weak and are not present on all long ribs beyond diameters of 100 mm. The adult body-chamber begins at about 125 mm diameter, but none of the specimens seen has well-preserved sutures.

Discussion. L. costatum differs from *L. fleuriausianum* in having a more compressed whorl section with flatter sides, weaker umbilical tubercles (which are, however, still stronger than in typical *Collignoniceras* spp.), siphonal clavi elevated above the outer ventrolateral clavi and persistent outer ventrolateral and upper lateral clavi through much of ontogeny, certainly from a diameter of 40 mm to about 125 mm.

Occurrence. All known French specimens are from the mid-Turonian Tuffeau Blanc of the Saumur region. In that formation ammonites are most common in the St. Cyr-en-Bourg Fossil Bed, but we have not found any specimens of *L. costatum* ourselves; as Amedro and Badillet (1978) have pointed out, ammonites do occur at other levels in the Tuffeau Blanc. The specimens figured by Petrascheck were from Labiatus-Pläner at Leubnitz and Briessnitz near Dresden in the German Democratic Republic.

EVOLUTIONARY AND STRATIGRAPHIC CONCLUSIONS

The origins of *Collignoniceras* and the Collignoniceratidae seem to lie in late *Thomelites* of Acanthoceratidae, the transition involving a raising of the mid-venter and forwards displacement of siphonal clavi and ribs to give a ventral chevron ornament. This is indicated by a few scraps we have seen from the Cenomanian–Turonian boundary beds in Devon. *Lecointriceras* may also arise in this way, or be a slightly later offshoot from already distinct *Collignoniceras*: the low Turonian record is too poor to be certain. In the United States *C. woollgari* overlaps late *Mammites nodosoides* (W. A. Cobban, *in litt.*); in Europe *C. woollgari* and *L. fleuriausianum* co-occur in the earliest of the French Tuffeau faunas. *C. woollgari* is a long-ranging species which occurs throughout the mid-Turonian zone of which it is the index species. In Europe we have detected no evolutionary changes in the successive *Collignoniceras* faunas studied. In contrast, W. A. Cobban's work on western interior sequences allows recognition of an early form, in which both long and short ribs persist in middle and later growth, and a late form in which long ribs dominate. That this is not seen in Europe suggests that typical individuals had reached the U.S. Western Interior by the beginning of *woollgari* Zone time, and underwent subsequent local differentiation which did not occur in European populations. The other collignoniceratids described here are mostly long ranging: *C. carolinum*, *C. papale* and *L. fleuriausianum* range through most of the *woollgari* Zone. *L. costatum* is restricted to the lower part, *L. carinatum*, *C. turoniense* and *C. canthus* to middle and low upper levels in the Zone.

These disappointingly meagre stratigraphic conclusions mean that any subdivision of the broad *woollgari* Zone must be based on other groups. We have already suggested that a local sequence of *Romaniceras* can be used in Touraine: *R.* (*R.*) *kallesi* (oldest) → *R.* (*Yubariceras*) *ornatissimum* → *R.* (*R.*) *deverianum* (youngest) (Hancock, Kennedy and Wright 1977; Kennedy, Wright and

Hancock, this volume). The lower two of these are clearly correlated with the *woollgari* Zone, but we are not entirely certain whether *R. deverianum* marks a level at the very top of the *woollgari* Zone or at the base of the succeeding *Subprionocyclus neptuni* Zone. Ammonites are too scarce at this level in both England and northern France for us to be sure either way; *Romaniceras* appears to be absent from the rich *neptuni* Zone fauna of the Chalk Rock (Wright 1979) but occurs in the Uchaux (Vaucluse) faunas.

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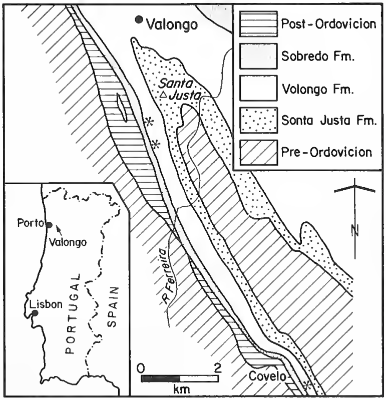
THE TRILOBITE *ECCOPTOCHILE* FROM THE ORDOVICIAN OF NORTHERN PORTUGAL

by M. ROMANO

ABSTRACT. The eccoptochilinid trilobite fauna from the Ordovician of the Valongo area, north Portugal, is revised. The holotype of *Eccoptochile* (?*Eccoptochile*) *mariana* (Verneuil and Barrande, 1855) is redescribed and figured and the species is restricted to the type specimen and two specimens from Valongo. Specimens previously described as *E.* (?*E.*) *mariana* from Spain, north Portugal, and southern England, together with other and new material from Portugal are here included within the new species *E.* (*Eccoptochile*) *almadenensis*. *E.* (*Eccoptochile*) cf. *clavigera* (Beyrich, 1845) is recorded from the Valongo area.

THIS revision of the genus *Eccoptochile* from the Ordovician of north Portugal forms part of a larger project concerned with systematic description and distribution studies of the Ordovician trilobite faunas of that region. The faunas from the Valongo area about 10 km east of Porto (text-fig. 1) have been well known since Delgado published extensive faunal lists from the beds (1908, pp. 106–109); only '*Uralichas Ribeiroi*' (Delgado, 1892, 1897) was described. Delgado listed '*Cheirurus claviger* Beyrich', '*Cheirurus Guillieri* Tromelin (aff. *C. claviger* Beyrich)', and '*Cheirurus* sp. n. (aff. *C. Sedgwicki* McCoy)' from his uppermost division, the 'Schistes à *Uralichas Ribeiroi*', of the '*Ordovician moyen*' from the Valongo area. Prior to this Sharpe (1849) had recorded '*Chirurus*' from the Porto region but this specimen was later recognized by Salter (1853) as '*Placoparia Zippei*, Boeck'. The most recent systematic work on this group was by Curtis (1961) who apparently regarded all three of the species listed by Delgado as conspecific and referred them to *Eccoptochile mariana* (Verneuile and Barrande).

The 'Schistes à *Uralichas Ribeiroi*' have generally been regarded as Llandeilo in age (Costa 1931;



TEXT-FIG. 1. Simplified geological map of the area south of Valongo (after Delgado 1908), showing localities (asterisks) where the species of *Eccoptochile* described in the text have been recorded.

[Palaeontology, Vol. 23, Part 3, 1980, pp. 605–616, pls. 78–79.]

Teixeira 1955; Thadeu 1956) and more recent work on certain elements of the fauna, notably harpids (Romano 1975), placopariids (Romano 1976), and dionidids (Henry and Romano 1978), suggests a possible Lower Llandeilo age, equivalent to the *Placoparia* (*Coplacoparia*) *tournemini* biozone of Spain and Brittany (Hammann 1971*a*; Henry and Clarkson 1975). The 'Schistes à *Uralichas Ribeiroi*' are included within the upper part of the Valongo Formation (Romano and Diggens 1973-1974) which is a thick sequence of argillaceous sediments ranging in age from Upper Llanvirn (*Didymograptus murchisoni* Zone) to ?Upper Llandeilo. The formation crops out about 10 km east of Porto and it is from this area that the bulk of the collections were made by Delgado, Wattison, and the present author with J. N. Diggens. The problem of accurately locating the material collected by Wattison was outlined earlier (Romano 1976) and similar difficulties arise with some of the specimens from the Delgado collection.

The collections used in this paper are housed in the British Museum (Natural History), London (Wattison Collection—(BM In)); École Nationale Supérieure des Mines, Paris (T); Serviços Geológicos, Lisbon (Delgado Collection—SG); Institute of Geological Sciences (GSM), and in the Geology Department, University of Sheffield (SU).

SYSTEMATIC PALAEONTOLOGY

General remarks. E. (*Eccoptochile*) *clavigera* (Beyrich, 1845), *E.* (*?Eccoptochile*) *mariana* (Verneuil and Barrande, 1855) and *E.* (*?Eccoptochile*) *guillieri* (Tromelin *in* Guillier, 1873) form a relatively homogeneous group within which the north Portuguese specimens clearly belong. The first two are generally regarded as valid species but *E.* (*?E.*) *guillieri* has fairly recently been placed into synonymy with *E.* (*?E.*) *mariana* by Hammann (1974, p. 105). *E.* (*?E.*) *guillieri* was compared with *E.* (*E.*) *clavigera* by Tromelin and Lebesconte (1876, p. 637) who noted that the glabella of the former differed from that in *E.* (*E.*) *clavigera* in being smooth, more convex, with the posterior end of the axial furrows curved inwards more strongly. The outline diagrams and locality information of the specimens of *E.* (*?E.*) *guillieri* shown in text-fig. 2 (g, h, i) were kindly sent to me by Dr. J.-L. Henry; they are of the holotype (2g) and a topotype (2h, i from the Kerforne collection). The latter is an incomplete but undeformed specimen, preserved in a nodule, from the type locality 'la Butte du Creux', near Saint-Denis-d'Orques (Sarthe); Dr. Henry informed me that it is Llanvirn or Llandeilo in age. This topotype shows a very narrow (sag.) frontal area and a strongly and evenly curved glabella in lateral view. From these two specimens *E.* (*?E.*) *guillieri* warrants retention as a separate species and is treated as such in this paper.

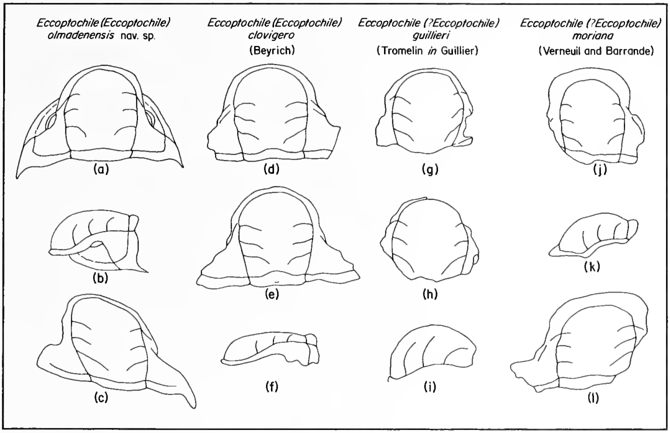
The most commonly reported species of *Eccoptochile* in Iberia and the Armorican Massif is *E. mariana* (Curtis, op. cit.; Hammann 1971, 1974; Lindström, Racheboeuf and Henry 1974), but a recent study of the holotype of this species by the author suggests that the species has been interpreted too widely in the past. The holotype of *mariana* is redescribed and figured here.

Prantl and Přibyl (1948) erected the subgenus *Eccoptochile* (*Eccoptochiloides*) on the basis of the thorax containing only ten segments and the four pairs of pleural spines on the pygidium. As the thorax and pygidium of *E.* (*?E.*) *mariana* are unknown the subgeneric status of *mariana* is still in doubt.

The morphological terms used are essentially those listed by Harrington *et al.* (*in* Moore, 1959). Lateral glabellar lobes and furrows are labelled 'L' and 'S' respectively and are numbered from the posterior forwards. The classification employed is that of Henningsmoen (*in* Moore, 1959) and Lane (1971).

Family CHEIRURIDAE Hawle and Corda, 1847
Subfamily ECCOPTOCHILINAE Lane, 1971
Genus ECCOPTOCHILE Hawle and Corda, 1847

Type species. Cheirurus claviger Beyrich, 1845



TEXT-FIG. 2. Outline sketches of the cephala or cranidia of the holotype and other material of selected species of *Eccoptochile*: *a–c*, *Eccoptochile* (*Eccoptochile*) *almadenensis* sp. nov. *a*, *b*, Holotype (selected), from Hammann, 1974, pl. 12, fig. 192c and 192b (reversed for comparison); *c*, from Curtis, 1961, pl. 2, fig. 1. *d–f*, *Eccoptochile* (*Eccoptochile*) *clavigera* (Beyrich); *d*, Holotype, from Beyrich, 1845, pl. (unnumbered), fig. 2; *e*, *f*, from Barrande, 1852, pl. 40, figs. 1, 2. *g–i*, *Eccoptochile* (?*Eccoptochile*) *guillieri* Tromelin *in* Guillier); *g*, Holotype, *h*, *i*, Topotype. Both drawings taken from photographs and drawings supplied by Dr. J.-L. Henry. *j–l*, *Eccoptochile* (?*Eccoptochile*) *mariana* (Verneuil and Barrande); *j*, *k*, Holotype, from Verneuil and Barrande, 1855, pl. 23, fig. 4 and present paper, pl. 1, figs. 1–4; *l*, Paratype, from Curtis, 1961, pl. 1, fig. 1 and refigured here, pl. 1, figs. 5, 6. Sketches drawn to approximately the same size.

Eccoptochile (?*Eccoptochile*) *mariana* (Verneuil and Barrande, 1855)

Plate 78, figs. 1–7; text-fig. 2 j–l

*1855 *Cheirurus marianus* Verneuil and Barrande, p. 970, pl. 23, fig. 4 (not p. 972, pl. 28 as stated by Hammann, 1974, p. 105).

1961 *Eccoptochile mariana* (Verneuil and Barrande); Curtis, p. 6, pl. 1, fig. 1 (not pl. 1, fig. 2, pl. 2; figs. 1, 2, ?pl. 3, fig. 1).

1974 *Eccoptochile* cf. *mariana* (Verneuil and Barrande); Hammann, p. 105 (referring to Curtis, 1961, pl. 1, fig. 1).

Diagnosis. (Modified from Verneuil and Barrande, 1855, p. 970.) A species of *Eccoptochile* with the following characteristics: strongly arched glabella with evenly curved longitudinal profile and, with occipital ring vertical, highest part level with the anterior part of L2. Wide frontal area over 12% of the glabellar length (excluding occipital ring) and consists of a more or less flat preglabellar field and a gently rounded anterior border. Palpebral lobe level with the posterior part of L2 to the posterior part of L3. Eye ridges are faintly visible running from the anterior of the palpebral lobe towards S3. Hypostoma, thorax, and pygidium unknown.

Type and figured material. Holotype: T 150 (Plate 78, figs. 1–4). Internal mould of incomplete cranidium (Verneuil and Barrande, 1855, pl. 23, fig. 4). Other figured material. BM In49177 (Plate 78, figs. 5, 6) (Curtis, 1961, pl. 1, fig. 1); BM In49182 (Plate 78, fig. 7).

Horizon and locality. Holotype from 'Puente de las Ovejas' near Ciudad Real, Spain; Upper Llandeilo (Hamman, 1974, p. 105). BM In49177 and In49182 from Covelo, near Valongo, north Portugal; upper part of Valongo Formation, probably Lower Llandeilo.

Description of holotype. Measurements with occipital ring vertical: length (sag.) of glabella (excluding occipital ring) and frontal area, 15·75 mm; length of glabella, 14·00 mm. Glabella longer than wide with even, outwardly curved lateral margins, slightly indented at S3, and a broadly rounded anterior margin; widest part of the glabella just anterior to the S2 furrows. L1 lobes subtriangular in outline, about one-quarter glabellar length and delimited by deep, well-marked S1 furrows which have an S-shaped trace and die out just under one-third glabellar width from axial furrows. L2 lobes rectangular in outline, shorter (trans.) than L1 and about the same length (exsag.). S2 furrows shorter and less well-marked than S1, evenly curved, parallel to the abaxial part of S1, starting just posterior to the midlength of the glabella. L3 similar in shape and orientation to L2, but appear to be very slightly longer. S3 furrows parallel to S2 but do not reach as far towards the midline. S3 start at nearly two-thirds the glabellar length from the posterior margin.

Glabella strongly arched transversely with a subtriangular cross section. Longitudinally (occipital ring vertical) the glabella is evenly curved dorsally, highest part lying above the anterior part of L2. Median glabellar lobe, L2 and L3 without independent convexity but L1 lobes are slightly bulbous. Frontal area wide (sag., exsag.), of more or less constant width around the frontal glabellar lobe but increasing at anterolateral corners where anterior margin of fixed cheek turns back rather sharply to give a more angular, although still rounded outline. Frontal area consists of an inner preglabellar field which is more or less flat or very slightly upwardly concave which grades into the frontal lobe of the glabella without a marked furrow. Preglabellar field also grades into anterior border which is gently rounded and lies horizontally. Anterolaterally the border is slightly wider. At anterolateral corners border appears to be directed more upwards but this may be an effect of deformation. Axial furrows well-marked from the occipital furrow to S3 where there is a deep pit just abaxial to axial furrow. Anterior to this pit axial furrow rapidly dies out. Occipital furrow curved forwards behind the median glabellar lobe and where it runs into the axial furrows, deep posterior to the L1 lobes and wide and shallow in the median part. Occipital ring not complete: posterior to the L1 lobes ring curves forwards. Incomplete free cheeks are narrow (trans.) opposite the palpebral lobes and fairly flat. Posterior border furrow deep, starting from the axial furrow just posterior to the occipital furrow. Posterior border narrow (exsag.) and convex. Convex (tr.) palpebral lobe slightly curved, lying oblique to sagittal line and separated from fixed cheek by a well-marked palpebral furrow which dies out anteriorly along length of lobe. Faint eye ridge extends from palpebral lobe to axial furrow at S3. Palpebral lobe level with posterior part of L2 to the posterior part of L3. Faint granular ornament on glabella but the distribution is not clear. On the fixed cheeks there is an irregular distribution of pits.

The figured material from Valongo assigned to this species is virtually identical to the holotype, differing mainly in convexity. The Portuguese specimens are flattened dorso-ventrally and slightly distorted obliquely. The transverse and longitudinal profiles of the cranidia do not show the high convex glabella of the holotype but the relative proportions of the cranidia are the same. This species is discussed further below.

EXPLANATION OF PLATE 78

Figs. 1–7. *Eccoptochile* (?*Eccoptochile*) *mariana* (Verneuil and Barrande). 1–4, holotype, internal mould; T 150. 'Puente de las Ovejas' near Ciudad Real, Spain; Upper Llandeilo. 1–3, dorsal, frontal, lateral views respectively, ×3. 4, detail of cheek ornament, ×9. 5, 6, internal mould; In49177. Covelo, north Portugal. Upper part of Valongo Formation; Lower Llandeilo. 5, dorsal view. 6, frontal view. Approximately ×2. 7, internal mould; In49182. Covelo, north Portugal. Upper part of Valongo Formation; Lower Llandeilo. Dorsal view, ×1.

Figs. 8, 9. *Eccoptochile* (*Eccoptochile*) *almadenensis* sp. nov. Internal moulds. 8, GSM CR 1526. Gorran Quartzites, Perhaver Beach, Cornwall; Llandeilo. Dorsal view, ×2. 9, SG 3A2. 1400 m S 32° E of Covelo church, north Portugal. Upper part of Valongo Formation; Lower Llandeilo. Dorsal view, ×1.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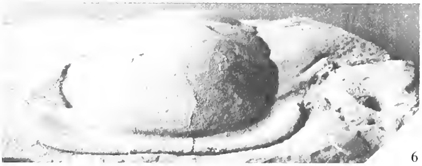
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ROMANO, Ordovician trilobite *Eccoptochile*

Eccoptochile (*Eccopotchile*) *almadenensis* sp. nov.

Plate 78, figs. 8, 9; Plate 79, figs. 1–7; text-fig. 2 *a–c*

1896 *Cheirurus* (*Eccoptocheile*) *marianus* (De Verneuil); Reed, p. 164.
1907 *Cheirurus sedgwicki* M'Coy; Lake *in* Reid, p. 39.
1908 *Cheirurus claviger* Beyrich; Delgado, ? p. 57 (refigured by Thadeu, 1947, pl. 3, fig. 2), ? p. 80, p. 106.
1908 *Cheirurus guillieri* Trom. (aff. *C. claviger* Beyr.); Delgado, p. 106.
1908 *Cheirurus* sp. n. (aff. *C. sedgwicki* McCoy); Delgado, p. 106.
1916 *Eccoptochile mariana* (Verneuil and Barrande); Barton, p. 106.
*1918 *Cheirurus claviger* var. *marianus* Verneuil and Barrande *emend.* Born; Born, p. 351, pl. 27, fig. 1.
1947 *Cheirurus claviger* Beyrich; Thadeu, p. 228, pl. 3, fig. 3.
1958 *Eccoptochile clavigera* (Beyrich); Whittard, p. 115 (specimen from Perhaven Beach, Cornwall).
1961 *Eccoptochile mariana* (Verneuil and Barrande); Curtis, p. 6, pl. 1, fig. 2 (*non* fig. 1), pl. 2, figs. 1, 2, pl. 3, ? fig. 1.
1969 *Eccoptochile* (*Eccoptochile*) sp. indet; Racheboeuf, p. 74, pl. 2, figs. 3*a*, *b*.
1971*b* *Eccoptochile marianus* (Verneuil and Barrande); Hammann, pp. 267, 270.
1974 *Eccoptochile clavigera* (Beyrich)?; Sadler, p. 73.
1974 *Eccoptochile* (*Eccoptochile*) *mariana* (Verneuil and Barrande); Lindström, Racheboeuf, and Henry, ? pp. 20, 21.
1974 *Eccoptochile mariana* (Verneuil and Barrande); Hammann, p. 105, text-fig. 39, pl. 11, figs. 188–191, pl. 12, figs. 192–198.
1978 *Eccoptochile mariana* (Verneuil and Barrande); Henry and Romano, p. 335.

Diagnosis. (Modified from Hammann, 1974, p. 106.) Species of *Eccoptochile* with glabella strongly convex, anterior lobe descending almost vertically to preglabellar field. Frontal area relatively narrow (sag.); anterior border steeply upturned forming an angle with lateral borders of free cheeks (viewed dorsally). Eyes start approximately level with S2 and reach back to S1. Fixed cheeks narrow (sag.). Anterior thoracic segments pointed, becoming gradually more rounded posteriorly. Internal surface of exoskeleton smooth except for pits on cheeks.

Type and figured material. Holotype: (SMG X 337a) Internal mould of cephalon with seven thoracic segments (figured Born, 1918, p. 351, pl. 27, fig. 1; Hammann, 1974, p. 105, pl. 12, figs. 192 *a–c*). Paratypes: (BM In49178–80) Curtis, 1961, p. 6, pl. 1, fig. 2, pl. 2, figs. 1 and 2 respectively; (SMF 24779–82, 24783_{1-3}, 24784, 24785a, 24787) Hammann, 1974, p. 105, pl. 11, figs. 188, ?189, 190–191, pl. 12, figs. 193–198. Other material: GSM GR 1526; SG 1704, SG 1711, and three unnumbered specimens in drawer labelled 3A2 in SG (figured here Pl. 78, fig. 9, Pl. 79, figs. 6, 7).

Horizons and locality. Holotype from Valdemosillo, approximately 16 km ENE of Almaden, Spain; Upper Llandeilo. Paratypes. BM In49178–80 from Covelo, near Valongo, north Portugal; upper part of Valongo Formation, probably Lower Llandeilo. SMF 24779, 24785a from Corral de Calatrava (near Ciudad Real, Spain); Co IIIf, Upper Llandeilo: SMF 24780–82, 24783_{1-3} from Corral de Calatrava; Co IIIe, Upper

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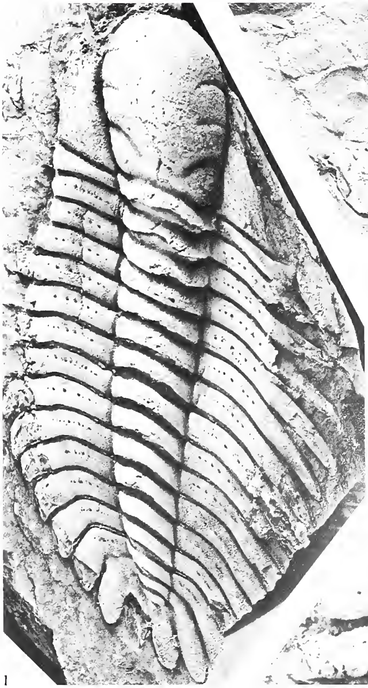
EXPLANATION OF PLATE 79

Figs. 1–7. *Eccoptochile* (*Eccoptochile*) *almadenensis* sp. nov. 1–6, internal moulds, 7, external impression. Upper part of Valongo Formation; Lower Llandeilo. 1–4, SG 1704. 1650 m S 20° W of the summit of Santa Justa, Valongo, north Portugal. 5, SG 1711, 6, 7 (both in drawer labelled 3A2), 1400 m S 32° E of Covelo church, north Portugal. 1–3, dorsal, lateral, frontal views respectively, ×2; 4, detail of thoracic segment, ×4. 5–7, dorsal views, ×1, ×0·75, ×1 respectively.

Fig. 8. *Eccoptochile* (?*Eccoptochile*) cf. *mariana* (Verneuil and Barrande). Internal mould; (no number, same box as SG 1704). 1650 m S 20° W of the summit of Santa Justa, Valongo, north Portugal. Upper part of Valongo Formation; Lower Llandeilo. Dorsal view, ×1.

Fig. 9. *Eccoptochile* (*Eccoptochile*) cf. *clavigera* (Beyrich). External impression. SG (no number, in drawer labelled 3A2). 1400 m S 32° E of Covelo church, north Portugal. Upper part of Valongo Formation; Lower Llandeilo. Dorsal view, ×1·5.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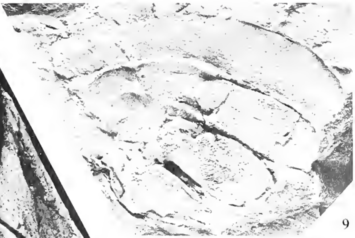
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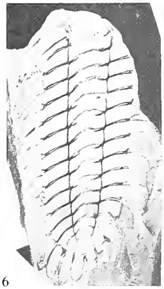
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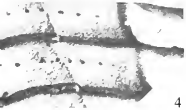
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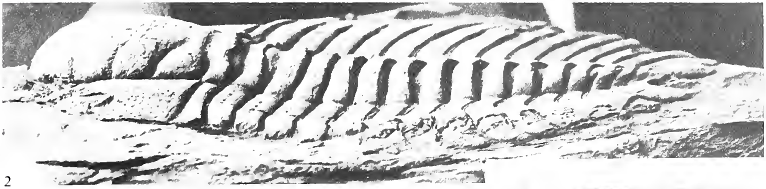
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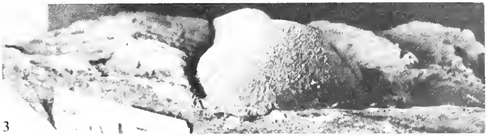
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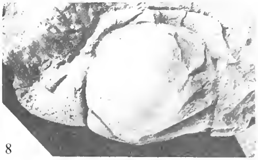
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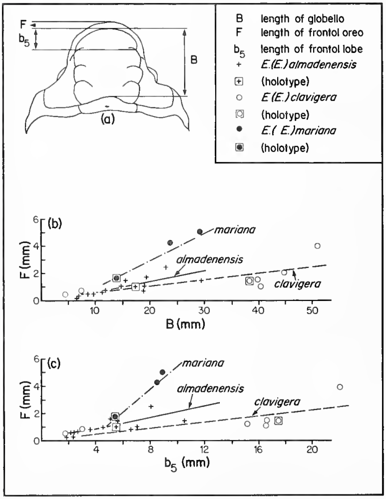
ROMANO, Ordovician trilobite *Eccoptochile*

Llandeilo: SMF 24784 from Navatrasierra (Montes de Toledo, Spain); Na Ia, Lower Llandeilo: SMF 24784 from Navatrasierra (Montes de Toledo, Spain); Na Ia, Lower Llandeilo: SMF 24787 from Navatrasierra (Montes de Toledo); Na Ia, basal Llandeilo.

Description. The types from Spain and Portugal have been well described and figured by Hammann (1974) and Curtis (1961). No further comments are necessary.

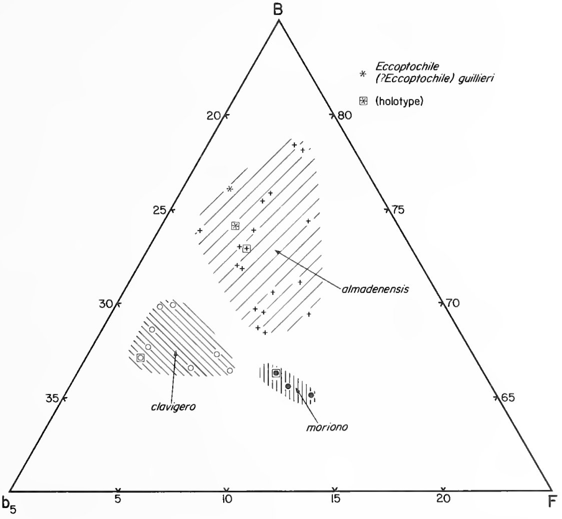
Discussion. Verneuil and Barrande erected *Eccoptochile* (?*Eccoptochile*) *mariana* (1855, p. 970, pl. 23, fig. 4) on the basis of it having a more dorsally convex glabella and a wider, flat anterior border than *Eccoptochile* (*Eccoptochile*) *clavigera* (Beyrich, 1845). They stated that the eye occupied the same relative position in both species. Curtis (1961, p. 8) listed four differences between the two species, including that in *E.* (?*E.*) *mariana* (*sensu* Curtis and Hammann) the frontal lobe is relatively shorter, the eye ridge starts level with the anterior glabella furrow and the eye is situated farther back. The specimen figured by Curtis (1961, pl. 1, fig. 1) as *E. mariana*, and later referred to *E.* cf. *mariana* by Hammann (1974, p. 105) possesses a wide frontal area which distinguishes it from other specimens of *E.* (?*E.*) *mariana* as understood by Curtis and Hammann. A reinvestigation of the holotype of *E.* (?*E.*) *mariana* also revealed the presence of a wide frontal area and it is thus clearly distinct from the majority of specimens previously assigned to that species. The evenly curved longitudinal profile of the glabella of the holotype (text-fig. 2*k* and Pl. 78, fig. 3) is also unlike that in *E.* (?*E.*) *mariana sensu* Hammann where maximum curvature occurs in the anterior part of the glabella (Hammann 1974, pl. 12, fig. 192*b*). Thus *E.* (?*E.*) *mariana* is restricted in this paper to include, with the holotype, only the two specimens from the Valongo area; that figured by Curtis (1961, pl. 1, fig. 1 and refigured here, Pl. 78, figs. 5, 6) and a previously unfigured specimen (Pl. 78, fig. 7).

The relative lengths (sag.) of the frontal glabellar lobe and frontal area appear to show significant differences in the species *almadenensis*, *clavigera*, and *mariana*. In an attempt to quantify these differences the three parameters B, F, and b_5 (text-fig. 3a) (symbols from Shaw, 1957 and Temple,



TEXT-FIG. 3. *a*, Outline of cranidium of *Eccoptochile* (*Eccoptochile*) *almadenensis* sp. nov. (after Hammann, 1974, text-fig. 39) showing parameters used in (*b*), (*c*) and text-fig. 4; *b*, *c*, Scatter diagrams of F against B and F against b_5 respectively with calculated regression lines for the species *almadensis*, *clavigera* and *mariana*.

1975) were selected since it is assumed the ratio of these measurements taken along a constant orientation will be virtually unaffected by deformation. When the three parameters are plotted on size frequency and scatter diagrams the species plot out in isolated and relatively restricted fields. Size/frequency histograms of the B:F and B : b_5 ratios (not illustrated) serve to distinguish *E.* (?*E.*) *mariana* from *E.* (*E.*) *almadenensis* and *E.* (*E.*) *clavigera* quite markedly. The regression lines of B against F and b_5 against F (text-fig. 3b and 3c) show that for *mariana* at least the lines appear to be clearly distinguishable and although few specimens were available to construct the graphs (*almadenensis*—14; *clavigera*—7; *mariana*—3) the contrast in gradient suggests the difference in growth rate is a useful criterion for separating this species. When the three parameters are plotted as ratios on a triangular graph (text-fig. 4) the three species plot out in discrete fields and the selected holotype for *E.* (*E.*) *almadenensis* occurs near the centre of scatter for that species. Since the number of specimens is small the fields have not been numerically defined. The species *clavigera* is clearly distinguishable by the presence of a long (sag.) frontal glabellar lobe (see text-fig. 2) and the flat profile of the glabella in lateral view. This difference in the relative length of the frontal lobe is shown in the groupings in text-fig. 4.



TEXT-FIG. 4. Triangular plot for the species *almadenensis*, *clavigera*, and *mariana* using the three parameters B, F, b_5 (see text-fig. 3). For material and references used to construct the graph see text. Additional sources include Dr. J.-L. Henry (pers. comm.) and author's collection, University of Sheffield.

Using the methods outlined above, *E.* (?*E.*) *guillieri* cannot be distinguished from *E.* (*E.*) *almadenensis* since measurements taken from the photographs supplied by Dr. J.-L. Henry plot out near the middle of the *E.* (*E.*) *almadenensis* field (text-fig. 4). However, the strong glabella convexity and subrounded outline of the glabella in dorsal view of *E.* (?*E.*) *guillieri* are characteristic enough to suggest it is a valid species. The specimen listed by Delgado (1908, p. 106), as '*Cheirurus* sp. n. (aff. *Ch. Sedgwicki* McCoy)', from 1400 m S 32° E of Covelo church (SG 1711) appears to show no important differences from *E.* (*E.*) *almadenensis*. The size of the free cheek, position, and structure of the eye in *Placoparina sedgwicki* (Whittard, 1958, pp. 112, 115) are distinctive, and although the Portuguese specimen listed by Delgado is imperfectly preserved (Pl. 79, fig. 5) it is assigned to *E.* (*E.*) *almadenensis*. Delgado (1908, p. 106) also recorded '*Cheirurus Guillieri* Trom. (aff. *Ch. claviger* Beyr.)' from the Valongo area, 1650 m S 20° W from the hill of Santa Justa (SG 1704), but the forwardly expanding and relatively longer glabella (Pl. 79, fig. 1) is unlike that of the holotype of *E.* (?*E.*) *guillieri* and this specimen is also identified as *E.* (*E.*) *almadenensis*. Another specimen (Pl. 79, fig. 8) identified by Delgado (op. cit.) as '*Cheirurus Guillieri*' is here referred to *E.* (?*E.*) cf. *mariana* because, although it closely resembles the holotype, the deformed specimen precludes a definite identification. The eccoptochilinid from Perhaver Beach, Cornwall, tentatively identified as *E.* (*E.*) *clavigera* by Whittard (1958, p. 115) and Sadler (1974, p. 73) is an incomplete cranidium (Pl. 78, fig. 8) which can now be confidently assigned to *E.* (*E.*) *almadenensis*.

Eccoptochile (*Eccoptochile*) cf. *clavigera* (Beyrich, 1845)

Plate 79, fig. 9

Figured material. One external impression of an incomplete flattened pygidium; specimen housed in Serviços Geológicos, Lisbon; drawer 3A2.

Horizon and locality. 1400 m S 32° E of Covelo church, Valongo; probably from upper part of Valongo Formation, probably Lower Llandeilo.

Description. Pygidium nearly twice as wide as long. Anterior margin gently rounded with nearly straight median portion and more strongly rounded posterior margin. Axis subtriangular in outline (articulating half ring not preserved) with outwardly curved axial furrows. Axis probably slightly wider than long, reaching back to about one-half length of pygidium; three axial rings and a small triangular terminal piece; rings decrease in length posteriorly, ring furrows shallow medially (except third axial ring furrow). Axial furrows shallow and weakly defined and not present posterior to the second axial ring furrow. Three pairs of broad, bluntly rounded, spinose pleural ribs. First and second ribs start opposite first two axial rings and curve gently outwards and backwards; third pair directed posteriorly. 7–8 shallow pits on first pleural ribs situated at about midlength (exsag.) of rib and extend for about one-quarter along the rib. Only 1–2 pits are present on the second rib and none on the third. Surface of pygidium covered with fine, closely spaced tubercles except in the shallow rib pits.

Discussion. The poor preservation of this specimen makes it difficult to compare length to width ratios with the type material of *E.* (*E.*) *clavigera* (Beyrich, 1845, plate (unnumbered), fig. 3), which appears to be relatively wider. In all other respects it closely resembles the holotype. The present material is very similar to the specimen referred to *E.* (*E.*) *clavigera* by Přibyl and Vaněk (1969, p. 3, fig. 8) except that in the latter the rows of pits on the pleural ribs extend further along the rib, although this is not so apparent in other specimens figured by those authors (op. cit. pl. 3, figs. 6, 7).

RANGE AND DISTRIBUTION OF *E.* (*E.*) *ALMADENENSIS*, *E.* (*E.*) *CLAVIGERA*, AND *E.* (?*E.*) *MARIANA*

E. (*E.*) *almadenensis* is the most widespread species in Iberia and the Armorican Massif and probably also occurs in southern Cornwall. It first appears in the basal Llandeilo of Navatrasierra in central Spain (Hamman 1974, p. 15) and occurs in the Lower Llandeilo of north Portugal, the Armorican Massif, and probably southern England. There is evidence that the species possibly also persists into the Caradoc in the region south of Rennes, Brittany (Lindström *et al.*, 1974, p. 20). There is no record of it continuing into the Ashgill. *E.* (?*E.*) *mariana* (as understood in this paper) is a relatively restricted species, recorded only from the Ciudad Real region in south central Spain where it is of Upper Llandeilo age and from the area around Covelo, near Valongo in north Portugal (Lower Llandeilo). *E.* (*E.*) *clavigera* is poorly represented in Spain and north Portugal; *E.* (*E.*) cf. *clavigera* (a deformed pygidium) occurs in probably Lower Llandeilo beds in the Valongo area and *E.* (*E.*) aff. *clavigera* (a hypostoma and pygidium) is recorded from Caradoc beds north of Almaden, central Spain (Hammann 1974, p. 111). A deformed eccoptochilinid cranidium from the ?Caradoc of central Portugal, 50 km SSE of Coimbra (A. H. Cooper collection), is probably referable to *E.* (*E.*) *clavigera* and the Delgado collection housed in the Serviços Geológicos, Lisbon, contains large specimens of *E.* (*E.*) *clavigera* from the Mação region 80 km SSE of Coimbra. The age of the Mação specimens is not known but the associated fauna contain *Actinopeltis* and *Eoharpes* and could indicate an Upper Llandeilo to Caradoc age. *E.* (*E.*) *clavigera* is common in Bohemia where it ranges from the Libeň Formation to the Bohdalec Formation (Havlíček and Vaněk 1966) and is associated with *Actinopeltis*. Havlíček and Marek (1973) have revised the chronostratigraphic terminology for the Bohemian sequence and they recognize a Beroun Series of middle Llandeilo to upper Caradoc age which includes the range of *E.* (*E.*) *clavigera*. In Bohemia *Eoharpes* dies out in the Dobrotivá Formation which is considered by these authors to be equivalent in age to the lower part of the Llandeilo.

Any conclusions regarding faunal migrations and phylogeny within the group must await further work in particular on the existing collections in Lisbon.

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THE MIOCENE HORSE *HIPPARION* FROM NORTH AMERICA AND FROM THE TYPE LOCALITY IN SOUTHERN FRANCE

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ABSTRACT. The three-toed horse *Hipparion* is diagnosed by the presence of a preorbital facial fossa that anteriorly is poorly defined and posteriorly is moderately pocketed with a well-developed and continuous rim. The concept of the genus *Hipparion sensu stricto* (*s.s.*) is presently restricted in the Old World to *H. prostylum* from the genotypic locality at Mt. Léberon, France, and the species *H. tehonense* and *H. forcei* from New World localities with a similar configuration of the preorbital facial fossa. It has previously been stated that, although *Hipparion* was common in the Old World Neogene, this genus was very rare in equivalent-aged sediments in the New World. Based on the concept of the genus presented here, *Hipparion s.s.* is found at numerous New World localities. There apparently was a generic-level continuity of *Hipparion s.s.* that existed throughout Holarctica during part of the Neogene. Hipparion horses (*sensu lato*) appear to represent a polyphyletic assemblage of several genera that arose independently from more than one merychippine ancestor during the Miocene. The presence of hipparion horses in the New and Old Worlds probably resulted from more than one dispersal event across Beringia.

FOR more than a century, the genus *Hipparion* has been used as a horizontal taxon, or 'form genus', to include Holarctic Mio-Pliocene horses with isolated protocones in the upper molars, and tridactyl limbs. The great geographic and geological abundance of this horse has made it biostratigraphically very useful for Neogene intercontinental correlations. More than one hundred species of '*Hipparion*' (*sensu lato*) have been named primarily on dental and postcranial characters. This large complex of species is so unwieldy that, rather than comparing a new sample to all the existing species, palaeontologists often propose new species out of despair and therefore perpetuate this taxonomic problem.

In recent years, several studies have been presented that attempt to sort out some of the different hipparion groups based principally on cranial morphology. Skinner and MacFadden (1977) analysed relatively large quarry samples from the North American mid-continent and showed that the development of the preorbital facial fossa appears to be a taxonomically valid character complex at the generic rank. In their study they proposed the genus *Cormohipparion* for hipparions with a diagnostic preorbital (also termed nasomaxillary) facial fossa that is pocketed posteriorly and has well-developed and continuous anterior and posterior rims. Skinner and MacFadden (1977) concentrated mostly on North American forms but also tentatively referred some Eurasian hipparions to this genus. MacFadden and Bakr (1979) studied the Siwalik hipparions from the Indo-Pakistan subcontinent and refer the large species *theobaldi* to the genus *Cormohipparion*. Woodburne and Bernor (1980) studied numerous museum collections of Eurasian hipparions and proposed several distinct groups, which probably represent separate lineages, based principally on their analysis of cranial characters. There is general agreement among students of equid systematics that one or more members of this polyphyletic hipparion assemblage arose in North America during the medial Miocene. Subsequently, it appears that more than one hipparion group (i.e. a few genera) dispersed into the Old World during the later Miocene. Many workers have suggested that the presence of hipparions in the Old World resulted from the dispersal of one monophyletic group or 'species' of '*Hipparion*' (e.g. Forstén 1968; Hussain 1971). Skinner and MacFadden (1977) suggested, based on different cranial morphologies, that the dispersal of hipparions from the New to the Old World was not monophyletic and probably involved several forms (or genera).

[Palaeontology, Vol. 23, Part 3, 1980, pp. 617–635.]

The concept of the genus *Hipparion sensu stricto* (*s.s.*) is based on the species *H. prostylum* described from the Turolian Mt. Léberon locality in southern France (de Christol 1832). One of the important problems in the study of hipparion systematics has been recognition of the genus *Hipparion s.s.* in North America. Gidley (1903) proposed the genus *Neohipparion* for most of the New World species that had been previously included in the genus *Hipparion*, and *Hipparion s.s.* was almost exclusively used for Old World forms. Osborn (1918) did not strictly follow Gidley's dichotomy between *Neohipparion* and *Hipparion* for New versus Old World forms, respectively. Since the early studies, many workers believed that *Hipparion s.s.* was abundant in the Old World Miocene and rare in the New World. Stirton (1940) stated that in North America *Hipparion s.s.* was represented by only a few species distributed in California, Oregon, Washington, and Florida.

The purpose of this report is to describe *Hipparion sensu stricto* from several localities in North America and to compare these samples with the material from the genotypic locality in southern France. This study shows that *Hipparion s.s.* was more widely distributed in North America than has been previously thought. Only the North American localities with well-preserved cranial material are discussed here. *Hipparion s.s.* is undoubtedly present at numerous other localities in North America, however, without relevant cranial material, it is difficult to distinguish these occurrences. It is not the purpose of this paper to revise the taxonomy of all species of *Hipparion* and related forms, as that task would certainly require a monograph. Therefore, the specific diagnoses and assignments essentially rely on previous studies. The phylogenetic and palaeogeographic implications presented at the end of the present study will focus on the recognition of a generic-level continuity of *Hipparion s.s.* throughout Holarctica during the late Miocene.

The following institutional abbreviations are used in the text: AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York; BMNH, Department of Palaeontology, British Museum (Natural History), London; CIT, California Institute of Technology Collection, now housed at the Los Angeles County Museum of Natural History, Los Angeles; F:AM, Frick American Mammals, The American Museum of Natural History, New York; MNHNP, Muséum National d'Histoire Naturelle, Institut de Paléontologie, 8 rue de Buffon, Paris 5, France; UCMP, University of California Museum of Paleontology, Berkeley; UF, Florida State Museum, University of Florida, Gainesville. The dental nomenclature follows Stirton (1940, 1941), Skinner and Taylor (1967), and Skinner and MacFadden (1977).

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821
Genus HIPPARION de Christol, 1832

Text-figs. 1–14

Type status. When de Christol (1832) first proposed the genus *Hipparion* based on material from Mt. Léberon in southern France (also called Mt. Luberon, Cucuron), no holotype was indicated. Later, Gervais (1849) designated a syntypic series of *Hipparion* from Mt. Léberon, including *H. prostylum*, *H. mesostylum*, and *H. diplostylum*. Osborn (1918) considered *H. prostylum* to be the type species for the genus *Hipparion*. Sondaar (1974) stated that the holotype of *H. prostylum*, which consists of a fragmentary palate with P^4–M^2 (see Gervais 1849, pl. 19, fig. 2), is probably contained in the collections in the Musée Requien, Avignon.

Revised generic diagnosis. Medium-sized, mesocephalic, and moderately hypsodont tridactyl horses. Nasal notch moderately developed and extends posteriorly to a position anterior to, or lying over, P^2. Infraorbital foramen lies over P^3. Preorbital facial fossa lies dorsal to P^3–M^1 on the nasal and maxillary bones well forward of the anterior rim of the orbit. The posterior portion of the fossa is usually developed on the nasal and maxillary bones, anterior to the lacrimal. Anteriorly the fossa is poorly defined and is confluent with the facial region. Posteriorly the fossa is moderately pocketed and has a well-developed and continuous rim. There is no ventral fossa associated with the malar crest as is the case in some other horses. In the upper cheek teeth the protocones vary from rounded to oval to lenticulate. There is a tendency for the protocone to be connected to the protoloph in earlier wear stages than some other hipparions, e.g. *Neohipparion*. The hypoconal groove is moderately developed and is distinct to the base of the tooth. In the lower cheek teeth there is a progressive deepening of the ectoflexids posteriorly. The metaconids and metastylids are widely separated. The parastylid (also termed ectoparastylid or protostylid) is often developed and is either connected to the protoconid or is isolated. In both the upper and lower cheek teeth the enamel plications vary from simple to moderately developed.

Distribution. Late Miocene (Clarendonian–?early Hemphillian) of North America, late Miocene–?Pliocene (Vallesian–?Villafranchian) of Eurasia, and possibly Miocene–Pliocene of Africa. *Note.* The questionable ranges listed here are taken from previous studies in which relevant cranial material is lacking. Therefore, it is difficult to allocate certain Old World species to the genus *Hipparion s.s.*

Included species. At this point it is impossible to list all the species that should be included in *Hipparion s.s.* (particularly in the Old World) because of the problems in recognition of this genus without cranial material. In the present report *H. tehonense* and *H. forcei* are described from North America and these are compared to *H. prostylum* from Europe.

Hipparion prostylum Gervais, 1849

Text-figs. 1–5, 13, 14

Selected synonymy

1849 *Hipparion prostylum* Gervais, pp. 284–285.
1873 *Hipparion gracile* Gaudry, pp. 32–42, pl. 5, figs. 7–10; pl. 6, figs. 1–11; pl. 7, fig. 1.
1956 *Hipparion mediterraneum* (in part), Pirlot, p. 28.
1968 *Hipparion mediterraneus* (in part), Forstén, pp. 40–53, 83–129, tables 12–15.
1974 *Hipparion prostylum* Sondaar, pp. 289–290, 296–299, 301–306, tables 2–4, pl. 46, figs. 1, 2; pl. 48, figs. 2, 3, 8–10; pl. 49, figs. 3, 4, 8, 9, 10.

Type specimen. See generic discussion.

Specific diagnosis. Same as for the genus with the limitation that *H. prostylum* has rounded (and infrequently oval) protocones in the upper molars. Sondaar (1974, p. 297, adapted from Gromova 1952) diagnoses *H. prostylum* as follows: 'Average size, length of the upper molar series P^2–M^2 123–145 mm. Enamel with little foldings, slender footbones with relatively long metapodials.' See discussion below.

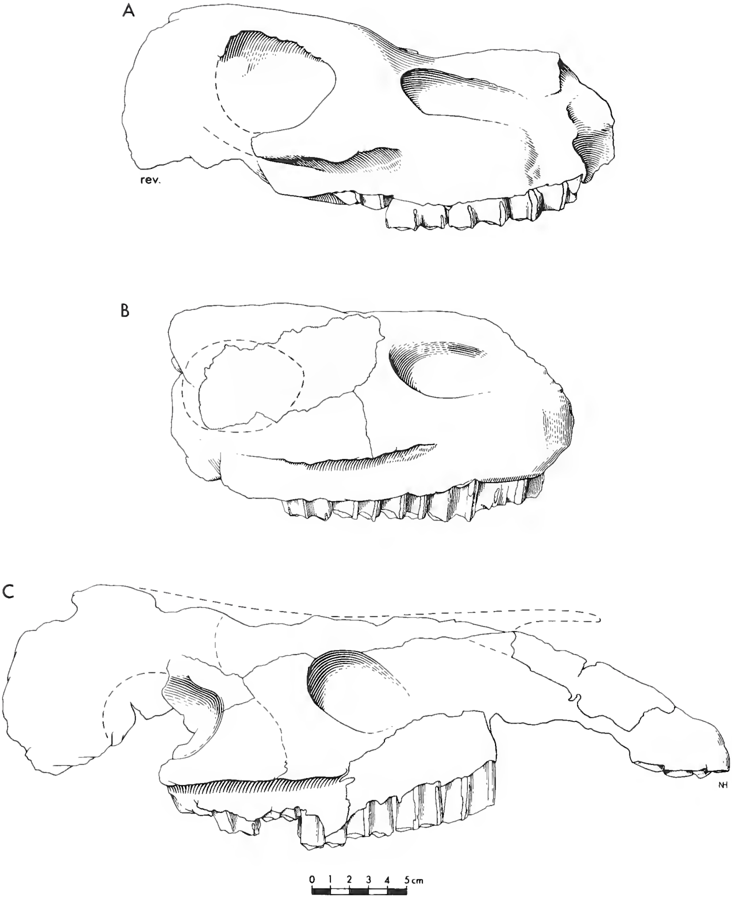
Referred material. This description is based on the collections of *H. prostylum* housed in Paris (NMNHP) and London (BMNH). These collections consist of four skulls, numerous dentitions, isolated teeth, and postcranials.

Distribution. Hipparion prostylum is recognized at the type locality, Mt. Léberon, which is of Turolian (late Miocene) age. This species is also part of the 'hipparionine Group 3' complex of Woodburne and Bernor (1980). Therefore, *H. prostylum* is probably represented at several other Old World localities of Turolian age listed in that publication. Pending a revision of hipparions from other Old World localities, *H. prostylum* is presently only known to occur for certain at the type locality, Mt. Léberon.

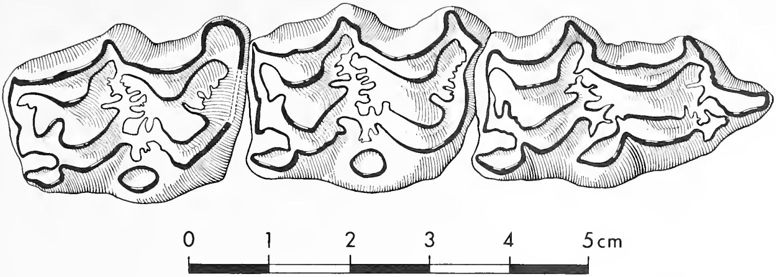
Description. Although *H. prostylum* has been described elsewhere (e.g. Gaudry 1873; Gromova 1952; Sondaar 1974) it is redescribed in this report in order to compare it to the North American representatives of this genus.

The description of skull morphology is based on four specimens; NMNHP Luberon 156, NMNHP 'unnumbered' (illustrated by Gaudry 1873, pl. 6, fig. 1, and Skinner and MacFadden 1977, text-fig. 3A), BMNH M33603, and BMNH M26617 (three of these are illustrated in text-fig. 1).

The skull is mesocephalic and of moderate size. The premaxillary and nasal regions are preserved in one specimen, BMNH M26617 (text-fig. 1C). It is unfortunate that in BMNH M26617 the nasal region is covered with matrix and therefore it is difficult to determine the posterior extent of the premaxillary bone and nasal notch. However, the reconstructed nasal region in this specimen suggests a well-retracted nasal notch. In the four skulls studied the buccinator fossa is either not preserved or it is covered with reconstructive material and therefore nothing can be said about the development of this region.



TEXT-FIG. 1. Skulls of *Hipparion prostylum* from the late Turolian of Mt. Léberon, France. A, NMNHP 'unnumbered'; B, NMNHP Lub. 156; C, BMNH M26617. Shading represents reconstruction or matrix.

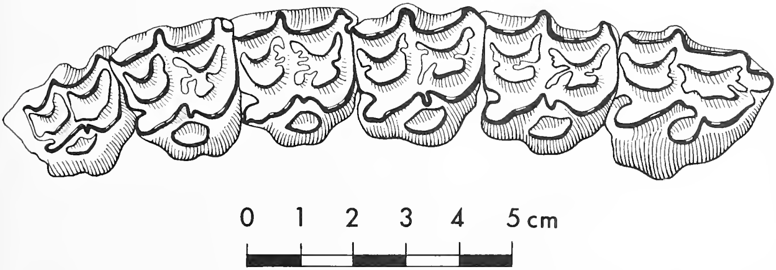


TEXT-FIG. 2. Deciduous upper cheek teeth (right dP^2–dP^4) of *Hipparion prostylum*, NMNHP Lub. 94, from the late Turolian of Mt. Léberon, France.

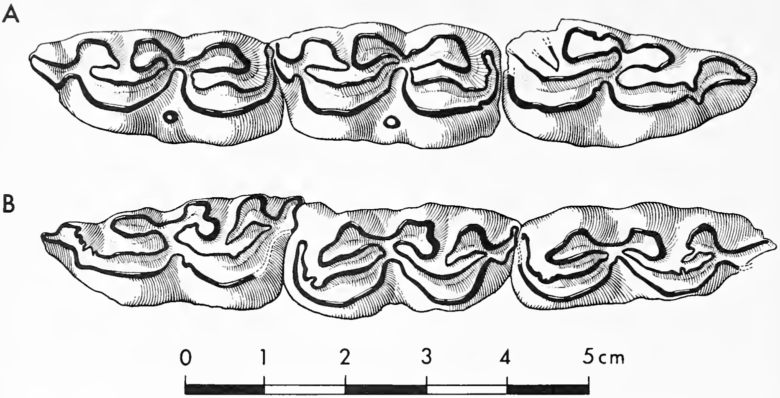
The preorbital facial fossa lies on the dorsal half of the cheek region. Anteriorly the fossa is poorly defined and it is confluent with the adjoining facial region. Posteriorly this fossa is usually moderately pocketed and has a well-developed continuous rim. The fossa lies in front of the lacrimal bone (as preserved in BMNH M26617, text-fig. 1) and well forward of the orbit. Postero-ventral to the nasomaxillary fossa is a moderately developed malar crest. There is no fossa associated with the malar crest as is the case in some other horses (e.g. *Pliohippus*). The teeth are moderately hypsodont, slightly curved, and covered with cement.

The upper incisors have cement-filled infundibula (cups). The precanine diastema is smaller than the post-canine diastema. DP^2–dP^4 are more rectangular in cross-section than the corresponding P^2–P^4 (text-fig. 2). The deciduous premolars are similar in dental pattern to the corresponding permanent premolars. In particular, the fossettes are moderately plicated, the protocones are usually rounded, and there is a tendency for the protocone of the dP^2 and P^2 to become connected to the protoloph during relatively early wear stages.

In the permanent upper dentition the protocone is isolated from the protoloph until late wear stages (except in the P^2 as noted above) when these two structures frequently connect. The protocone is characteristically rounded but infrequently varies to oval or lenticulate in shape with anterior and posterior spurs (text-fig. 3). The hypoconal groove is relatively well developed until late wear stages. The enamel plications are simple to moderately well developed. The posterior border of the anterior lake (prefossette) and the anterior border of the posterior lake (postfossette) show the most complexity of plications within a given tooth or tooth row. As in North American hipparions, the anterior border of the prefossette and posterior border of the postfossette lack complex foldings. The plicaballin consists of either a single or double loop.

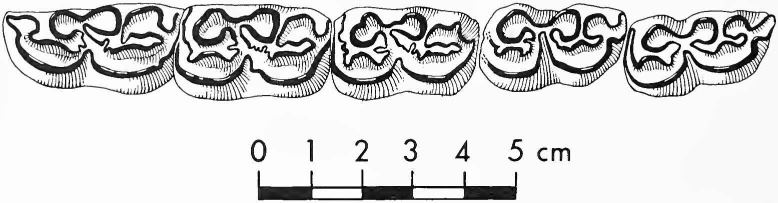


TEXT-FIG. 3. Permanent right upper cheek teeth (P^2–M^3) of *Hipparion prostylum*, BMNH 27590, from the late Turolian of Mt. Léberon, France.



TEXT-FIG. 4. Deciduous lower cheek teeth of *Hipparion prostylum* from the late Turolian of Mt. Léberon, France. A, NMNHP Lub. 14, right dP_2–dP_4; B, NMNHP Lub. 26, left dP_2–dP_4.

The lower incisors have cement-filled infundibula. The precanine diastema is very small and the canine is nearly appressed to the I_3. The postcanine diastema is moderate in length, with the mental foramen situated approximately midway between the C and P_2. The premolars are larger in cross-section than the molars. As exemplified by NMNHP Luberon 14 and 26 (text-fig. 4), the lower deciduous teeth are similar to the permanent premolars in dental pattern. In the anterior region of dP_2 and P_2 there is a moderately developed anterior projection of the paralophid-parastylid complex characteristic of hyposodont horses. The P_2 through M_3 are generally similar in dental pattern except as noted below (text-fig. 5). There is a well-developed parastylid on the antero-external portion of the cheek tooth. This structure is similar to that seen in some other hipparions, e.g. *Cormohipparion*. The metaconids and metastylids are well separated and vary from equal to subequal in size. The entoconid is significantly larger than the hypoconulid. On the M_3 the posterior portion of the tooth is expanded to form a projection of the hypoconulid or 'heel'. The protoconids and hypoconids are crescentic. In contrast to e.g. *Neohipparion eurystyle* and Pleistocene hipparions from Africa, the ectoflexid is moderately developed in the premolars. In the molars the deep ectoflexid almost separates the metaconid and metastylid. The plicaballinid and other enamel plications are usually absent or infrequently they are poorly developed.



TEXT-FIG. 5. Permanent left lower cheek teeth (P_2–M_2) of *Hipparion prostylum*, NMNHP Lub. 40, from the late Turolian of Mt. Léberon, France.

The metapodials of *H. prostylum* from Mt. Léberon are of moderate size relative to other Eurasian hipparions. Sondaar (1974) studied the metapodials of *H. prostylum* and concluded that this species was smaller than the slender form from Pikermi, *H. gracile*. As is the case in Eurasian hipparions of Turolian age, *H. prostylum* usually has a well-developed ectocuneiform facet on the MT III (Sondaar 1974, Sondaar, pers. comm. 1979).

Discussion. Woodburne and Bernor (1980) and Woodburne (pers. comm. 1980) suggest that two forms of hipparions are represented at Mt. Léberon. This assertion is based on the fact that, besides the facial morphotype described as *Hipparion s.s.*, Pirlot (1956) described one skull from the BMNH collection that had a well-developed preorbital facial fossa. From his description, one might be concerned that this skull possibly represented *Cormohipparion*. If that were true, then the validity and proper assignment of the species *prostylum* to *Hipparion* would be questionable. Pirlot (1956) unfortunately did not refer to the skull in question by its catalog number. I have studied the BMNH collection, and unless this skull has been lost, it seems almost certain that based on Pirlot's description, he was referring to BMNH M26617 (text-fig. 1C). It is not necessary to refer this skull to another taxon besides *H. prostylum* because BMNH M26617 appears to be the same facial morphotype as the other cranial specimens from Mt. Léberon.

Hipparion tehonense (Merriam 1916), new combination

Text-figs. 6-8, 13, 14

Selected synonymy

1907 ?*Hipparion lenticularis* (in part), Gidley, pp. 915-917. Synonymy restricted to Clarendonian sample from Texas Panhandle.
1918 *Hipparion lenticulare* (in part), Osborn, pp. 184-185, text-figs. 147, 148; pl. 32, fig. 2; pl. 33, figs. 5-7. Synonymy restricted to Clarendonian sample from Texas Panhandle.
1916 *Neohipparion gratum tehonense*, Merriam, pp. 118-120, text-figs. 1-7.
1918 *Hipparion lenticulare* Osborn, pp. 184-185, text-figs. 147, 148; pl. 32, fig. 2; pl. 33, figs. 5-7.
1939 *Nannippus tehonensis* Stirton, pp. 347-352, text-figs. 13, 24.
1942 *Nannippus tehonensis* Drescher, pp. 11-15, text-fig. 3.
1969 *Nannippus tehonensis* Webb, pp. 130-135.

Type specimen and locality. UCMP 21780, right upper M^1?, described by Merriam (1916, p. 119, fig. 1), Chanac ('Santa Margarita') Formation, south Tejon Hills, California, early Clarendonian.

Diagnosis. Characters same as for other species of the genus *Hipparion s.s.* In particular, the preorbital facial fossa is well developed posteriorly, but anteriorly becomes poorly defined (text-figs. 6, 7). The nasal notch is retracted to a position that lies above P^2. In addition, *H. tehonense* is characterized by very simple enamel plications and the anterior region of the P^2 is not as well developed as some other *Hipparion s.s.*

Referred material. H. tehonense from the California localities is represented by numerous specimens in the UCMP and CIT collections (see, e.g., Merriam 1916 and Drescher 1942). The Texas occurrence of this species is represented by F:AM 74400-74585 and also numerous uncatalogued F:AM specimens from MacAdams Quarry (locality 17), collected by the Frick Laboratory between 1934-1960, Donley County, Texas Panhandle and also specimens from other localities in Donley County, e.g. AMNH 10854 (see Osborn 1918, pl. 32, fig. 2).

Distribution. Besides the type locality, *H. tehonense* is also known from the Orinda Formation, early Clarendonian, San Francisco Bay Area, California, and the 'Clarendon Beds', Ogallala Group, early Clarendonian, Donley County, Texas.

Description. In most characters, *H. tehonense* is similar to *H. prostylum*. Only those characters that show certain important similarities and differences between *H. tehonense* and *H. prostylum* or characters not represented in the hypodigm of *H. prostylum* will be discussed here.

The description of skull morphology of *H. tehonensis* is based on a large sample from MacAdams Quarry, as exemplified by F:AM 74478 (text-fig. 6A), F:AM 74537 (text-fig. 7A), and AMNH 10854 ('neotype' of *H.* '*lenticulare*', see Osborn 1918, pl. 32, fig. 2) from the 'Clarendon Beds' of the Texas Panhandle. The skull of *H. tehonensis* is small relative to other species of *Hipparion s.s.*

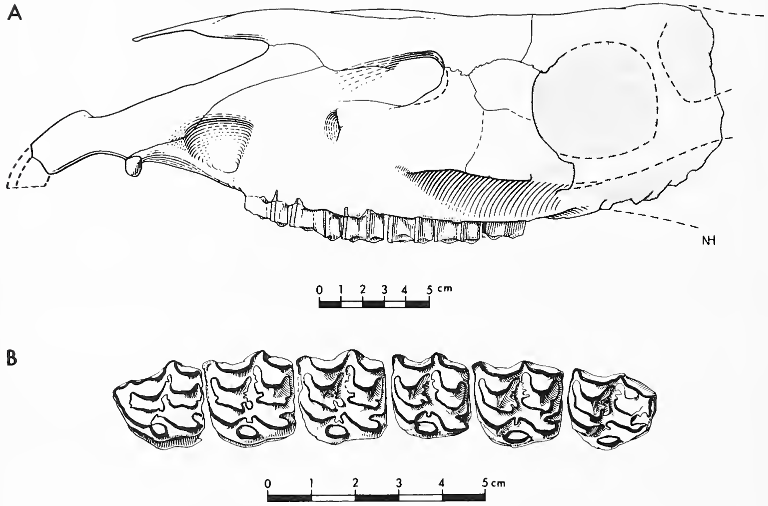
The premaxilla extends postero-dorsally to above the P^2–P^3. The nasal notch, which lies above P^2, is well retracted in contrast to other hipparions such as *Neohipparion whitneyi* (see Osborn 1918, pl. 32, fig. 1) but certainly less retracted than e.g. '*H.*' *proboscideum* (see Sondaar 1971, pl. III).

The infraorbital canal lies above P^3. As seen in *H. prostylum*, the preorbital facial fossa lies on the dorsal half of the facial region. Anteriorly, the fossa is poorly defined and it is confluent with the adjoining facial region. Posteriorly, this fossa is usually moderately pocketed and has a well-developed continuous rim. The fossa lies well forward of the lacrimal bone and orbit. As evidenced by the MacAdams Quarry sample, there is no significant morphological change in the preorbital facial fossa during ontogeny (compare text-figs. 6A and 7A).

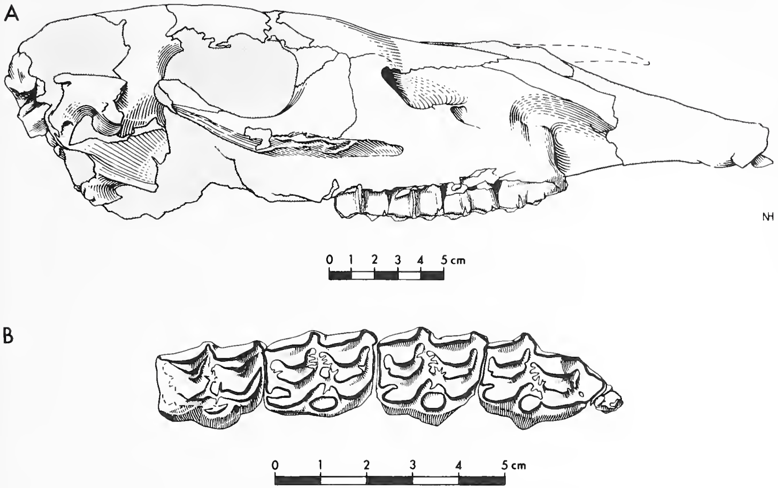
The dentition of *H. tehonense* is similar in pattern to other species of this genus. The enamel plications are very simple relative to other hipparions. The protocones are rounded to oval and these structures tend to become connected to the protoloph during later wear stages, particularly in the P^2. There are well-developed parastylids, and the ectoflexids are deep with few, if any, plicaballinids (text-figs. 6B, 7B, and 8).

Discussion. The large sample from MacAdams Quarry is assigned to *H. tehonense* as defined by the topotypic material from the Tejon Hills based on the following distinctive characters; (1) small size relative to other *Hipparion s.s.*, (2) extreme simplicity of the enamel plications, (3) a poorly developed anterior extension of the parastyle on P^2, and (4) similar degree of hypsodonty.

Because of its distinctively small size, the species *H. tehonense* from California has in the past been assigned to two different taxa of small hipparions. Merriam (1916) originally named the topotypic material from Tejon Hills a subspecies of the tiny *Pseudhipparion gratum*. Subsequent workers have assigned *tehonensis* to *Nannippus*, a genus of dubious monophyletic significance. Skinner and Hibbard (1972, p. 117) stated that: 'The practice of assigning all small forms of *Hipparion*-like



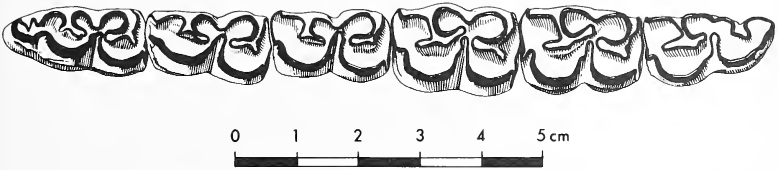
TEXT-FIG. 6. Adult specimen of *Hipparion tehonense*, F:AM 74478, from the Frick MacAdams Quarry, early Clarendonian of the Texas Panhandle. A, left lateral view of skull; B, occlusal view of left upper dentition. Shading represents reconstruction or matrix.



TEXT-FIG. 7. Immature specimen of *Hipparion tehonense*, F:AM 74537, from the Frick MacAdams Quarry, early Clarendonian of the Texas Panhandle. A, right lateral view of skull; B, occlusal view of dP^1–dP^4. Shading represents reconstruction or matrix.

equids to *Nannippus* without careful consideration of other characters clouds the relationship of many of the dwarf forms and prevents the recognition of true *Nannippus*. For example, *Griphippus* [= *Pseudhipparion*] *gratus*, which has quite different skull, dental, and postcranial characters, has often been assigned to *Nannippus*.'

Although there are no skulls preserved for the Californian sample of *H. tehonense*, the MacAdams Quarry specimens clearly demonstrate a similarity in facial morphology with *Hipparion s.s.* MacFadden and Waldrop (1980) described the facial morphology of *N. phlegon* from Mt. Blanco in the Texas Panhandle, which is the genotypic locality and therefore central to the concept of that genus. *N. phlegon* has a smooth preorbital cheek region with no facial fossa. Therefore, there is no doubt that the small hipparion species *tehonense* is best referred to the genus *Hipparion s.s.*



TEXT-FIG. 8. Right lower cheek teeth (P_2–M_3) of *Hipparion tehonense*, F:AM 105440, from the Frick MacAdams Quarry, early Clarendonian of the Texas Panhandle.

'*H.*' *lenticularis*, as it is used for Clarendonian hipparions from Donley County, Texas, is synonymized here with *H. tehonense*. The species '*H.*' *lenticularis* has been inconsistently used in the literature and it is appropriate to comment on its nomenclature here. In 1893 Cope assigned the species *lenticularis* to *Protohippus* based on material of late Hemphillian age from Mulberry Canyon, near Goodnight, in the Texas Panhandle (see Schultz 1977). Gidley (1907) referred material from the Clarendon beds of Donley County in the Texas Panhandle to *H. lenticularis*. Osborn (1918) designated a well-preserved skull (also described previously by Gidley 1907), AMNH 10584, as the neotype of *H. lenticularis*. This judgement was apparently made by Osborn because the early workers thought that the Clarendon and Goodnight beds were correlative and the topotypic material from Mulberry Canyon was not abundant. Despite these previous taxonomic decisions, it remains to be demonstrated that '*H.*' *lenticularis* from Donley County is conspecific with the material from Mulberry Canyon and numerous other late Hemphillian localities, e.g. Coffee Ranch (Matthew and Stirton (1930). It is unfortunate that no skulls are known of late Hemphillian '*H.*' *lenticularis*. The Clarendonian *H. tehonense* and Hemphillian '*H.*' *lenticularis* are remarkably similar in dental pattern, however, the younger species is noticeably more hypsodont. In this report the species '*H.*' *lenticularis* is restricted to the late Hemphillian forms. Based on dental and temporal similarities, the Clarendonian '*H.*' *lenticularis* as used by workers such as Gidley and Osborn is synonymized with *H. tehonense*.

Hipparion forcei Richey 1948

Text-figs. 9, 13, 14

Selected synonymy

1919 *Hipparion mohavense* Merriam, pp. 549–553, text-figs. 163–170.
1948 *Hipparion forcei* Richey, pp. 9–25, text-figs. 4–12, pl. 2, figs. *a–c*; pl. 3, figs. *a–d*.
1969 *Nannippus forcei* Webb, pp. 130–135.

Type specimen and locality. UCMP 33051, P^3, from Green Valley Formation, Black Hawk Ranch Quarry, Mount Diablo area, California, late Clarendonian.

Diagnosis. Characters same as for other species of the genus *Hipparion s.s.*, in particular, configuration of the preorbital facial fossa and nasal region listed above for *H. prostylum* and *H. tehonense*. Specific characters for *H. forcei* include an apparently higher frequency of connection of the protocone to the protoloph in P^2 (Richey 1948). Also the protocone-protoloph connection is very well developed with less of a constriction between these parts than is seen in many other hipparions. The protocone is smaller in *H. forcei* than in *H. tehonense* relative to the occlusal area of the tooth. *H. forcei* has higher crowned cheek teeth with larger occlusal cross-sectional areas than in *H. tehonense* (Webb 1969).

Referred material. Numerous UCMP specimens from the Black Hawk Ranch Local Fauna, Green Valley Formation, San Francisco Bay region, California, and the Dove Springs Fauna, Ricardo Formation, Mohave Desert, California (see Richey 1948).

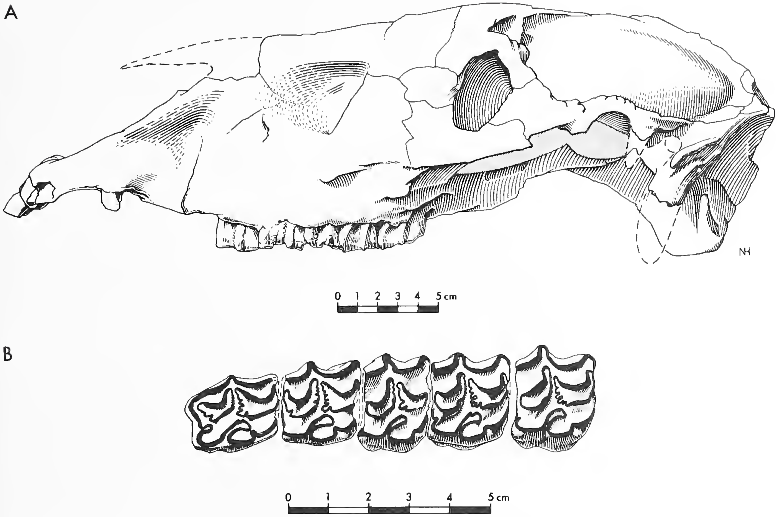
Distribution. Besides the type locality, *H. forcei* is probably represented in the Ricardo Formation (Dove Springs Fauna), Mohave Desert, California. These localities are late Clarendonian in age (Tedford *et al*., in press).

Description. In most characters the material of *H. forcei* is similar to other species of this genus, including *H. prostylum* and *H. tehonense*. The cranial morphology of *H. forcei* is known from one crushed but relatively complete skull from Black Hawk Ranch (text-fig. 9A), UCMP 34511, originally described in detail by Richey (1948). The important characters that are similar among these species include a relatively well-developed nasal notch that is retracted to a position that lies over P^2. The infraorbital canal lies above P^3. As is diagnostic of *Hipparion s.s.*, the preorbital facial fossa is poorly defined anteriorly but posteriorly it is characterized by a well-developed continuous rim that is pocketed. The fossa lies well forward of the lacrimal bone and orbit.

The most complete dentition of *H. forcei* is known from the skull, UCMP 34511 (text-fig. 9B). However, the dental pattern in this specimen is not characteristic because it represents an old individual in late wear stage. There are numerous isolated teeth known from the type locality and Richey (1948) described them in detail.

The following characters are diagnostic of *H. forcei*; relatively simple enamel plications, small protocone, high frequency of protocone-protoloph connection in the P^2, and lowers with deep ectoflexids but without plicaballinids. Richey (1948, p. 15) stated that: 'Another character that distinguishes *H. forcei* from many other species is the frequency of connection of the protocone with the protoconule [protoloph]. Many hipparions have a connected protocone in the P^2. This is particularly true of *H. forcei*. In fact, in none of the specimens thus far studied is the protocone separate.'

Richey (1948) studied the limbs of *H. forcei* and concluded that they were of moderate size in contrast to smaller forms such as *Nannippus* and larger, more robust, forms such as '*H.*' (= *Cormohipparion*) *theobaldi* from the Siwaliks and *H. gracile* from Pikermi.



TEXT-FIG. 9. *Hipparion forcei*, UF 22656 (cast of UCMP 34511) from the late Clarendonian Black Hawk Ranch Local Fauna, California. A, left lateral view of skull; B, occlusal view of right upper cheek teeth.

Discussion. H. forcei and *H. tehonense* are very similar in many characters. Webb (1969) has suggested an ancestral-descendent relationship between these two species. The samples from Tejon Hills–Chanac Formation–Black Hawk Ranch appear to approximate a morphocline in characters such as hypsodonty. However, in other characters such as the high frequency of protocone-protoloph connection, *H. forcei* seems more primitive than *H. tehonense*. The relative primitiveness of certain dental characters in *H. forcei* would, as Richey (1948) suggested, imply independent evolution in parallel of *H. forcei* and *H. tehonense* from a common ancestor rather than a single ancestral-descendent sequence as suggested by Webb (1969). It is not within the scope of this paper to resolve the phylogenetic relationships of the species *H. tehonense* and *H. forcei*. This short note is included as an introduction to the next section below, i.e. the provisional assignment of forms from the mid-continent of North America to *H.* cf. *tehonense* or *forcei*.

Hipparion cf. *tehonense* or *forcei*

Text-figs. 10–14

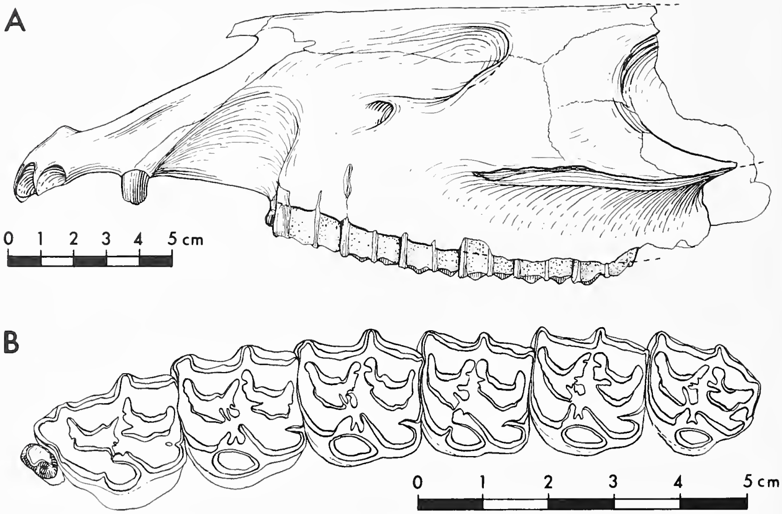
Referred material. Numerous specimens in the F:AM collection including well-preserved skulls, e.g. F:AM 107664, from Trail Side Kat Quarry Channel, Cherry County, Nebraska, late Clarendonian; F:AM 107663, Rosebud Agency Quarry, Todd County, South Dakota, late Clarendonian; F:AM 71887, Olcott Quarry, Hipparion Channel, Olcott Hill, Sioux County, Nebraska, late Clarendonian.

Distribution. Snake Creek and Ash Hollow Formations, Ogallala Group, north-central Nebraska and adjacent South Dakota, and north-western Nebraska, late Clarendonian (see Skinner *et al.* 1977; Tedford *et al.* in press).

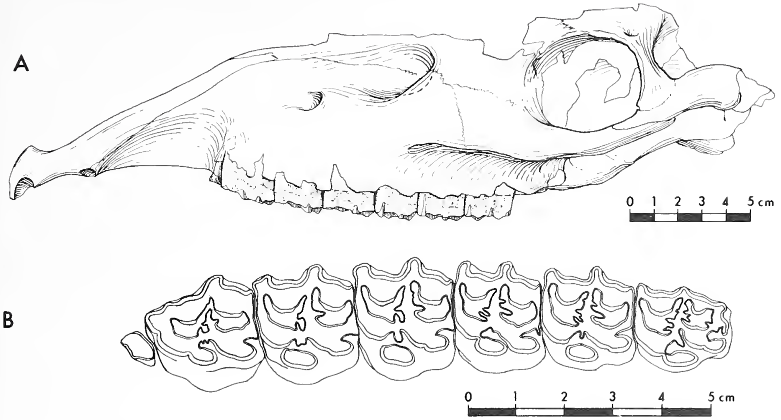
Description. Well-preserved cranial material from the northern Great Plains localities are referred to *Hipparion s.s.* based on the configuration of certain skull characters, particularly the preorbital facial fossa.

There appears to be a significant size difference among the individuals of *H.* cf. *tehonense* or *forcei*. In F:AM 107664 (text-fig. 10) and F:AM 107663 (text-fig. 11) the premaxillary extends posteriorly to a position that lies over the P^2. There is some variation in the posterior extent of the nasal notch. In F:AM 107664 and F:AM 71887 (text-fig. 12) the nasal notch extends to a position that lies over the buccinator fossa, which is slightly less retracted than in other skulls of *Hipparion s.s.* described here. Although the nasal bones are not preserved in F:AM 107664, the nasal notch appears retracted to a position over P^2 similar to that seen in other skulls of *Hipparion s.s.* In the skulls illustrated in text-figs. 10–12 the infraorbital foramen lies above the P^3 just ventral to the antero-ventral margin of the preorbital facial fossa. This fossa is poorly defined anteriorly but posteriorly it consists of a well-defined continuous rim. Posteriorly there also is a moderately well-developed pocket. This fossa lies well forward of the lacrimal bone and orbit. There is a moderately developed malar crest.

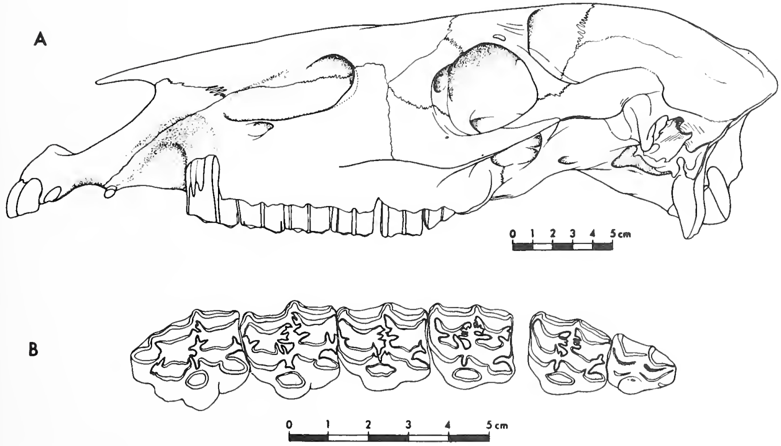
The dentitions are similar to other species of *Hipparion s.s.* In particular, the enamel plications are relatively simple. The protocone is oval and relatively large. In the P^2 of F:AM 107663 and F:AM 107664 the protocone is strongly connected to the protoloph.



TEXT-FIG. 10. *Hipparion* cf. *tehonense* or *forcei*, F:AM 107664, from the late Clarendonian Trail Side Kat Quarry Channel, Nebraska. A, left lateral view of skull; B, occlusal view of left upper cheek teeth.



TEXT-FIG. 11. *Hipparion* cf. *tehonense* or *forcei*, F:AM 107663, from the late Clarendonian Rosebud Agency Quarry, South Dakota. A, left lateral view of skull; B, occlusal view of left upper cheek teeth.



TEXT-FIG. 12. *Hipparion* cf. *tehonense* or *forcei*, F:AM 71887, from the late Clarendonian Olcott Quarry, Hipparion Channel, Olcott Hill, Nebraska. A, left lateral view of skull; B, occlusal view of left upper cheek teeth.

Discussion. The configuration of the skull, particularly in the development of the preorbital facial fossa, justifies the allocation of the material from these mid-continental sites to *Hipparion s.s.* However, the specific allocation is, at this point, somewhat uncertain. It is not implied that the sample from these three localities represents one discrete species. For example, the smaller size of F:AM 107664 and F:AM 107663 possibly indicates an affinity with *H. tehonense*, whereas the larger size of F:AM 71887 possibly indicates an affinity with *H. forcei* (following Webb 1969). On the other hand, the very strong connection of the protocone and protoloph in both F:AM 107663 and F:AM 107664 indicates an affinity with *H. forcei* (following Richey 1948). The resolution of this species-level problem would require further study beyond the scope of the present paper. The important point is that this mid-continental sample is referred to *Hipparion s.s.* Therefore, this genus was relatively widespread in North America during the Clarendonian.

BIOSTRATIGRAPHY AND PALAEOBIOGEOGRAPHY

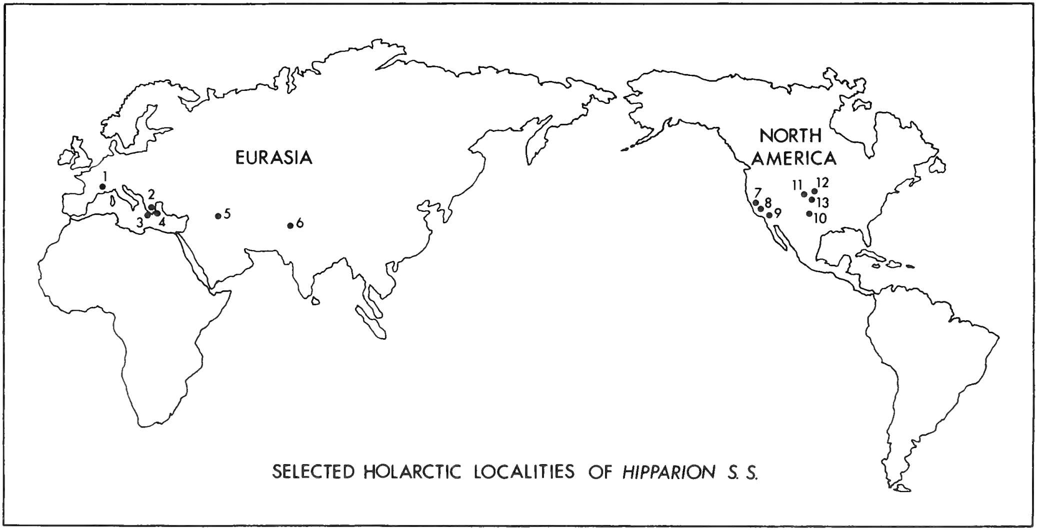
The temporal and geographic distribution of *Hipparion s.s.* from North America and Mt. Léberon is summarized in text-figs. 13 and 14. In these text-figs. several other Eurasian localities of *Hipparion s.s.* have been added, based on recent studies of cranial morphology (MacFadden and Bakr 1979, Woodburne and Bernor 1980). Undoubtedly *Hipparion s.s.* (as recognized by cranial morphology) occurs at other Holarctic localities and possibly also in Africa. For this discussion only the selected localities shown in text-figs. 13 and 14 will be presented.

The radiometric time scale and European Stages in text-fig. 14 were taken from several works, including Berggren and Van Couvering (1974), Aguirre (1975), Fahlbusch (1976), and Van Couvering and Berggren (1977). The age of the 'Hipparion Datum Plane' is shown to range from about 12·0 mybp to about 10·8 mybp. This range is a result of alternative interpretations of radiometric dating of critical Old World sites, particularly Höwenegg (e.g. Berggren and Van Couvering 1974; Van Couvering and Berggren 1977; Becker-Platen *et al.* 1977; Barndt *et al.* 1978, also see discussion in MacFadden and Bakr 1979). The boundary between the Astarcian (*sensu* Fahlbusch 1976) and Vallesian, which is usually taken as the first appearance of 'Hipparion', is dashed in text-fig. 14 in order to indicate the uncertainty involved in the calibration of this event. The calibration and nomenclature of the North American localities is taken from Tedford *et al.* (in press).

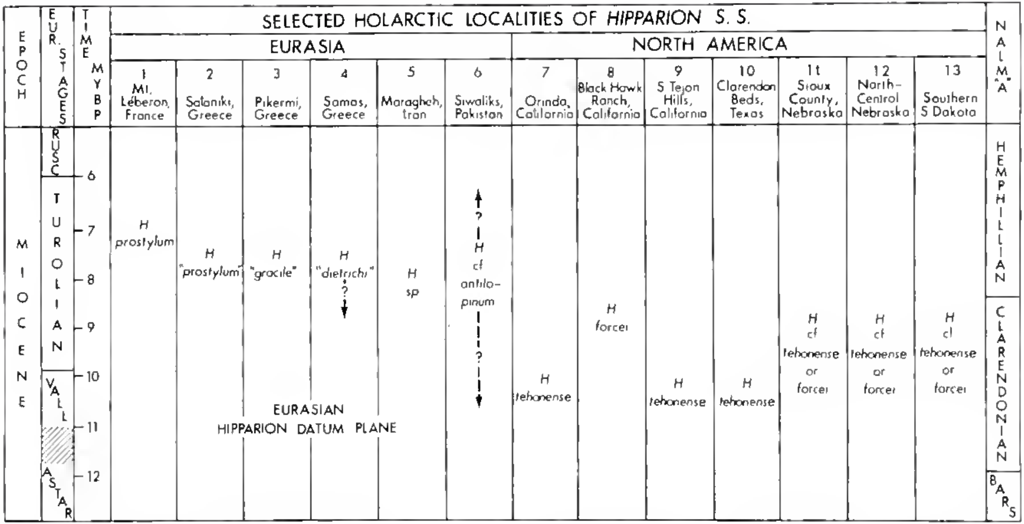
Sondaar (1974) and Sen *et al.* (1978) consider the Mt. Léberon locality, and, therefore, the type material of *Hipparion s.s.* to be of late Turolian age. Woodburne and Bernor (1980) studied facial morphotypes from selected Old World localities. Their 'Group 3' consists of a morphologically distinct group including *H. prostylum* from Mt. Léberon and forms from several localities in Greece and Iran. This facial morphotype agrees with the concept of the genus presented in this report for *Hipparion s.s.* The *Hipparion s.s.* from Saloniki, Greece (Group 3 of Woodburne and Bernor 1980, here referred to as *H. 'prostylum'*), and Pikermi, Greece (also Group 3, here referred to as *H. 'gracile'*), are considered to be of medial Turolian age and slightly older than Mt. Léberon (Berggren and Van Couvering, 1974; Sen *et al.* 1978).

For a long time it was thought that at Samos, Quarries 1–4 were older than Quarry 5, and that this succession spanned medial to late Turolian time (e.g. Berggren and Van Couvering 1974; Aguirre 1975; Sen *et al.* 1978). Recent field work at Samos (Solunias, pers. comm. 1977), suggests that all the quarries are approximately contemporaneous. Therefore, depending upon the stratigraphic interpretation, the *Hipparion s.s.* (Group 3, here referred to as *H. 'dietrichi'*) from Samos either spans medial to late Turolian time or is restricted to the late Turolian. Woodburne and Bernor (1980) state that *Hipparion* Group 3 (here referred to *H.* sp.) is found in the middle and upper parts of the Maragheh, Iran, sequence. Based on this range, the Maragheh *Hipparion s.s.* spans medial to late Turolian time.

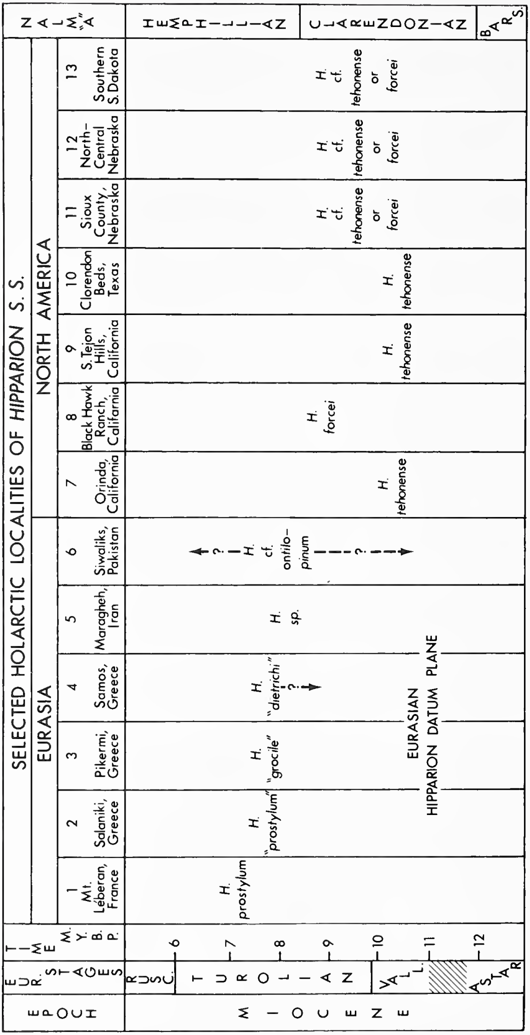
The Siwalik hipparions of Pakistan and adjacent India have been the subject of numerous publications because of their association with a very rich Neogene sequence including the oldest-known hominoid fossils (Pilbeam *et al.* 1977). Hussain (1971) presented the most recent revision of Siwalik hipparions. MacFadden and Bakr (1979) recognize two, or perhaps three, supraspecific taxa of



TEXT-FIG. 13. Selected Holarctic localities of *Hipparion s.s.* as recognized by skull morphology. Eurasian localities (1–6) are taken from this report, MacFadden and Bakr (1979) and Woodburne and Bernor (1980). North American localities (7–13) are taken from this report. The locality numbers in this text-fig. correspond to the numbers of the columns in text-fig. 14.



TEXT-FIG. 14. Temporal and geographic distribution of the Holarctic *Hipparion s.s.* localities shown in text-fig. 13. Epoch, Stage, North American Land Mammal 'Ages' (NALMA), and time (mybp) calibrations are taken from numerous references cited in the text. Dashed zone between Astarcian and Vallesian European Stages indicates the uncertainty involved in the calibration of the Hipparion Datum Plane. The arrows in columns 4 and 6 indicate questionable ranges depending upon stratigraphic interpretations (for Samos) and lack of well-preserved cranial material (for the Siwaliks). See discussion in text.



TEXT-FIG. 14. Temporal and geographic distribution of the Holarctic *Hipparion s.s.* localities shown in text-fig. 13. Epoch, Stage, North American Land Mammal 'Ages' (NALMA), and time (mybp) calibrations are taken from numerous references cited in the text. Dashed zone between Astarcian and Vallesian European Stages indicates the uncertainty involved in the calibration of the Hipparion Datum Plane. The arrows in columns 4 and 6 indicate questionable ranges depending upon stratigraphic interpretations (for Samos) and lack of well-preserved cranial material (for the Siwaliks). See discussion in text.

Siwalik hipparions. Some specimens of their 'small hipparion complex' (here termed *H.* cf. *antilopinum*) are tentatively referred to *Hipparion s.s.* Based on teeth, hipparions are known to range in the Siwaliks from the early Vallesian (roughly 10·5 mybp following Barndt *et al.* 1978) to the early Villafranchian (roughly 3·0 mybp following Keller *et al.* 1977). It is impossible at present to determine the exact range of *H.* cf. *antilopinum* because the relevant cranial material either has poor stratigraphic data (particularly from the early collections) or is limited to the upper Dhok Pathan Formation, which is probably late Turolian in age.

The stratigraphic range in North America of *Hipparion s.s.* as recognized by cranial morphology is from early to late Clarendonian. The individual ages of each locality are represented in text-figs. 13 and 14.

There are several important conclusions based on the present study of *Hipparion s.s.* First, in contrast to the hypotheses of earlier workers, *Hipparion s.s.* was widespread in North America as well as Eurasia during the Miocene. The stratigraphic distribution (text-fig. 14) of the several species of *Hipparion s.s.* demonstrates a generic-level continuity throughout Holarctica during the medial to late Turolian and early to late Clarendonian. The slightly older occurrences of *H. tehonense* in North America may be significant in a phylogenetic context depending upon the accuracy of the intercontinental correlations. If *H. tehonense* is older than the other *Hipparion s.s.*, at present there is no implication of primitiveness or ancestry for this species. The interspecific relationships of the species assigned to *Hipparion s.s.* require a detailed analysis beyond the scope of this paper.

Another interesting conclusion, based on the limited number of localities and relevant cranial material discussed here, is that Eurasian *Hipparion s.s.* appears to be common in Turolian age localities but is not recognized from the Vallesian. Therefore, it appears that *Hipparion s.s.* was not involved in the Eurasian 'Hipparion Datum Plane' that defines the base of the Vallesian. MacFadden and Skinner (1977) and Skinner and MacFadden (1977) suggested that the presence of hipparions in the Old World could have been a result of more than one dispersal event rather than only one event as has been suggested by some other workers (e.g. Forstén 1968; Hussain 1971).

As was stated in the Introduction, the species-level taxonomy of Holarctic *Hipparion s.s.* needs to be revised in light of cranial morphology. Based on numerous cranial characters it appears that *Hipparion s.s.* is composed of a monophyletic group of several species. It is important to determine the ancestral stock from which the *Hipparion s.s.* species were descended. It is clear that the closest relative of *Hipparion s.s.* is within the merychippine horses (e.g. Matthew 1924; Colbert 1935; Stirton 1940; Forstén 1968; Skinner and MacFadden 1977). A study is needed that demonstrates the relatedness of several hipparion groups that apparently arose independently from the horizontal merychippine complex. A striking consequence of recent studies of hipparion cranial morphology is that these three-toed horses are certainly polyphyletic and arose from more than one merychippine lineage. In short, several distinct supraspecific groups of hipparions originated independently and evolved in parallel during the Neogene in the Old and New Worlds.

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THE TOARCIAN AGE OF THE UPPER PART OF THE MARLSTONE ROCK BED OF ENGLAND

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ABSTRACT. The 'Transition Bed' of Oxfordshire, Northamptonshire, and Leicestershire is the weathered or altered top of the Marlstone Rock Bed. In the top 0·05 m–0·3 m of the bed, the green ferrous minerals were oxidized to limonite, partly before deposition of overlying beds, partly recently in some areas. In another type of alteration, best seen at Harston, Leicestershire, much granular iron-pyrites was deposited in a highly irregular zone up to 0·08 m thick at the top of the bed. In these Midland counties the whole of the Tenuicostatum Zone, the basal zone of the Toarcian, is represented in the top 1–3 m of the Marlstone Rock Bed, the lower 3–6 m of which belongs to the Spinatum Zone. Regardless of the depth of weathering or alteration, *Tiltoniceras antiquum* and *Dactylioceras semicelatum* of the Semicelatum Subzone occur widely in the top 0·1 m of the bed, *D. tenuicostatum* occurs more locally at a slightly lower horizon, and lower still one *D. crosbeyi* is evidence for the Clevelandicum Subzone. Ammonites from the Semicelatum, Tenuicostatum, and Paltum Subzones occur in the Dorset coast Marlstone Rock Bed. North of Lincoln the top of the Bed is at about the top of the Spinatum Zone, while the Tenuicostatum Zone is divided between an overlying hard mudstone and higher grey shales. The change from the underlying ironstone/limestone facies to the overlying clays/shales-with-nodules facies took place at the top of the Spinatum Zone in Yorkshire, but at the top of the Tenuicostatum Zone in the Midland counties.

THE Marlstone Rock Bed is one of the most distinctive lithological horizons in the English Lias. It is typically an oolitic limestone, though the sand content becomes significant in a few places, and the ferrous iron content is high enough in two areas for it to be used as an iron-ore. The outcrop (text-fig. 1), known from numerous building-stone and iron-ore quarries in the past, extends from the Dorset coast generally north-eastwards to north of the Humber. Although it is represented immediately north of the Mendips and also at Dundry, south of Bristol, it is generally absent around and to the south of Bath. There is another gap in north Northamptonshire and south Leicestershire, where it is absent altogether or only about 0·3 m thick, owing to a combination of thin deposition and subsequent erosion. For several miles north and south of Lincoln it disappears and is represented by a layer of phosphatic pebbles and possibly some thin overlying shales. North of the Humber it thins out against the Market Weighton block, and it does not reappear farther north in Yorkshire, where equivalent beds are developed in a different facies.

Traditionally the top of the Marlstone Rock Bed was the junction between the Middle and Upper Lias, or more specifically the junction between the Spinatum and Tenuicostatum Zones (Arkell 1933, pp. 153–159; Whitehead *et al.* 1952, pp. 97, 105, 144–150). In fact the Marlstone Rock Bed was referred to a single zone, the Spinatum Zone, because in some areas it has a rich fauna of species of *Pleuroceras* (Howarth 1958, pp. ix–xi). The beds above the Marlstone Rock Bed are clays and shales in most areas, but in some parts of the Midlands the 'Transition Bed', a bed of oolitic limestone up to 0·15 m thick, is the immediately overlying bed. It was first described from the Banbury area, north Oxfordshire, and later at Tilton, Leicestershire, and contains a rich fauna of the Upper Lias ammonites *Dactylioceras* and *Tiltoniceras* '*acutum*' (Blake). It was called the Acutum Zone or hemera by Buckman (1910*b*, p. 86) and the Acutum Subzone by Arkell (1933, p. 179), and placed at the base of the Upper Lias, below the Tenuicostatum Subzone, as the lower of the two subzones of the Tenuicostatum Zone. This subzonal position of the Transition Bed has not been challenged until recently, though Spath (1942, p. 265; 1956, p. 143) did not accept the validity of this subdivision of the Tenuicostatum Zone. The identification of the horizon to which the Transition Bed belonged was made more difficult by the naming of an atypical representative of its *Dactylioceras* fauna as

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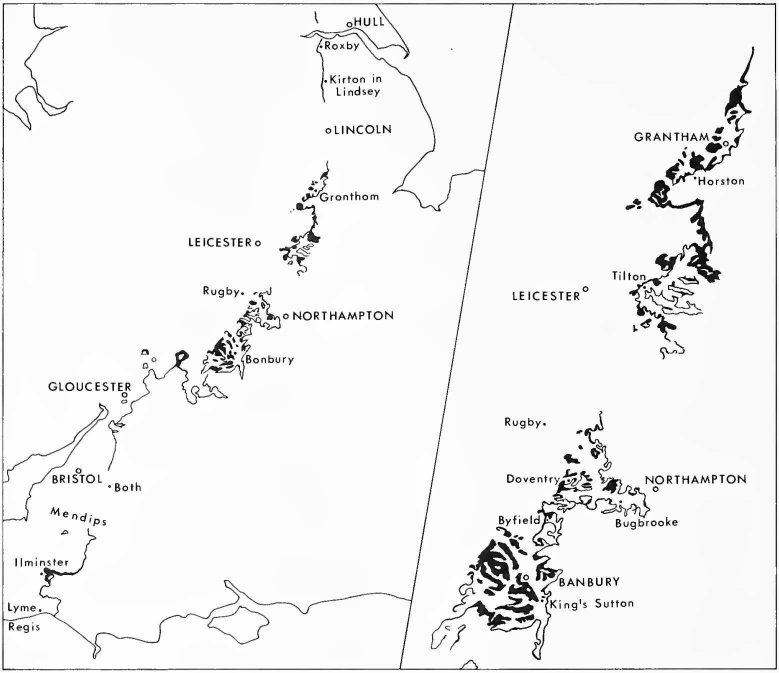
Orthodactylites directus Buckman (1926*a*, pl. 654), and also by the inability of anyone to find either this ammonite or *Tiltoniceras* in the Yorkshire coast Upper Lias succession. In a more recent investigation of the succession at Tilton, Hallam (1955, p. 21) discovered that *D. directum* occurred in the top 0·9 m of the Marlstone Rock Bed as well as in the Transition Bed, and suggested that it would be necessary to place the base of the Toarcian (i.e. the Upper Lias) at least 0·9 m below the top of the Marlstone Rock Bed. A more conservative view was taken by Howarth (1958, p. xi), and followed later by Hallam (1967, p. 397), that it was best to retain the Middle/Upper Lias boundary at the top of the bed, because the relationships between the last *Pleuroceras* and the first *Dactylioceras* in Britain were not known at that time.



TEXT-FIG. 1. Sketch map of the outcrop of the Marlstone Rock Bed, showing the principal localities described in the text.

No further advance could be made until the succession of ammonites in the Tenuicostatum Zone of the Yorkshire coast was worked out. When this was done (Howarth 1973, enlarging on the collecting of the late Professor P. C. Sylvester-Bradley, whose preliminary results were published in Dean, Donovan, and Howarth 1961, p. 476) the following sequence of ammonites, and of subzones derived from them, was established:

Zone	Subzone	Ammonite faunas
Dactylioceras tenuicostatum	*Dactylioceras semicelatum*	*Tiltoniceras antiquum* and *Dactylioceras semicelatum*
		D. semicelatum
	D. tenuicostatum	*D. tenuicostatum*
	D. clevelandicum	*D. clevelandicum*
		D. crosbeyi
	Protogrammoceras paltum	*Protogrammoceras paltum*

Abundant faunas of *Tiltoniceras* were found at the top of the Tenuicostatum Zone in Yorkshire, not at the base of the zone where the genus had always been expected before (e.g. Hallam 1967, p. 415). This alone was sufficient to suggest that the Transition Bed of the Midlands belonged to the top subzone of the Tenuicostatum Zone, and confirmation of this correlation was obtained when it was found that most of the *Dactylioceras* in that bed, to which the name *D. directum* had always been given before, were typical examples of *D. semicelatum*. In fact the populations of the latter species in the Transition Bed and in the Semicelatum Subzone of the Yorkshire coast are very similar, having almost identical ranges of variation. One end of the variation consists of evolute specimens with fine rectiradiate ribs, and Buckman gave the name *D. directum* to the most extreme example of this type from the Transition Bed.

Shortly after the Yorkshire coast Tenuicostatum Zone succession had been described, an abundant ammonite fauna was found in the top of the Marlstone Rock Bed in a quarry at Harston, north Leicestershire. The top 0·08 m of the bed contained many *D. semicelatum* and a few *Tiltoniceras*, and was clearly equivalent to the Transition Bed, though it was not developed as a distinct bed at Harston. The main discovery, however, was the presence of *D. tenuicostatum* in abundance in the next 0·05 m below, an ammonite that had hardly ever been found in the Marlstone Rock Bed before. This proved the presence of the Tenuicostatum Subzone in the bed, and further minor discoveries showed that the Clevelandicum Subzone occurred lower still in the bed.

The presence of the whole of the Tenuicostatum Zone in the Marlstone Rock Bed at Harston, and the discovery in existing museum collections of specimens of *Tiltoniceras* from Tilton preserved in green oolitic limestone typical of the Marlstone Rock Bed, led to further investigation of the Tilton Railway Cutting. It was found that, just as had been originally described by Wilson and Crick (1889), the Transition Bed is not a lithologically distinct bed, it is merely the weathered top of the Marlstone Rock Bed. There is no lithological break or disconformity that marks off a distinct bed at the top, only a highly irregular zone of oxidation of the green ferrous-iron content of the oolite to brown limonite. The Semicelatum Subzone ammonite fauna occurs in the top 0·9 m of this complete Marlstone Rock Bed (i.e. including the 'Transition Bed') at Tilton. Unfortunately there is no evidence for lower subzones of the Tenuicostatum Zone at Tilton, though there is plenty of room for them above the highest recorded *Pleuroceras* at about 3 m below the top of the Marlstone Rock Bed.

The 'Transition Bed' and its distinct ammonite fauna is also well developed in the Banbury–Byfield area of north Oxfordshire and west Northamptonshire. Although more constant in thickness, it appears possible to interpret it similarly in that area as the weathered top of the Marlstone Rock Bed, weathering that probably occurred before deposition of any overlying beds. Between north

Oxfordshire and south Somerset Tenuicostatum Zone ammonites are rarely found and the presence of the zone within the Marlstone Rock Bed has yet to be demonstrated. On the Dorset coast, however, where the Marlstone Rock Bed is very thin (0–0·6 m), ammonites are frequent and prove the presence of the Paltum, Tenuicostatum, and Semicelatum Subzones. The new stratigraphical work and ammonite collections, and reinterpretation of older collections are described in detail below.

STRATIGRAPHICAL DESCRIPTIONS

1. *Dorset coast.* The Marlstone Rock Bed forms the lowest part of the Middle and Upper Liassic Junction Bed in the cliffs between Seatown and Eype, and has been described in detail by Buckman (1922*b*), Jackson (1922, 1926), and Howarth (1957). The bed is never more than 0·6 m thick and consists of three layers, the lithological differences and ammonite faunas of which were discussed by Howarth (1957, pp. 192–193). The lowest layer R is a coarse conglomeratic and oolitic limestone that contains many *Pleuroceras* indicative of the Apyrenum Subzone of the Spinatum Zone. The middle layer Px is a hard grey and pink limestone with scattered ooliths that contains only a few *P.* cf. *spinatum* and probably belongs to the Hawskerense Subzone. The top layer P is a brown finely oolitic limestone that contains a rich ammonite fauna. Previously (Howarth 1957, p. 193) it was said to be of Hawskerense Subzone age only, but now that the sequence within the Tenuicostatum Zone is known in Yorkshire, it is clear that layer P is a highly condensed bed that contains most horizons from the Hawskerense up to the Semicelatum Subzones. The following is a list of the ammonites that have been collected from layer P:

Dactylioceras semicelatum (BM C.17548, C.74719; IGS GSM 22475, 22514; SM J.44225–44226; NMW 26.135 G123), *D. tenuicostatum* (NMW 26.135 G5–8 (9 specimens), G124), *Protogrammoceras paltum* (BM 67939, C.2200, C.30769, C.68536; IGS GSM 47160–47161, 49291; SM J.44789), *Pleuroceras spinatum* (Bruguière), *P. spinatum* var. *buckmani* (Moxon), *P. yeovilense* Howarth, *P. hawskerense* (Young and Bird), *P. apyrenum* (Buckman).

These ammonites are characteristic of the Semicelatum, Tenuicostatum, Paltum, and Hawskerense Subzones, and the only horizon for which there is no evidence is the Clevelandicum Subzone. The examples of *D. semicelatum* (Pl. 81, figs. 3, 4, and Howarth 1957, pl. 17, figs. 5, 6) are typical of the species and match Yorkshire coast examples closely. The ten specimens of *D. tenuicostatum* (Pl. 82, figs. 5–8) are small and very similar to examples from near the top of the Marlstone Rock bed at Harston, Leicestershire; they all came from a layer of fine brown oolite which also contained one specimen of *D. semicelatum*, many gastropods, and a unique Terebratulid that was later described as '*Terebratula*' *reversa* Ager (1956*a*, p. 4, pl. 1, fig. 6) (possibly a *Lobothyris*). This association of fossils found in only a single block was the basis for the proposal of the layer At by Jackson (1926, p. 497) (At was derived from Buckman's hemera '*athleticum*', a term used for the Transition Bed of the Midlands that was said to contain a similar Terebratulid). However, the lithology is not different from layer P, the brachiopod has no special age significance, and the ammonites are intermediate in age between the Semicelatum and Paltum Subzones ammonites that are found in many other blocks of layer P. Therefore, there is no justification for the recognition of a separate At layer. Well-preserved specimens of *Protogrammoceras paltum* in layer P include the holotype and paratype (Buckman 1922*a*, pl. 362A; 1923*a*, pl. 362B), an example figured by Wright (1884, pl. 81, figs. 4–6), and the specific synonym *Platyharpites platypleurus* Buckman (1927*a*, pl. 698). So layer P, though never more than 0·3 m thick, contains highly condensed representatives from the Hawskerense to Semicelatum Subzones. The Marlstone Rock Bed of the Dorset coast, i.e. layers R, Px, and P, belongs to the whole of the Spinatum and Tenuicostatum Zones, so it is approximately equally divided between the Middle and Upper Lias. The next higher blocks of the Junction Bed are the layers N, O, and D, which are lateral equivalents of each other, and contain specimens of *Harpoceras exaratum*, from about the middle of the Exaratum Subzone. There are no records of *Eleganticeras* that would indicate the presence of the lower part of the Exaratum Subzone.

2. *North Dorset, Somerset, Avon, and Gloucestershire.* Northwards from the Dorset coast the Marlstone Rock Bed thickens quickly, and the term Junction Bed is now applied to the overlying sequence of clays and limestones of the Upper Lias. Both beds are very rich in ammonites in the Ilminster area of south Somerset. In the well-known Barrington succession described by Hamlet (1922), Spath (1922), and Pringle and Templeman (1922), the Marlstone Rock Bed contains many *Pleuroceras*, and is overlain by bed 1 (of Hamlet), a 0·175 m bed of 'sandy marl' which contains *D.* cf. *tenuicostatum* in addition to more examples of *Pleuroceras*. Bed 2, a 0·1 m bed of grey oolitic limestone, contains *D. semicelatum*, of which an example is figured here (Pl. 81, figs. 1, 2). The overlying bed 3 is clay containing argillaceous limestone nodules, and is of Exaratum Subzone age. So the Tenuicostatum

Zone is confined to bed 2 and part of bed 1, and these may be a local lithological variation of the Marlstone Rock Bed.

The Marlstone Rock Bed is well developed around Batcombe and Evercreech, near Shepton Mallet on the south side of the Mendips (Richardson 1906, 1909), but evidence for the presence of the Tenuicostatum Zone has not been obtained. After a gap north of the Mendips, the bed reappears north of Bath, thickens quickly, and was formerly extensively quarried along the western escarpment of the Cotswolds in Gloucestershire. There is little ammonite evidence for the age of the top of the bed. Species of *Pleuroceras* from both subzones of the Spinatum Zone are common at some localities (e.g. Alderton Hill), but data about their stratigraphical position in the Marlstone Rock Bed are lacking. There are no Tenuicostatum Zone ammonites in existing museum collections from this area. One record is intriguing, however: in an exposure of the Marlstone Rock Bed near Stow-on-the-Wold, about 25 km east of the Cotswolds escarpment, Hull (1857, pp. 19, 20) saw a 'band of deep reddish purple ironstone' 0·15 m thick at the top of the bed 'filled with good specimens of *Ammonites annulatus*'. It is likely that these were examples of *D. tenuicostatum* or *D. semicelatum* and they would show that most of the Tenuicostatum Zone was in the Rock Bed. The exposure was not extant in 1929 when Richardson (1929, p. 31) quoted the record, and the ammonites are not preserved in the Institute of Geological Sciences, so the occurrence cannot be investigated further. In the Stowell Park bore-hole, 18 km south-west of Stow-on-the-Wold, the Marlstone Rock Bed did not yield any ammonites, but 1 m of overlying shales contained *Tiltoniceras* and *Dactylioceras* of the Semicelatum Subzone. This shows that at least some of the Tenuicostatum Zone is above the Marlstone Rock Bed, though it need not be more than the upper half of the Semicelatum Subzone.

3. *Oxfordshire and Northamptonshire*. The Marlstone Rock Bed used to be extensively quarried for iron-ore and building stone over a large area between Banbury and Northampton, and details of the many former quarries can be found in Whitehead *et al.* (1952). It was in this district that the term 'Transition Bed' was first proposed by Walford (1878, p. 2) for a pale-brown oolitic and ferruginous 'marl' 0·050–0·075 m thick that forms the top of the Marlstone Rock Bed. The type area is around Banbury, and the best-known localities were quarries at Adderbury, King's Sutton, and Middleton Cheney, south and east of Banbury. Large numbers of *T. antiquum* (Wright) and *D. semicelatum* (including the holotype of *D. 'directum'* Buckman) and many small gastropods were obtained from the Transition Bed in these quarries, and they show that the bed belongs to the Semicelatum Subzone. Arkell (1947, p. 21) proposed that the term 'Acutum Bed' (after *Tiltoniceras 'acutum'* Blake, the holotype of which came from Adderbury) should supercede Transition Bed in the north Oxfordshire area, but this change of name has not been adopted by other authors ('Acutus Subzone' had been used earlier by Walford (1899, p. 33)). This lithology and 0·050–0·075 m thickness is fairly constant over the whole of north Oxfordshire and west Northamptonshire as far north as Daventry. At Iron Cross Farm, Byfield, the last locality at which it was well exposed (Howarth 1978, p. 240), it forms the upwards continuation of the Marlstone Rock Bed, with which it has a sharp and irregular junction. The Transition Bed appears to be the altered top of the Marlstone Rock Bed, alteration that is mainly oxidation and leaching of the green ferrous iron, and which probably took place before deposition of the overlying Abnormal Fish Bed. The latter is separated by a parting from the top of the Transition Bed, and is of mid and upper Exaratum Subzone age (Howarth 1978, p. 241).

In areas further east, and especially around Milton and Bugbrooke west of Northampton, a series of beds up to 0·35 m thick has been referred to the Transition Bed (Thompson 1889, 1892). This is due to the inclusion of an overlying sandy or shaly clay that does not contain the characteristic Transition Bed ammonites or gastropods. The age of the clay is not accurately known, but it may bridge the small disconformity that occurs everywhere else between the Transition Bed and the Abnormal Fish Bed, and it should not be included in the Transition Bed. At Bugbrooke Thompson (1892, p. 337) said that the Transition Bed was not present as a distinct bed, but was nevertheless clearly shown by the altered character of the top of the Marlstone Rock Bed which contained the Transition Bed fossils. Thus it appears that throughout the area the Transition Bed is the altered top of the Marlstone Rock Bed, alteration which probably took place before deposition of the overlying beds.

Evidence for the subzonal age of the remainder of the Marlstone Rock Bed is meagre in this area. Only one specimen of *D. tenuicostatum* has been found (Pl. 82, figs. 3, 4), at Rothersthorpe, 5 km south-west of Northampton, from an unrecorded horizon, but judging from the grey-green finely oolitic matrix, probably from immediately below the altered top of the Marlstone Rock Bed. This ammonite is evidence for the Tenuicostatum Subzone, but there are no ammonites to prove the presence of lower subzones. The majority of the Marlstone Rock Bed belongs to the Spinatum Zone and the characteristic brachiopods *Tetrarhynchia tetrahedra* and *Lobothyris punctata* are abundant except at the extreme top. *Pleuroceras* is rare in Northamptonshire: a few *P. spinatum* have been found and at least one *P. apyrenum* is known, but their horizons are not recorded. The Middle/Upper Lias junction occurs near the top of the Marlstone Rock Bed, probably within the top 0·25 m.

4. *Tilton, Leicestershire*. The well-known section at Tilton Railway Cutting (SK 762055) was first described by Wilson and Crick (1889) and there is a good photograph of it in its original state in Fox-Strangways (1903, p. 30, pl. 2). Wilson and Crick saw the Marlstone Rock Bed soon after it was uncovered below a thickness of up to 9 m of Upper Lias shales and it had been little affected by recent subaerial weathering. The 'Transition Bed' was described as a flaggy limestone 0·15–0·23 m thick containing a distinctive fauna, especially the ammonite *Tiltoniceras*, even though they said that 'it possesses the mineral characters of and is welded to the top of the Marlstone Rock Bed' (Wilson and Crick 1889, p. 297). Woodward (1893, p. 236) repeated this interpretation of the Transition Bed, but Whitehead *et al.* (1952, p. 135) made no mention of a Transition Bed at Tilton, nor anywhere in the surrounding area. The railway section was again described by Hallam (1955; 1968, p. 208) who recognized the 0·15–0·23 m Transition Bed, and observed that it lapped 'over minor irregularities at the top of the ironstone' and 'rested non-sequentially on the ironstone'. The lithology of the Transition Bed has been described as a pale-brown or cream finely oolitic limestone, sometimes flaggy, and sometimes passing up into sandy marl. *Tiltoniceras* preserved in such brown oolitic limestone is very common, but many others also occur preserved in the deep-green oolitic ironstone that is typical of the Marlstone Rock Bed at Tilton. Hallam (1955, p. 21) explained the latter by saying that the genus occurred rarely in the ironstone immediately below the Transition Bed.

Examination of the Tilton Railway Cutting exposures in recent years shows that the Transition Bed does not exist as a separate bed. It is the weathered top of the Marlstone Rock Bed, in which the siderite and chamosite of the deep green oolitic limestone are oxidized to limonite; partial decalcification gives it a friable, granular texture, which has been described as sandy, though the bed is not arenaceous. The depth of weathering varies greatly between 0·01 m and 0·25 m below the top surface, and the lowest extent is marked by an undulating thin sheet of brown limonite. Many specimens of *T. antiquum* (Wright), *D. semicelatum* (Pl. 81, figs. 5, 6) and *Gibbirhynchia tiltonensis* Ager, and many small gastropods (Wilson and Crick 1889, pp. 298–305, pl. 9) occur in the top 0·2 m of the Marlstone Rock Bed. Whether they occur preserved in deep-green ironstone or pale-brown oolitic limestone depends entirely on how deeply the weathering has penetrated at any particular point. Several fine examples of *Tiltoniceras* preserved in green ironstone were obtained from only 0·025 m below the top, but most of the green specimens occur lower down. In some specimens that are orientated approximately vertically in the bed, the upper half of the ammonite is pale brown and the lower half deep green. Weathering also penetrates deeply down some of the vertical joints and can convert fossils much lower down into pale-brown friable limestone. In a few places horizontal bedding planes lead to greater penetration of weathering, and rarely the whole of the top 0·2 m is affected giving the appearance of a distinct lithological bed at the top of the ironstone. Such beds fade out rapidly laterally, and the usual state is dark-green Marlstone Rock Bed weathered brown to a highly variable depth.

D. semicelatum is commonest in the top 0·2 m, but unlike *Tiltoniceras* it also occurs lower down to depths of 0·9 m below the top of the ironstone. This is the amount of the Marlstone Rock Bed that must be referred to the Semicelatum Subzone. No Upper Lias ammonites belonging to lower subzones occur at Tilton. The only Pleuroceras found *in situ* is a specimen of *P.* cf. *hawskerense* (Young and Bird) 3·0 m below the top of the Marlstone Rock Bed, and it indicates the Hawskerense Subzone of the Spinatum Zone. The brachiopods *Tetrarhynchia tetrahedra* (J. Sowerby) and *L. punctata* (J. Sowerby) range higher in the ironstone, the last ones being about 1·2 m below the top (Hallam 1955, p. 20). These two are usually held to be good indicators of the Spinatum Zone in England, but there are rare records from the Upper Lias, the genus *Tetrarhynchia* ranges up into the Bajocian (Ager 1956*b*, p. 3), and *T. tetrahedra* occurs in the Upper Lias, Bifrons Zone, in Spain (Hallam 1972, p. 408). So in the absence of ammonites, it does not seem safe to take the highest occurrence of these brachiopods as unequivocal evidence of the Spinatum Zone. The evidence available at present suggests that the Spinatum/Tenuicostatum Zone boundary occurs between 1 m and 3 m below the top of the Marlstone Rock Bed at Tilton. There is room in this thickness for condensed representatives of the three lower subzones of the Tenuicostatum Zone, and a disconformity need not be postulated to explain their absence. There is also no lithological evidence for such a disconformity.

The beds above the Marlstone Rock Bed are clays and shales with a few thin beds of limestone or limestone nodules. The basal 2·8 m belongs to the Exaratum Subzone, and uncrushed examples of *Harpoceras elegans* (J. Sowerby) and *H. serpentinum* (Schlotheim) occur at about the 2 m level. These indicate the top part of the Exaratum Subzone, and the absence of *H. exaratum* suggests that the non-sequence between the top of the Marlstone Rock Bed and the shales represents at least the lower half of the Exaratum Subzone. All the higher shales up to the top of the cutting belong to the Falciferum Subzone and contain the index ammonite commonly throughout. The following is a summary of the section exposed in the Tilton Railway Cutting (SK 762055), Leicestershire:

Zone and subzone of *Harpoceras falciferum*

Grey shale, with two rows of small limestone nodules about 0·5 m and 0·6 m below the top. *H. falciferum*	5·50 m
Grey clay containing large calcite ooliths. *H. falciferum*, *Phylloceras heterophyllum* (J. Sowerby)	0·70 m

Subzone of *Harpoceras exaratum*

Grey clay, oolitic. Large specimens of *H. serpentinum* (Schlotheim)	0·80 m
Grey oolitic limestone. *H. elegans* (J. Sowerby) (BM C.80481–80483) and *H. serpentinum* common (BM C.80484–80485), and many *Dactylioceras* sp. indet.	0·20 m
Grey shales, paper shales, and clays. *H. serpentinum* in top 0·5 m	1·80 m

Zones of *Dactylioceras tenuicostatum* and *Pleuroceras spinatum*

Marlstone Rock Bed:

a.	Ironstone. Dark-green finely oolitic limestone, containing chamosite and siderite, weathered brown to an irregular depth, and sometimes more deeply along joints and bedding planes. *Tiltoniceras antiquum* (Wright) (BM C.10265–10267, C.41733, C.48753–48757, C.80242–80276, C.80470–80480) and *D. semicelatum* (BM C.36186–36188, C.49766, C.80277–80282, C.80466–80469) are abundant in the top 0·2 m and 0·9 m respectively and indicate the Semicelatum Subzone; *P.* cf. *hawskerense* (Young and Bird) (BM C.73686) occurs at the bottom and indicates the Hawskerense Subzone	3·0 m
b.	Green oolitic limestone, containing numerous specimens of *Tetrarhynchia tetrahedra* and *Lobothyris punctata*, and many bivalves (band B of Hallam 1955, p. 18)	0·45 m
c.	Sandrock. Green massive calcareous sandstone	1·4 m
d.	Calcareous sandstone as bed c, but with many nests of the brachiopods *T. tetrahedra* and *L. punctata* (band A of Hallam 1955, p. 18)	0·3 m
e.	Sandrock, as bed c	0·75 m

Other exposures of the Marlstone Rock Bed in the Tilton area were in iron-ore quarries, where the bed had been less deeply buried than in the railway cutting. Consequently the top of the bed had been more strongly weathered. Of those described by Whitehead *et al.* (1952) and Hallam (1955, 1968), few now remain. One that can still be seen is the old quarry 1·3 km east of Tilton (SK 756056), where the top 0·2 m of the Marlstone Rock Bed is highly weathered into a pale-brown oolitic limestone that contains *Tiltoniceras antiquum* and *Dactylioceras semicelatum*. Other quarries, now obscured, were similar, and it is thought that the 'Transition Bed' is, in all cases, the weathered top of the Marlstone Rock Bed.

5. *Grantham area, north Leicestershire and south Lincolnshire*. Two quarries working the Marlstone Rock Bed as iron-ore existed, until closed down and filled in in 1975, at Harston, 12 km south-west of Grantham. Here the top of the Marlstone Rock Bed contains more Dactylioceratidae than any other exposure of the bed in England, and it is the most important section for dating the Upper Lias part of the bed. A section for the Upper Lias shales above the bed was given in Hallam (1968, p. 210), but a more detailed description is now given, so that the position of the disconformities can be established. Section at Harston Quarry (SK 843305), 1·5 km south-south-east of Harston:

Zone and subzone of *Harpoceras falciferum*

Clay. Impressions of *H. falciferum* and *Dactylioceras* sp. indet.	2·00 m
Brown rubbly limestone, oolitic or pisolitic in places. *H. falciferum*	0·20 m

Subzone of *Harpoceras exaratum*

Grey shale	1·20 m
Scattered flat nodules of blue limestone, weathered red-brown and white. *H. elegans* (J. Sowerby) abundant, *Dactylioceras anguiforme* Buckman abundant, *Nodicoeloceras crassoides* (Simpson), *Phylloceras heterophyllum* (J. Sowerby), *Coelodiscus minutus* (Schübler)	0·10 m
Grey shale	*c.* 10·00 m
Grey calcareous clay, forming a hard massive bed. A few limestone nodules occur in a row at the top. Large specimens of *H. elegans*, *H. serpentinum* (Schlotheim) and *Hildaites murleyi* (Moxon)	1·30 m
Shale, with a row of 0·025 m thick flat limestone nodules at the top. *H. serpentinum*, *H. elegans*	0·05 m
Scattered lenticles of coarse sandstone, cross-bedded, with many granules of iron pyrites and some small pebbles. Much shell debris broken into small fragments. Fragments of *Harpoceras* (?*H.* cf. *exaratum*)	0–0·05 m

Zone of *Dactylioceras tenuicostatum*

Marlstone Rock Bed:

a. Pale-brown limestone, consisting of numerous calcite ooliths and minute shell fragments in a calcareous matrix; the top 0·05 m contains patches of crystalline calcite and occasional pebbles of brown limestone; the lower half becomes green-coloured, more coarsely oolitic, with chamosite and siderite, and much recrystallized calcite; the top 0·025–0·080 m is full of fine granules of iron-pyrites and is grey-green in colour; its very uneven lower boundary is marked by a solid line of iron-pyrites, and the bed below is pale brown with only a few granules of iron-pyrites . . . 1·20 m

Subzone of *Dactylioceras semicelatum*

The top 0·08 m contains *Tiltoniceras antiquum* (Wright) (BM C.80237–80241), *D. semicelatum* common (BM C.80169, C.80171–80235), *Acrocoelites vulgaris* (Young and Bird), *Gibbirhynchia* sp. and gastropods.

Subzone of *Dactylioceras tenuicostatum*

Between 0·08 m and 0·13 m below the top *D. tenuicostatum* is abundant (BM C.80099–80168) and *Gibbirhynchia* sp. occurs.

Subzone of *Dactylioceras clevelandicum*

0·23 m below the top one specimen of *D. crosbeyi* (Simpson) (BM C.80170) was found.

Zone of *Pleuroceras spinatum*

b. Deep-green oolitic limestone, with much chamosite and siderite, and many bands of recrystallized calcite. Abundant *Tetrarhynchia tetrahedra* and *Lobothyris punctata* in nests. One *Pleuroceras* cf. *spinatum* (Bruguière) 0·25 m below the top, and several other specimens not *in situ* . . . 3·00 m

This quarry contained one of the best sections of the Marlstone Rock Bed for demonstrating that the top part that contains *Tiltoniceras* is a typical part of the bed that has been diagenetically altered. The alteration is due to pyritization from the top surface downwards. It consisted of the deposition of a large amount of fine granular iron-pyrites, which penetrated to a depth varying between 0·025 m and 0·080 m and the very uneven lower boundary is marked by a thin sheet of solid iron-pyrites. *Tiltoniceras* and *D. semicelatum* (Pl. 81, figs. 10, 11; Pl. 82, figs. 11, 12) occur in the top 0·080 m, so some of the Semicelatum Subzone is in the pyritized part and some in the unaltered part below. Most ammonites lie parallel to the bedding plane, but a few are at a high angle and occasionally the lower boundary of pyritization has reached half down an ammonite. There is no lithological break or change other than the pyritization, except for a few pebbles just below the top surface.

D. tenuicostatum (Pl. 82, figs. 1, 2, 9, 10) occurs in abundance between 0·08 m and 0·13 m below the top of the Bed, and this is the extent of the Tenuicostatum Subzone, which is below the pyritized zone. A single *D. crosbeyi* 0·23 m below the top is evidence for the presence of the Clevelandicum Subzone. There are no ammonites to prove the presence of the Paltum Subzone, but there is plenty of room for it between 0·25 m and 1·2 m below the top of the Bed. Marlstone Rock Bed division b of the above section is a natural downward continuation of the upper part where it becomes richer in iron, and several specimens of *Pleuroceras* occur of the Spinatum Zone.

The whole of the Tenuicostatum Zone is in the top 1·2 m of the Marlstone Rock Bed at Harston, and there are no major lithological discontinuities within that part of the bed. The main disconformity is at the top of the bed where the lithology changes to shale facies, and the bottom one-third of the Exaratum Subzone is missing (because of the absence of *Eleganticeras*). The middle third of that subzone is represented only by the lenticles of sandstone that contain *Harpoceras*, and continuous deposition starts only in the upper third of the subzone where more than 11 m of shales contain *H. elegans* and *H. serpentinum*.

At Denton Park Quarry (SK 856316), 1·5 km north-east of Harston Quarry, a similar succession was seen at the top of the Marlstone Rock Bed, though ammonites were much less common. The top 0·03–0·08 m of the bed contains much granular iron-pyrites as at Harston, but it is more of a shell bed containing a great number of broken bivalve shells and large numbers of the belemnite *Acrocoelites vulgaris* (Young and Bird). A few fragments of large specimens of *Tiltoniceras* were also seen. The lower non-pyritized part of the bed is similar to that at Harston, but Tenuicostatum Subzone ammonites were not found.

6. *North Lincolnshire and south Humberside*. North of Grantham the Marlstone Rock Bed thins steadily and disappears altogether before Lincoln. At Lincoln the Spinatum Zone is absent or is represented by a bed of

phosphatic pebbles (Trueman 1918; Howarth 1958, p. xii, bed 11), but there is no ammonite evidence for the presence of the zone nor for the lowest three subzones of the Tenuicostatum Zone. The presence of the Semicelatum Subzone is shown, however, by specimens of *T. antiquum* (Trueman Coll., Nottingham University, and BM C.48429–48432) in the top 0·15 m of the 0·60 m of overlying shales (Howarth 1958, p. xi, bed 12). *D. semicelatum* also occurs in these shales, and probably in the shales of bed 14 above.

The Marlstone Rock Bed reappears north of Lincoln and it was well exposed in recent years in quarries at Kirton in Lindsey (Howarth and Rawson 1965) and Roxby (Penny and Rawson 1969, pp. 194–197). The distribution of ammonites in the Upper Lias shales was poorly known in these quarries, and better records have been obtained from boreholes in the same area. Most information came from boreholes near Worlaby, 8 km east of Roxby, where many specimens of *T. antiquum* occurred in shales between 4 m and 5·7 m above the Marlstone Rock Bed (Richardson 1979). The following succession for part of the Middle and Upper Lias in this area incorporates details of the Kirton in Lindsey Quarry (Howarth and Rawson 1965, pp. 262–263), the north end of the Roxby Quarry (Penny and Rawson 1969, p. 196), and some records from the Worlaby boreholes. Thicknesses and lithology show little variation, though the rows of doggers are more obvious in the quarries, especially at Kirton in Lindsey. The ammonite distribution is the same, and records from all three places are included.

Subzone of *Harpoceras exaratum*

Shale, with two rows of doggers and a band of limestone. Beds 25–29 at Kirton in Lindsey; bed 29, a row of doggers 0·13 m from the top, contains many *H. elegans* (J. Sowerby); bed 27, a bed of limestone 1·2 m from the top, contains *H.* cf. *exaratum* (Young and Bird); bed 25 is a row of doggers at the base	4·60 m

Subzone of *Dactylioceras semicelatum*

Shale, close-bedded, but sandy in basal 0·3 m. Beds 23 and 24 at Kirton in Lindsey. Many crushed *Tiltoniceras antiquum* (Wright), sometimes in shell beds, through most of the thickness . .	3·50 m
Shale, with scattered limestone nodules, especially near the base. Crushed *D. semicelatum* in the shales in the borehole, and well-preserved solid specimens in the basal nodules at Roxby . .	1·70 m

Subzone of *Dactylioceras tenuicostatum*

Shale. A few *D.* cf. *tenuicostatum*	1·30 m

Subzones of *Dactylioceras tenuicostatum* (part), *D. clevelandicum*, and *Protogrammoceras paltum*

Hard, pale-grey, calcareous mudstone, silty and micaceous, with some phosphatic and calcareous nodules. Bed 21 at Kirton in Lindsey. Many well-preserved ammonites and belemnites: *D. tenuicostatum* and *D. clevelandicum* common; one large *P. paltum* (Buckman) known from Roxby	0·40–1·10 m

Zone of *Pleuroceras spinatum*

Marlstone Rock Bed. Green oolitic limestone. Rare *Pleuroceras* cf. *hawskerense* (Young and Bird) (level unknown). Many brachiopods	3·00 m

The Dactylioceratidae that were recorded previously (Howarth and Rawson 1965, p. 262) in bed 21 at Kirton in Lindsey have been reassessed in the light of the succession of species now known in the Yorkshire coast Grey Shales (Howarth 1973). *Dactylioceras tenuicostatum* and *D. clevelandicum* are both present, and with the single large *Protogrammoceras paltum* at Roxby, they show that the Paltum, Clevelandicum, and part of the Tenuicostatum Subzones are present in that bed. *D. tenuicostatum* also occurs in the shales above, and then *D. semicelatum* and *Tiltoniceras antiquum* occur higher up. So it can be shown that the Tenuicostatum Zone lies wholly above the Marlstone Rock Bed in the area north of Lincoln. Approximately the lower half of the zone is condensed in a bed up to 1·1 m thick, but unlike the 'Transition Bed' of Oxfordshire to Leicestershire, it is a calcified silty mudstone significantly different in lithology from the Marlstone Rock Bed. The upper half of the zone occurs in shales 6·5 m thick that resemble the Grey Shales of the Yorkshire coast in thickness and lithology, except for the absence of pyritized doggers.

SYSTEMATIC DESCRIPTIONS

Family DACTYLIOCERATIDAE Hyatt, 1867
Genus DACTYLIOCERAS Hyatt, 1867
Subgenus ORTHODACTYLITES Buckman, 1926
Dactylioceras (*Orthodactylites*) *semicelatum* (Simpson)

Plates 80, 81; Plate 82, figs. 11, 12; text-figs. 2, 3

1819	*Ammonites annulatus* J. Sowerby, p. 41, pl. 222, figs. 1, 2 (*non* figs. 3–5) (*non Ammonites annulatus* Schlotheim, 1813).
1843	*Ammonites semicelatus* Simpson, p. 20.
1855	*Ammonites semicelatus* Simpson, p. 50.
1884	*Ammonites semicelatus* Simpson, p. 81.
1911*a*	*Dactylioceras semicelatum* (Simpson); Buckman, pl. 31.
1926*a*	*Orthodactylites directus* Buckman, pl. 654.
1927*a*	*Kryptodactylites semicelatus* (Simpson); Buckman, pl. 31A.
1927*a*	*Orthodactylites mitis* Buckman, pl. 738.
1957	*Dactylioceras directum* (Buckman); Howarth, p. 197, pl. 17, figs. 5, 6.
1957	*Dactylioceras semicelatum* (Simpson) and spp.; Maubeuge, figs. 1–3, ?18–21, 41, 42, 44, ?46, 47, 48, ?49, ?58, ?59 (1), 59 (2).
1957	*Dactylioceras pseudocrassoides* Maubeuge, p. 201, pl. 13, fig. 28.
1957	*Dactylioceras densicostatum* Maubeuge, p. 202, pl. 13, fig. 29.
1960	*Dactylioceras* sp. indet.; Hoffmann and Martin, p. 114, pl. 9, fig. 5; pl. 10, figs. 2*a*, 2*b*.
1968	*Dactylioceras* cf. *toxophorum* (Buckman); Hoffmann, p. 4, pl. 2, figs. 3, 4; pl. 3, fig. 1.
1968	*Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson); Hoffmann, p. 6, pl. 2, figs. 1, 2.
1968	*Dactylioceras* (*Orthodactylites*) *eikenbergi* Hoffmann, p. 8, pl. 1, fig. 2.
1968	*Dactylioceras* (*Orthodactylites*) *wunnenbergi* Hoffmann, p. 7, pl. 1, fig. 1.
1968	*Dactylioceras ernsti* Lehmann, p. 46, pl. 17, figs. 5, 6; pl. 19, figs. 2, 4.
1971	*Dactylioceras* (*Orthodactylites*) *anguinum* (Reinecke); Pinna and Levi-Setti, p. 90, pl. 2, figs. 1, 2, 5.
1971	*Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson); Pinna and Levi-Setti, p. 90, pl. 2, figs. 3, 4, 15.
1973	*Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson); Howarth, p. 262, pl. 6, fig. 1; pl. 7, figs. 1, 2; pl. 8, figs. 1–4; pl. 9, figs. 1–3.

Occurrence. Dorset coast: Marlstone Rock Bed layer P, fairly frequent; Somerset: bed 2 (Hamlet 1922) at Barrington, Ilminster, about four specimens known; north Oxfordshire and Northamptonshire: abundant in the top of the Marlstone Rock Bed at many localities from south and east of Banbury to Byfield, Daventry, and Northampton; Leicestershire: abundant in the top of the Marlstone Rock Bed in the Tilton area and common at Harston; Lincoln: shales of beds 12 and 14 (Howarth 1958, p. xi); north Lincolnshire and south Humberside: shales 2·3–4·0 m above the Marlstone Rock Bed at Kirton in Lindsey and Roxby.

Discussion. The occurrence of *Dactylioceras* (*Orthodactylites*) *semicelatum* in the Grey Shales Formation of the Yorkshire coast has already been described in detail by Howarth (1973, p. 262), and

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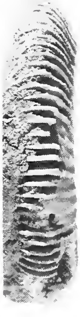
EXPLANATION OF PLATE 80

Figs. 1–12. *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson). All from top 0·1 m of the Marlstone Rock Bed ('Transition Bed'), Semicelatum Subzone, Tenuicostatum Zone, of the Banbury area, Northamptonshire. 1, 2, 5, 6, King's Sutton, 6 km SE of Banbury, BM C.67697, C.67376. 3, 4, Middleton Cheney, 4 km ENE of Banbury, originally figured Buckman (1926*a*, pl. 654) as holotype of *Orthodactylites directus*, IGS GSM 47847. 7, 8, Adderbury, 6 km SSE of Banbury, IGS GSM 22566. 9, 10, Chipping Warden, 10 km NE of Banbury, BM C.67388. 11, 12, Copredy, 6 km north of Banbury, originally figured J. Sowerby (1819, p. 41, pl. 222, fig. 1), paralectotype of *Ammonites annulatus*, BM C.40125. All figures × 1.

PLATE 80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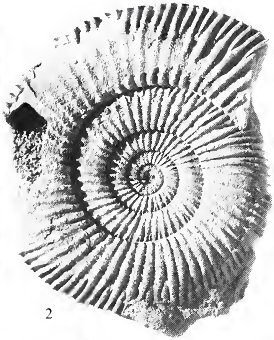
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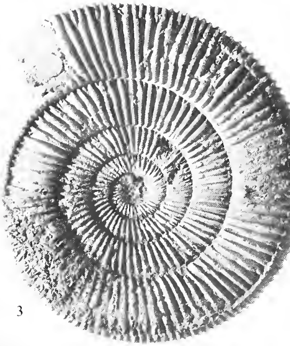
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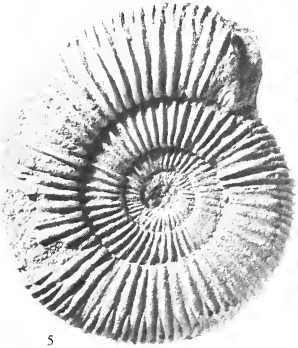
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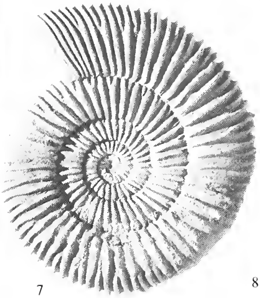
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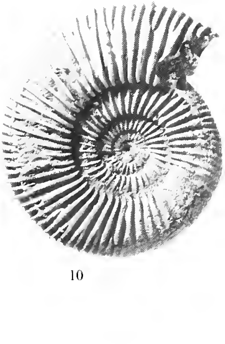
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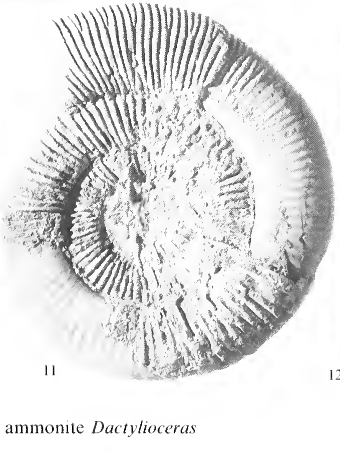
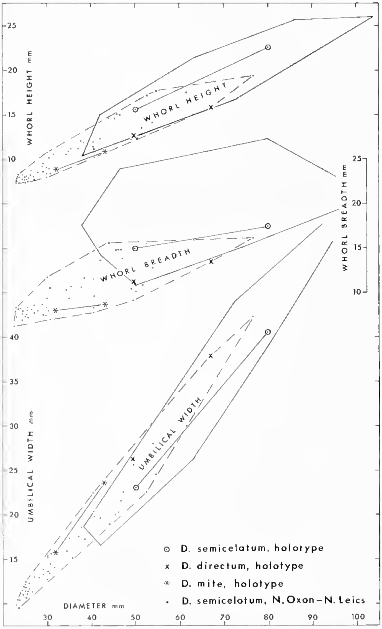

11


12

HOWARTH, ammonite *Dactylioceras*

reference should be made to that paper for an account of the type specimen, the diagnosis and the general description of the species. Outside Yorkshire, the commonest occurrence is in the topmost part of the Marlstone Rock Bed (the 'Transition Bed') in Northamptonshire and Leicestershire. The name *Orthodactylites directus* Buckman (1926*a*, pl. 654) has always been used for these examples previously (including Howarth 1973, pp. 266–267). However, analysis of the west Northamptonshire fauna shows that it agrees closely with the Yorkshire fauna of *D.* (*O.*) *semicelatum* in all characters. Whorl dimensions and rib-density are expressed graphically in text-figs. 2 and 3, where it can be seen that there are no significant differences from the Yorkshire fauna, and that the Yorkshire holotype occupies an approximately central position within the variation of the Northamptonshire fauna. An average specimen from the Marlstone Rock Bed of Northamptonshire is figured in Plate 80, figs. 1, 2, an example with higher whorls and more rectiradiate ribs in Plate 80, figs. 5, 6, and a more involute example with higher whorls in Plate 80, figs. 9, 10. Text-figs 2 and 3 also show that the holotype of *D. directum* (Pl. 80, figs. 3, 4) is an extreme form being more evolute, more compressed, and more finely ribbed than most Northamptonshire specimens. Nevertheless, it does fall within the range of variation of the population, and it matches some Yorkshire specimens closely (e.g. Howarth 1973, pl. 8, fig. 1), so the specific name *directum* should be placed in synonymy with *semicelatum*.

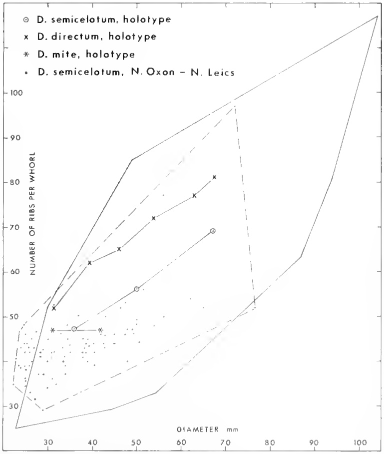
The only west Northamptonshire specimen that is more finely ribbed is one of the paralectotypes of *Ammonites annulatus* J. Sowerby (1819, pl. 222, fig. 1). Previously (Howarth 1973, p. 262) it was determined as *D.* (*O.*) *tenuicostatum*, but, although it is evolute and finely ribbed (Pl. 80, figs. 11, 12), it has the characteristic compressed oval (not near-circular) whorls and prorsiradiate ribs of *D.* (*O.*)



TEXT-FIG. 2. Scatter diagrams of whorl dimensions (whorl height, whorl breadth, and umbilical width, plotted against diameter) for fifty-nine specimens of *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson) from the top of the Marlstone Rock Bed in north Oxfordshire, Northamptonshire, and Leicestershire. The dashed lines are the envelopes of these points, while the solid lines are the envelopes of the scatter diagrams of the Yorkshire coast population of the same species (from Howarth 1973, p. 259, fig. 5).

semicelatum and is matched closely by several specimens from bed 30 in Yorkshire (e.g. Howarth 1973, pl. 8, figs. 1, 2, and BM C.77304). Another west Northamptonshire specimen was made the holotype of *O. mitis* Buckman (1927*a*, pl. 738): it also is not typical of the Northamptonshire fauna, being more evolute than most specimens and it has flat whorl sides and widely spaced ribs near the aperture (text-figs. 2, 3; Pl. 81, figs. 7–9). It is an incomplete immature specimen 44 mm diameter, and it is matched very closely by two specimens from bed 28 in Yorkshire and by some from Harston, Leicestershire (e.g. Pl. 82, figs. 11, 12). These are only another form in the variation of the species, with a different combination of characters, being evolute with fewer ribs, and *O. mitis* should also be placed in synonymy with *D.* (*O.*) *semicelatum*. A larger west Northamptonshire example with similar widely spaced ribs is figured in Plate 80, figs. 7, 8. It is one of the few complete adults that are known from the Marlstone Rock Bed, and has a mouth border at 55 mm diameter. A specimen from Tilton, Leicestershire (C.80278), has a mouth border at 54 mm diameter, and two other Northamptonshire and Harston specimens are 97 and 99 mm diameter at their adult mouth borders respectively. This 54–99 mm range compares with an adult diameter range of 75–120 mm for the Yorkshire coast fauna. A typical example from the top 0·1 m of the Marlstone Rock Bed at Tilton is figured in Plate 81, figs. 5, 6. Two small and indifferently preserved Dorset coast specimens were figured previously (Howarth 1957, p. 197, pl. 17, figs. 5, 6); a large, better preserved example is figured in Plate 81, figs. 3, 4, which is a typical involute specimen with the high, oval whorls of the species. At Barrington, Somerset, specimens occur in a bed about 0·2 m above the Marlstone Rock Bed, and the best one is figured in Plate 81, figs. 1, 2.

The only occurrence of *D.* (*O.*) *semicelatum* outside Britain that was not dealt with in the Yorkshire coast paper (Howarth 1973) consists of those specimens in north-west Germany described as *D. ernsti* by Lehmann (1968, p. 46, pl. 17, figs. 5, 6; pl. 19, figs. 2, 4; also figured by Hoffmann 1968) and smaller specimens figured by Hoffmann and Martin (1960). These show all the usual characters of *D.* (*O.*) *semicelatum*, and the holotype of *D. ernsti* has whorl proportions and rib-density that are close to the average of the Yorkshire and Northamptonshire populations. All the north-west German specimens come from the Semicelatum Subzone, and *D. ernsti* is considered to be a synonym of *D.* (*O.*) *semicelatum*.



TEXT-FIG. 3. Scatter diagram of number of ribs per whorl for seventy-one specimens of *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson) from the top of the Marlstone Rock Bed in north Oxfordshire, Northamptonshire, and Leicestershire. The dashed line is the envelope of these points; the solid line is the envelope of the scatter diagram of the Yorkshire coast population of the same species (from Howarth 1973, p. 261, fig. 6).

Dactylioceras (*Orthodactylites*) *tenuicostatum* (Young and Bird)

Plate 82, figs. 1–10, 13, 14

1822 *Ammonites tenuicostatus* Young and Bird, p. 247, pl. 12, fig. 8.
1828 *Ammonites annulatus* Sowerby; Young and Bird, p. 253, pl. 12, fig. 11.
1884 *Stephanoceras annulatum* (J. Sowerby); Wright, p. 475, pl. 84, figs. 7, 8.
1920*a* *Dactylioceras tenuicostatum* (Young and Bird); Buckman, pl. 157.
1927*a* *Tenuidactylites tenuicostatus* (Young and Bird); Buckman, pl. 157A.
1933 *Dactylioceras tenuicostatum* (Young and Bird); Arkell, pl. 32, fig. 6.
1956 *Dactylioceras tenuicostatum* (Young and Bird); Arkell, pl. 33, fig. 6.
1957 *Dactylioceras tenuicostatum* (Young and Bird); Maubeuge, p. 208, figs. ?41, 42, 43.
1961 *Dactylioceras tenuicostatum* (Young and Bird); Dean, Donovan, and Howarth, pl. 72, fig. 1.
1973 *Dactylioceras* (*Orthodactylites*) *tenuicostatum* (Young and Bird); Howarth, p. 258, pl. 5, figs. 1, 2; pl. 6, figs. 2, 3.

Occurrence. Dorset coast: Marlstone Rock Bed layer P, uncommon; Somerset: bed 1 (Hamlet 1922) at Barrington, Ilminster, poorly preserved crushed specimens; Northamptonshire: Rothersthorpe, one specimen; Leicestershire: 0·08–0·13 m below the top of the Marlstone Rock Bed at Harston, abundant; north Lincolnshire and south Humberside: hard mudstone and 1 m of shales above the Marlstone Rock Bed at Kirton in Lindsey and Roxby, common.

Discussion. A full account of the type specimen, diagnosis, and the Yorkshire coast fauna is found in Howarth (1973, pp. 258–262). Outside Yorkshire, *D. tenuicostatum* is much less widely distributed than *D. semicelatum*, and the only substantial collection from the Marlstone Rock Bed was that obtained from Harston, Leicestershire. About seventy specimens were collected, all of them immature and less than 60 mm maximum diameter. Most have part of their body chambers preserved but they are incomplete, and no adult specimens, indicated by constricted mouth borders or approximated final suture-lines, were found. All have the typical rounded whorl section and fine ribs of *D. tenuicostatum*. An immature of average size is figured in Plate 82, figs. 9, 10, and the largest of 58 mm diameter in Plate 82, figs. 1, 2. The top part of the Marlstone Rock Bed at Harston is highly condensed, and although the main occurrence of *D. semicelatum* is higher up, a few specimens of the latter species are found at the same level as the highest *D. tenuicostatum*. Specimens of *D. semicelatum* are always separable by their higher whorls, oval whorl section, more widely spaced ribs, and by the considerably thicker whorls in some individuals.

A single well-preserved specimen has already been referred to (p. 641) from the top of the Marlstone Rock Bed at Rothersthorpe, 5 km south-west of Northampton (Pl. 82, figs. 3, 4). It is immature, 46 mm diameter, and has a body chamber one whorl long. About ten examples of *D. tenuicostatum* are known from layer P of the Marlstone Rock Bed on the Dorset coast. Again they are all immature or inner whorls of less than about 60 mm diameter, and two of the best specimens are figured in Plate 82, figs. 5–8. In north Lincolnshire the species occurs in the hard mudstone that overlies the Marlstone Rock Bed, and one of the more complete, though small, specimens is figured in Plate 82, figs. 13, 14.

EXPLANATION OF PLATE 81

Figs. 1–11. *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson). 1, 2, bed 2 (Hamlet 1922), 0·2 m above Marlstone Rock Bed, Barrington Quarry, near Ilminster, Somerset, IGS GSM 31612. 3, 4, Marlstone Rock Bed layer P, Seatown, Dorset, BM C.17548. 5, 6, Marlstone Rock Bed, top 0·1 m, Tilton Railway Cutting, Leicestershire, BM C.80277. 7–9, top of Marlstone Rock Bed ('Transition Bed'), Byfield, Northamptonshire, originally figured Buckman (1927*a*, pl. 738) as holotype of *Orthodactylites mitis*, IGS GSM 38384. 10, 11, Marlstone Rock Bed, 0·08 m below top, Harston Quarry, north Leicestershire, BM C.80169. All figures × 1.

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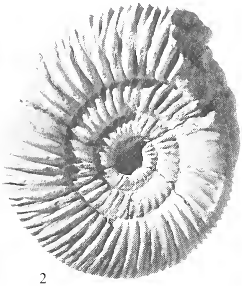

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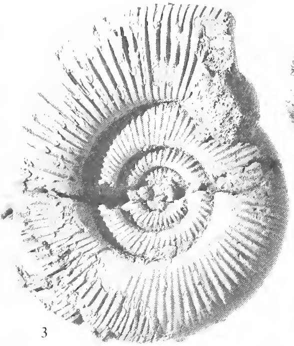

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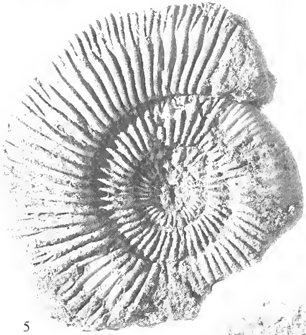

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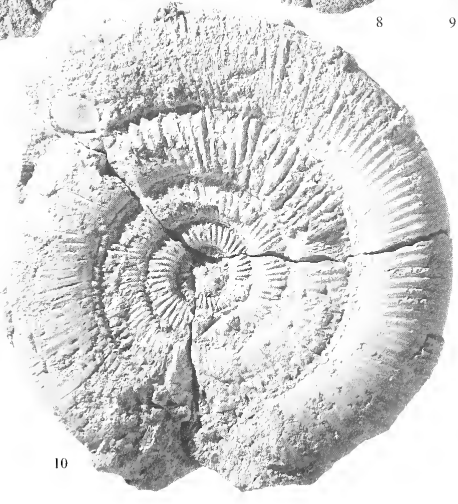

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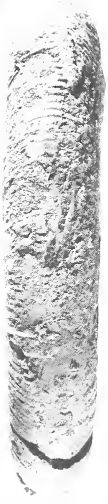

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HOWARTH, ammonite *Dactylioceras*

Dactylioceras (*Orthodactylites*) *clevelandicum* Howarth

Plate 82, figs. 15, 16

1973 *Dactylioceras* (*Orthodactylites*) *clevelandicum* Howarth, pp. 257–258, pl. 3, figs. 1–3; pl. 4, figs. 1, 2; pl. 5, fig. 3.

Occurrence. About eight specimens known in bed 21 at Kirton in Lindsey, north Lincolnshire, and an equivalent horizon in the near-by Worlaby borehole.

Discussion. The most difficult problem in describing the Tenuicostatum Zone Dactylioceratidae that occur in the Marlstone Rock Bed area in England is the identification of the well-preserved specimens in the hard mudstone and the calcareous nodules (bed 21) that overlie the Rock Bed at Kirton in Lindsey, north of Lincoln. Specimens, though well preserved, are not very numerous, and considered on their own they could be a condensed mixture of *D. semicelatum*, *D. tenuicostatum*, and *D. clevelandicum*. Some limit to the age range can be obtained, however, from the ammonites in the overlying beds, for crushed *Dactylioceras* that appear to be *D. tenuicostatum* occur in the overlying 1·3 m of shale, then *D. semicelatum* appears in the next higher 1·7 m of shale, and unmistakable specimens of *Tiltoniceras* occur in the next 3·5 m. These ammonites are in the correct stratigraphical sequence for the Tenuicostatum and Semicelatum Subzones. So it is probable that only the lower part of the Tenuicostatum Subzone, together with lower horizons, occurs in the hard mudstone. This mudstone, and especially the calcareous nodules within it, contains a number of small or fragmentary specimens of *D. tenuicostatum* (Pl. 82, figs. 13, 14), and also a small collection of larger and better-preserved individuals that are identified with *D. clevelandicum*. One of the best specimens from the mudstone at Kirton in Lindsey is figured in Plate 82, figs. 15, 16. Although it is like *D. semicelatum* in some respects, it has rectiradiate ribs, not the prorsiradiate ribs of compressed specimens of *D. semicelatum*. Nor does it have the typical oval whorl section of the latter species. Other examples in this bed have a range of variation from rounded whorls with fine ribs, to depressed whorls with coarse ribs and tubercles. The few that are measurable all fall within the ranges for whorl dimensions and rib-density measured for the Yorkshire coast population of *D. clevelandicum* (Howarth 1973, pp. 259, 261). No examples of this species have been found anywhere else in the Marlstone Rock Bed area.

EXPLANATION OF PLATE 82

Figs. 1–10, 13, 14. *Dactylioceras* (*Orthodactylites*) *tenuicostatum* (Young and Bird). 1, 2, 9, 10, Marlstone Rock Bed, 0·1 m below top, Harston Quarry, north Leicestershire, BM C.80122, 80100. 3, 4, Marlstone Rock Bed, immediately below 'Transition Bed', Rothersthorpe, 5 km SW of Northampton, BM C.82051. 5–8, Marlstone Rock Bed layer P, Doghouse Cliff, Seatown, Dorset, NMW 26.135 G124 and G5.2. 13, 14, bed 21 (Howarth and Rawson 1965), 0·3 m above Marlstone Rock Bed, quarry 2 km north of Kirton in Lindsey, north Lincolnshire, BM C.73560. All figures × 1.

Figs. 11, 12. *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson). Marlstone Rock Bed, 0·08 m below top, Harston quarry, north Leicestershire, BM C.80173, × 1.

Figs. 15, 16. *Dactylioceras* (*Orthodactylites*) *clevelandicum* Howarth. Bed 21 (Howarth and Rawson 1965), 0·3 m above Marlstone Rock Bed, quarry 2 km north of Kirton in Lindsey, north Lincolnshire, BM C.73561, × 1.

Figs. 17, 18. *Dactylioceras* (*Orthodactylites*) *crosbeyi* (Simpson). Marlstone Rock Bed, 0·23 m below top, Harston quarry, north Leicestershire, BM C.80170, × 1.


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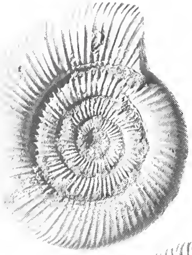
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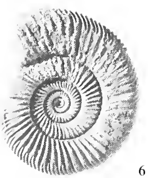
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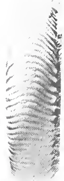
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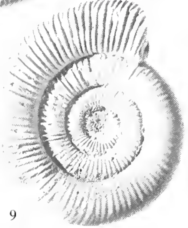
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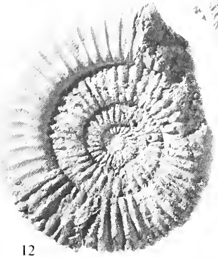
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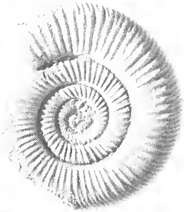
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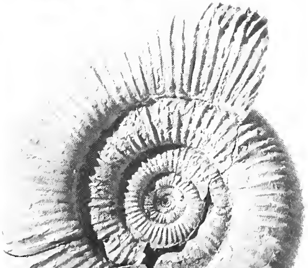
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HOWARTH, ammonite *Dactylioceras*

Dactylioceras (*Orthodactylites*) *crosbeyi* (Simpson)

Plate 82, figs. 17, 18

1843 *Ammonites crosbeyi* Simpson, p. 22.
1855 *Ammonites crosbeyi* Simpson, p. 58.
1884 *Ammonites crosbeyi* Simpson, p. 90.
1912*a* *Coeloceras crosbeyi* (Simpson); Buckman, pl. 60.
?1957 *Dactylioceras pseudosemicelatum* Maubeuge, p. 193, pl. 3, fig. 6.
?1957 *Dactylioceras podagrosum* Maubeuge, p. 193, pl. 4, fig. 7.
1973 *Dactylioceras* (*Orthodactylites*) *crosbeyi* (Simpson); Howarth, p. 255, pl. 1, figs. 2–4; pl. 2, figs. 1–4.

Occurrence. North Leicestershire: 0·23 m below the top of the Marlstone Rock Bed, Harston quarry, one specimen.

Discussion. This broken half ammonite is about 74 mm diameter, and the final one-third of a whorl is probably body-chamber. It has relatively high and broad whorls that are about one-quarter involute, and the whorl section has an evenly rounded venter. The preservation is mainly as an internal cast, so the ribbing is of very low relief, and consists of prorsiradiate primary ribs, about half of which bifurcate at the ventro-lateral edge. The ribs on the venter swing slightly more forwards, and only the slightest traces of ventro-lateral tubercles are present. At 74 mm diameter the whorl height is 21·5 mm and the breadth is 21·0 mm, and these whorl dimensions agree well with those of Yorkshire coast specimens of *D.* (*O.*) *crosbeyi.* It compares well with the more compressed, more finely ribbed examples of the species such as were figured by Howarth (1973, pl. 1, fig. 2; pl. 2, fig. 2). The whorl height and the amount of overlap of the whorls are both too large for *D.* (*O.*) *clevelandicum.* The specimen occurs 0·1 m below a rich population of *D.* (*O.*) *tenuicostatum* in the Marlstone Rock Bed at Harston, a stratigraphical position that agrees with its occurrence in Yorkshire. No trace was found at Harston of the intervening species *D.* (*O.*) *clevelandicum.* No other examples of *D.* (*O.*) *crosbeyi* have been found outside Yorkshire.

CONCLUSIONS

The 'Transition Bed' is the weathered or altered top of the Marlstone Rock Bed. The main change is oxidation of the green ferrous minerals to limonite, and associated partial decalcification leaves the bed crumbly or 'sandy' in some places. The weathering occurred partly before deposition of the overlying beds in some areas, e.g. Banbury and west Northamptonshire, though at Tilton most of the weathering is more recent. Another type of alteration that took place before deposition of overlying beds, was the pyritization of the bed in the Harston area, Leicestershire. There is no evidence that the bed is otherwise mineralogically different from the Marlstone Rock Bed, and there is no sedimentary discontinuity at its base. The term Marlstone Rock Bed should be applied to the whole of the bed.

In south Dorset and from north Oxfordshire to south Lincolnshire the Marlstone Rock Bed was deposited during all the period represented by the Spinatum and Tenuicostatum Zones, and there is no lithological division between the two zones. The ammonite faunas at the boundary are poor, but generally the top 1–3 m belongs to the Tenuicostatum Zone and the bottom 3–6 m to the Spinatum Zone. From north Somerset to south Oxfordshire there is no ammonite evidence for the age of the top of the bed.

The following ammonite faunas have been found in the Marlstone Rock Bed:

(*a*) *Dactylioceras semicelatum* (*D. directum* is a synonym) and *Tiltoniceras antiquum* of the Semicelatum Subzone. This is abundant at many localities and is the fauna of the 'Transition Bed'.

(*b*) *D. tenuicostatum* of the Tenuicostatum Subzone. Abundant only at Harston, Leicestershire, present on the Dorset coast, and rare elsewhere.

(*c*) *D. crosbeyi* of the Clevelandicum Subzone. One specimen at Harston.

(*d*) *Protogrammoceras paltum* of the Paltum Subzone. Only on the Dorset coast.

(*e*) *Pleuroceras* spp. of the Spinatum Zone. Abundant in Dorset, Somerset, and Gloucestershire. Much rarer from Oxfordshire to north Humberside, but sufficient are known to show that both the Apyrenum and Hawskerense Subzones are present.

From north of Lincoln to north Humberside deposition of the Marlstone Rock Bed stopped at the end of the Spinatum Zone, and ammonites of all four subzones of the Tenuicostatum Zone occur in an overlying, lithologically distinct, hard mudstone and in shales above. The latter are similar to the Grey Shales Formation of the Yorkshire coast.

The change from the lower, regressive ironstone/limestone facies to the upper transgressive clays/shales-with-nodules facies (Hallam 1967, pp. 431–440) did not occur simultaneously in Britain. In Yorkshire it occurred at the top of the Spinatum Zone at the Upper Pliensbachian/Toarcian (i.e. Middle/Upper Lias) boundary, but from Dorset to south of Lincoln it occurred at the top of the Tenuicostatum Zone. In a small transitionary area between north of Lincoln and Market Weighton the change took place in the middle of the Tenuicostatum Subzone. The extent of the time disparity for the facies change may be judged from the fact that 14 m of Grey Shales Formation on the Yorkshire coast were being deposited while 1–3 m of Marlstone Rock Bed was being deposited in England south of Lincoln.

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JURASSIC ARAUCARIAN CONE FROM SOUTHERN ENGLAND

by RUTH A. STOCKEY

ABSTRACT. A well-preserved araucarian cone measuring 4·5 × 5·0 cm is described from Jurassic age limestone from near Osmington Mills, Dorset. Four pieces of cone material representing a single specimen are somewhat flattened and lignitic, with intact seed and cone-scale tissues. The cone axis and bract apophyses are replaced with a calcitic matrix. Helically arranged cone-scale complexes with a prominent ligular sulcus surround a wide pith. One recurved wingless ovule 0·8 cm long is deeply sunken into the cone-scale tissue. Seed integuments are relatively mature and contain three distinct layers the most prominent of which is the sclerotesta constructed of interlocking zig-zag sclereids. The nucellus, in some cases still cellular, is free from the integuments except at the chalaza and has the characteristic wavy apex common to extant araucarians at a comparable developmental stage. A well-developed vascular system like that in *Araucaria bidwillii* Hooker is present near the seed chalaza. Cellular megagametophyte and embryos are present within some seeds. The specimen is described as a new species, *A. brownii* sp. nov. in which the cone structure most closely resembles that of the section *Bunya* of the genus *Araucaria*. This discovery extends the range of this section to the Northern Hemisphere during the Mesozoic.

THE Araucariaceae, an extant conifer family with a very restricted distribution, has often been considered primitive among conifer families. Two genera, *Agathis* and *Araucaria*, grow as natives in South America, Australia, New Caledonia, New Guinea, and a few South Pacific islands. Although the group has only a few relict species today, it was at one time widespread and included numerous species in the Northern Hemisphere during the Mesozoic Era. Araucarian cones display what have been suggested as primitive characters that readily distinguish them from those of other conifer groups (Wieland 1935; Thomson 1905*a*, 1907, 1913; Eames 1913; Wilde and Eames 1948, 1952; Burlingame 1913, 1914, 1915; Chamberlain 1935; Hirmer 1936; Seward and Ford 1906). The genus *Araucaria*, usually believed to be the more primitive of the two genera, has ovulate cones with large bracts and partially fused ovuliferous scales. *Agathis* exhibits cone-scales composed of completely fused bracts and scales, believed to be a derived condition (Eames 1913). Well-preserved fossil conifer cones of any type are rare; however, a few well-preserved araucarian fossils have been found, and these have revealed important information about the geologic history of this family, its distribution, and reproductive biology (Kendall 1949; Wieland 1935; Darrow 1936; Calder 1953; Stockey 1975, 1977, 1978; Vishnu-Mittre 1954). The uniquely preserved fossil conifer cone reported here is closely compared with other fossil and living araucarians. The information obtained has proved useful in elucidating phylogenetic trends within the family, and in particular, within the genus *Araucaria*.

MATERIALS AND METHODS

The cone was found in 1973 by Mr. P. A. Brown of Dorset in a block of limestone lying on the beach under Black Head, west of Osmington Mills. Specimens are lignitic, in a matrix best described as a compacted bio-pel-micrite with pelecypod shells, fecal pellets, tests of foraminifera, and corals which have all undergone a considerable amount of diagenesis. The recrystallized calcite composing these fragments is held together with a $CaCO_3$ cement that has infiltrated many of the preserved cone parts including the seeds. Specimens were prepared for study by a modified coal ball peel technique (Joy, Willis, and Lacey 1956) using 76 μm cellulose acetate sheets and by thin sections after epoxy

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infiltration of the cut face. Some cone parts were examined after gold sputter coating using an AMR 1000 scanning electron microscope at 20 kV. A few whole seeds and cone fragments were demineralized in 2% HCl overnight and washed in distilled water. These parts were then embedded in glycol methacrylate and sectioned with a rotary microtome after a technique by Robison and Miller (1975).

Since the cone was not found in place its exact age needs some discussion. The area west of Osmington Mills, Dorset, to Black Head where the cone was found consists of cliffs composed of Corallian and Kimmeridge Clay sediments. These correspond to the Oxfordian and Kimmeridgian Stages respectively of the Upper Jurassic (Arkell 1947). The cone most likely comes from the Osmington Oolite Series which is exposed along the shore west to Shortlake. The beds within this series contain several clay layers with nodules, in addition to the oolites and marlstones (Arkell 1947). The matrix surrounding the specimen closely resembles these beds. Its age is therefore certainly Upper Jurassic, and probably Upper Oxfordian.

SYSTEMATIC DESCRIPTION

Order CONIFERALES
Family ARAUCARIACEAE
Genus ARAUCARIA de Jussieu, 1789
Section BUNYA Wilde and Eames, 1952
Araucaria brownii sp. nov.

Plates 83–86

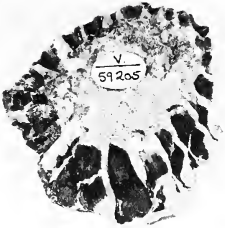
Diagnosis. Ovulate cone, 4·5 × 5·0 cm diameter, pith 1·4 cm diameter near point of attachment to peduncle, expanding to 3·2 cm wide near centre of cone. Cortical resin canals present. Winged cone-scales 1·7 cm long × 1·1 cm wide. Bract and ovuliferous scale free for two-thirds of length, both with a system of resin canals. Ovules 0·8 cm long × 0·3 cm wide, wingless, embedded in ovuliferous scale tissue with micropyle oriented towards cone axis; one seed per cone-scale complex. Seed integuments with prominent branched sclereids of sclerotesta arranged in a zig-zag pattern. Complex system of vasculature at ovule chalaza. Nucellus with wavy apex free from integuments except at base, 0·2 mm thick. Megaspore membrane thin (7 μm) and discontinuous. Megagametophyte composed of polygonal cells 30–50 μm in diameter.

Holotype. British Museum (Natural History) London, V59205, and one fragment housed at Corfe Castle Museum, Dorset.

Etymology. This cone is named after Mr. P. Anthony Brown of Corfe Castle, Dorset who discovered the specimen and made it available for study.

EXPLANATION OF PLATE 83

Figs. 1–8. *Araucaria brownii* sp. nov. Holotype, BMNH V59205 from Osmington Mills, Dorset. *b*, bract; *end*, endotesta; *i*, integument; *ls*, ligular sulcus; *m*, megagametophyte; *n*, nucellus; *os*, ovuliferous scale; *scl*, sclerotesta. 1, cone axis region showing position of ovules, and arrangement of cone-scale complexes, × 1. 2, reverse side of cone in fig. 1, showing cone axis region, rhomboidal cone-scale complexes, and flattened nature of cone, × 1. 3, tangential portion showing seed transverse sections, × 1. 4, cone portion with part of axis and many closely spaced cone-scale complexes, × 1. 5, reverse side of portion in fig. 4, showing limestone nodule matrix and numerous cone-scale complexes with ovules, × 1. 6, V59205 B 25. Cone tangential section with ovule transverse sections. Note large calcite crystals replacing most bract tissue, × 7. 7, V59205 B 21, longitudinal section of cone-scale showing the separation of bract and scale resulting in a wide ligular sulcus, × 23. 8, peel of V59205 B 6, ovule micropylar end showing well-developed seed integuments, megagametophyte tissue and wavy nucellar apex, × 15.



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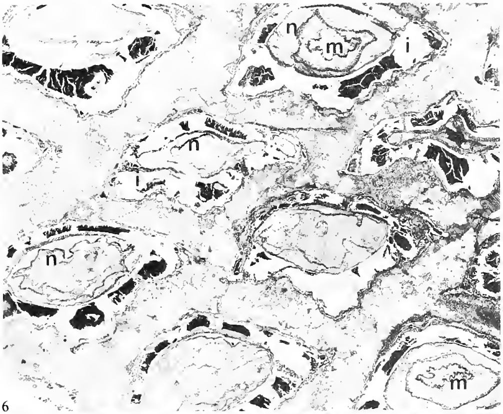

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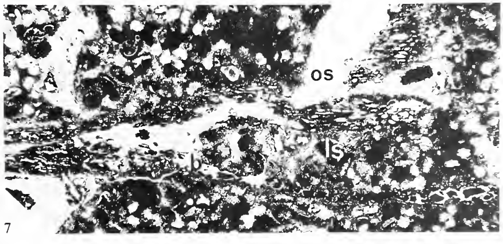

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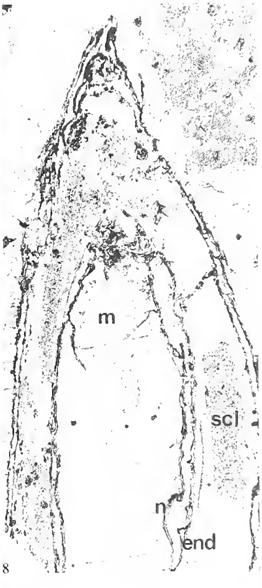

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STOCKEY, Araucarian cone

Description. Cone represented by four pieces which are slightly flattened. Plate 83, figs. 1 and 2 show both sides of central portion of cone revealing position of cone axis and numerous helically arranged, seed-bearing cone-scales. Plate 83, figs. 4 and 5 show an external portion of the cone. This piece was attached to that shown in Pl. 83, fig. 1 with an epoxy before sectioning. Plate 83, fig. 3 shows a third cone fragment, a tangential cone piece belonging to the same cone. The remaining part of this specimen was retained by Mr. Brown and is housed at Corfe Castle Museum in Dorset.

Cone measures 4·5 × 5·0 cm in diameter and was probably spherical in shape before burial. Pith of cone axis reaches a width of 3·2 cm and approaches 1·4 cm in the most basal portions. Little organic material preserved in central part of cone, and no peduncle is present in available material. Organic remains are found in some cases in a region corresponding to the cortex of the cone axis (Pl. 86, fig. 6). Small parenchymatous cells are often found in groups surrounding resin canals, some of which contain a dark opaque substance (Pl. 86, fig. 6, arrows). A few isolated tracheids have been identified in the cone axis region; these exhibit scalariform secondary wall thickenings. Unfortunately these tracheids are isolated and their exact position within the axis stele is questionable.

Cone-scales measure 1·7 cm long and 1·1 cm wide, and are distinctly winged. On first examination the cone appears similar in size, shape, and appearance to those of the genus *Agathis* Salisbury. The bract and scale, however, are free for most of their length, a character typical of species of *Araucaria* (Pl. 83, fig. 7). Vascular system of the ovuliferous scales consists of at least four bundles (Pl. 84, fig. 5). Bract apophyses are replaced by coarsely crystalline calcite making vascular bundles generally difficult to observe. There is a system of resin canals in the scale as well as the bract, although their number and placement is difficult to determine because the cone-scales are flattened.

Ovules of *A. brownii* measure 0·8 cm in length by 0·3 cm in diameter (Pl. 84, figs. 1, 4). One wingless seed per cone-scale complex deeply embedded in ovuliferous scale tissue with its micropyle oriented towards the cone axis. Although both *Agathis* and *Araucaria* have one seed per scale, only seeds of *Araucaria* are wingless. Ovules show an advanced state of integumentary development. The sarcotesta, or outer layer, is represented by a thin layer of crushed cells 20 μm thick (Pl. 85, fig. 1). The middle sclerotesta or stony layer is quite thick (up to 0·2 cm) and is composed of thick-walled branched sclereids, each about 30 μm in diameter (Pl. 83, fig. 8; Pl. 84, fig. 2; Pl. 85, fig. 5). These cells are hexagonal in transverse section (Pl. 85, fig. 3) with very small lumens and thick walls. In many cases the walls are no longer distinguishable, but the entire cell, or layer, has been replaced by calcite (Pl. 85, figs. 1, 3). The endotesta, or inner integumentary layer, is thin, up to three cells in thickness and often crushed (Pl. 85, fig. 1). In places where it is present, the cells are short and often barrel-shaped with relatively thin walls (Pl. 85, fig. 2). Integumentary differentiation within the ovules indicates a nearly mature developmental stage.

The non-adnate nature of the nucellus and integument is shown in all of the ovules examined (Pl. 83, fig. 8; Pl. 84, fig. 7). Where well preserved the nucellus has a thick cuticle (Pl. 83, figs. 6, 8; Pl. 84, figs. 3, 6; Pl. 86, figs. 1, 2). It is basally attached to the inner integumentary layer and appears somewhat shrunken (Pl. 86, fig. 2). The nucellar apex appears convoluted as in living araucarians (Pl. 83, fig. 8). In extant plants it protrudes out of the micropyle at the time of pollination and later may retract by drying or by subsequent integumentary growth (Eames 1913). Some authors (Darrow 1936; Eames 1913) have suggested that the convoluted apex was the result of pollen tube damage; however, on examining some living araucarian ovules, a disruption of the apex by pollen tube damage seems unlikely. Plate 85, fig. 4 shows the wavy nucellar apex of the extant *A. montana* Brongn. *et* Gris. and is typical of most known araucarians at this stage of development. The configuration of the apex appears to represent a drying phenomenon rather than the result of extensive pollen

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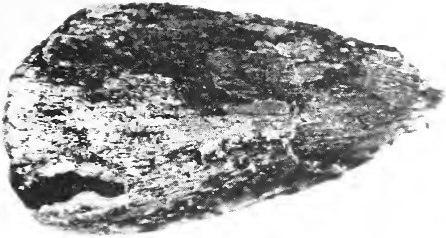
EXPLANATION OF PLATE 84

Figs. 1–7. *Araucaria brownii* sp. nov. Holotype, BMNH V59205. *b*, bract; *i*, integument; *m*, megagametophyte; *n*, nucellus; *os*, ovuliferous scale; *s*, seed. 1, isolated seed, × 10. 2, paradermal section of sclerotesta cells showing zig-zag cell arrangement. Arrows indicate branched sclereids, × 380. 3, isolated nucellus with apex removed, × 17. 4, V59205 B 6, cone longitudinal section showing sunken nature of seeds within the cone-scale complex, × 7. 5, V59205 B 25 transverse section of ovule showing lateral vascular bundle of ovuliferous scale outside of the seed integuments, × 37. 6, V59205 A 40, ovule transverse section showing thick wavy nucellus and cellular megagametophyte tissue, × 90. 7, V59205 B 26, ovule transverse section showing the relationship of integument, nucellus, and cellular megagametophyte, × 85.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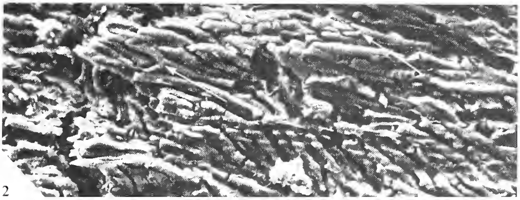
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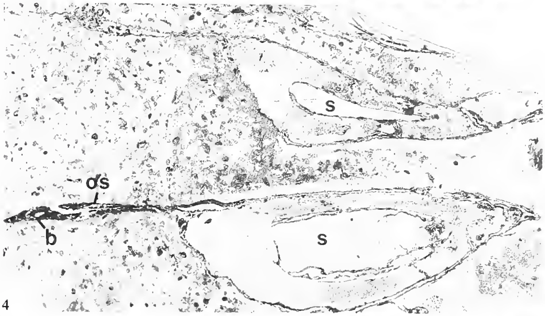

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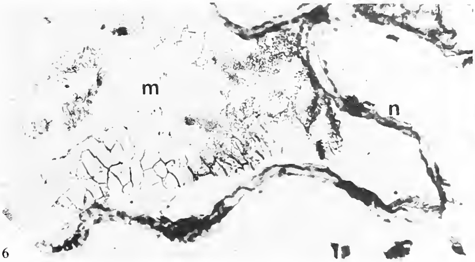

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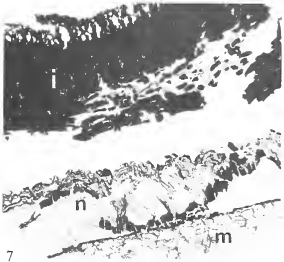

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STOCKEY, Araucarian cone

tube damage. The ease with which the nucellus is removed from isolated ovules is due to its narrow attachment as well as its thick cuticle (Pl. 84, fig. 3). External surface shows little cellular detail while internally outlines of elongate, rectangular cells are visible (Pl. 85, fig. 7).

Ovule attachment and vascularization are difficult to determine with peels. However, thin sections of the chalaza of some ovules where preservation of the bract and ovuliferous scale is partial show a well-developed system of conducting cells (Pl. 86, fig. 5). Using scanning electron microscopy, the chalazal end of each ovule exhibits a series of small holes penetrating the sclerotesta (Pl. 84, fig. 6, arrows), as in the living *A. bidwillii* Hooker. There appears to be what Wilde and Eames (1948, p. 326) term a vascular 'plexus', a complex system of vascularization near the ovule base. Holes in the mature seed integuments correspond to points of entry of numerous vascular bundles. The same type of attachment also occurs in *A. mirabilis* from the Jurassic Cerro Cuadrado Petrified Forest (Stockey 1975).

Most ovules show some tissue remains inside the nucellar cavity. The megaspore membrane of some ovules is thin (7 μm) (Pl. 84, fig. 7), and similar to that in living araucarian cones at a comparable stage of development (Eames 1913; Burlingame 1915; Thomson 1905*b*). Many of the ovules reveal preservation of tissues within this membrane. In most, megagametophyte tissue is either poorly preserved or represented by a free nuclear stage of development at the time of preservation (Pl. 84, fig. 8; Pl. 86, figs. 2, 7). Other ovules show cellular preservation of the megagametophyte (Pl. 84, fig. 6; Pl. 86, fig. 4). These polygonal cells (30–50 μm in diameter) occur in the outer portions of the megagametophyte proper. No ovules have been found with solid megagametophyte tissue preserved within the seed cavity. However, some ovules do show two distinct regions of poorly preserved tissue (Pl. 86, fig. 2). The boundary between the two regions appears to be a discontinuous layer. In other ovules (Pl. 86, fig. 4) the cellular megagametophyte and a centrally located region probably representing the embryo are replaced by calcite. Other specimens contain a four-parted cellular structure that may represent an embryo with four cotyledons (Pl. 86, fig. 3, arrows). An alternate possibility is that this may have been a partially formed megagametophyte at the time of preservation. The seed itself is not crushed, even though parts of the integuments are very crumbly.

DISCUSSION

The spherical shape of the Osmington Mills cone with helically arranged cone-scales, large pith in the cone axis region, cortical resin canals, and presence of one seed per ovuliferous scale are general characteristics of cones from the family Araucariaceae. The presence of a ligular sulcus (space between the ovuliferous scale tip and the bract) and wingless seeds suggest affinities with the genus *Araucaria*. The cone of *A. brownii* was apparently in a relatively mature state of development at the time of fossilization. The appearance of the three-layered integument with a thin sarcotesta, thick sclerotesta composed of elongate branched sclereids, and a thin layer of endotesta composed of thin-walled cells is characteristic of araucarian cones near maturity (Eames 1913; Burlingame 1915; Wilde and Eames 1948; Stockey 1978). The seed contents including the configuration of the nucellus and thin megaspore membrane support this view. A cellular megagametophyte is present with a hollow central cavity (Pl. 86, figs. 2, 4) that probably represents the remains of an embryo rather than free nuclear megagametophyte. This embryo may have aborted or more likely deteriorated prior to preservation since it is likely that the cone remained floating in water for some time prior to its

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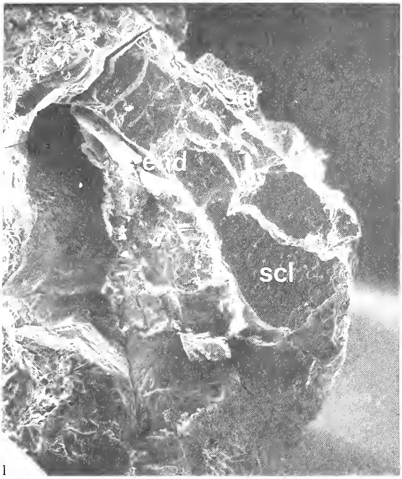
EXPLANATION OF PLATE 85

Figs. 1–7. *Araucaria brownii* sp. nov. Holotype, BMNH V59205, scanning electron micrographs. *end*, endotesta; *n*, nucellus; *sar*, sarcotesta; *scl*, sclerotesta. 1, ovule transverse section showing three integumentary layers at a late developmental stage, ×90. 2, cells of the endotesta, ×425. 3, transverse section of integument showing hexagonal sclerotesta cells completely replaced by calcite, ×400. 4, *A. montana* Brongn. *et* Gris., nucellar apex from a mature seed, ×100. 5, surface view of sclerotesta with sarcotesta removed showing elongate interlocking sclereids, ×425. 6, seed chalaza, surface of sclerotesta. Arrows indicate holes of the ovular vascular bundles in the plexus, ×90. 7, elongate nucellar cells, ×450.



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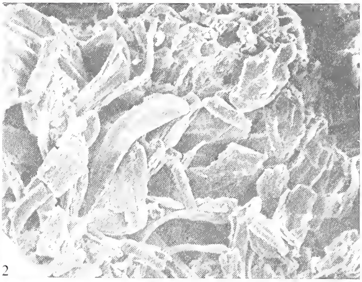

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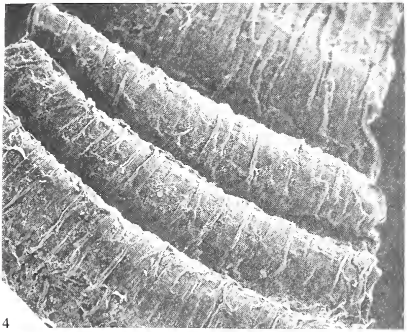

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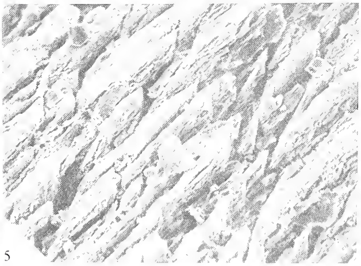

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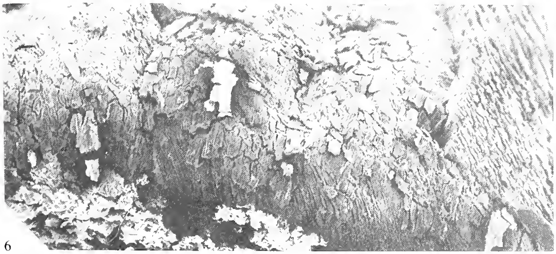

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STOCKEY, Araucarian cone

burial. Plate 86, fig. 3 may show the cellular remains of such an embryo. Extant araucarian cones, at the time when free nuclear megagametophyte is present (about the time of pollination), show ovules with the integumentary layers of approximately equal thickness with little if any expansion and thickening of the sclerotesta (Wilde and Eames 1948; Stockey 1978).

According to Wilde and Eames (1952) the living genus *Araucaria* may be divided into four sections: *Columbea*, *Bunya*, *Eutacta*, and *Intermedia* based on seedling morphology, foliage type, and cone morphology. The differences in cone structure between the section *Columbea* and the other three sections is distinct, while the differences between the other three are more subtle. The *Columbea* species found only in South America have wingless cone-scales, the bract and scale are nearly completely fused and never separate after the scales are shed from the cone axis. Sections *Eutacta*, *Intermedia*, and *Bunya* have winged cone-scales, those of *Intermedia* being widest, up to 10 cm in *A. klinkii* Lauterb. (White 1947). Seeds in the closely related *Eutacta* and *Intermedia* sections are never removed from the tightly fused bract and scale. The winged cone-scale complex is the unit of dispersal for these species. Seeds from *A. bidwillii*, the only living member of the section *Bunya*, are easily removed from the cone-scales which are more fleshy than those of the *Eutacta* and *Intermedia* sections. These seeds are often dispersed by birds and small animals in Queensland but are easily removed from the cone-scale complex even though the cone disaggregates as in the other species.

A. mirabilis from the Jurassic Cerro Cuadrado Petrified Forest is also included within the Section *Bunya* (Calder 1953; Stockey 1975, 1978). These ovulate cones are only one-third as large as those of *A. bidwillii* at maturity and have winged cone-scales, a zig-zag pattern of sclereids in the sclerotesta of the seed integument, a complex system of vasculature at the seed chalaza, and a dicotyledonous embryo characteristic of *A. bidwillii* (Wilde and Eames 1948; Stockey 1975, 1978). There is some evidence to suggest that these cones shed their seeds and not their scales at maturity (Stockey 1978).

Another ovulate cone which can be considered to be closely related to these three *Bunya* species is *Araucarites bindrabunensis* (Vishnu-Mittre 1954) from the Jurassic of India which shows a slightly larger size than most *Araucaria mirabilis* cones, and is also larger than the cone from Osmington Mills. The origin of the cone-scale complex vascular supply, nature of the winged cone-scales, presence of a ligular sulcus, and vascularization of the ovuliferous scale tip (ligule) place it in the section *Bunya*.

The cone described here from Osmington Mills in Dorset should also be considered under the section *Bunya* of the genus *Araucaria*. The winged cone-scales, zig-zag sclereid pattern and vascular plexus, and deep ligular sulcus are similar to *A. mirabilis* and *A. bidwillii*. These comparisons extend the range of the section *Bunya* into the Northern Hemisphere where it was probably widespread during the Jurassic and Cretaceous.

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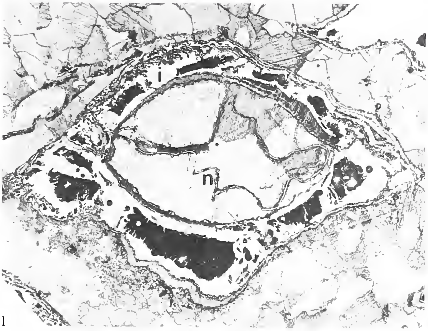
EXPLANATION OF PLATE 86

Figs. 1–7. *Araucaria brownii* sp. nov. Holotype, BMNH V59205. *e*, embryo; *i*, integument; *m*, megagametophyte; *n*, nucellus; *p*, plexus. 1, V59205 B 24, ovule transverse section showing lateral extensions of the seed integuments and well-preserved endotesta cells, ×9. 2, V59205 A 40, seed transverse section with well-preserved nucellus, megagametophyte, and a possible embryo, ×25. 3, V59205 B 23, transverse section of seed showing possible embryo with four cotyledons, ×35. 4, V59205 B 25, transverse section of seed with cellular megagametophyte and crystalline central area, possibly representing an embryo, ×50. 5, V59205 B 26, transverse section near seed chalaza showing vascular plexus leading into ovule, ×15. 6, V59205 C 8, longitudinal section of resin canal (arrows) in cortex of cone axis, ×30. 7, transverse section of ovule showing disorganized megagametophyte tissue, ×925.



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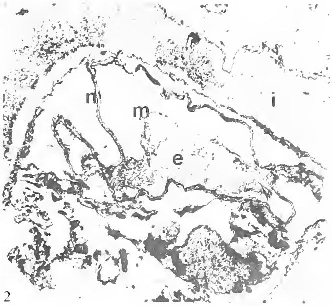

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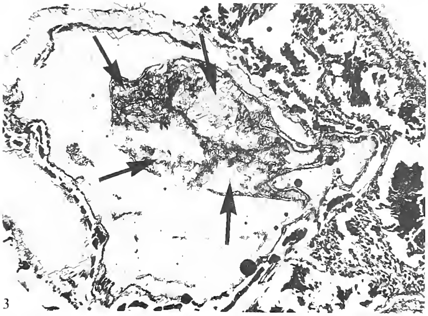

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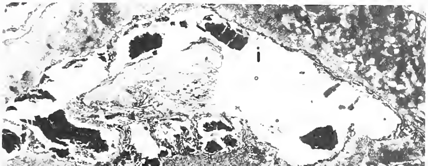

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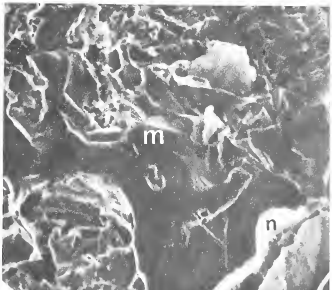

7

STOCKEY, Araucarian cone

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NOMENCLATURE AND HOMOLOGY IN PERIDINIALEAN DINOFLAGELLATE PLATE PATTERNS

by GEOFFREY L. EATON

ABSTRACT. The apical and antapical series of peridinialean dinoflagellate thecal plates are redefined relative to the cingulum. They are then compatible with the Kofoidian pre- and postcingular series, and the need to recognize anterior and posterior intercalary series is removed. The concept of apical closing and antapical closing series is introduced. Homologous and corresponding plates are recognized in fifteen selected modern and fossil dinoflagellates by comparing interseries relationships with respect to a model plate pattern. The differences between the selected patterns are due to three variable effects. First, the reduction in plate number through simplification, where one plate in one pattern corresponds to two or more plates in another pattern. This critically affects interseries relationships. Secondly, the primary development of fewer plates without affecting interseries relationships. Thirdly, the variation in the relative size of certain plates. The interaction of these three effects resulted in the comparatively independent evolution of epithecae and hypothecae. Reduction in over-all plate number, particularly through the primary development of fewer plates, may well represent a fundamental trend in the evolution of peridinialean plate patterns.

THE dinoflagellates of the Order Peridiniales Haeckel 1894 are often informally described as 'armoured'. They are so called because their cell covering includes a layer of rigid, polygonal, suturally united, cellulosic plates, termed the theca. Text-fig. 1 shows thecal morphology and nomenclature in two typical peridinialean dinoflagellates, *Protoperidinium depressum* (Bailey) Balech 1974 and *Gonyaulax spinifera* (Claparède and Lachmann) Diesing 1866. The theca is divided into two parts, epitheca (anterior) and hypotheca (posterior), which are separated by an equatorial groove termed the cingulum. The two ends of the cingulum are separated on the ventral surface by a more or less longitudinal groove termed the sulcus. Motility is achieved by the beating of two flagella (not shown in text-fig. 1) which originate from the sulcus. The transverse flagellum lies within the cingulum, while the longitudinal flagellum lies within, and extends posteriorly beyond, the sulcus. The thecal plates are arranged in roughly parallel transverse series. Differences in tabulation; that is the number, shape, and arrangement (plate pattern) of the thecal plates, have long been used as the main criterion for taxonomic separation within the Peridiniales. The accepted system of thecal plate nomenclature was defined by Kofoid (1907, 1909, 1911).

The fossil peridinialean dinoflagellate record ranges back at least 200 million years into the Late Triassic period. However, in terms of representing the absolute geological history of the Peridiniales, this record has only limited effectiveness. This is because all fossilized dinoflagellates attributed to the Peridiniales are non-motile cysts rather than motile thecae, and modern studies show that only a very small proportion of living peridinialeans produce potentially fossilizable cysts. Comparisons between modern thecae and fossil cysts show that not all modern plate patterns have been recognized in the fossil record, and some fossil plate patterns are unknown in modern dinoflagellates. Accepting the limitations of the fossil record, and the fact that cysts only rarely show full details of their parent thecal tabulation, it is still possible that the relative distribution of the different plate patterns through geological time may provide some evidence of trends in plate pattern evolution. The recognition of such trends is dependent on the critical assessment of the similarities and differences between different plate patterns. Such an assessment will involve the recognition of homologous plates in different patterns. In my own studies on fossil dinoflagellates I have found that a strict application of Kofoid's

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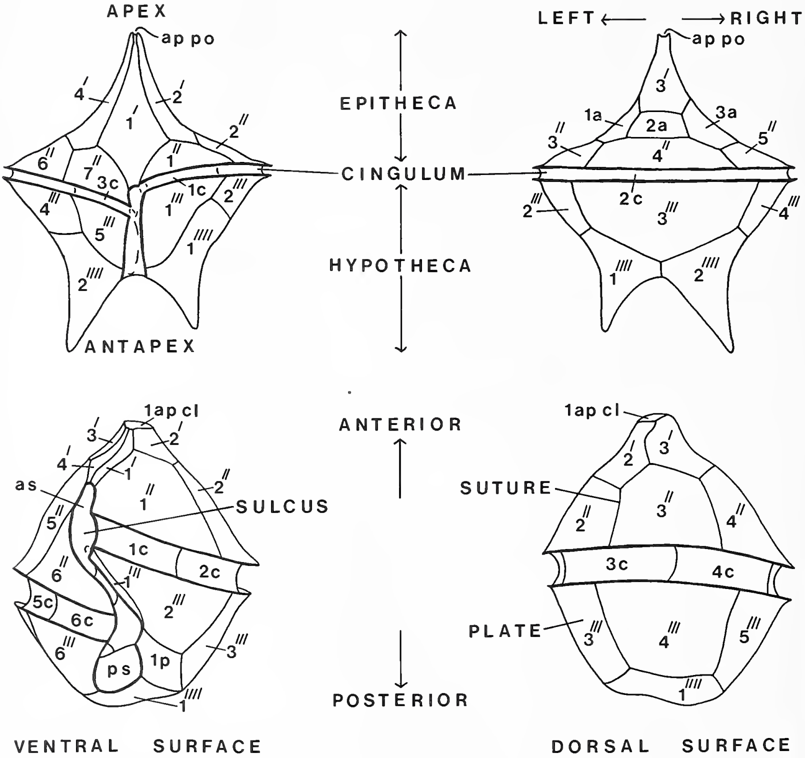
plate nomenclature often results in apparently homologous plates in different patterns, being assigned to different transverse plate series. I believe that compatibility between nomenclature and homology is essential for the recognition of evolutionary trends, and that it can only be achieved by modifying certain aspects of Kofoid's system. Discussion of the need for this modification and a way of effecting it, forms the basis of this paper.

According to Evitt *et al.* (1976) fossil cyst plate patterns should be discussed in terms of their paratabulatory nomenclature (paraplates, parasutures, etc.). However, in this paper on modern



TEXT-FIG. 1. Thecal morphology of two modern peridinialean dinoflagellates. Upper, *Protoperidinium depressum* (Bailey) Balech 1974. Lower, *Gonyaulax spinifera* (Claparède and Lachmann) Diesing 1866. Interpretation of the transverse plate series is conventional Kofoidian. The distribution and number of cingular and sulcal plates in *P. depressum* is assumed to be typical of the genus. In *G. spinifera* only the anterior (a.s.) and posterior (p.s.) sulcal plates are annotated.

thecae and fossil cysts I wish to avoid the use of a dual 'tabulation/paratabulation' nomenclature. Therefore I assume that the fossil cyst paraplate patterns are a fair representation of their parent thecal plate patterns, and treat them all, modern and fossil, simply as plate patterns.

ORIGIN AND DEVELOPMENT OF THE KOFOID SYSTEM OF THECAL PLATE NOMENCLATURE

Although the system of peridinialean thecal plate nomenclature which has been generally used for the past seventy years is attributed to Kofoid, it should be remembered that he was clearly influenced by several nomenclatural systems proposed by earlier workers, e.g. Stein, Bütschli, Schütt, Paulsen, Fauré-Fremiet (see Kofoid 1909, p. 44). All these earlier workers recognized that thecal plates are arranged in transverse rows, and that there are four major plate series, two anterior to the equator and two posterior to the equator. Various names had been applied to these series (see Kofoid 1909, p. 44), but those used by Bütschli (1885) were closest to Kofoid's subsequent terminology. Bütschli described the most anteriorly positioned series as apical, and the most posteriorly positioned as antapical. The two intervening series were termed pre-equatorial (anterior) and post-equatorial (posterior).

Kofoid recognized seven transverse plate series, comprising the four major series plus the cingular series and two incomplete intercalary series. Each series was designated by superscript acute accent marks, figures or letters, or simply by letters. The series were named from apex to antapex as: apical (′), anterior intercalary (a), precingular (″), cingular (c), postcingular (‴), posterior intercalary (p), antapical (⁗). The plates in each series were numbered in sequence, anticlockwise (in apical view) from the ventral surface. Additional plates at the extreme apex or within the sulcus were individually designated, e.g. apical closing plate (cl. pl.). During subsequent use, Kofoid's system has remained unchanged except for the designation of the sulcal plates (s) and the use of various abbreviations to designate additional individual plates. The typical application of Kofoid's nomenclature to *P. depressum* and *G. spinifera* is shown in text-fig. 1. These two forms together illustrate all seven of Kofoid's transverse plate series. Their respective tabulation formulae are: 4′, 3a, 7″, 3c, 5‴, Op, 2⁗, 6–7s, and 1 ap. cl., 4′, Oa, 6″, 6c, 6‴, 1p, 1⁗, 5s.

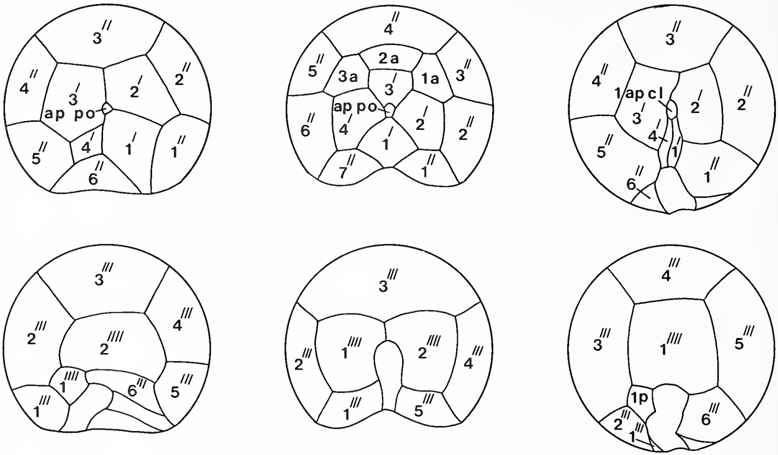
The most extensive discussion of thecal plate nomenclature is given in Kofoid (1909, pp. 40–45), but definitions of the various plate series are also found in Kofoid (1907, 1911).

Kofoid (1907, p. 179) defined the four major plate series with reference to modern *Ceratium* Schrank 1793. Kofoid stated: 'I shall use the term apical for the anterior series of plates only, and shall designate the series anterior to and contiguous to the girdle [cingulum] as precingular (prec.), and that posterior to and contiguous to it as postcingular (postc.) and the posterior ones as antapicals (antap.).'

Kofoid (1909, pp. 26–28) next applied his nomenclature to modern peridiniacean dinoflagellates, using *P. steini* (Jörgensen) as an example. His nomenclatural interpretation of *P. steini* is equally applicable to *P. depressum* (text-fig. 1). Kofoid interpreted the apical plates as 'those whose apical ends border the apical pore' (ap. po. in text-fig. 1). The combination of this interpretation of the apicals and Kofoid's earlier interpretation of the precingulars leaves three plates unaccounted for on the dorsal surface. These plates 'intercalate' between the apicals and precingulars and were referred to the anterior intercalary series (1a–3a), a term Kofoid had previously used in his original description of *Heterodinium* Kofoid 1906.

In his studies on modern *Gonyaulax* Diesing 1866, Kofoid (1911, p. 194) interpreted the apical plates as 'those in contact with the apex'. He recognized that in this genus the apex does not have an open pore, but is occupied by a small apical closing plate (1 ap. cl. in text-fig. 1). Kofoid designated as anterior intercalary those plates anterior to the precingular series but not in contact with the apex. This series was not recognized in all species of *Gonyaulax*. Kofoid also introduced the concept of a posterior intercalary series with reference to *Gonyaulax*. The single plate (1p) assigned to this series lies posterior to postcingulars 1‴ and 2‴, and anterior to antapical 1⁗ which occupies the antapex.

Kofoid realized that thecal plates are arranged in rows roughly parallel to the cingulum. This led him to use the cingulum rather than the geometric equator as a basis for defining transverse plate series. This approach recognized the fundamental importance of the structure which divides the theca into epitheca and hypotheca. Kofoid (1909, p. 43) believed that his recognition of transverse series throughout the theca clarified the confused situation that had previously existed over the nomenclature of plates anterior to the precingulars. His beliefs would seem to have been justified by the subsequent application of his nomenclature to modern dinoflagellates and to fossil forms ranging back to the Triassic period.



C. HIRUNDINELLA **P. DEPRESSUM** **G. SPINIFERA**

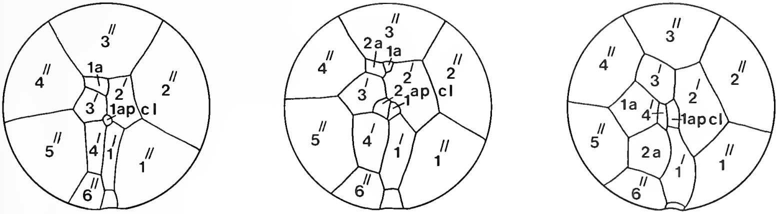
TEXT-FIG. 2. Conventional Kofoidian interpretation of tabulation in polar views of *Ceratium hirundinella* (Müller) Schrank 1793, *Protoperidinium depressum* (Bailey) Balech 1974, *Gonyaulax spinifera* (Claparède and Lachmann) Diesing 1866. Upper, epithecae. Lower, hypothecae.

A problem in designating apparently homologous plates

Although Kofoid did not recognize any intercalary plates in *Ceratium*, a case can sometimes be made for a single anterior intercalary in *Ceratium hirundinella* (Müller) Schrank 1793 (text-fig. 2). In a particular form of this species, Wall and Evitt (1975, p. 21) designated as apical 4′ a plate which does not reach the tip of the apical horn. They admitted that strictly speaking this plate should be designated anterior intercalary, but to do so would only lead to confusion. They argued that since the homology of this plate and the fourth apical of other species of *Ceratium* is so obvious, it is better to consider this plate as a shortened apical. In this particular case Wall and Evitt considered the recognition of 'obvious' homology to be more important than the strict application of a definition or rule.

This approach can also be applied to other dinoflagellates, for instance, the fossil taxon *Hystrichogonyaulax cladophora* (Deflandre) Stover and Evitt 1978 and certain species of fossil

Ctenidodinium Deflandre 1938. In some well-preserved specimens of *H. cladophora* (text-fig. 3) a plate can be recognized anterior and adjacent to 3″ and 4″. This plate does not touch the apical closing plate (1 ap. cl.) and is therefore designated anterior intercalary 1a. Two such plates are recognizable in *Ctenidodinium pachydermum* (Deflandre) Gocht (1970, pl. 29, fig. 5) and *Ctenidodinium* sp. (text-fig. 3), and 2a in this pattern appears to be homologous with 1a in *H. cladophora*. Also, 2a in *Ctenidodinium* sp. and 1a in *H. cladophora* appear to be homologous with apical 3′ in *Gonyaulax polyedra* Stein 1883 (text-fig. 3). If this interpretation of homology is correct, then this particular anterior intercalary plate in the two fossil taxa could be interpreted as a shortened apical.



H. CLADOPHORA　　CTENIDODINIUM SP.　　G. POLYEDRA

TEXT-FIG. 3. Conventional Kofoidian interpretation of epithecal tabulation in *Hystrichogonyaulax cladophora* (Deflandre) Stover and Evitt 1978, *Ctenidodinium* Deflandre 1938 sp., *Gonyaulax polyedra* Stein 1883.

Kofoid's (1911, pp. 194–195) own comments on the anterior intercalaries in gonyaulacacean dinoflagellates are significant here. Kofoid designated as anterior intercalary, plates in the apical region which are 'crowded away from contact with the apex . . . as well as other plates lying between the apical and precingular series'. He also considered the two anterior intercalaries lying laterally and ventrally to the right of the greatly reduced apical 4′ in *G. polyedra* (text-fig. 3) to be plates which had been 'crowded away' from the apex. Kofoid remarked further (Kofoid 1911, p. 239) that the area of 1a had probably 'split off' from the edge of apical 4′, and he also illustrated one specimen of *G. polyedra* (Kofoid 1911, pl. 14, fig. 29) in which intercalary 2a actually touches the apical closing plate. There is no doubt that Kofoid considered intercalaries 1a and 2a in *G. polyedra* to be territorially apical, but their spatial relationship with the extreme apex required their designation as anterior intercalary.

The anterior intercalary plates in *H. cladophora* and *Ctenidodinium* sp. seem to be apicals which have been shortened and crowded away from the apex, and according to Kofoid's comments on *G. polyedra* their designation as intercalary is entirely justified. Also, it can be argued that Wall and Evitt should have adopted this approach with *C. hirundinella*. Apical 4′ could be interpreted as being crowded away from the apex to occupy an anterior intercalary position, and this plate could then be designated 1a. This would not lead to the confusion Wall and Evitt suggested. It would simply reflect the strict application of a universally recognized rule, and any discussion of homologous relationships with the apical plates of other taxa would be of secondary importance. However, against this it can be argued that the recognition of homologous plates in different dinoflagellates is in fact of primary importance, and is critical to the understanding of the evolution of thecal plate patterns. Therefore, since the Kofoid rules require that apparently homologous plates in different taxa are assigned to different plate series, Kofoid's method of defining these series should be re-evaluated.

An inconsistency in plate series definition

The foregoing comments are specifically concerned with the anterior intercalary and apical series in gonyaulacacean epithecae. More important is the concept of these series in peridiniacean dinoflagellates. The partially developed anterior intercalary series is a characteristic feature of the peridiniacean plate pattern, and there can be little doubt that Kofoid considered these intercalaries to be additional plates between the precingulars and apicals. However, a polar view of the peridiniacean epitheca does not support this interpretation. In *Protoperidinium depressum* (text-fig. 2) for instance, the three anterior intercalaries 1a–3a and apicals 1′, 2′, and 4′ form a perfect ring of plates, effectively concentric with the precingular series. The interpretation of these six plates as the apical series would leave only Kofoidian apical 3′ unaccounted for. Thus Kofoid's concept of the anterior intercalary series seems to be an artificial one which resulted directly from his interpretation of the apical series in peridiniacean dinoflagellates.

I can only speculate on the reasons why Kofoid defined the apical series in the way he did. He may simply have believed that the apical plates should occupy or at least touch the morphological apex. He may have been influenced by the fact that his concept of the apical series resulted in the recognition of four apical plates in *Ceratium*, peridiniacean taxa, and certain species of *Gonyaulax*, and this consistency might be significant. Whatever reason is suggested, one major criticism is inescapable: Kofoid's concept of the apical series in peridiniacean dinoflagellates is incompatible with his basic statement on plate series definition. That is, since the division of the theca into epitheca and hypotheca is of such fundamental importance, the intervening cingulum should be used as the basis for defining the transverse plate series (Kofoid 1909, pp. 41, 43).

For consistency, after the precingular series had been defined as the plates anterior to and contiguous to the cingulum, the next series should have been defined as the plates anterior to and contiguous to the precingulars. This consistent definition of the apical series would not have affected Kofoid's interpretation of *Ceratium*, but it would have greatly affected his interpretation of the peridiniacean plate pattern. In *P. depressum* there would be six apicals rather than four, a residue of one plate at the apex (Kofoid's apical 3′), and no anterior intercalaries. In species of *Gonyaulax* such as *G. polyedra* there would be five apicals (Kofoid's 1′–3′, 1a, 2a) rather than four, a residue of two plates at the apex (1 ap. cl. and Kofoid's apical 4′), and again no anterior intercalaries. In *H. cladophora* there would be five apicals, in *Ctenidodinium* sp. there would be six, and the conventional intercalary plate in both patterns previously suggested to be homologous with apical 3′ in *G. polyedra* would now be designated apical. Also, apical 4′ in *C. hirundinella* would be designated apical, independent of its relationship with the morphological apex.

A similar argument can be made against Kofoid's interpretation of the antapical series in *Gonyaulax* and his resulting concept of a posterior intercalary series. After the postcingular series had been defined as the plates posterior to and contiguous to the cingulum, the next series should have been defined as the plates posterior to and contiguous to the postcingulars. This consistent definition of the antapical series would not have affected Kofoid's interpretation of *Ceratium* or the basic peridiniacean plate pattern, but it would have affected his interpretation of *Gonyaulax*. In the latter genus, the plate conventionally designated posterior intercalary 1p would become first antapical 1′′′′, conventional 1′′′′ would become 2′′′′, and there would be no posterior intercalaries.

Thus initially on the grounds of consistency in plate series definition and some limited evidence of plate homology, redefinition of the apical and antapical series is justified.

MODIFICATION OF KOFOID'S SYSTEM OF PLATE SERIES NOMENCLATURE

Definition of all the transverse plate series relative to the cingulum generally results in the recognition of two major plate series on both the epitheca and hypotheca. Any remaining plates occur at or near the poles of the theca and can be accommodated in a third epithecal or hypothecal series. Although this approach differs from Kofoid's concept of transverse plate series, only the apical and antapical series need to be redefined. Also, almost all of Kofoid's terms are still applicable and there is only one completely new plate series.

I would emphasize here that the following definitions are only intended to be broad guides to the recognition of the various plate series and the designation of individual plates. I do not believe that such definitions should be rigidly applied. Subjective interpretation is unavoidable, and interplate relationships must be considered for each plate pattern before individual plates can be assigned to the various plate series.

Definition of the transverse series

Three transverse series are recognized on the epitheca: precingular, apical, apical closing; and three are also recognized on the hypotheca: postcingular, antapical, antapical closing.

The precingular series (″) was satisfactorily defined by Kofoid (1907, p. 179) as the row of plates anterior to and contiguous to the cingulum. This definition is retained here.

The apical series (′) is redefined as the row of plates anterior to and contiguous to the precingular series. Also included is the plate (or plates) anterior to and contiguous to the sulcal area, as suggested by Kofoid. The apical series may be interrupted by a posterior extension of the apical closing series and in certain circumstances apical plates may touch the cingulum (e.g. *Helgolandinium subglobosum*, text-fig. 7).

The apical closing series (ap. cl.) is defined as the plates anterior to and contiguous to the apical series. The concept of apical closing plates was discussed by Kofoid (1911, p. 194) with respect to the small plate occupying the extreme apex of *Gonyaulax*. My idea of the apical closing series includes this and any other plates anterior and contiguous to the apical series, with the term ‘closing’ being used in a geometric rather than a biologically functional sense. This series may be represented by a distinct row of plates, and in certain circumstances apical closing plates may interrupt the apical series and touch the precingular series (e.g. *Shublikodinium arcticum*, text-fig. 8).

The postcingular series (‴) was satisfactorily defined by Kofoid (1907, p. 179) as the row of plates posterior to and contiguous to the cingulum. This definition is retained here.

The antapical series (⁗) is redefined as the plates posterior to and contiguous to the postcingular series.

The antapical closing series (an. cl.) is proposed as a new series, and is defined as the plates posterior to and contiguous to the antapical series. Again, ‘closing’ is used in a purely geometric sense. So far this series has been recognized only in *S. arcticum* and *Rhaetogonyaulax rhaetica* (both text-fig. 8).

Application to selected modern and fossil dinoflagellate plate patterns

The plate patterns of five modern and ten fossil dinoflagellates are illustrated in text-figs. 4–8 as diagrammatic polar (epithecal and hypothecal) views, in which I have tried to retain true interplate relationships with minimum distortion of observed plate geometry. This type of illustration is used rather than conventional ventral and dorsal views (text-fig. 1) because it allows a better appreciation of the geometric relationship between individual plates or groups of plates. Hypothecae are illustrated with the sulcus to the south rather than the conventional north, to emphasize certain similarities with epithecae. The plates are numbered in terms of the modified plate series nomenclature, and the direction of numbering is conventional. Individual cingular and sulcal plates are not indicated.

The listed data for each pattern include the specific name with its authorship, geological age (where relevant), the source of the plate pattern, and the modified tabulation formula. The formula is expressed in terms of the epithecal (E) and hypothecal (H) transverse series only. Changes in plate designation are indicated, with the reinterpreted designation first, followed by the conventional Kofoidian designation in parentheses. Where necessary, changes in dinoflagellate cyst archaeopyle nomenclature are indicated for the fossil taxa, in terms of the notation previously discussed by Evitt (1967) and Stover and Evitt (1978).

Gonyaulax spinifera (Claparède and Lachmann) Diesing 1866, Recent, text-fig. 4.

From: Kofoid (1911, text-figs. A–D) and Wall and Dale (1970, text-figs. 19–22).
Modified tabulation formula, E: 1 ap. cl., 4′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 1⁗ (1p), 2⁗ (1⁗).

Gonyaulax polyedra Stein 1883, Recent, text-fig. 4.

From: Kofoid (1911, pl. 12, figs. 16–20).
Modified tabulation formula, E: 2 ap. cl., 5′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 2 ap. cl. (4′), 4′, 5′ (1a, 2a), 1⁗ (1p), 2⁗ (1⁗).

Hystrichogonyaulax cladophora (Deflandre) Stover and Evitt 1978, Late Jurassic, text-fig. 4.

From: Deflandre (1938, text-figs. 5, 6) and my own observations.
Modified tabulation formula, E: 1 ap. cl., 5′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 3′ (1a), 4′, 5′, (3′, 4′), 1⁗ (1p), 2⁗ (1⁗).

Ctenidodinium Deflandre 1938 sp., Middle Jurassic, text-fig. 5.

From: my own observations.
Modified tabulation formula, E: 2 ap. cl., 6′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 3′, 4′ (1a, 2a), 5′, 6′ (3′, 4′), 1⁗ (1p), 2⁗ (1⁗).

Paragonyaulacysta Johnson and Hills 1973 *s.l.*, Middle Jurassic, text-fig. 5.

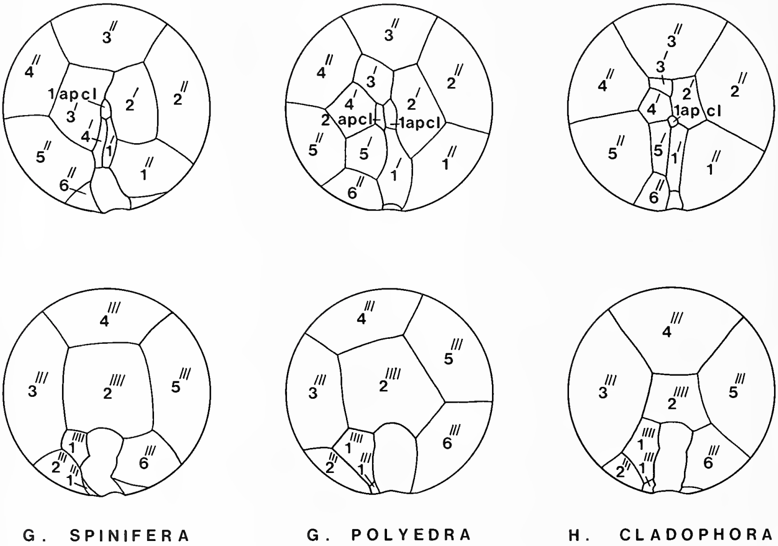
From: Johnson and Hills (1973, text-fig. 9) and my own observations.
Modified tabulation formula, E: 1 ap. cl., 5′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 3′–5′ (1a–3a), 1⁗ (1p), 2⁗ (1⁗).
Cyst archaeopyle type: dorsal apical, type A, 2A or 3A (conventionally intercalary, type I, 2I or 3I).

Luehndea spinosa Morgenroth 1970, Early Jurassic, text-fig. 5.

From: Morgenroth (1970, pl. 9, figs. 1–4), Evitt (unpublished data).
Modified tabulation formula, E: 1 ap. cl., 6′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 1 ap. cl. (3′), 3′–5′ (1a–3a), 6′ (4′), 1⁗ (1p), 2⁗ (1⁗).

Canninginopsis denticulata Cookson and Eisenack 1962, Mid Cretaceous, text-fig. 6.

From: Cookson and Eisenack (1962, text-fig. 2), Wall and Evitt (1975, text-fig. 11).
Modified tabulation formula, E: 1 ap. cl., 4′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 1⁗ (1p), 2⁗ (1⁗).



TEXT-FIG. 4. Modified interpretation of tabulation in polar views of *Gonyaulax spinifera* (Claparède and Lachmann) Diesing 1866, *Gonyaulax polyedra* Stein 1883, *Hystrichogonyaulax cladophora* (Deflandre) Stover and Evitt 1978. Upper, epithecae. Lower, hypothecae.

Ceratium hirundinella (Müller) Schrank 1793, Recent, text-fig. 6.

From: Wall and Evitt (1975, text-figs. 5, 6).
Modified tabulation formula, E: 4′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 1⁗ (1p), 2⁗ (1⁗), relative to Wall and Evitt (1975).

Thalassiphora delicata Williams and Downie 1966, Eocene, text-fig. 6.

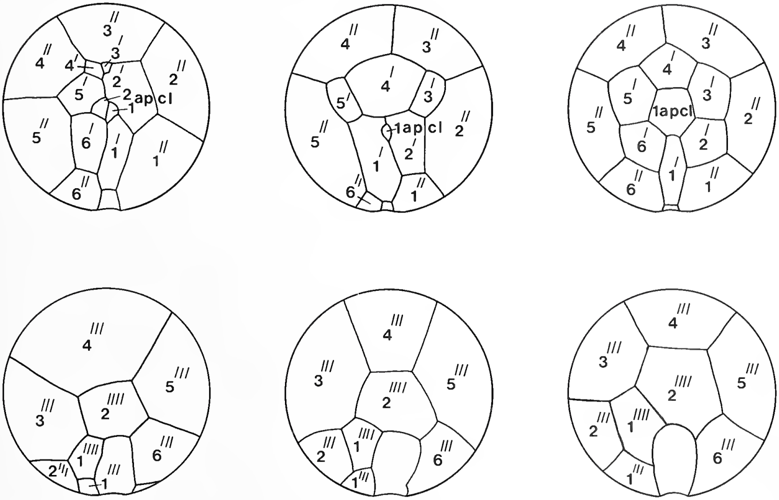
From: Eaton (1976, text-figs. 18, 20).
Modified tabulation formula, E: 1 ap. cl., 4′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 1 ap. cl. (4′), 4′ (1a), 2⁗ (1p). Also, the sixth pre- and postcingulars are now recognized.

Protoperidinium depressum (Bailey) Balech 1974, Recent, text-fig. 7.

From: Gocht and Netzel (1974, text-fig. 1).
Modified tabulation formula, E: 1 ap. cl., 6′, 7″; H: 5‴, 2⁗.
Changes in plate designation: 1 ap. cl. (3′), 3′–5′ (1a–3a), 6′ (4′).

Phthanoperidinium tritonium Eaton 1976, Eocene, text-fig. 7.

From: Eaton (1976, text-fig. 24).
Modified tabulation formula, E: 1 ap. cl., 6′, 7″; H: 5‴, 2⁗.
Changes in plate designation: 1 ap. cl. (3′), 3′–5′ (1a–3a), 6′ (4′).
Cyst archaeopyle type: dorsal apical, type A (conventionally intercalary, type I).



CTENIDODINIUM SP. PARAGONYAULACYSTA S.L. L. SPINOSA

TEXT-FIG. 5. Modified interpretation of tabulation in polar views of *Ctenidodinium* Deflandre 1938 sp., *Paragonyaulacysta* Johnson and Hills 1973 *s.l.*, *Luehndea spinosa* Morgenroth 1970. Upper, epithecae. Lower, hypothecae.

Helgolandinium subglobosum von Stosch 1969, Recent, text-fig. 7.

From: von Stosch (1969, text-fig. 3).
Modified tabulation formula, E: 5′, 7″; H: 7‴, 3⁗.
Changes in plate designation: 1′ (1″), 2′–5′ (1′–4′), 1″–7″ (2″–8″).

The very small plate designated 9″ by von Stosch (1969, text-fig. 3*f*) which lies anterior to the anterior sulcal plate and touches the first cingular plate is here referred to the sulcus as a second anterior sulcal plate, 2 a.s. A similarly positioned plate can sometimes be recognized in *Paragonyaulacysta s.l.*

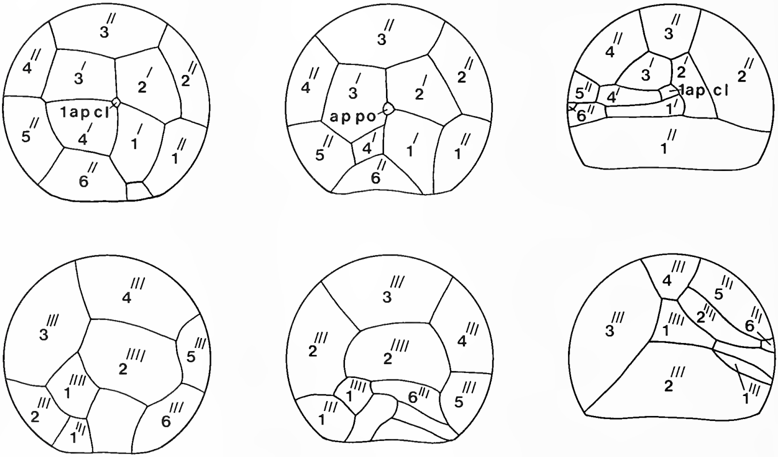
Dapcodinium priscum Evitt 1961, Early Jurassic, text-fig. 8.

From: Evitt (1961, text-figs. 1–20).
Modified tabulation formula, E: 1 ap. cl., 7′, 7″; H: 7‴, 3⁗.
Changes in plate designation: 1 ap. cl. (3′), 3′–6′ (1a–4a), 7′ (4′), 2‴–7‴ (1‴–6‴), 1⁗, 2⁗ (1p, 2p), 3⁗ (1⁗).

On the hypotheca, Evitt originally recognized only six postcingulars, but several of his drawings (Evitt 1961, text-figs. 5–10, 15–17, 19) show an undesignated plate comparable in position to the reduced first postcingular of *Gonyaulax*. This plate is designated 1‴ here, and the number of postcingulars is increased from six to seven.

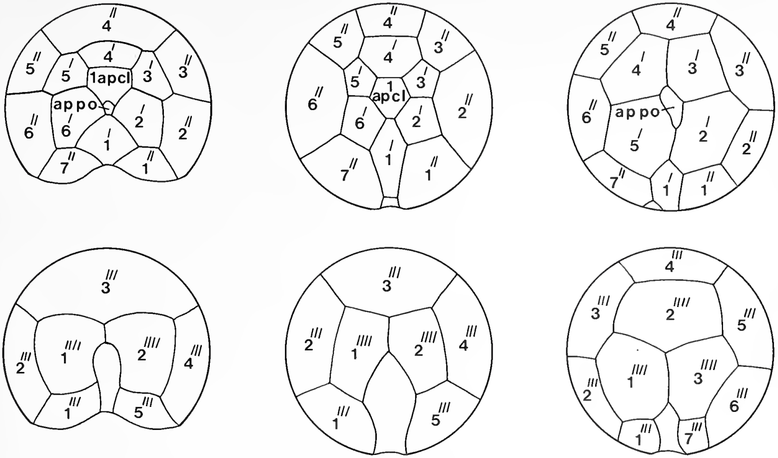
Shublikodinium arcticum Wiggins 1973, Late Triassic, text-fig. 8.

From: Wiggins (1973, text-fig. 3).
Modified tabulation formula, E: 6 ap. cl., 6′, 7″; H: 7‴, 3⁗, 1 an. cl.
Changes in plate designation: 1 ap. cl. (va. cl.), 2–6 ap. cl. (2′–6′), 2′–6′ (1a–5a), 1 an. cl. (ppl).
Cyst archaeopyle type: combination apical closing-apical, type $\overline{\mathrm{tACL\ tA}}$ (conventionally combination apical-intercalary, type $\overline{\mathrm{tA\ tI}}$).



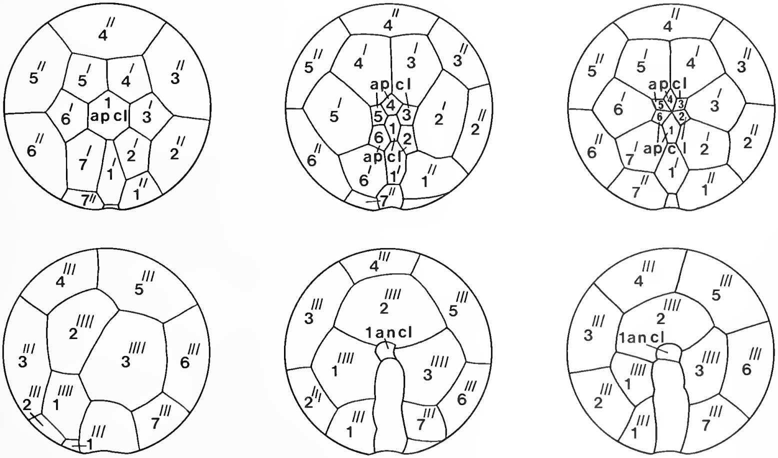
C. DENTICULATA C. HIRUNDINELLA T. DELICATA

TEXT-FIG. 6. Modified interpretation of tabulation in polar views of *Canninginopsis denticulata* Cookson and Eisenack 1962, *Ceratium hirundinella* (Müller) Schrank 1793, *Thalassiphora delicata* Williams and Downie 1966. Upper, epithecae. Lower, hypothecae.



P. DEPRESSUM P. TRITONIUM H. SUBGLOBOSUM

TEXT-FIG. 7. Modified interpretation of tabulation in polar views of *Protoperidinium depressum* (Bailey) Balech 1974, *Phthanoperidinium tritonium* Eaton 1976, *Helgolandinium subglobosum* von Stosch 1969. Upper, epithecae. Lower, hypothecae.



D. PRISCUM S. ARCTICUM R. RHAETICA

TEXT-FIG. 8. Modified interpretation of tabulation in polar views of *Dapcodinium priscum* Evitt 1961, *Shublikodinium arcticum* Wiggins 1973, *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich 1968. Upper, epithecae. Lower, hypothecae.

Rhaetogonyaulax rhaetica (Sarjeant) Loeblich and Loeblich 1968, Late Triassic, text-fig. 8.

From: Harland, Morbey and Sarjeant (1975, text-fig. 2).
Modified tabulation formula, E: 6 ap. cl., 7′, 7″; H: 7‴, 3⁗, 1 an. cl.
Changes in plate designation: 1–6 ap. cl. (1′–6′), 1′ (a.v.), 2′–7′ (1a–6a), 1⁗, (1p), 1 an. cl. (1⁗).
Cyst archaeopyle type: combination apical closing-apical, type tACL tA (conventionally combination apical-intercalary, type tA tI).

HOMOLOGOUS AND CORRESPONDING PLATES IN SELECTED DINOFLAGELLATE PLATE PATTERNS

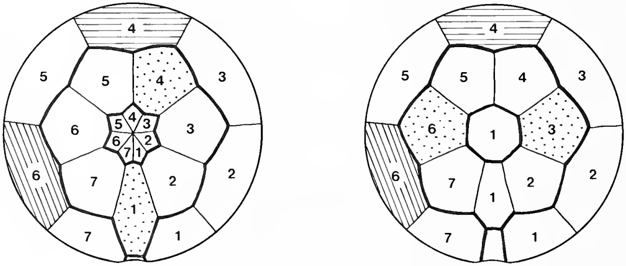
Method

The method used here for recognizing homologous and corresponding plates in different plate patterns involves critical comparisons of their interplate relationships. These comparisons are made with respect to a model plate pattern (text-fig. 9) whose epitheca and hypotheca both show a very high degree of radial symmetry and plate regularity. The model plate series are interpreted in terms of the modified nomenclature, but to emphasize the model nature of the pattern, the Kofoidian style notation is not applied. Instead, the series are referred to as 'ap.' (apical), 'prec.' (precingular), 'postc.' (postcingular) and 'antap.' (antapical). Also, the plates in each series are simply numbered consecutively 1, 2, 3 etc., and referred to as ap. 1, postc. 3, etc. The idea of this model plate pattern is based on the following observations.

In the fifteen epithecal patterns illustrated in text-figs. 4–8, the maximum number of plates in any of the transverse series is seven (7′, e.g. *D. priscum*; 7″, e.g. *P. depressum*). Also, the most regular interseries relationship involves groups of three plates (3-plate relationship) with one plate in one series touching two plates in an adjacent series. This relationship is fully developed between the precingular and apical series in *L. spinosa* and *D. priscum* for instance, and between six of the apicals (2′–7′) and five of the apical closing plates (2–6 ap. cl.) in *R. rhaetica*.

The model epitheca shows a full development of the 3-plate interseries relationship in a pattern with seven plates in all three transverse series. The direction of numbering the epithecal plates is conventional, i.e. anticlockwise relative to the apical pole. When an observed epithecal pattern does not show counterparts of all the model plates, it is the highest numbered model plates which are considered to be unrepresented.

A similar interpretation of such observations on the fifteen hypothecal patterns illustrated in text-figs. 4–8 would lead to a model pattern closely comparable to *S. arcticum* and *R. rhaetica*. The



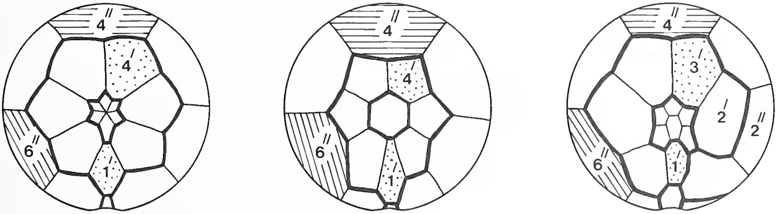
TEXT-FIG. 9. The model plate pattern. Left, epitheca, E: 7 ap. cl., 7 ap., 7 prec. Right, hypotheca, H: 7 postc., 7 antap., 1 an. cl.

maximum number of plates in any of the transverse series is again seven, but this maximum only occurs in the postcingular series (e.g. *H. subglobosum*). The maximum number of antapicals is only three (e.g. *D. priscum*), with a single antapical closing plate developed only in *S. arcticum* and *R. rhaetica*. All four patterns with seven postcingulars and three antapicals (*H. subglobosum*, *D. priscum*, *S. arcticum*, *R. rhaetica*) show a constant relationship between these two series. This involves groups of four plates (4-plate relationship) with one antapical touching three postcingulars. However, this arrangement can be interpreted in terms of the fundamental 3-plate relationship (fully developed in the model epitheca), if each of the three antapicals is treated as two plates, and the intervening mid-ventral area is also considered to be an antapical plate.

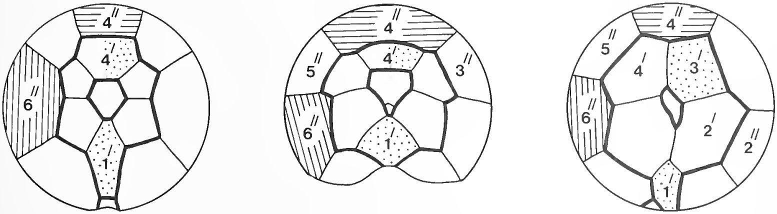
Thus the model hypotheca shows a full development of the 3-plate relationship between the postcingulars and antapicals, with seven plates in both series. The model hypothecal plates are numbered anticlockwise relative to the antapical pole. This is the reverse of convention, but is more convenient for the discussion of observed hypothecal patterns which do not show counterparts of all the model plates. As with the epithecae, it is the highest numbered model plates which are considered to be unrepresented.

In text-fig. 9, four plates on both the epitheca and hypotheca are ornamented. I consider these to be key reference plates in the discussion of homologous plate relationships and the comparison of different plate patterns.

For ease of comparison with the model pattern, the epithecae and hypothecae of the selected modern and fossil dinoflagellates are discussed and illustrated separately (text-figs. 10–12). The modified system of plate series nomenclature is applied throughout with a Kofoidian style notation.



R. RHAETICA D. PRISCUM S. ARCTICUM



P. TRITONIUM P. DEPRESSUM H. SUBGLOBOSUM

TEXT-FIG. 10. Epithecal plate patterns of six selected dinoflagellate taxa. The key reference areas are ornamented.

The direction of numbering the plates is conventional. In the text-figures the interseries boundaries are thickened for emphasis, and only those plates critical to the discussion are numbered. A maximum of four such plates on both the epitheca and hypotheca are also ornamented, either in full or in part. Each ornamented area corresponds to one key plate in the model pattern.

Epithecal plate patterns (text-figs. 9, 10, 11)

The model epithecal pattern (text-fig. 9) has twenty-one plates arranged in three series (7 ap. cl., 7 ap., 7 prec.). This discussion is primarily concerned with the apical and precingular series in which the key reference plates are ap. 1, ap. 4 (stippled), and prec. 4, prec. 6 (shaded).

Rhaetogonyaulax rhaetica and *Dapcodinium priscum* (text-fig. 10) both have a 7′, 7″ pattern, and also show a full development of the 3-plate relationship. Because of this, the seven apicals and seven precingulars in both patterns are considered to be respectively homologous with ap. 1–7 and prec. 1–7.

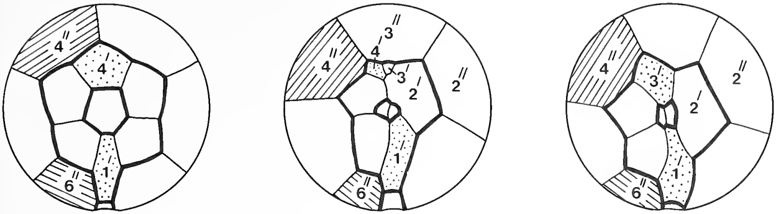
In *Shublikodinium arcticum* (text-fig. 10) which has a 6′ 7″ pattern, the 3-plate relationship is lost in the vicinity of precingular 2″ which is touched by only one apical, 2′. Compared with the model pattern, plate 2′ occupies the position of two plates, ap. 2 and ap. 3. Thus apical 2′ in *S. arcticum* corresponds to two plates in the model pattern, and as a result, apical 3′ in *S. arcticum* is homologous with key ap. 4. The interruption of the apical series in *S. arcticum* by a posterior extension of the apical closing series between 1′ and 2′, does not affect the over-all interpretation of the 3-plate relationship. *Phthanoperidinium tritonium* (text-fig. 10) also has a 6′, 7″ pattern, but the 3-plate relationship is lost in the vicinity of 4″. Thus apical 4′ corresponds to two plates in the model pattern, and only its stippled area corresponds to key ap. 4. In the 6′, 7″ pattern of *Protoperidinium depressum* (text-fig. 10), the 3-plate relationship is lost in the vicinity of three consecutive precingulars, 3″–5″. Even so, I still consider that only apical 4′ corresponds to two plates in the model pattern, and this accounts for the loss of the 3-plate relationship between the apical series and 4″. The further loss in the vicinity of 3″ and 5″ is due to a relative lateral displacement of the two intra-apical sutures which border 4′. Thus only the stippled area of 4′ in *P. depressum* corresponds to key ap. 4. In *Helgolandinium subglobosum* (text-fig. 10) which has a 5′, 7″ pattern, the 3-plate relationship is lost in the vicinity of two separated precingulars, 2″ and 5″. Thus apicals 2′ and 4′ each correspond to two plates in the model pattern, and 3′ is homologous with key ap. 4.

In *Luehndea spinosa* (text-fig. 11) there are only six plates in both the apical and precingular series (6′, 6″ pattern), but the 3-plate relationship is maintained throughout. Because of this the twelve plates comprising the apical and precingular series are considered to be respectively homologous with ap. 1–6 and prec. 1–6. Thus the highest numbered model plates, ap. 7 and prec. 7, have no counterparts in *L. spinosa*. This last comment also applies to the eight remaining patterns discussed here.

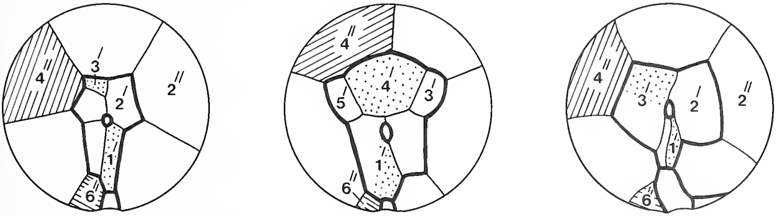
Ctenidodinium sp. (text-fig. 11) has a 6′, 6″ pattern, but the 3-plate relationship is lost in the vicinity of two consecutive precingulars, 2″ and 3″. Plate 2″ has one apical touching it, 2′, while 3″ has three apicals touching it, 2′–4′. The loss of the 3-plate relationship is due to the critical shortening of 3′, accompanied by the relative enlargement of 2′. Plate 4′ is also shortened, but not critically. As in *L. spinosa*, the twelve plates comprising the apical and precingular series in *Ctenidodinium* sp. are respectively homologous with ap. 1–6 and prec. 1–6.

In *Gonyaulax polyedra* and *Hystrichogonyaulax cladophora* (text-fig. 11) which both have a 5′, 6″ pattern, the 3-plate relationship is lost in the vicinity of precingular 2″. Applying the principle used in the interpretation of *S. arcticum*, *P. tritonium* etc., apical 2′ corresponds to two plates in the model pattern. Thus 3′ in *G. polyedra* and *H. cladophora* is homologous with key ap. 4. The shortening of 3′ in *H. cladophora* is not critical, and is comparable to 4′ in *Ctenidodinium* sp. In *Paragonyaulacysta s.l.* (text-fig. 11) which also has a 5′, 6″ pattern, the 3-plate relationship is lost in the vicinity of precingular 6″. Thus only the stippled area of 1′ corresponds to key ap. 1, and the unornamented area of 1′ corresponds to ap. 6. The shortening of apicals 3′–5′ in *Paragonyaulacysta s.l.* is not critical.

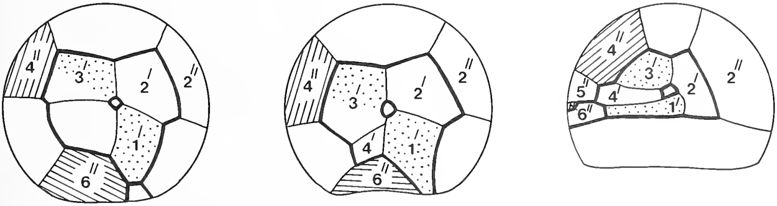
Gonyaulax spinifera, *Canninginopsis denticulata*, and *Ceratium hirundinella* (text-fig. 11) all have a 4′, 6″ pattern and identical homologous and corresponding plate relationships. Loss of the 3-plate



L. SPINOSA CTENIDODINIUM SP. G. POLYEDRA



H. CLADOPHORA PARAGONYAULACYSTA S.L. G. SPINIFERA



C. DENTICULATA C. HIRUNDINELLA T. DELICATA

TEXT-FIG. 11. Epithecal plate patterns of a further nine selected dinoflagellate taxa. The key reference areas are ornamented.

relationship occurs in the vicinity of precingulars 2″ and 4″. Thus 2′ and 3′ each correspond to two plates in the model pattern, and therefore the stippled area of 3′ corresponds to key ap. 4. The further loss of the 3-plate relationship in *G. spinifera* is due to the critical shortening of 6″. The shortening of 4′ in *C. hirundinella* is not critical.

In *Thalassiphora delicata* (text-fig. 11) which also has a 4′, 6″ pattern, the 3-plate relationship is lost in the vicinity of three precingulars, 2″, 5″, and 6″. Thus 2′ and 4′ each correspond to two plates in the model pattern, and 3′ is homologous with key ap. 4. Plate 6″ is critically shortened and is not touched by any of the apical series.

Only limited comments can be made on possible homologous relationships in the apical closing series, because of the great variation in its development. It is reasonable to suggest that 1 ap. cl. in *R. rhaetica* and *S. arcticum* corresponds to the first and seventh apical closing plates in the model pattern, and that the five remaining plates in all three patterns are respectively homologous. Also that the large single apical closing plate in *D. priscum*, *L. spinosa*, *P. tritonium*, and *P. depressum* corresponds to all seven apical closing plates in the model pattern. However, the relationship between these two extremes of development, and the apical closing plates in *G. spinifera* and *Ctenidodinium* sp. for instance, is undetermined.

Hypothecal plate patterns (text-figs. 9, 12)

The model hypothecal pattern (text-fig. 9) has fifteen plates arranged in three series (7 postc., 7 antap., 1 an. cl.). This discussion is only concerned with the postcingular and antapical series in which the key reference plates are postc. 4, postc. 6 (shaded) and antap. 3, antap. 6 (stippled). The fifteen selected hypothecae do not show the same range of variation as their epithecae, and can be discussed in terms of only eight patterns.

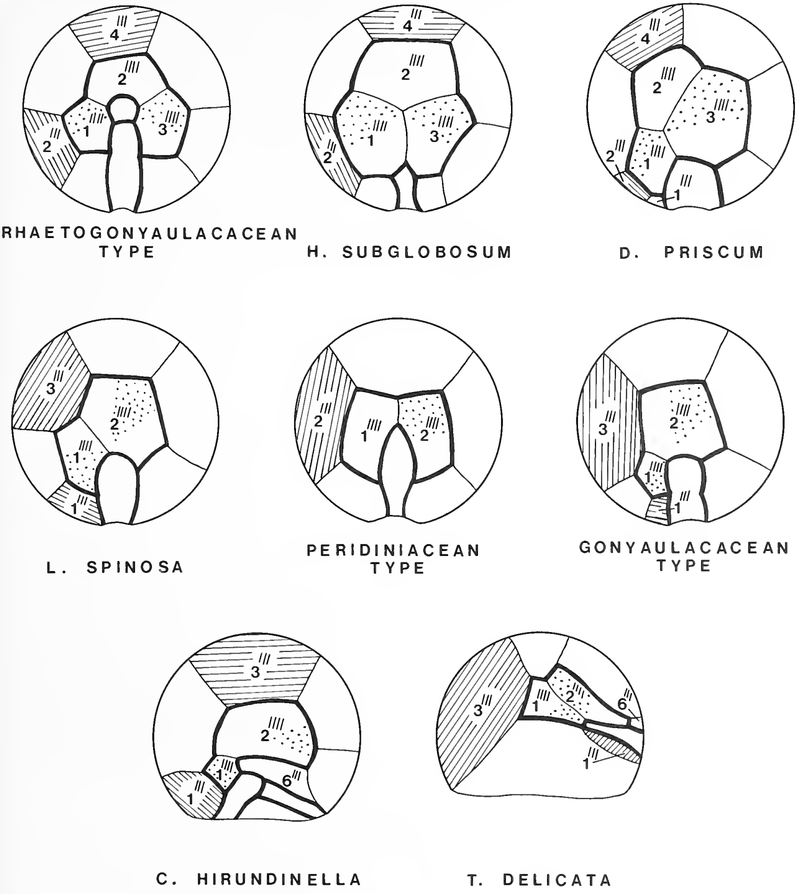
The 'rhaetogonyaulacacean' type (*Rhaetogonyaulax rhaetica*, *Shublikodinium arcticum*), *Helgolandinium subglobosum*, and *Dapcodinium priscum* (text-fig. 12) all have a 7‴, 3⁗ pattern. The seven postcingulars in these patterns and the model pattern are respectively homologous. The antapical-postcingular interseries relationship is constant, with each antapical touching three postcingulars. As stated earlier, each antapical corresponds to two plates in the model pattern. Since 1⁗–3⁗ occupy the position of antap. 2–7, 1⁗ corresponds to antap. 6–7, 2⁗ to antap. 4–5, and 3⁗ to antap. 2–3. Thus, only the stippled area of 3⁗ corresponds to key antap. 3, and only the stippled area of 1⁗ corresponds to key antap. 6.

Although no counterpart of antap. 1 is shown in the 7‴, 3⁗ patterns, it may be represented by the posterior area of the sulcus. However, in fossil dinoflagellates the individual sulcal plates are often very poorly defined, and it is by no means certain that all areas designated posterior sulcal (p.s.) are respectively homologous. Consequently this relationship is only questionably applied to the fifteen selected patterns (Table 1).

A significant feature of *D. priscum* is the anticlockwise rotation of its plate pattern relative to the model pattern, and the associated reduction of 2‴ and 1‴. These reduced plates correspond to the highest numbered model postcingulars, postc. 6, postc. 7, and this influenced my earlier statement that when a hypothecal pattern does not show counterparts of all the model plates, it is the highest numbered model plates which are unrepresented. Consequently it is convenient to discuss the plate relationships of the five remaining patterns in an anticlockwise direction, i.e. in terms of 6‴–1‴ and 2⁗–1⁗.

In *Luehndea spinosa* there are only six postcingulars and two antapicals (6‴, 2⁗ pattern). Plates 6‴–1‴ are respectively homologous with postc. 1–6, and there is no counterpart of postc. 7. Thus 3‴ is homologous with key postc. 4, and 1‴ is homologous with key postc. 6. Antapical 2⁗ touches four postcingulars and therefore corresponds with three plates in the model pattern, antap. 2–4. Thus only the stippled area of 2⁗ corresponds to key antap. 3. Plate 1⁗ touches three postcingulars and therefore corresponds to two plates in the model pattern, antap. 5, 6. Thus only the stippled area of 1⁗ corresponds to key antap. 6, and there is no counterpart of antap. 7.

In the 'peridiniacean' type pattern (*Protoperidinium depressum* and *Phthanoperidinium tritonium*) there are only five postcingulars and two antapicals (5‴, 2⁗ pattern). Plates 5‴–1‴ are respectively



RHAETOGONYAULACACEAN TYPE

H. SUBGLOBOSUM

D. PRISCUM

L. SPINOSA

PERIDINIACEAN TYPE

GONYAULACACEAN TYPE

C. HIRUNDINELLA

T. DELICATA

TEXT-FIG. 12. Eight hypothecal plate patterns representative of the fifteen selected dinoflagellate taxa. The key reference areas are ornamented.

PLATE SERIES	MODEL PATTERN	R RHAETICA	D PRISCUM	S ARCTICUM	H SUBGLOBOSUM	P TRITONIUM	P DEPRESSUM	L SPINOSA	PARAGONYAULACYSTA s l	CTENIDODINIUM sp.	G POLYEDRA	H. CLADOPHORA	G SPINIFERA	C DENTICULATA	C. HIRUNDINELLA	T. DELICATA
APICAL	1	1	1	1	1	1	1	1	1(pt)	1	1	1	1	1	1	1
	2	2*	2	}2*	2	2	2	2	2	2	}2	2	2	2	2	2
	3	3*	3*			3*	3*	3*	3*	3*						
	4	4*	4*	3*	3	}4*	4*	4*	4*	4*	3	3*	}3	3	3	3
	5	5*	5*	4*	}4			5*	5*	5	4*	4				}4
	6	6*	6*	5*		5*	5*	6	1(pt)	6	5*	5	4	4	4	
	7	7*	7	6*	5	6	6	—	—	—	—	—	—	—	—	—
PREC.	1	1	→	→	→	→	→	→	→	→	→	→	→	→	→	1
	↓	↓														↓
	6	6	→	→	→	→	→	→	→	→	→	→	→	→	→	6
	7	7	→	→	→	→	7	—	—	—	—	—	—	—	—	—
POSTCINGULAR	1	7	7	7	7	5	5	6	→	→	→	→	→	→	6(?pt)	6
	2	6	6	6	6	4	4	5	→	→	→	→	→	→	→	5
	3	5	5	5	5	3	3	4	→	→	→	→	→	→	→	4
	4	4	4	4	4	2	2	3	→	→	→	→	→	→	→	3
	5	3	3	3	3	1	1	2	→	→	→	→	→	→	→	2
	6	2	2	2	2	—	—	1	→	→	→	→	→	→	→	1
	7	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—
ANTAPICAL	1	←					?ps.	→	→	→	→	→	→	→	?6'''(pt)	
	2	}3	3	3	3	2	2								}2	}2*
	3							}2	→	→	→	→	→	2		
	4	}2	2*	2	2	1	1									
	5															}1
	6	}1*	1*	1	1	—	—	}1*	→	→	→	→	→	1*	1*	
	7					—	—	—	—	—	—	—	—	—	—	—

TABLE 1. Homologous and corresponding plates in the fifteen selected plate patterns and the model pattern. The modified interpretation of transverse series is applied throughout. Plates with an asterisk would be designated intercalary using the conventional Kofoidian system.

PLATE SERIES	MODEL PATTERN	R. RHAETICA	D. PRISCUM	S. ARCTICUM	H. SUBGLOBOSUM	P. TRITONIUM	P. DEPRESSUM	L. SPINOSA	PARAGONYAULACYSTA s.l.	CTENIDODINIUM sp.	G. POLYEDRA	H. CLADOPHORA	G. SPINIFERA	C. DENTICULATA	C. HIRUNDINELLA	T. DELICATA
APICAL	1	1	1	1	1	1	1	1	1(pt)	1	1	1	1	1	1	1
	2	2*	2	}2*	2	2	2	2	2	2	}2	2	2	2	2	2
	3	3*	3*			3*	3*	3*	3*	3*						
	4	4*	4*	3*	3	}4*	4*	4*	4*	4*	3	3*	}3	3	3	3
	5	5*	5*	4*	}4			5*	5*	5	4*	4				}4
	6	6*	6*	5*		5*	5*	6	1(pt)	6	5*	5	4	4	4	
	7	7*	7	6*	5	6	6	—	—	—	—	—	—	—	—	—
PREC.	1	1	→													1
	↓	↓														↓
	6	6	→													6
	7	7	→				7	—	—	—	—	—	—	—	—	—
POSTCINGULAR	1	7	7	7	7	5	5	6	→						6(?pt)	6
	2	6	6	6	6	4	4	5	→							5
	3	5	5	5	5	3	3	4	→							4
	4	4	4	4	4	2	2	3	→							3
	5	3	3	3	3	1	1	2	→							2
	6	2	2	2	2	—	—	1	→							1
	7	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—
ANTAPICAL	1	←						?p.s.	→						?6'''(pt)	
	2	}3	3	3	3	2	2	}2	→					2	}2	}2*
	3															
	4	}2	2*	2	2	1	1									}1
	5							}1*	→					1*		
	6	}1*	1*	1	1	—	—								1*	
	7					—	—	—	—	—	—	—	—	—	—	—

TABLE 1. Homologous and corresponding plates in the fifteen selected plate patterns and the model pattern. The modified interpretation of transverse series is applied throughout. Plates with an asterisk would be designated intercalary using the conventional Kofoidian system.

homologous with postc. 1–5 and there are no counterparts of postc. 6, 7. Thus 2‴ is homologous with key postc. 4. Antapicals 2⁗ and 1⁗ each touch three postcingulars and therefore each corresponds to two plates in the model pattern. Thus only the stippled area of 2⁗ corresponds to key antap. 3, and there are no counterparts of antap. 6, 7.

The 'gonyaulacacean' type pattern (*Gonyaulax spinifera*, *G. polyedra*, *Hystrichogonyaulax cladophora*, *Ctenidodinium* sp., *Canninginopsis denticulata*, *Paragonyaulacysta s.l.*) with six postcingulars and two antapicals (6‴, 2⁗ pattern) differs from *L. spinosa* only in showing considerable reduction of 1‴, 2‴, and 1⁗. The interseries relationships of the gonyaulacacean pattern are directly comparable with *L. spinosa*. Thus 3‴ is homologous with key postc. 4, and 1‴ is homologous with key postc. 6. Also, only the stippled area of 2⁗ corresponds to key antap. 3 and only the stippled area of 1⁗ corresponds to key antap. 6.

Ceratium hirundinella also has a 6‴, 2⁗ pattern, but is unusual in that postcingular 6‴ touches 1⁗ as well as 2⁗. A possible explanation of this relationship is that 6‴ in *C. hirundinella* actually represents two plates, 6‴ *s.s.* and the conventional posterior sulcal plate (p.s. in text-fig. 1). The latter plate has not been precisely identified in *C. hirundinella*, although it must be admitted that the sulcal area of *Ceratium* in general is poorly known (Wall and Evitt 1975, p. 19). Plates 5‴–1‴ are respectively homologous with postc. 2–6, and there is no counterpart of postc. 7. Thus 3‴ is homologous with key postc. 4, and 1‴ is homologous with key postc. 6. Antapical 2⁗ touches five postcingulars and therefore corresponds to four plates in the model pattern, antap. 2–5. Thus only the stippled area of 2⁗ corresponds to key antap. 3. Plate 1⁗ touches 1‴ and 2‴ and is therefore homologous with key antap. 6. There is no counterpart of antap. 7.

Thalassiphora delicata also has a 6‴, 2⁗ pattern, but its interseries relationships effectively represent a lateral reversal of the gonyaulacacean arrangement. This affects the antapicals, where 2⁗ only touches three postcingulars and therefore corresponds to two plates in the model pattern, and 1⁗ touches four postcingulars and therefore corresponds to three plates in the model pattern. Thus only the stippled area of 2⁗ corresponds to key antap. 3, and only the stippled area of 1⁗ corresponds to key antap. 6.

The interpreted homologous and corresponding plate relationships of the fifteen selected plate patterns and the model pattern (excluding the apical closing, cingular and antapical closing series) are summarized in Table 1. This emphasizes the fact that plates conventionally designated intercalary (*) in one pattern, are homologous with or partially correspond to conventional apical or antapical plates in another pattern. Examples include apical 4′ (conventional 2a) in *Protoperidinium depressum* homologous with apical 3′ in *Gonyaulax spinifera*, and antapical 1⁗ (conventional 1p) in *G. spinifera* which partially corresponds to part of antapical 1⁗ in *Helgolandinium subglobosum*. This table also shows that when a series is represented by the same number of plates in different patterns, the plates need not all be respectively homologous. Examples include the four apicals in *G. spinifera* and *T. delicata*, and the two antapicals in *G. spinifera*, *T. delicata*, and *P. depressum*.

DISCUSSION

The differences between the fifteen selected plate patterns (text-figs. 10–12) reflect an over-all trend of reduction in the total number of plates. This reduction is effected in two particular ways. There may be simplification through the development of a single plate in one pattern which spatially corresponds with two or more plates in another pattern. This critically affects interseries relationships. Alternatively there may be a primary development of fewer plates in particular series, without affecting interseries relationships. These two styles of reduction may occur independently or together. They may also be accompanied by variation in the relative size of certain plates which may affect interseries relationships through critical shortening or lateral reduction.

Reduction through simplification affects the apical closing, apical and antapical series. The development of a single large apical closing plate in *D. priscum* for instance, represents simplification of the six-plate arrangement in *R. rhaetica* and *S. arcticum*. In the apical series, simplification occurs in specific areas, e.g. mid-ventral (1′) in *Paragonyaulacysta s.l.*; left lateral (2′) in *S. arcticum*; mid-dorsal (4′) in *P. tritonium*; left and right lateral, (2′, 3′) in *G. spinifera*, (2′, 4′) in *T. delicata*; left ventral and right lateral (2′, 4′) in *H. subglobosum*. In the antapical series, simplification is best defined with reference to the model antapicals, antap. 2–7. For instance, the three antapicals in *H. subglobosum* reflect simplification of antap. 2–7 in the form 2–3, 4–5, 6–7. In the patterns with only two antapicals this simplification takes several forms, e.g. 2–3, 4–5 (peridiniacean type), 2–4, 5–6 (gonyaulacacean type), 2–5, 6 (*C. hirundinella*), 2–3, 4–6 (*T. delicata*).

Reduction through the primary development of fewer plates is best defined with reference to the position of plates which are homologous with or in part correspond to model key reference plates.

In the six epithecae in text-fig. 10 (*R. rhaetica* etc.) the position of these plates is virtually constant. In particular, the equivalent of key prec. 4. is invariably mid-dorsal. A similar constancy is shown by eight of the epithecae in text-fig. 11 (*L. spinosa* etc., but not *T. delicata*). However, in these patterns the equivalent of key prec. 4 is invariably right dorso-lateral in position. Compared with *R. rhaetica* etc. (text-fig. 10), this represents a rotation of the epithecal pattern, anticlockwise relative to the apical pole. This accommodates the primary development of one less apical and one less precingular plate (i.e. no counterparts of ap. 7, prec. 7).

In the eight hypothecae in text-fig. 12 there is considerable variation in the position of the key reference areas. In particular, the equivalent of key postc. 4 rotates from mid-dorsal in the rhaetogonyaulacacean type and *H. subglobosum*, through left dorso-lateral in *D. priscum* and *L. spinosa*, to left lateral in the gonyaulacacean and peridiniacean types. This rotation, which affects the over-all hypothecal pattern, is anticlockwise relative to the antapical pole. This accommodates the primary development of fewer postcingulars and antapicals (i.e. no counterparts of two or more of postc. 6, 7, antap. 6, 7).

The effect of variation in the relative size of certain plates is well shown by the epithecae of *Ctenidodinium* sp., *H. cladophora*, *Paragonyaulacysta s.l.* and *G. spinifera* (text-fig. 11), in which there is enlargement of the lateral and left ventral precingulars (compared with *L. spinosa*). This is at the expense of the apical series which becomes longitudinally aligned, and 6″ which is reduced. In the somewhat bizarre pattern of *T. delicata* (text-figs. 11, 12) the considerable enlargement of 1″ and 2‴, 3‴ is accommodated by the displacement of the sulcus, 1′, 4′, 1‴, 6‴ and 1⁗, 2⁗ to a right lateral position. There is also reduction of 5″ and 6‴, and 6″ is critically shortened. Other examples of critical shortening include 3′ in *Ctenidodinium* sp. and 6″ in *G. spinifera*, while 4′ in *P. depressum* is critically reduced laterally.

Reduction in the total number of thecal plates may well represent a fundamental trend in the evolution of peridinialean plate patterns. If this is so, then available evidence from the fossil record suggests that primary development of fewer plates was the most important means of achieving this reduction. This evidence is provided for epithecae by the appearance in the Late Triassic of patterns with counterparts of ap. 7, prec. 7 (*R. rhaetica*, *S. arcticum*), followed in the Jurassic by the appearance of patterns without counterparts of these two plates (e.g. *L. spinosa*, *Ctenidodinium* sp.). The hypothecal evidence is provided by the successive appearance of the rhaetogonyaulacacean type (Late Triassic), *D. priscum* and *L. spinosa* (Early Jurassic), gonyaulacacean type (Middle Jurassic) and the peridiniacean type (Late Jurassic). The great range of variation shown by Late Triassic and younger plate patterns resulted from the effects of reduction through simplification, and variation in relative plate size, being superimposed on the effect of primary reduction. The interaction of these three variables resulted in epithecae and hypothecae evolving comparatively independently and this is emphasized by the way in which the epitheca and hypotheca accommodated the effects of primary reduction. In both, rotation is anticlockwise relative to their respective pole, and therefore the hypotheca rotates in the opposite direction to the epitheca relative to the polar axis of the theca. The model plate pattern appears to represent an evolutionary base to which all Late Triassic and younger peridinialeans of the selected type are related. This type is characterized by having up to seven plates in each of its epithecal and hypothecal transverse series. In view of this relationship, the complex model pattern could be representative of a pre-Late Triassic ancestral peridinialean.

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MODE OF LIFE OF A GIANT CAPULID GASTROPOD FROM THE UPPER CRETACEOUS OF SAGHALIEN AND JAPAN

by ITARU HAYAMI *and* YASUMITSU KANIE

ABSTRACT. The life habits of a huge Campanian patelliform gastropod, hitherto called '*Helcion giganteus*', from Saghalien and Japan are discussed on the basis of several specimens adhering to enormous shells of *Inoceramus* (*Sphenoceramus*) *schmidti*. This gastropod is here transferred to the Capulidae of Mesogastropoda, and a new generic name, *Gigantocapulus*, is proposed for it. Its ecological relation with *I.* (*S.*) *schmidti* is regarded as parasitic by analogy to some living species of *Capulus* that attach to the valves of pectinids. This interpretation is supported by stratigraphic and geographic distribution patterns and by its functional morphology.

'*Helcion giganteus*', originally described by Schmidt (1873) from the Upper Cretaceous at Cape Dui near Alexandrovsk, north Saghalien, is probably the largest patelliform gastropod known. Its shell sometimes exceeds 400 mm in maximum length, and shows a wide range of morphological variation. This species, though restricted to the lower to middle Campanian (Zone of *Inoceramus schmidti*), occurs at various localities in Saghalien, Japan (mainly Hokkaido), Koryak Highland of eastern Siberia (Dundo and Efremova 1974), Southern Alaska (Jones, pers. comm.), and British Columbia (Whiteaves 1903). The association of this species with *I.* (*Sphenoceramus*) *schmidti* Michael, 1899, is important. Almost all the specimens of '*I. digitatus*' described by Schmidt (1873) together with '*H. giganteus*' from Cape Dui seem to be referable to *I.* (*S.*) *schmidti*, as revised in Michael (1899) and Nagao and Matumoto (1940). Their coexistence in the same fossil bed (commonly fine-grained sandstone) was also recorded at many other localities: Naibuchi (= Naibuti) (Matumoto 1942, p. 167) in south Saghalien, Abeshinai (Matumoto 1942, p. 205), Hetonai (Matumoto 1942, p. 251), Urakawa (Matumoto 1942, p. 268; Kanie 1966, p. 322; 1977, p. 54) and some other places in Hokkaido, and Dogo-Himezuka, Matsuyama City (Kashima 1972; Matsumoto 1973) in Shikoku.

Summarizing the classification and evolutionary history of Cretaceous patelliform gastropods in the northern Pacific region, Kanie (1975) concluded that '*H. giganteus*' belongs to the Mesogastropoda and that they possibly attached to some other shelled organism. Since '*H. giganteus*' is seldom accompanied by molluscs assumed to have lived on near-shore rocky substrates, it was assumed that it may have been attached to large bivalves such as *I.* (*S.*) *schmidti*, but at that time there was no direct evidence. Subsequently Hayami found a specimen of '*H. giganteus*', in growth position attached to the shell surface of *Inoceramus*, in the collection of the University Museum, University of Tokyo. We have now examined the relation between the two molluscs on the basis of many specimens stored at various institutions. In the present article we describe some of these specimens, discuss the interpreted life habit of this gastropod, and compare it with some living species of similar habit. The taxonomic position of '*H. giganteus*' is also reconsidered.

SYSTEMATIC PALAEONTOLOGY

Order CAENOGASTROPODA Cox, 1959
Suborder MESOGASTROPODA Thiele, 1925
Superfamily CALYPTRAEACEA Lamarck, 1809
Family CAPULIDAE Fleming, 1822
Genus *Gigantocapulus* Hayami and Kanie, gen. nov.

[Palaeontology, Vol. 23, Part 3, 1980, pp. 689–698, pl. 87.]

Type species. Helcion giganteus Schmidt, 1873, northern Pacific region, Campanian.

Diagnosis. Shell very large, cap-shaped or conical, bilaterally symmetrical but more or less irregular in outline; apex located anteriorly from the centre, sometimes marginal; surface commonly ornamented with irregularly disposed radial costae in addition to concentric rings on the apical region; anterior elevated sector and internal septum absent; outermost layer prismatic, while other and inner layers are crossed-lamellar; some species living upon the shells of *Inoceramus*.

Remarks. The taxonomic position of '*H. giganteus*' and its allied species from the Cretaceous of northern Pacific has been debatable; *Capulus*, *Patella*, *Scurria*, *Acmaea*, and *Brunonia* also have been used as their generic names. Living patelliform gastropods occur in various unrelated taxonomic groups, e.g. the Patellacea of Archaeogastropoda, the Neritacea and Calyptraeacea of Mesogastropoda and the Siphonariacea of Pulmonata. Because their shell forms sometimes show remarkable convergence, such essential characters as muscle impression, presence or absence of internal septum and shell structure as well as inferable life habit may be important for determination of the taxonomic position of fossil species.

Kanie (1975) assigned these Cretaceous species in question to the genus *Anisomyon* Meek and Hayden, 1860, which had been included in the Basommatophora (an order of Pulmonata), and proposed a new family Anisomyonidae in the Mesogastropoda. This treatment was primarily based on the resemblance of muscle impressions and shell form of some species to the Capulidae and the difference of shell structure from the Siphonariidae. As noted elsewhere (Hayami and Kase 1977, p. 55), however, one of us (I. H.) doubted if the type species of *Anisomyon* [*H. patelliformis* Meek and Hayden,1856] should be transferred from the Basommatophora to the Mesogastropoda, and presumed that '*H. giganteus*' may represent an unnamed genus of the Capulidae. This is proposed here, which modifies the previous classification (Kanie 1975) of Cretaceous patelliform gastropods from the northern Pacific region.

Kanie (1975) distinguished two 'morphotypes' in '*H. giganteus*': type A is characterized by the relatively small size, small apical angle, and irregularly noded ornament, while type B has relatively large size, large apical angle, and almost persistent and not noded radial ribs. Of the originally figured specimens of *H. giganteus*, most individuals including the lectotype (Schmidt 1873, pl. 2, fig. 17, designated by Kanie (1975) as 'holotype') belong to type B, and only two small specimens (Schmidt 1873, pl. 3, figs. 8, 9) may belong to type A. Numerous individuals of type A are preserved in various Japanese institutions, but none of them actually shows any intimate relation to the shell of *Inoceramus*. All the observed specimens attached to the surface of *I.* (*S.*) *schmidti* belong to type B. Moreover, significant morphological differences are newly recognized between the two 'morphotypes'. First, a trace of an internal septum is often seen in type A (see Kanie 1975, p. 9, fig. 2), but has never been observed in type B. Secondly, the apex is always located subcentrally or even posteriorly in type A, while it is commonly located very anteriorly or even near the anterior margin in type B. Thirdly, a tongue-like projection, as described later, occurs only in type B. Host-determined non-genetic variation is actually known in a living capulid species (Thorson 1965), and dwarf males are also seen in such semi-parasitic gastropods. Yet, such great differences of essential characters are hardly explicable by individual variation. At present, we consider that the two 'morphotypes' belong to different species, and that the use of the specific name *Gigantocapulus giganteus* should be restricted to the type B of Kanie (1975). The specimens of type A seem to be close to '*A. transformis*' Dundo and Efremova (1974) from the Koryak Highland. The presence of an internal septum may suggest that they belong to the Calyptraeidae.

EXPLANATION OF PLATE 87

Figs. 1, 2. *Gigantocapulus giganteus* (Schmidt, 1873). UMUT MM5535 attached to the surface of *Inoceramus* (*Sphenoceramus*) *schmidti* Michael, 1899. Loc. N469, north-west of Miho (gorge of Ryugase), Naibuchi area, south Saghalien. Collected by T. Matsumoto. 1, upper view, × 0·42; 2, left lateral view, × 0·42. (See also text-fig. 1.)

1

2

HAYAMI and KANIE, Cretaceous patelliform gastropod

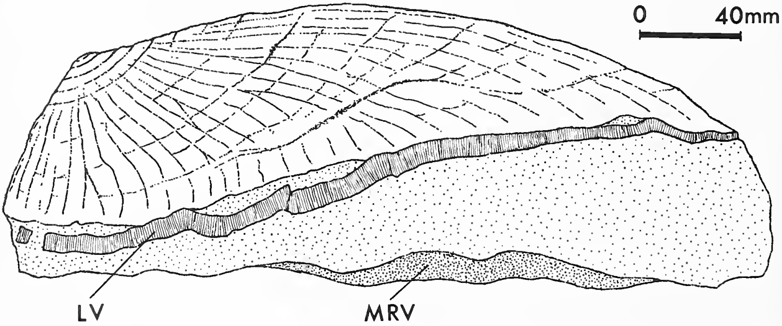
In the Western Interior of the United States some specimens of *Anisomyon* have also been found adhering to the shells of *Inoceramus* (Sohl 1967*a*). The association may be comparable with the present case. According to Sohl's (1967*b*) redescription of *A. patelliformis* (Meek and Hayden, 1856), however, one of the paratypes reveals clearly asymmetric muscle impression, which resembles that of *Siphonaria*, although the posterior carination of *Siphonaria*-type is undeveloped in that species. No specimen of *G. giganteus* shows clear muscle impression, but *Capulus*-like horseshoe-shaped muscle scars are recognized in *C. cassidarius* Yokoyama, 1890, which is considered to be ancestral to *G. giganteus* (Kanie 1975, p. 9, fig. 2). The genus *Anisomyon* is represented by much smaller species without radial costae, and we are now inclined to consider that it is not directly related to *Gigantocapulus*.

The genus *Brunonia* Müller, 1898, may be another Late Cretaceous patelliform gastropod comparable with our new genus from morphological and paleoecological standpoints. The genus was generally referred to the Siphonariidae, but in the *Treatise* (Knight *et al.* 1960) it was doubtfully included in the suborder Patellina. The concentrically ornamented shell of its type species [*B. grandis* Müller, 1898, from the Santonian of Germany] resembles the apical part of *G. giganteus*. Unfortunately, Müller's original specimen of *B. grandis* is said to have been lost, and further comparative study is now difficult. At present we think that *Gigantocapulus* is at least generically separable from *Brunonia* by the developed radial costae on the surface. Judging from the original figures of *B. grandis*, the apex is more constantly located near the centre of shell, and no projection is developed on its anterior periphery.

DESCRIPTION OF SELECTED SPECIMENS

Among a large number of specimens of *G. giganteus* in the collection of the University Museum, University of Tokyo (UMUT), and the Institute of Geology and Palaeontology, Tohoku University, Sendai (IGPS), several show an intimate association with the shells of *I.* (*S.*) *schmidti*. UMUT MM5535 (Pl. 87; text-fig. 1) has well-preserved shells of the two species, and shows the position and orientation of attachment. It was found in T. Matsumoto's collection from a greenish fine-grained sandstone of the Ray 1 Member of the Ryugase Group at loc. N469 (gorge of Ryugase), about 4·5 km north-west of Miho, Naibuchi area, south Saghalien (see the locality map in Matsumoto 1942). The following description is entirely based on this specimen.

The shell of *G. giganteus*, though a considerable part of the marginal area is broken off, exceeds 290 mm in maximum length and 250 mm in breadth, showing a suboval, nearly bilaterally symmetrical, cap-shaped outline with a somewhat irregularly undulating marginal area. The apex is located at about one-fifth of maximum length

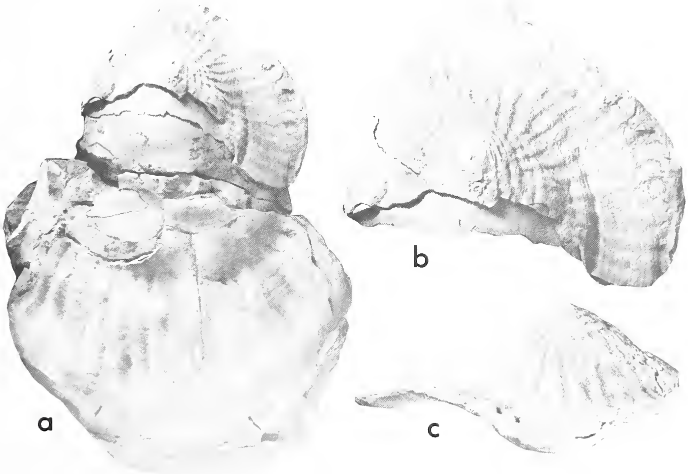


TEXT-FIG. 1. Sketch of Specimen I (UMUT MM5535) of *Gigantocapulus giganteus* (Schmidt) from the left side. LV: Fracture of the left valve (prismatic outer layer) of *Inoceramus* (*Sphenoceramus*) *schmidti* Michael; MRV: Internal surface of the right valve of the same individual, on which characteristic divergent ribs are impressed.

from the anterior end, but the growth-lines indicate that it was situated near the centre of shell in the early growth stage. The pre-apical area steeply descends towards the anterior margin, while the post-apical area is widely expanded and broadly convex. The maximum inflation of shell lies far behind the apex. The surface is ornamented with several subconcentric ribs and about fifty radial costae. Subconcentric ribs are distinct and widely spaced, and their distribution is confined to the apical area (within 50 mm from the apex). On the contrary, radial costae are at first indistinct but become prominent after the effacement of subconcentric ribs. They are commonly irregularly dichotomous but sometimes convergent. The thickness of test does not exceed 10 mm. The outermost layer is thin and prismatic, and the outer and inner layers are crossed-lamellar and solid.

The associated shell of *Inoceramus* is evidently a part of an articulated individual. The shell of *G. giganteus* adheres closely to the surface of its left valve. The shell margin of *G. giganteus*, though its right side is incomplete, fits perfectly the undulating surface of *Inoceramus* without any perceptible gap (text-fig. 1). The opposite valve of *Inoceramus* has been almost entirely exfoliated and lost, but the divergent ribs impressed on the internal surface are unmistakably characteristic of *I.* (*S.*) *schmidti*. The radial ribs of *G. giganteus* are evidently denser than the divergent ribs of *I.* (*S.*) *schmidti*; the former does not necessarily correspond with the latter. Judging from the orientation of the divergent ribs as well as the nearly closed valves of *I.* (*S.*) *schmidti* below the anterior margin of *G. giganteus*, this gastropod appears to have sat on the antero-ventral area of the living shell of *I.* (*S.*) *schmidti* with the apex located on the antero-ventral side. The axis of symmetry of *G. giganteus* forms an angle of about 30° with the line of maximum length of *I.* (*S.*) *schmidti*. The prismatic layer of *Inoceramus*, which represents the outer layer of the shell, is about 7·0 mm and 3·0 mm thick below the anterior and posterior margins of *G. giganteus*, respectively. The original size of this inoceramid shell would exceed 500 mm, provided that the thickness of this layer increases isometrically to the attained shell length. If the allometric growth indices calculated by Tanabe (1973, p. 177) on some specimens of *I.* (*S.*) *schmidti* from Hokkaido are applied, the restored shell of this individual may exceed 700 mm in maximum length.

UMUT MM5711 (= Cr.1217) (text-fig. 2) is interesting because its right-anterior margin is nearly complete. It belongs to an old collection from the Cape Khoi Beds at Cape Jonquière near Alexandrovsk, north Saghalien.



TEXT-FIG. 2. *Gigantocapulus giganteus* (Schmidt). Specimen II (UMUT MM5711) attached to a crushed shell of *Inoceramus* (*Sphenoceramus*) *schmidti* Michael. Loc. Cape Jonquière near Alexandrovsk, north Saghalien. *a*, upper view, ×0·36; *b*, bird's-eye anterior view of the anterior part of the specimen showing a tongue-like projection and nearly complete right-anterior margin of shell, ×0·55; *c*, anterior view of the same specimen, ×0·55.

This individual is also closely associated with an enormous articulated shell of *I.* (*S.*) *schmidti*, which, however, is so strongly crushed that the original state of attachment is difficult to restore.

This specimen is about 250 mm long and 190 mm wide, and the shell of post-apical part has been considerably exfoliated and lost. The matrix was successfully removed from the pre-apical part of shell, and both the external and internal characters are well exhibited. The marginal area of the pre-apical part is remarkably depressed and gently folded like a brim (text-fig. 2*c*). Furthermore, there is a curious tongue-like projection at the anterior extremity, which is unusually thickened with a rounded edge. The internal surface is nearly smooth, and neither a septum nor a muscle scar is observed below the apical area. Radial costae are not impressed on the internal surface even near the margin.

The following specimens of *G. giganteus* are also intimately associated with some crushed shells of *I.* (*S.*) *schmidti*: UMUT MM5710 (= Cr.1418) and UMUT MM5709 (= Cr.998): old collection from the Zone of *I. schmidti* in Naibuchi area, south Saghalien (exact locality unknown). UMUT MM5713 (= Cr.1228): old collection from the same locality as UMUT MM5711. UMUT MM5712 (= Cr.1218): old collection from the Zone of *I. schmidti* in Alexandrovsk area, north Saghalien (exact locality unknown). These specimens show a wide range of morphological variation. One of the illustrated paralectotypes of *Helcion giganteus* from the type locality (Schmidt 1873, pl. 3, fig. 2) may be another example of an attached specimen, because a fragmentary prismatic shell was indicated below it.

VARIABILITY OF SOME MORPHOLOGICAL CHARACTERS

When *H. giganteus* was originally described by Schmidt (1873), four varieties were distinguished by the different position of the apex. All the original specimens are included either in var. α *depressa*, var. β *nasuta*, var. γ *retracta* or var. δ *centralis*. Kanie (1975, p. 23) designated a specimen of var. *depressa* as the 'holotype' of *H. giganteus*, but (Hayami and Kase 1977, p. 56) this procedure can be regarded as constituting valid lectotype designation. Dundo and Efremova (1974) regarded some of these varieties as distinct species, and referred *centralis* and *nasutus* to *Patella* and *Helcion*, respectively. However (Kanie 1975; Hayami and Kase 1977), none of these varieties (except for two small specimens of var. *depressa* (Schmidt 1873, pl. 3, figs. 8, 9) seems to constitute a distinct taxon, because the difference of apical position as well as other characteristics appears to be gradational within a single fossil population. The growth-lines of the present specimens show that the variability of apical position is partly due to ontogenetic transformation: the apex evidently shifts from the central part to the anterior portion of shell with growth. There is also a change of the direction of apex in the young stage. As shown in UMUT MM 5709 and some other small specimens, the very apex, if preserved, seems to point in the direction opposite to the expansion of shell. Although the apex is generally located posteriorly in many living species of *Capulus* and related genera, this ontogenetic change is one of the main reasons why we suspect here, unlike a previous interpretation (Kanie 1975), that the shorter end is actually anterior.

The shell form and surface ornamentation are also quite variable. Among the forty specimens we have observed at various institutions in Japan, the angle of ultimate apex in lateral view varies from 120° to 145°. The number of radial costae ranges from thirty-five to sixty-five. The thickened tongue-like projection at the anterior end of shell is also observable in some other specimens, e.g. one of the paralectotypes (Schmidt 1873, pl. 3, fig. 10) and IGPS no. 50910 (Kanie 1975, pl. 15, fig. 1*a*, *b*; Kanie 1977, pl. 2, fig. 4). It may be a widespread character in this species, but, as shown by the growth-lines on UMUT MM5535, 5711, its development is seen only in the later ontogenetic stage.

The range of morphological variation of *G. giganteus* is thus unusually wide. Such a great variability is unknown in any living species of the Patellacea, but comparable with that of some species of the Capulidae. The variable shell form and ornamentation of this species were probably influenced by the nature of the surface of the host.

INTERPRETATION OF MODE OF LIFE

From our observation on *in situ* specimens, it is likely that at least some individuals of *G. giganteus* grew on living shells of *Inoceramus* (*Sphenoceramus*) *schmidti*. This is supported by the fact that the associated inoceramid shells are, even if crushed, commonly articulated. Moreover, the stratigraphic and geographic distribution of the two species is identical, which suggests not only their intimate ecological relation but also that the evolutionary history of the former depended on the latter.

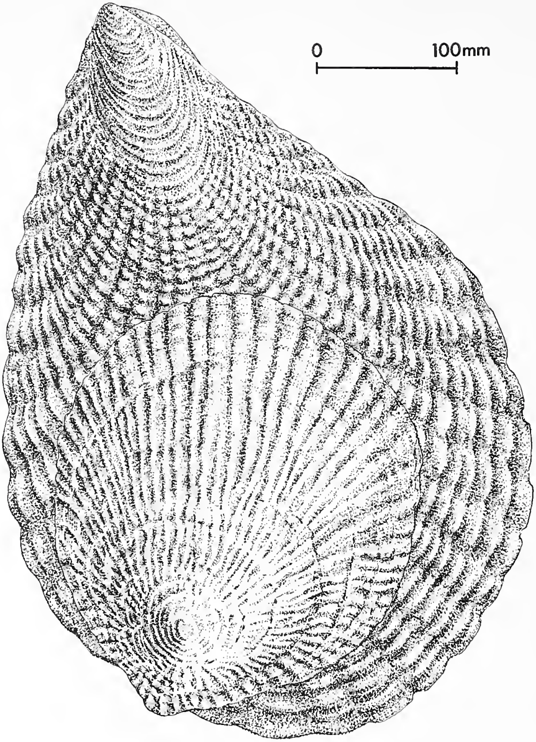
A large number of malacologists and marine ecologists have paid attention to the parasitic or semi-parasitic life of *Capulus* species and their hosts (Orton 1912, 1949; Yonge 1938; Otuka 1939; Teramachi 1942; Kuroda 1951; Sharman 1956; Burch and Burch 1961; Orr 1962; Thorson 1965; Kosuge and Hayashi 1967; Habe 1967). The hosts are commonly epifaunal bivalves, especially large species of the Pectinacea, though in a few cases the epibionts rest also on the surface of certain gastropods, brachiopods, and annelids. Sometimes an almost exclusive relation exists between the epibiont and host species (e.g. *C.tosaensis* on *Propeamussium sibogae* in Japan), but in other cases an epibiont species can grow on various hosts (e.g. *C. dilatatus* on *Amusium japonicum*, *Pecten albicans*, *Decatopecten striatus*, *Chlamys nobilis*, etc. in Japan; *C. ungaricus* on *P. maximus*, *Aequipecten opercularis*, *Modiolus modiolus*, *Monia patelliformis*, *Turritella communis*, etc. in Great Britain and North Sea). According to Yonge (1938) and others, *C. ungaricus* is a ciliary feeder. It intercepts the food, which has been collected on the gills of a bivalve, by inserting its long proboscis inside the bivalve shells. The ecological relation was regarded as semi-parasitic by Sharman (1956) and as commensalistic by Thorson (1965). Although the epibiont does not seem to cause the bivalves any mortal harm, this state is most certainly disadvantageous to the host. We consider that this is a case of external parasitism, but the term 'semi-parasitic' may be more appropriate for this species, because it also attaches to dead shells and rocks.

The life habits of such parasitic individuals of *Capulus* can be classified into two types. One is represented by *C. dilatatus*, in which (Kosuge and Hayashi 1967) the epibiont bores a small hole through the pectinid shell (commonly up-facing valve) in order to insert its proboscis. The boring position is concentrated on the anterior half of the disc (corresponding to the position of gills) and sometimes on the anterior wing. The orientation of attachment seems to be almost random. The other type is exemplified by *C. ungaricus*, which rests preferentially on the anterior and ventral marginal part of down-facing valves of living pectinids. Sharman (1956) examined the attaching position and orientation of many individuals of this species on the shells of *A. opercularis* from off the coast of the Isle of Man, noting: 'in its characteristic position the gastropod sits at the edge of the valve with the front margin of the shell projecting a little over it and the apex pointing inwards.' *C. ungaricus* never makes a borehole, but the edge of the valve margin is said to be frequently chipped so that this gastropod can easily insert its proboscis into the pectinid valves. Somewhat similar feeding habits are known in *C. tosaensis* from the Japanese deep waters, although this species is said to attach preferentially to the left (? up-facing) valve of *Propeamussium sibogae*.

On the shell surface of the many specimens of *I.* (*S.*) *schmidti* neither a borehole nor a scar of attachment has been recognized, and it may be difficult to know whether the valve margin was actually chipped or not by other organisms. However, the attaching position and orientation in the specimens on text-fig. 1 seem to indicate that the life habit of *G. giganteus* was analogous to the second type, especially to the case of *C. ungaricus* as illustrated by Sharman (1956, figs. 1–3). We interpret the function of the curious tongue-like anterior projection as protecting the head of the gastropod which presumably protruded a little beyond the edge of the valve margin, because otherwise the remarkable, declined margin of this projection could not adhere closely to the surface of inoceramid shell. Such a hanging front margin of the shell is also commonly seen in *C. ungaricus*. Text-fig. 3 shows a putative living position of *G. giganteus* on the left valve of *I.* (*S.*) *schmidti*, although it is still unknown whether the valve is actually up-facing or down-facing.

SUMMARY

The observation of *in situ* specimens and the functional interpretation of the shell shows that *G. giganteus* was a parasitic gastropod to *I.* (*S.*) *schmidti*. Considering the much smaller size of other associated molluscs, only this inoceramid seems to have offered the solid ground of attachment for such a large patelliform gastropod. Although complete specimens of *I.* (*S.*) *schmidti* can seldom be



TEXT-FIG. 3. Reconstruction of the living position of *Gigantocapulus giganteus* (Schmidt) on *Inoceramus* (*Sphenoceramus*) *schmidti* Michael. Their periostracum is not drawn, because nothing is known about its development. This is not a sketch but chiefly based on Specimens I and II.

obtained, we have actually observed several extraordinarily large specimens of this species (exceeding 700 mm in maximum length) in the collections from Saghalien and Hokkaido. The gigantism of this gastropod is evidently related to the unusually large size of the host. If such a parasitic relation was developed, it can be readily imagined that an ecologically specialized epibiont was compelled to become extinct by the decline of the host species. *G. giganteus* seems to have shared its evolutionary lot with *I.* (*S.*) *schmidti*, because their stratigraphic and geographic distribution is identical.

The history of this external parasitism possibly goes back to earlier times. As interpreted previously (Kanie 1975), *G. giganteus* may have been derived from *C. cassidarius* Yokoyama through some intermediate form. *C. cassidarius* is common in the Turonian to Santonian strata of the same region and is frequently accompanied by *I.* (*S.*) *naumanni* Yokoyama, which seems to be ancestral to *I.* (*S.*)

schmidti, and some other small-sized species of *Inoceramus*. Therefore, it is possible that the parasitism was already established between the ancestors, although *in situ* preservation has not been found. The inferred mode of life also explains shell orientation, the wide range of morphological variation, and the curious tongue-like anterior projection in *G. giganteus*. Its taxonomic reference to the Capulidae of Mesogastropoda is also consistent with the parasitic mode of life. There is still a shortage of *in situ* material showing life orientations, which will provide more evidence of the paleoecological relation between this peculiar limpet and other organisms.

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TWO NEW JURASSIC BRYOZOA FROM SOUTHERN ENGLAND

by PAUL D. TAYLOR

ABSTRACT. *Reptomultisparsa tumida* sp. nov. and *Reptoclausa porcata* sp. nov. are described respectively from the Bathonian Bradford Clay of Bradford-on-Avon and the Aalenian/Bajocian Inferior Oolite of the Cotswold Hills. The genus *Reptoclausa* was previously known only from the Cretaceous. *Reptoclausa* colonies have autozooecia located on longitudinal ridges which are separated by furrows composed of kenozooecia. This unusual arrangement of zooecia can be explained by the action of physiological growth gradients during colony life.

DURING a revision of some Jurassic Bryozoa from England and Normandy (Taylor 1977) two new species were recognized and are described for the first time in this paper. Both species are encrusting forms belonging to the Order Cyclostomata, the most abundant group of bryozoans during a period of relatively low species diversity. A tentative estimate of known Jurassic bryozoan diversity based on available data suggests the existence of about ninety species belonging to approximately thirty genera, although these figures are undoubtedly an underestimate of total worldwide diversity for three main reasons. First, almost all known Jurassic bryozoans have been described from either England, France, or Germany; they are extremely poorly known from other parts of the world (see Taylor 1977, pp. 336–338). Secondly, high levels of phenotypic variation within species of simple morphology has hindered taxonomic discrimination and quite probably has led to undersplitting. Genetic studies (e.g. Thorpe *et al.* 1978) of living bryozoans are beginning to reveal the presence of 'cryptic' species that are difficult to distinguish morphologically. Thirdly, non-calcified ctenostome bryozoans with a low fossilization potential were perhaps much more common during the Jurassic than is immediately obvious (Voigt 1977; Pohowsky 1978; Taylor 1978). Despite their low apparent diversity Jurassic bryozoans are ubiquitous in marine sediments, which accumulated in aerobic environments containing firm substrates (e.g. brachiopod shells) suitable for colony attachment. Some species developed erect growth from an attached base but the commonest species were totally encrusting, as are the two new species described here.

Type and figured specimens are housed in the British Museum (Natural History) (BMNH).

FAMILIAL CLASSIFICATION OF JURASSIC TUBULOPORINID BRYOZOA

The order Cyclostomata was represented in the Jurassic by two suborders, the Tubuloporina and the Cerioporina. Six major Jurassic families of the Tubuloporina may be distinguished: Stomatoporidae, Oncousoeciidae, Macroeciidae (= Multisparidae), Plagioeciidae, Theonoidae, and Frondiporidae. The stomatoporids are typically encrusting uniserial or narrow multiserial ('ribbon-shaped') genera, apparently lacking the larval brooding polymorphs known as gonozooids which characterize the other tubuloporinid families. Oncousoecids have branching adnate colonies and gonozooids with minute ooeciopores. Macroecid and plagioecid genera developed a variety of convergent colony forms, both erect (e.g. '*Entalophora*', '*Pustulopora*') and encrusting (e.g. '*Berenicea*'), but the two families may be distinguished from one another by the structure of their gonozooids. Macroecid gonozooids are longitudinally elongate and possess comparatively large ooeciopores (the orifice through which the larvae were released). Plagioecid gonozooids are broad, bulbous and possess

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ooeciopores which are considerably smaller than the apertures of autozooids in the same colony. In both the theonoids and the frondiporids, groups of contiguous autozooidal apertures form fascicles elevated above the general level of the colony surface. Frondiporid zooids are typically longer than those of theonoids and, whereas zooidal budding occurred within the lengthening frondiporid fascicles, within-fascicle zooidal budding is not known in the theonoids.

SYSTEMATIC PALAEONTOLOGY

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order CYCLOSTOMATA Busk, 1852
Suborder TUBULOPORINA Milne-Edwards, 1838
Family MACROECIIDAE Canu, 1918
Genus REPTOMULTISPARSA d'Orbigny, 1853

(see Walter 1969, p. 75, for a revised generic diagnosis)

Reptomultisparsa tumida sp. nov.

Plate 88, fig. 1; text-fig. 1

Derivation of name. The trivial name *tumida* refers to the broad, swollen appearance of the gonozooecia.

Holotype. BMNH D13346 Bathonian, Bradford Clay (*discus* Zone), Bradford-on-Avon, Wiltshire.

Paratypes. BMNH D52651a–c, Bathonian, Bradford Clay, locality unknown. Other specimens in the authors collection are from the Bathonian White Limestone Formation of Foss Cross, Gloucestershire.

Diagnosis. *Reptomultisparsa* with delicate unilamellar zoaria; autozooecia with maximum width midway along their frontal walls and possessing small apertures; gonozooecia broad and inflated.

Description. Zoaria (Pl. 88, fig. 1) are unilamellar, fan-shaped, or discoidal (bereniciform). Zooecia arise at divisions of existing interzooecial walls on a basal lamina.

Autozooecia have moderately long frontal walls characteristically attaining maximum width midway along their length. Interzooecial walls form conspicuous traces on the relatively flat zoarial surface. The small, circular autozooecial apertures are widely spaced and have raised rims but lack distinct peristomes.

Kenozooecia may occur around gonozooecial borders. Their proximal portions are identical to those of autozooecia but the kenozooecia are truncated distally by gonozooecial dilation and consequently lack an aperture.

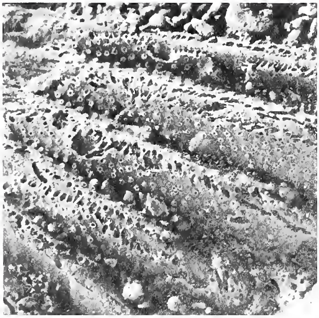
Gonozooecia (text-fig. 1) have narrow proximal portions and well-defined inflated distal portions with a circular to oval shape. The sub-terminal ooeciopores lack ooeciostomes and are transversely elongate and slightly smaller than autozooecial apertures.

EXPLANATION OF PLATE 88

Fig. 1. *Reptomultisparsa tumida* sp. nov. BMNH D13346, Holotype colony, Bathonian, Bradford Clay, Bradford-on-Avon, × 7.

Figs. 2–6. *Reptoclausa porcata* sp. nov. 2, BMNH B4855, immature colony prior to ridge development, Bajocian, Lower Ragstone, Cold Comfort, × 7. 3–5, BMNH D8724, Holotype, Aalenian, Pea Grit, Birdlip. 3, intracolony overgrowth by a new layer of zooecia, × 11. 4, furrow occupied by kenozooecia (centre right), × 13. 5, autozooecia with rounded distal terminations, × 30. 6, BMNH D10091, zoarium showing conspicuous furrows and ridges with a ridge dichotomy, Aalenian, Pea Grit, Crickley Hill, × 8.

Figs. 1 and 2 are of ammonium chloride coated specimens.



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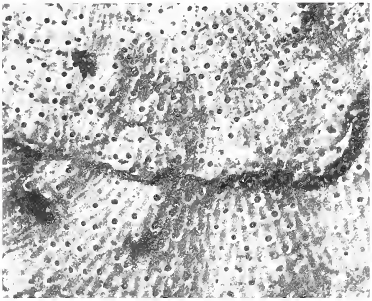

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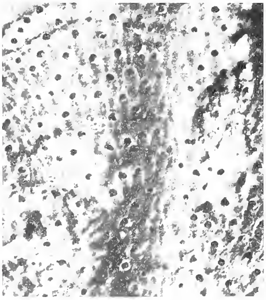

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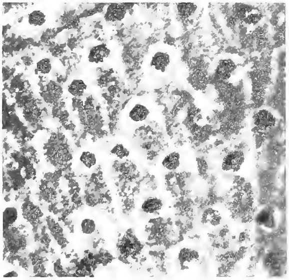

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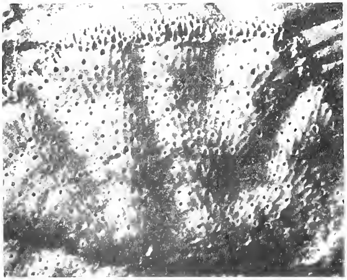

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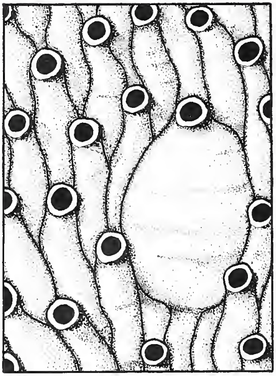
TAYLOR, Jurassic Bryozoa



TEXT-FIG. 1. *Reptomultisparsa tumida* sp. nov. BMNH D13346 (holotype), Upper Bathonian, Bradford Clay, Bradford-on-Avon, Wiltshire. A group of autozooecia and a bulbous gonozooecium. × 38.

Dimensions. See Table 1.

Remarks. The relatively broad and inflated gonozooecia of *Reptomultisparsa tumida* distinguish it from other species in the genus, and the subterminal position of the ooeciostome contrasts with the terminal ooeciostomes developed in plagioecids with similar bereniciform colonies.

Stratigraphical range. Upper Bathonian.

TABLE 1. Dimensions (in mm) of *Reptomultisparsa tumida* zooecia. Abbreviations of morphological characters: law, longitudinal autozooecial aperture width; taw, transverse autozooecial aperture width; fwl, autozooecial frontal wall length; fww, autozooecial frontal wall width (maximum); tgl, total gonozooecial frontal wall length; igl, length of inflated portion of the gonozooecial frontal wall; gw, gonozooecial frontal wall width (maximum); low, longitudinal ooeciopore width; tow, transverse ooeciopore width. Abbreviations of statistical functions: Nc, number of colonies from which measurements were taken; Nz, number of zooecia measured; x̄, mean value; Rc, range of colony means; Rz, total range of values.

	Nc	Nz	x̄	Rc	Rz
law	3	55	0·08	0·08	0·06–0·10
taw	3	55	0·08	0·08	0·06–0·09
fwl	3	55	0·67	0·63–0·69	0·46–0·88
fww	3	55	0·18	0·17–0·19	0·14–0·21
tgl	3	3	1·44	1·20–1·82	1·20–1·82
igl	3	6	1·11	0·92–1·34	0·86–1·34
gw	3	6	0·62	0·53–0·67	0·51–0·80
low	3	5	0·06	0·06	0·05–0·07
tow	3	5	0·07	0·06–0·08	0·06–0·10

Genus REPTOCLAUSA d'Orbigny, 1853

Reptoclausa porcata sp. nov.

Plate 88, figs. 2–6; text-fig. 2

?1894 *Berenicea allaudi* (Sauvage); Gregory, p. 60.
1896*a* *Berenicea Allaudi* (Sauvage); Gregory, p. 44 (*partim*.).
1896*b* *Berenicea allaudi* (Sauvage); Gregory, p. 77 (*partim*.), pl. 3, fig. 6.
1969 *Idmonea triquetra* Lamouroux; Walter, p. 52 (*partim*.), pl. 3, figs. 11–13 only.

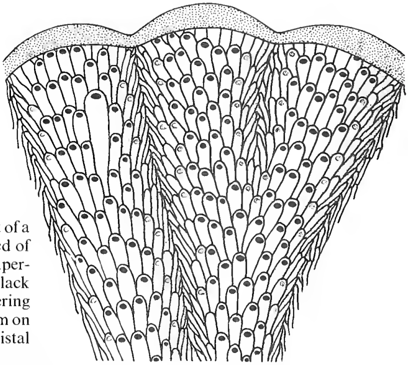
Derivation of name. The trivial name *porcata* refers to the ridged and furrowed form of the zoarium.

Holotype. BMNH D8724, Aalenian, Pea Grit (*murchisonae* Zone), Birdlip, Gloucestershire.

Paratypes. BMNH D7526a–b, Aalenian, Pea Grit (*murchisonae* Zone), near Stroud, Gloucestershire. BMNH D31586, Aalenian, Lower Limestone (*murchisonae* Zone), Crickley Hill, Gloucestershire. BMNH B2290a–c, Inferior Oolite, Crickley Hill, Gloucestershire. BMNH B4855, Lower Ragstone (*discites* Zone), Cold Comfort, Gloucestershire. BMNH D1795, Inferior Oolite, ?locality. BMNH D10091, Pea Grit (*murchisonae* Zone), Crickley Hill, Gloucestershire. BMNH D30002a–c, Lower Limestone (*murchisonae* Zone), Kimsbury, Painswick, Gloucestershire.

Diagnosis. *Reptoclausa* with continuous autozooecial ridges separated by furrows of kenozooecia; zoaria commonly unilamellar, occasionally multilamellar.

Description. Zoaria are adnate, fan-shaped (Pl. 88, fig. 2) to discoidal, commonly unilamellar but occasionally multilamellar (Pl. 88, fig. 3). Zooecia arise where existing interzooecial walls divide on a basal lamina at the colony growth margin. Rounded ridges of low profile cross the zoarial surface parallel to the direction of growth and form lobate projections where they meet the colony growth margin (Pl. 88, fig. 6). Ridge crests are about 2 mm apart and new ridges appear at dichotomies of established ridges. Ridges are occupied by autozooecia orientated with their long axes slightly divergent from the ridge crest. Zooecium size, particularly width, decreases progressively away from ridges towards intervening furrows occupied by kenozooecia (text-fig. 2). Multilamellar growth was achieved either by spiral overgrowth around irregularly distributed pivot points (Taylor 1976), or by a process, comparable with the frontal budding known in cheilostomes (Banta 1972), in which an overgrowing zooecium arose from an autozooecial aperture to initiate a fan-shaped expansion on the zoarial surface. The first zooecium of each new frontally budded layer has a short frontal wall and a longitudinally elongate aperture.



TEXT-FIG. 2. Semidiagrammatic representation of part of a *Reptoclausa porcata* colony showing ridges composed of autozooecia and furrows of kenozooecia lacking apertures. Open autozooecial apertures are shown in black and the occluded apertures of autozooecia bordering kenozooecial furrows are stippled. The large zooecium on the left-hand ridge is a gonozooecium. The lobate distal growth margin is evenly stippled. Approx. × 18.

Frontal walls of autozooecia are thick, have rounded distal terminations (Pl. 88, fig. 5), and are clearly defined by traces of vertical interzooecial walls on the zoarial surface. Autozooecial apertures are slightly transversely elongate. Thin-walled peristomes are preserved only when immured by intracolony overgrowths. Terminal diaphragms, level with the frontal walls, frequently occlude zooecia, particularly those situated at boundaries between ridges and furrows (text-fig. 2). Ontogenetic zonation (Silén and Harmelin 1974) of autozooecia is not apparent.

Kenozooecia, occurring regularly in furrows between autozooecial ridges (Pl. 88, fig. 4), have narrow frontal walls defined by the faint traces on the zoarial surface of their vertical interzooecial walls. Less elongate kenozooecia may occur at growth margin anastomoses and in the vicinity of zoarial lateral walls.

Gonozooecia are developed in about 50% of the zoaria examined. They are elongate, slightly dilated in width and inflated, and are situated on zoarial ridges. The transversely elongate ooeciopores are about the same size as autozooecial apertures.

Dimensions. See Table 2.

TABLE 2. Dimensions (in mm) of *Reptoclausa porcata* zooecia. Abbreviations as in Table 1.

	Nc	Nz	$\bar{x}$	Rc	Rz
law	5	125	0·10	0·09–0·10	0·07–0·11
taw	5	125	0·10	0·09–0·11	0·08–0·13
fwl	5	125	0·61	0·52–0·66	0·40–0·80
fww	5	125	0·22	0·22–0·23	0·18–0·29
tgl	4	34	1·70	1·62–1·77	1·17–2·25
gw	4	36	0·43	0·37–0·46	0·35–0·59
low	3	19	0·09	0·08–0·09	0·07–0·13
tow	3	19	0·12	0·11–0·14	0·10–0·15

Remarks. Among the specimens included by Gregory (1869*b*) in *Berenicea allaudi* (Sauvage) are two (BMNH D1794, D1795) belonging to this new species. *Rosacilla allaudi* of Sauvage (1888) is a simple, multiserial tubuloporinidean lacking ridged zoaria and quite distinct from the species figured as *Berenicea allaudi* by Gregory (1896*b*, pl. 3, fig. 6). Walter (1969, p. 52) includes specimens of *Reptoclausa porcata* within *Idmonea triquetra* Lamouroux 1821. *Reptoclausa porcata*, however, differs from *Idmonea triquetra* in the following features:

1, *R. porcata* zoaria have a fan-shaped to discoidal form whereas zoaria of *I. triquetra* consist of dichotomising narrow multiserial branches. 2, The branches of *I. triquetra* have a well-defined triangular cross-section distinct from the rounded ridges of *R. porcata*. 3, Ooeciopores of *I. triquetra* are about half the diameter of *R. porcata* ooeciopores. 4, *I. triquetra* zooecia are usually arranged in distinct rows. Those of *R. porcata* are not usually arranged in rows and have larger frontal wall dimensions.

Furthermore, *R. porcata* is known only from the Upper Aalenian and Lower Bajocian, whereas the probable range of *I. triquetra* is Upper Bajocian to Lower Callovian (Walter 1969).

Hillmer (1971, p. 42) noted the similarity between Lower Cretaceous *Reptoclausa* and two of Walter's (1969) figured *Idmonea triquetra* specimens (BMNH D10091, D31586) which are here included in *R. porcata*. *R. porcata* differs from the Lower Cretaceous type-species of *Reptoclausa*, *R. neocomiensis* d'Orbigny (redescribed by Hillmer 1971), which has autozooecial ridges discontinuous in the direction of colony growth and kenozooecia occupying a larger proportion of the zoarial surface. The known range of the genus *Reptoclausa* is extended back from the Lower Cretaceous into the Middle Jurassic by the description of *R. porcata*.

R. porcata is abundant in the Lower Inferior Oolite of the Cotswolds where, along with *Reptomultisparsa cricopora* and *R. ventricosa*, it is found encrusting a variety of substrates including the large terebratulid brachiopod *Pseudoglossothyris simplex* and limestone intraclasts. Some of the brachiopod-encrusting colonies may represent associations with a living brachiopod because bryozoan growth is frequently found to terminate at a growth line on the brachiopod shell suggesting that growth of both bryozoan and brachiopod were checked simultaneously but, whereas brachiopod growth later recommenced, bryozoan growth did not (Ager 1961).

Stratigraphical range. Upper Aalenian–Lower Bajocian.

Discussion. The morphology of *Reptoclausa porcata* contrasts with that of most other multiserial encrusting tubuloporinideans (e.g. *Reptomultisparsa tumida*) and deserves further consideration. In colonies of *Reptoclausa porcata* zooecium size, particularly frontal wall width, decreases progressively passing from the crests of the ridges to the bottoms of the furrows (text-fig. 2). Ridge crests bear broad autozooecia, furrows are composed of narrow kenozooecia, and the intervening regions between ridge crests and furrows possess comparatively narrow autozooecia typically occluded by terminal diaphragms. This type of morphological gradient perpendicular to the growth direction of the colony suggests the presence during life of a physiological gradient (Bronstein 1939; Anstey *et al.* 1976), perhaps hormonal, which determined zooid structure according to position of budding. Comparatively large zooids were budded at regularly spaced loci along the growing edge of the colony. Here, the zoarium was differentially thickened to give a ridge which formed a lobate projection where it intersected the colony growing edge. These large zooids displayed a dominance over zooids budded between loci causing them to be crowded and reduced in size. The smallest zooids budded between loci were too small to support a functional polypide (gut and tentacles) and thus became kenozooids. It seems that zooids of intermediate size could support only a short-lived polypide whose degeneration was followed by early occlusion of the zooecial aperture by a terminal diaphragm. The functional significance of the unusual arrangement of autozooecia and kenozooecia in *Reptoclausa* is unclear but may relate to the maintenance of efficient colony feeding, with autozooid exhalent currents departing from the colony surface above regions of non-feeding kenozooids (see Taylor 1979).

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ANOMALOUS OCCURRENCES OF THE LOWER PALAEOZOIC BRACHIOPOD *SCHIZOCRANIA*

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ABSTRACT. There are rare occurrences of Ordovician and Silurian species of the inarticulate brachiopod *Schizocrania* attached to orthoconic cephalopod shells. These were probably transported considerable distances prior to their deposition in onshore sediments, in which *Schizocrania* is not normally found. Relationships between host and encruster are discussed with a view to elucidating both encrustation sequences and inferred ecological associations.

DURING the course of studies of Upper Llanvirn, Ordovician (MGL) and Whitcliffian, Silurian (DDJA) successions in the Anglo-Welsh region, we noted rare occurrences of orthocones with *Schizocrania* (Trematidae) attached to either the inner or outer walls of their body chambers; in both cases the associated clastic sediments are of a coarse arenaceous type associated with demonstrably shallow-water facies (Williams 1953; Antia 1979). Havlíček (1972, p. 230) reported that the Upper Ordovician trematid *Ptychopeltis incola* Perner from Bohemia '. . . lived attached only to the cylindrical shells of orthocone nautiloids'; he also noted that its ancestor *P. hornyi* Havlíček sometimes encrusted orthocones. We therefore consider that these examples of apparent host-specific relationships may be paralleled elsewhere amongst the Trematidae (e.g. *Schizocrania*) by similar associations between host and encruster.

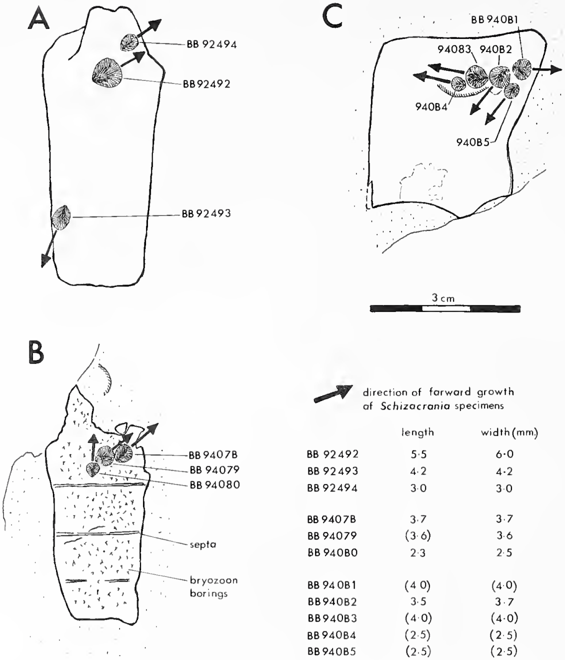
MATERIAL

The Upper Llanvirn specimen is an incomplete, poorly preserved internal mould of a body chamber of an orthoconic nautiloid of unknown taxonomic affinity. It was recovered from a shell-bed in the upper part of the Flags and Grits Formation of the Ffairfach Group exposed at Coed Duon, 3 km south of Llangadog, Dyfed (Grid Ref. SN 709256), where it lay parallel to bedding. The orthocone has three specimens of *Schizocrania* cf. *salopiensis* Williams attached to the inner surface of the body chamber; the brachial valves all face inwards (text-fig. 1A) but show no obvious preference for any particular attachment site although two of the specimens are aligned subparallel to each other near the anterior end.

The Whitcliffian specimens are represented by poorly preserved fragmentary moulds of *Orthoceras* sp. (diameters *c.* 20 mm and > 30 mm respectively) from the Lower Whitcliffe Beds of Mortimer Forest, south of Ludlow (Grid Ref. SO 497725) and the Upper Whitcliffe Beds near Broadstone Farm (SO 544900). The older specimen, an internal mould of a large portion of the conch (text-figs. 1B, 2B) has three specimens of *S. striata* (Sowerby) attached to the anterior part of its external surface. The specimens all occur close to each other on the exposed section of the orthocone mould which faces downwards from the undersurface of a bedded unit; relative to the final entombment position of the orthocone the *Schizocrania* specimens occur on its 'underside' and following the dissolution of the cephalopod shell have become impressed on to the preserved mould. The younger (upper Whitcliffian) specimen consists of the internal and external moulds of a curved fragment of a large body chamber; it has five poorly preserved specimens of *S. striata* attached to its inner (concave) surface which faces downwards. The specimens are aligned transversely, parallel to the peristome (text-figs. 1, 2C).

The lectotype (Geol. Surv. Mus. No. 6631) of *S. striata* (Sowerby) from the Leintwardinian–Whitcliffian beds of Delbury, Salop (Grid Ref. SO 501854) is the only other known British *Schizocrania* which we have discovered attached to an orthoconic nautiloid fragment; the specimen is attached to the convex surface of the free part of a septum, probably the last one; it differs from the other examples in its larger size (length 9 mm) and posterior attachment site (text-fig. 2A).

[Palaeontology, Vol. 23, Part 3, 1980, pp. 707–713.]



	length	width (mm)
BB 92492	5·5	6·0
BB 92493	4·2	4·2
BB 92494	3·0	3·0
BB 9407B	3·7	3·7
BB 94079	(3·6)	3·6
BB 940B0	2·3	2·5
BB 940B1	(4·0)	(4·0)
BB940B2	3·5	3·7
BB940B3	(4·0)	(4·0)
BB940B4	(2·5)	(2·5)
BB940B5	(2·5)	(2·5)

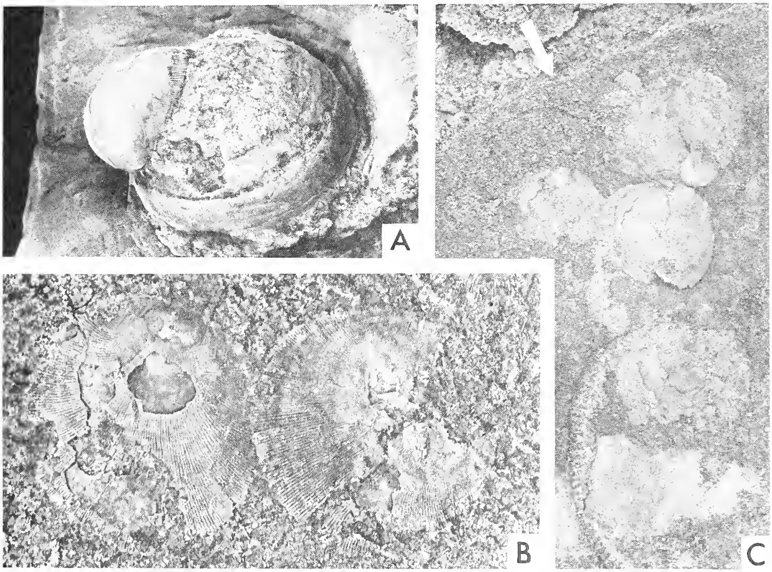
TEXT-FIG. 1. Scale drawings of *Schizocrania* encrusted orthoconic nautiloids from Upper Llanvirn strata exposed near Llangadog, Mid Wales (A) and from lower (B) and upper (C) Whitcliffe strata exposed near Ludlow, Salop. All *Schizocrania* specimens have British Museum numbers, specimens BB94078–94080 are attached to the outer surface of the shell mould (B) whilst the remaining specimens are attached to the inner surfaces of the shell moulds. Approximate length, width measurements, listed bottom right.

OBSERVATIONS AND INTERPRETATION

All twelve of these *Schizocrania* specimens exhibit only their convex brachial valves facing away from the cephalopod shell surface. *Schizocrania* is known to attach to substrates by its flat pedicle valve (Hall and Whitfield 1875; Rowell *in* Williams *et al.* 1965, p. H283). However, pedicle valves are exceptionally rare, being either altogether absent from assemblages or hidden from view beneath the brachial valve. The three orthocone specimens shown in text-fig. 1 indicate that the anterior edge of the phragmacone was the preferred encrustation site for all but two of the *Schizocrania* specimens. The orientation of these *Schizocrania* inside the phragmacone and on the shell exterior is apparently not random since all adjacent shells are aligned with their umbones pointing in approximately the same direction (i.e. transverse or oblique to the orthocones' long axis).

The orthocones may have been encrusted while they were alive and mobile, or when they were dead and floating, or dead and semi-buoyant, being washed around on the sea floor, or dead and settled on the sea floor, or, finally, when being reworked.

In addition to the numerous examples of fossil cephalopod (ammonoid) encrustation recorded from Mesozoic assemblages (e.g. Seilacher 1960; Meischner 1968) and the few broadly analogous Lower Palaeozoic examples involving orthoconic nautiloids (Holland 1971; Havlíček 1972), we have noted Ordovician and Silurian collections containing several varied and undescribed examples of orthocone encrustation (e.g. National Museum of Wales specimen NMW 79. 5G. Map loc. 771; Hunterian Museum specimens S.25129/1–3 and S.25114 a/b). *Schizocrania* is ornamented by numerous radial capillae (Williams 1974, p. 44). According to Williams and Wright 1963, p. 19 and Williams and Rowell (*in* Williams *et al.* 1965, p. H81) such radial ornament probably supported setal follicles at the commissure, and it is reasonable to assume that *Schizocrania* was particularly setiferous. Sudarson (1969, p. 65) noted that *Disciniscа* larvae have well-developed principle setae and that 'there may be a prolonged larval stage . . . with chaetae increasing in number to facilitate floatation'. Both the *Schizocrania* species discussed here exhibit high capillae densities at the same



TEXT-FIG. 2. A. *Schizocrania striata* lectotype showing attachment to mould of orthocone septum from upper Ludlow beds, Delbury, Shrops., × 3. B, Detail of *S. striata* specimens BB94078 (*left*) and BB94079 (*right*) from Lower Whitcliffe Beds, Mortimer Forest, Ludlow, × 12·5; see also text-fig. 1B. C, *S. striata* specimens BB94081 (*top*) to BB94085 showing attachment to orthocone body chamber fragment, the edge of which is arrowed, from Upper Whitcliffe Beds, Broadstone farm, Ludlow, × 6. Text-fig. 1C is a scale-drawing of the counterpart of this specimen.

growth stage (i.e. 10–12 per mm, 5 mm antero-medianly of the dorsal umbones) and probably therefore had a juvenile epiplanktic stage.

Holland (1971, p. 18) considered that strophomenid (aegeromenid) and rhynchonellid (*Microsphaeridorhynchus nucula*) brachiopods might have attached to living orthocone hosts but concluded that due to the size of the brachiopods this was 'unlikely'. Havlíček (1967, p. 21) demonstrated the attachment of epiplanktic strophomenids to the 'stems of algae' (Havlíček 1967, p. 21). He subsequently suggested (Havlíček 1972, p. 230) that aegeromenids attached to live orthocones and considered that inarticulates such as *Ptychopeltis incola* 'were attached to the shells of living nautiloids' (Havlíček 1972, p. 230) whilst related trematids attached both to orthocones and other specific 'freely moving organisms' (Havlíček 1972, p. 229). An orthocone encrusted with *Conchiolites* (Ordovician) was described by Prantl (1948, p. 6). Seilacher (1954, 1968) concluded (1968, p. 284) that the preferentially orientated epizoans on this specimen were adjusted to the 'head-on motion of their host'. Both Havlíček (1972, p. 230) and Seilacher (1968) suggested that *preferred* orientation of encrusters is of prime importance in testifying to pre-mortem attachment. This suggests that the majority of known *Schizocrania* specimens were attached at various stages in the orthocone's post-mortem history. Although Havlíček (1972, p. 229) presumed that aegeromenid brachiopods such as those depicted by Holland (1971, fig. 1*b*) attached to live orthocones, direct evidence for this is insubstantial. Although these authors, and Bergström (1968) have shown such brachiopods attached in rows along orthocones and 'algal stems' such arrangements do not constitute the type of preferred orientation referred to above.

Since modern spirorbids are known to be host specific and capable of seeking a preferred attachment site and orientation (Knight-Jones 1951), it is almost certain that the occurrence of fossil spirorbids aligned along the growth margins of orthocones (Holland 1971) indicates a comparable relationship. This may mean that the similar alignment of *Schizocrania* specimens noted here (text-fig. 1) could also be indicative of a host-specific relationship. Such a contention tends to be supported by our observation that the Anglo-Welsh *Schizocrania* have not been found attached to any other host organisms and would also offer a possible explanation for the virtual absence of pedicle valves, which could have either remained attached to a host when the brachial valve disarticulated, or become obscured during fossilization by the substrate to which they were attached.

The *Schizocrania* on the internal surface of the body chambers of the Llanvirn and upper Whitcliffian specimens indicate encrustation beginning no earlier than the post-mortem drifting phase (following decay of mantle lining the body chamber) but prior to the infilling of the body chamber. Interpretation of the lower Whitcliffian orthocones' pre-entombment history is problematical; it could have been encrusted at any one of a number of stages in its history as a live or dead mobile organism. However, since the *Schizocrania* are attached to its 'underside' they must have settled and had time to grow prior to its final entombment in this position. The *S. striata* lectotype must have become attached to the posterior side of its septal substrate after the separation of the orthocone's body chamber from the remaining posterior part of the shell (i.e. at a relatively late stage in the orthocones' post-mortem history).

On the lower Whitcliffian orthocone the internal mould (text-fig. 1*b*) is covered by numerous irregular markings consisting mainly of small elongated raised protruberances averaging about 0·1 mm in height and width and between 0·3 and 0·7 mm in length. These apparently represent the internal moulds of bryozoan borings on the inner surface of the orthocone shell although it is not altogether clear whether some of the flatter or even slightly indented markings may not result from the fossilization of external borings. In any event where the *Schizocrania* shells are slightly broken, and around their edges, it is evident that the borings affect the orthocone shell beneath. Unfortunately the absence of a counterpart of this specimen renders this evidence inconclusive.

Distribution of Schizocrania

The Llanvirn orthocone and *Schizocrania* discussed here are virtually the only representatives of these taxa known from the predominantly arenaceous and rudaceous Ffairfach Group of the Llandeilo area. Since *S. salopiensis* is common in penecontemporaneous, argillaceous successions elsewhere in South Wales and the Welsh Borderlands (Williams 1974; Bassett *et al.* 1974, p. 9; Lockley and Williams, in press) where there are different benthic and pelagic faunas (i.e. trilobites, graptolites, and cephalopods), it is reasonable to assume that the exotic Ffairfach occurrence may have been related to the drifting or migration of a stray cephalopod beyond the normal limits of its indigenous environment. Such post-mortem drifting of modern cephalopods is well known (House 1973; Kennedy and Cobban 1976; Hewitt and Pedlay 1978) and may result in individual specimens being transported for hundreds or even thousands of kilometres.

Similarly *S. striata* is rare in the Whitcliffe Beds of the Ludlow region where it constitutes only about 0·01 to 0·005% of the total fauna with specimens generally occurring in a fragmentary condition and random orientations. It is more common in unbioturbated, parallel-laminated, alternating light and dark siltstones (rhythmites) of deeper-water facies (e.g. Upper and Lower Leintwardinian Beds, Holland *et al.* 1963, p. 154; Lawson 1973, p. 274) and is recorded only rarely in shallow-water bioturbated siltstones (Facies B *sensu* Antia 1979). Again, the Whitcliffian cephalopods drifted into inshore deposits from an offshore source, although limited evidence also points to later phases of encrustation (e.g. lectotype). Williams (1969, p. 143) discussed the potential range of larval dispersal and its bearing on brachiopod migration during the Ordovician. Clearly his suggested figure (up to 250 km) is only a fraction of the range potential for brachiopods capable of encrusting live or drifting orthocones.

Trematid hosts

Encrusting Trematidae such as *Schizocrania*, *Drabodiscina*, and *Ptychopeltis* appear to have been host specific. *S. salopiensis*, *S. striata*, and *P. incola* have hitherto only been observed attached to orthoconic nautiloids generally presumed to have been alive or floating at the time of their encrustation. Other members of the family, e.g. *P. hornyi* Havlíček and *D. grandis* Barrande, are commonly attached to conularids which are considered by Havlíček (1972) to have been mobile during life, and the American species *S. filosa* Hall frequently attached to the brachiopod *Rafinesquina* (e.g. Cooper 1956 and Rowell *in* Williams *et al.* 1965). With respect to trematid-nautiloid associations, it is intriguing to note that Titus and Cameron (1976) record *S. filosa* only in their deep-water *Geisonoceras* (Orthocerida) community. Dr. R. A. Hewitt and Mrs. D. Evans (pers. comm. 1979) inform us that they know of no Silurian or Ordovician examples of cephalopod encrustation by brachiopods other than those reported here, which is suggestive of host-specific relationships.

CONCLUSIONS

Faunal associations with abundant *Schizocrania* in the Ordovician and Silurian of the Anglo-Welsh region are almost invariably confined to argillaceous deep-water facies where species of the genus are represented almost exclusively by assemblages of brachial valves. Such exceptionally disproportionate valve ratios are considered to result from their encrustating habits which might account for the obscuring or removal of pedicle valves. Known associations between trematid encrusters and hosts such as those reported here and elsewhere (e.g. Havlíček 1972; Rowell *in* Williams *et al.* 1965) point to some form of host-specific relationship between representatives of the family and other larger invertebrate hosts. Whether such relationships could be termed symbiotic, commensal, or parasitic is unclear because we lack evidence which demonstrates that hosts were encrusted during life. However, we can establish that encrustation of orthocones, which may in some cases have begun during their life, often began no earlier than the post-mortem drifting phase, and may have continued or begun at a time when the orthocones were resting or rolling on the sea floor. Since encrustation of many of these orthocones could not have taken place when they were in the final 'resting' position it must have occurred during the middle phases of their pre-entombment history.

The following suggestions on the time of encrustation can be made: (1) The encrusting *Schizocrania* noted here are not currently known to attach to non-orthocone skeletal components within the deposits from which they were recovered and are therefore likely to have settled preferentially on orthocone shells prior to their final deposition. (2) The apparent high-density, orderly clustering of *Schizocrania* towards the anterior of the conch suggests that possibly the orthocone was colonized as a specific host whilst it was floating. (3) Since both *Schizocrania* and its nautiloid hosts are normally indigenous to sparsely fossiliferous, low-density offshore facies, it is probable that encrustation occurred in an offshore region before the orthocones finally became entombed in more diverse, fossiliferous, onshore facies where *Schizocrania* is invariably rare. This inference is supported by the observation that the setiferous *Schizocrania* may well have been adapted to a prolonged larval stage which would have enhanced its chances of encountering a suitable encrustation site. If *Schizocrania* even occasionally encrusted orthocones in a manner analogous to the attachment of epiplanktic aegeromenids to buoyant organisms noted by Bergstrom (1968), then the combined effect of nautiloid mobility during life and drifting after death would offer an explanation for exceptionally widespread occurrences of certain kinds of brachiopods.

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Cover: *Edriophus levis* (Bather, 1914) from the Middle Ordovician Trenton Group of Kirkfield, Ontario. × 2·5.
Specimen in the Smithsonian Institution; photograph by H. B. Whittington.

THE TRILOBITE *TRETASPIS* FROM THE UPPER ORDOVICIAN OF THE OSLO REGION, NORWAY

by ALAN W. OWEN

ABSTRACT. All known Norwegian species of *Tretaspis* are described. Six are established taxa: *T. ceriodes* (Angelin) *angelini* Størmer, *T. seticornis* (Hisinger), *T. anderssoni* Størmer, *T. hadelandica hadelandica* Størmer, *T. sortita* (Reed) *broeggeri* Størmer, and *T. kiaeri* Størmer. Three are new: *T. hisingeri*, *T. askerensis*, and *T. latilimbus* (Linnarsson) *norvegicus*. Most of these taxa have a broad range of variation encompassing two or more morphs. The relative proportions of these morphs are used to distinguish *T. latilimbus norvegicus* and *T. sortita broeggeri* from their nominate subspecies. The British form *T. convergens* Dean and its subspecies are reinterpreted as subspecies of *T. hadelandica*. Ingham's concept of species groups within *Tretaspis* is revised with the North American species and, provisionally, *T. kiaeri* and *T. calcaria* Dean being recognized as a distinct group centred on *T. sagenosus* Whittington. Neoteny is considered to have played a part in the evolution of *Tretaspis*.

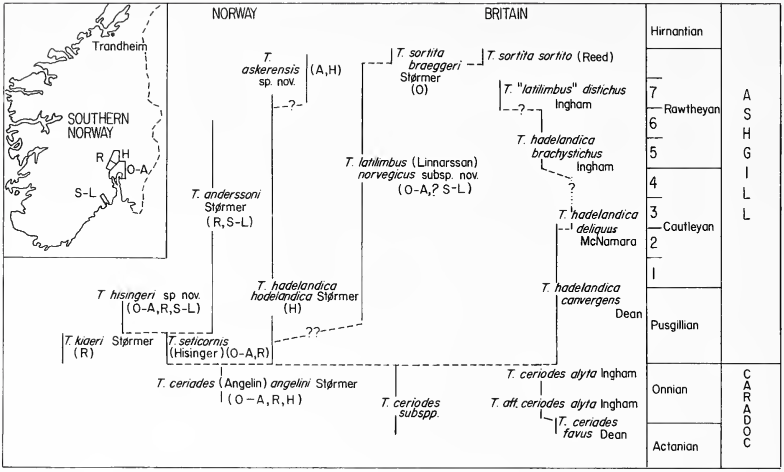
SPECIES of the trinucleid *Tretaspis* have played an important part in the correlation of late Caradoc and Ashgill successions in Britain over the past two decades (Dean 1961, 1963; Ingham 1970; Price 1973, 1977; McNamara 1979). The classical studies by Størmer (1930, 1945) on the Scandinavian trinucleids include a number of species of *Tretaspis*, most of which are closely related to British forms. The present study is part of a broader project aimed at revising the late Caradoc and Ashgill stratigraphy and trilobite faunas of the Oslo Region. This area was divided into eleven districts by Størmer (1953, text-fig. 1) and *Tretaspis* is known from four of them (text-fig. 1). Of these, the upper Ordovician stratigraphy of two, Hadeland and Ringerike, has been revised by Owen (1978, 1979) and summaries of the successions in the other two, Oslo-Asker and Skien-Langesund, are given by Strand and Henningsmoen (1960, pl. 7). In the case of Oslo-Asker, the youngest Ordovician units were redescribed by Brenchley and Newall (1975). The present study includes an examination of all available museum material and samples of *Tretaspis* collected by the writer from 117 localities in Oslo-Asker, Hadeland, and Ringerike, now housed in the Paleontologisk Museum, Oslo (PMO) and the Hunterian Museum, Glasgow (HM).

TREATMENT OF DATA

The distribution of pits on the bilamellar fringe of trinucleids is one of the major taxonomic features of the group (Hughes, Ingham, and Addison, 1975, pp. 550–552) and the terminology applied herein is that advocated by Hughes *et al.* (1975, pp. 543–545, text-figs. 3, 4). Hughes (1970) demonstrated that although individual specimens of *Trinucleus fimbriatus* Murchison may show slight asymmetry in the development of fringe pits, there is no significant statistical difference between the left and right sides of the fringe when populations are considered. It has thus become standard practice to present data in terms of half-fringe pit counts and this is followed herein. Moreover, Hughes also demonstrated that the distribution and number of pits is independent of holaspid specimen size and this also is assumed for other trinucleids.

The number of arcs of pits and the number of pits in each arc has been used for defining species and subspecies in various trinucleids, not least *Tretaspis*. These features can be determined even in heavily distorted material and lend themselves to simple univariate techniques of display and analysis. Such an approach is adopted here and enables direct comparisons to be made with data presented in other studies. Moreover, few horizons in the Oslo Region have yielded more than a

[Palaeontology, Vol. 23, Part 4, 1980, pp. 715–747, pls. 89–93.]



TEXT-FIG. 1. Stratigraphical ranges and suggested phylogeny of Norwegian and closely related British species of *Tretaspis* in terms of the standard British succession. The geographical distribution of Norwegian forms is given also: O-A = Oslo-Asker (Oslo is in the eastern part of this district), H = Hadeland, R = Ringerike, S-L = Skien-Langesund. The British species are revised to some extent herein.

dozen or so specimens and although many thousands of specimens have been examined, these comprise relatively few complete half-fringes, let alone entire fringes and thus most specimens have provided information on only a small proportion of the possible parameters. Univariate analysis therefore is preferred.

PROBLEMS OF POLYMORPHISM

Hughes *et al.* (1975, p. 590) noted that in many trinucleid stocks there is a progressive increase in the number of I arcs between I_1 and I_n. This is broadly the case in *Tretaspis* and in general terms the fringe criteria used in defining species and subspecies are, in decreasing order of importance: (1) the number of arcs present, (2) whether these arcs are complete anteriorly and/or posteriorly, (3) the range of variation in pit number per arc and along the posterior margin of the fringe. These features are closely related in most forms in that there is a threshold value (4–7 pits in Norwegian forms) for the number of pits present in the I arc adjacent to I_n before that arc can be complete anteriorly and a greater threshold (7–13 pits in Norwegian forms) before another incomplete arc can be developed between it and I_n. Other taxonomic fringe features are more dependent on preservation and include the extent of pits in adjacent arcs sharing sulci, the size of individual pits and the development of lists between arcs.

Many of the species and subspecies of *Tretaspis* described from Britain appear to have a fairly narrow range of variation with a purely typological concept based on characters 1 and 2 listed above being sufficiently diagnostic for both the taxon and all the individuals within it. In some cases this may be simply an artefact of small sample sizes. In contrast, Price (1977, pp. 764–772) found that some populations of *Tretaspis* from Wales have a range of variation in fringe characters which encompasses that seen in two named taxa which he considered to be end-member subspecies. Similarly, Lespérance and Bertrand (1976) distinguished a number of different morphotypes within

Cryptolithus although this needs reassessment in relation to the development of F pits on the posterior part of the fringe (Owen 1980).

Most of the Norwegian populations of *Tretaspis* have a broad range of variation, in some instances comprising morphotypes which correspond to the type specimens of described taxa. This presents great problems which, if taken to extremes could produce a taxonomy which is either very divisive and unweildy with each population sample comprising a number of formally named taxa or one which is grossly simplified to the extent of masking potentially useful affinities.

A fairly conservative approach is therefore adopted with different phenotypes within populations being recognized by the neutral term 'morphs' (Mayr 1969, p. 46). In the case of *T. ceriodes angelini* there is evidence for the progressive establishment of distinct phenotypes (see Hayami and Ozawa 1975 for a discussion of this process). In all the other Norwegian taxa only slight non-directional temporal and geographical changes in the relative proportions of constituent morphs are seen. To some extent the morphs are simply the product of variation exceeding the threshold values noted above. Thus, for example, it is not surprising that *T. ceriodes angelini* morph D (see below), which has arc I_4 developed, commonly has more pits in I_3 than does morph B. Moreover, I_3 is always continuous anteriorly in morph D but, by definition, is incomplete frontally in morph B. Nevertheless, the recognition of morphs is found to be very useful in describing variation and in making comparisons with named taxa from elsewhere which typologically resemble particular portions of the Norwegian range of variation.

The Norwegian species and subspecies therefore are defined in terms of recurrent associations of morphs (Table 1) and to some extent the relative percentages of these morphs. The boundaries between formally named taxa in some instances are ones of convenience, allowing for maximum stability of present usage within the new framework. Thus as Table 1 shows, the Norwegian taxa *T. latilimbus norvegicus* sp. nov. and *T. sortita broeggeri* are distinguished by the relative abundance of two morphs and the presence in the latter taxon of a third morph. This allows for formal expression of the greater similarity of *T. latilimbus norvegicus* to the Swedish *T. latilimbus latilimbus* (in which morph B is virtually absent) and of *T. sortita broeggeri* to the coeval *T. sortita sortita* from Scotland which is composed almost entirely of morph C.

Toxon	Morph %	Rodii	E_2	I_2	I_3			I_4			I_5		
					% P.	% C. Post.	% C. Ant.	% P.	% C. Post.	% C. Ant.	% P.	% C. Post.	% C. Ant.
T. ceriodes ongelini	A 34	1	▨	C	96	8	48	▨	▨	▨	▨	▨	▨
	B 13	1	C	C	90	0	0	▨	▨	▨	▨	▨	▨
	C 26	1	C	C	100	18	100	▨	▨	▨	▨	▨	▨
	D 27	1	C	C	100	66	100	100	0	14	▨	▨	▨
T. hisingeri sp. nov		2	Inc	Inc	▨	▨	▨	▨	▨	▨	▨	▨	▨
T. seticornis		2	Inc	C	▨	▨	▨	▨	▨	▨	▨	▨	▨
T. oskerensis sp. nov		2	Inc	C	29	0	0	▨	▨	▨	▨	▨	▨
T. anderssoni		2	Inc	C	100	0	0	▨	▨	▨	▨	▨	▨
T. hadelandica hadelondico	A 37	2	Inc	C	100	0	61	▨	▨	▨	▨	▨	▨
	B 56	2	Inc-C	C	100	100	23	▨	▨	▨	▨	▨	▨
	C 7	2	Inc	C	100	67	100	100	0	0	▨	▨	▨
T. latilimbus narvegicus subsp. nov	A 59	2	▨	C	100	100	100	100	10	29	▨	▨	▨
	B 41	2	Inc	C	100	100	100	100	0	17	▨	▨	▨
T. sortito broeggeri	A 5	2	▨	C	100	100	100	100	0	0	▨	▨	▨
	B 58	2	Inc	C	100	100	100	100	0	75	▨	▨	▨
	C 37	2	Inc	C	100	100	100	100	0	93	100	0	0
T. kiaeri	A 65	2	C	C	100	100	100	100	3	100	▨	▨	▨
	B 35	2	C	C	100	100	100	100	9	100	100	0	22

TABLE 1. The basic fringe development in the Norwegian species and subspecies of *Tretaspis*. Where more than one morph is recognized, the pit distribution in each morph is given. Note that the range in pit number in each arc also serves to differentiate between the morphs and this is detailed in text-figs. 2–9. The shading marks the complete absence of an arc, Inc = incomplete, C = complete, P = present, Post. = posteriorly, Ant. = anteriorly

The revision of the Norwegian *Tretaspis* material has entailed a reassessment of some of the well-documented British forms. In addition, Dr. J. K. Ingham of Glasgow University has given me access to his data on some of the Swedish forms. Most of the numerous citations in the literature of Swedish and other European material are based on very limited collections, as is the North American *T. clarkei*. The polymorphic Norwegian material indicates that individual specimens with a particular fringe morphology could belong to one of a number of taxa. Large samples are required to determine the range of variation and presence of morphs before taxonomic assignment can be carried out with any confidence. Thus whilst the known material of *Tretaspis* from outside Norway and Britain is discussed, it would be premature to make more than general comments on its affinity.

SYSTEMATIC PALAEONTOLOGY

Family TRINUCLEIDAE Hawle and Corda, 1847
Subfamily TRINUCLEINAE Hawle and Corda, 1847
Genus TRETASPIS McCoy, 1849

Type species. Asaphus seticornis Hisinger, 1840, p. 3, pl. 37, fig. 2; from the Fjäcka Shale (early Ashgill), Dalarna, Sweden; by subsequent designation of Bassler (1915, p. 1285).

Discussion. Ingham (1970, pp. 41–45) divided *Tretaspis* into three species groups centred on *T. moeldenensis* Cave, *T. seticornis* (Hisinger), and '*T.*' *granulata* (Wahlenberg). Hughes *et al.* (1975, pp. 503–505) reassigned the species constituting the last-mentioned group to *Nankinolithus* Lu and slightly revised the other two groups.

The *T. seticornis* group was originally stated to be characterized by an incomplete or absent E_2, the I_1–E_{1-2} radii 'out of phase' with those containing the remaining I arcs, the number of pits in E_1 ranging from 16 to 23, rarely up to 27 (half-fringe), the thoracic rachial rings relatively broad (tr.) and bearing a median tubercle and the pygidium never having more than six pairs of apodemes. Populations described below as *T. hadelandica hadelandica* include specimens with E_2 complete and up to ten pairs of pygidial apodemes. Similarly, populations of *T. anderssoni* have seven pairs of apodemes. In all other respects these forms correspond to the *T. seticornis* group. *T. persulcatus* from the Upper Drummuck Group at Girvan, south-west Scotland, has a complete E_2 but otherwise corresponds to the *T. seticornis* group and was almost certainly derived from an unnamed form which has E_2 incomplete (see discussion of *T. hadelandica* below). Thus the extent of E_2 and the number of pygidial apodemes are not, *per se*, indicative of the *T. seticornis* group.

Ingham (1970, pp. 44–45) had difficulty in assigning *T. kiaeri* Størmer to his groups but Hughes *et al.* (1975, p. 563) assigned it to the *T. moeldenensis* group. *T. kiaeri* is redescribed here and has E_2 complete frontally, two sets of radii, up to $27\frac{1}{2}$ pits in E_1 and up to ten pairs of pygidial apodemes. It is therefore intermediate between the *T. seticornis* and the *T. moeldenensis* groups. *T. kiaeri* and its probable derivative *T. calcaria* Dean resemble a number of middle Ordovician species from North America: *T. canadensis* Staüble, *T. reticulata* Ruedemann, and *T. sagenosus* Whittington and broadly coeval allied species from Scotland and Ireland. (Hughes *et al.* 1975, pp. 564–565). These middle Ordovician forms are older than all other known species of *Tretaspis* and have a single set of radii, a large number of pit arcs and in most cases a high pit count in most arcs. They were assigned to the *T. moeldenensis* group by Hughes *et al.* (1975, pp. 563–564). Specimens from the low Carodoc of Belgium assigned to *Tretaspis* by Hughes *et al.* (1975, p. 564) belong to *Nankinolithus* (= *N.* sp. of Hughes *et al.* 1975, p. 559).

The *T. seticornis* group as presently defined seems to be a natural grouping derived in the earliest Ashgill from *T. ceriodes* (Angelin), a member of the *T. moeldenensis* group. The removal of *T. kiaeri*, *T. calcaria*, and the middle Ordovician species listed above would leave the *T. moeldenensis* group as a close grouping within which phylogenetic relationships are fairly clear. The American province forms are poorly known but probably closely related and are here termed the *T. sagenosus* group. They almost certainly gave rise to *T. ceriodes*, the earliest known member of the revised *T. moeldenensis* group possibly by neoteny (giving a much simplified fringe morphology) and at a time of major immigration into the Scandinavian area (Bruton and Owen 1979). *T. kiaeri* and *T. calcaria* have the typical large number of arcs and high pit counts of the *T. sagenosus* group and whilst having two sets of radii developed the possibility exists that they are more closely related to that group than to the other two groups and thus are provisionally included in it.

Tretaspis moeldenensis group

Tretaspis ceriodes (Angelin, 1854) *angelini* Størmer, 1930

Plate 89, figs. 1–12; text-fig. 2

1887 *Trinucleus*; Brøgger, p. 23.
1930 *Tretaspis cerioides* [*sic*] (Angelin); Størmer, pp. 44–48, pl. 9, figs. 1–4; text-fig. 21*b*.
1930 *Tretaspis cerioides* var. *angelini* Størmer, pp. 48–50, pl. 9, figs. 5–10.
1934 *Tretaspis cerioides*; Størmer, p. 331.
1945 *Tretaspis ceriodes* (Angelin); Størmer (*pars*), p. 402, pl. 1, fig. 6; *non* pp. 387, 404–405, pl. 1, fig. 7; pl. 4, fig. 16 (= *T. hadelandica hadelandica*).
1945 *Tretaspis ceriodes* var. *angelini* Størmer; Størmer, p. 402, pl. 1, fig. 5.
1945 *Tretaspis ceriodes* var. *donsi* Størmer, pp. 388, 402, 405, pl. 1, fig. 8.
1953 *Tretaspis ceriodes*; Størmer, pp. 68, 87, 94.
1953 *T. c. angelini*; Størmer, p. 68.
1973 *Tretaspis cerioides*; Lauritzen, p. 29.
1978 *Tretaspis ceriodes* (*sensu lato*) (Angelin); Owen, pp. 9, 14, 15.
1979 *Tretaspis ceriodes*; Owen, pp. 250, 251.
1979 *Tretaspis ceriodes* (Angelin) (*sensu lato*); Bruton and Owen, text-figs. 3–6.

Holotype. A cranidium (PMO H226) from 2 m below the top of the Upper Chasmops Limestone on Terneholmen, Asker.

Material, localities, and horizons. The subspecies has a short stratigraphical range and, although no complete specimens are known, a large number of disarticulated skeletal elements are known from the uppermost parts of the Upper Chasmops Limestone in Baerum and Asker in the western part of Oslo-Asker (see Bruton and Owen 1979 for detailed information), from 0·85–1·02 m above the base of the Lower Tretaspis Shale on Nakholmen, Oslo, from the uppermost parts of the Solvang Formation throughout Hadeland and at Norderhov in Ringerike, and from the lowest part of the Gagnum Shale Member of the Lunner Formation in the northern part of Hadeland.

Description. Sagittal length of glabella equal to 50–60% of width between posterior fossulae. Occipital ring arched gently upwards and rearwards and defined anteriorly by a shallow furrow which bears deep slot-like pits laterally. Occiput short (sag., exsag.), very weakly swollen. 1p furrows deep, transversely oval. 2p furrows large, deep, situated a very short distance in front of 1p furrows and diverging forwards at approximately 90°. Composite lateral glabellar lobes very narrow (tr.) adjacent to 2p furrows, anteriorly and posteriorly to which they are very weakly developed. 3p furrows developed as very shallow depressions on the pseudofrontal lobe directly in front of the mid-length of the glabella. Pseudofrontal lobe very strongly swollen, almost circular in dorsal view, occupying approximately 70% of the sagittal glabellar length. Median node situated on the highest part of the glabella at 60% of the sagittal glabellar length. Dorsal furrows broad (tr.) and shallow posteriorly, narrowing and deepening a little frontally, diverging forwards at approximately 30° to a level a short distance in front of the 2p furrows, anteriorly to which they are gently convex abaxially and bear deep fossulae frontally. Genal lobes quadrant-shaped, gently inclined from the dorsal furrows, more steeply declined towards the fringe. Lateral eye tubercles situated opposite or slightly in front of 2p furrows. Low but distinct eye ridges converge adaxially forwards at about 145° from the eyes to the outer parts of the dorsal furrows. Posterior border furrows deeply incised, transversely directed, bearing deep fossulae distally. Posterior borders ridge-like, transversely directed to behind posterior fossulae abaxially to which they are deflected steeply downwards and rearwards at approximately 60°. External surface of glabella and genal lobes bears a variable but usually strong reticulation which is coarsest around the glabellar node and lateral eye tubercles. On internal moulds the glabella is commonly smooth and the genal lobes bear a very subdued reticulation. Fringe flat-lying over the inner one or two I arcs anteriorly and anterolaterally, otherwise almost vertical.

All specimens have arcs E_1, I_1, I_2, and I_n complete but there is considerable variation in the development of arcs E_2, I_3, and I_4. On the basis of these arcs, four morphs are recognized (Table 1). Morph A lacks E_2 and I_4 and has I_3 continuous in front of the glabella in 48% of 31 specimens where this could be determined and extending to the posterior margin in 8% of 24 specimens. I_3 is absent in 4% of 24 specimens. Morph B has a complete E_2, I_3 developed in 90% of 20 specimens but never continuous anteriorly or posteriorly and I_4 is absent. Morph C has a complete E_2, no I_4, and an I_3 arc which is always continuous anteriorly and extends to the posterior margin in 18% of 36 specimens. Morph D has E_2 complete, I_3 invariably complete anteriorly and complete posteriorly in 66% of 25 specimens and a short I_4 developed. The range of variation in arcs E_1, I_3, I_n, and the number of pits along the posterior margin of the fringe for *T. ceriodes angelini* as a whole and in the constituent morphs, is given on text-fig. 2 along with data on the development of I_4 in morph D. With the exception of the number of pits in I_3, these ranges are very similar for all the morphs although the mean values for morph A are lower than those of the other morphs. Arcs I_1, E_1, and E_2 (when present) commonly share sulci on the anterior and lateral parts of the fringe in most specimens. Although the extent of this feature was recorded wherever possible, there is often some difficulty in assessing the precise extent of the sulcation which may also be partially dependent on preservation and consequently this is not presented in histogram form. In a few specimens the sulcation does not extend laterally beyond the dorsal furrows and in a few it extends almost to the posterior margin. The mean extent is to about bR9 (fifty specimens, standard deviation 4) and there is no apparent difference between the morphs. Only one set of radii is developed. On external surfaces, lists are developed between all the I arcs. Genal spines parallel, length unknown.

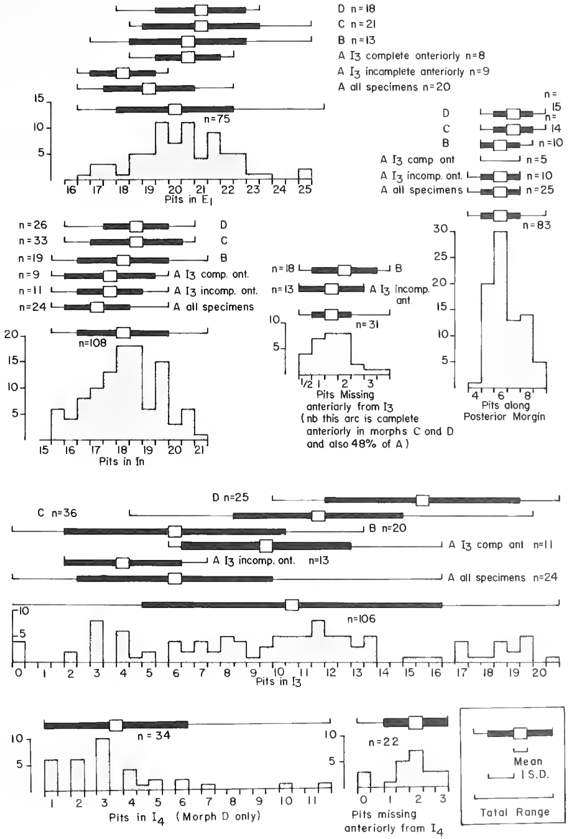
Hypostoma and thorax not known.

Pygidium sub-semicircular in outline with sagittal length equal to approximately 35% of the anterior width. Rachis occupies 25% of the anterior width of the pygidium, tapers rearwards at about 30°, and is composed of an anterior articulating half-ring and five or six rings. Ring furrows progressively less well-defined rearwards along the rachis, bearing deep apodemal pits a short distance in from the weakly incised dorsal furrows. Pleural lobes flat-lying, bearing four pairs of very broad furrows which define three or four ribs which die out some distance from the weakly developed marginal rim. Pygidial border very steeply declined, broad, maintaining constant width. Antero-lateral corners of pygidium bear steeply declined facets which diverge abaxially backwards at about 120°.

Discussion. The absence of arc E_2 from morph A clearly distinguishes it from the other morphs where this arc is not only present, but complete. Morphs B, C, and D could be viewed as representing a single morphological type with a broad range of variation. However, three morphs are recognized because two, B and C, are similar to, or correspond to, the holotypes of named taxa, and there is also some evidence for a progressive development of levels of phenotype organization from morph A through B and C to D. In Hadeland, a sample of thirty-three specimens from an exposure of the Lieker Member of the Solvang Formation illustrated by Owen (1978, text-fig. 6) from a level near the first appearance of the species has the following morph composition: A88%, B6%, and C6%. Higher levels in the formation in the nearby stratotype section have yielded morph D, and ten specimens from broadly equivalent levels in the Gagnum Shale (including the holotype of *T. ceriodes donsi*) comprise B10%, C80%, and D10%. Similar results have been obtained from Oslo-Asker with early populations having morph A dominant over B and C; morph D being restricted to the later populations where A is rare or absent.

It can be argued, therefore, that morph A represents the primitive condition, the development of a complete E_2 arc in some members of the population giving morphs B and C and individuals of morph D type developed from morph C parents. It must be stressed, however, that the morphs are regarded as representing fairly broad portions of the range of variation in interbreeding populations.

Angelin's original material of *T. ceriodes* (1854, p. 65, pl. 34, fig. 2–2*b*) from the Upper Mossen Formation (late Caradoc) at Kinnekulle, Västergötland, Sweden, was reported by Størmer (1930, p. 45) to be lost and a neotype from the Solvang Formation in Ringerike was chosen. This neotype could not have any standing as it was not from the type locality and recently Angelin's probable syntypes have come to light in the collections of the Riksmuseum, Stockholm. A full examination of the E pit development can be made in only one of these and E_2 is not developed. Two specimens show the development of I_3 which in both cases is short (3–4 pits) and not present anteriorly. I_4 is absent. Thus these probable syntypes resemble *T. ceriodes angelini* morph A. Two other specimens in the Riksmuseum collections from the Upper Mossen Formation (locality not known) show an extensive I_3 development and while one lacks E_2, the other has it developed mesially but not beyond R4. This



TEXT-FIG. 2. Histograms showing the range of variation in fringe characters of all available specimens of *Tretaspis ceriodes angelini* with a comparison of the range, mean, and one sample standard deviation on each side of the mean of the four morphs (A, B, C, and D) present in the subspecies. Morph A is also subdivided to compare these parameters in specimens with arc I_3 incomplete anteriorly (i.e. like morph B) with those in which this arc is complete anteriorly (i.e. like morphs C and D). It may prove useful to define separate morphs on this basis once more material is available. In all instances n = number of specimens in the sample.

condition is not known from any Norwegian specimen. Detailed comparisons of the Swedish and Norwegian forms must await the documentation of more material from Kinnekulle.

T. ceriodes alyta Ingham, 1970, from the upper part of the Onnian Stage in northern England has arcs E_2 complete, I_4 absent, and I_3 extensive or complete posteriorly but incomplete anteriorly. It thus resembles *T. ceriodes angelini* morph B, differing only in having a more extensive I_3 arc and the I_1–E_{1-2} sulci commonly extending almost to the genal angles. Examination of specimens from the Onnian Stage in the Cross Fell Inlier in northern England figured by Dean (1961, 1962) shows that Ingham was correct in suggesting that they belong to *T. ceriodes alyta* (1970, p. 5). Some of the specimens of supposed Onnian age in Dean's collections in the Cross Fell Inlier (localities A12 and A15 of Dean, 1959, text-fig. 1) have a very large number of pits in I_n ($25\frac{1}{2}$–$28\frac{1}{2}$) and up to $9\frac{1}{2}$ pits in I_4 and most closely resemble *T. moeldenensis* Cave, 1960 (see Price 1977, pp. 764–772 for a discussion of this species).

T. ceriodes favus Dean, 1963, is a poorly known form based on specimens from the upper part of the Actonian Stage and the lowest beds of the Onnian Stage in the Onny River section and supposed Actonian strata near Cardington, Salop, England. The subspecies was diagnosed as having arc E_2 developed only laterally and I_3 complete anteriorly but not posteriorly. Whilst the latter is true for the holotype and other specimens from the Onny River, the material is too poorly preserved for the E pit development to be discerned fully although E_2 is certainly present. The I_3 development is closest to that seen in *T. ceriodes angelini* morph C. All of the sixteen specimens from near Cardington in the British Museum (Natural History) (including Dean collection) and the Hunterian Museum (Owen and Ingham collection) in which the E arc development is clear, undoubtedly have E_2 complete. I_3 is incomplete anteriorly in this material (eleven specimens) and has 2–14 pits. Arcs I_1–E_{1-2} are sulcate over almost the whole fringe. The Cardington material therefore is similar to both *T. ceriodes angelini* morph B and *T. ceriodes alyta* and, as noted by Bruton and Owen (1979, p. 220), its association with *Onnia gracilis* may indicate an Onnian age for the strata here.

T. ceryx Lamont, 1941, from the Raheen Shales (late Caradoc–early Ashgill) of Co. Waterford, Eire, differs from *T. ceriodes angelini* morph C only in having very long, slot-like I_1–E_{1-2} sulci anteriorly and anterolaterally. The Irish form is probably best viewed as a geographical subspecies of *T. ceriodes*.

T. colliquia Ingham, 1970, from the Pusgillian Stage in the Cautley district of northern England is probably a derivative of *T. ceriodes alyta* and some specimens, like *T. ceriodes angelini* morph D have a short I_4 developed. The English species is distinguished by its very large, deep, extensive I_1–E_{1-2} sulci and in having a very high E pit count (twenty-eight in the two specimens showing this feature).

Dr. J. K. Ingham of Glasgow University has informed me of an undescribed form of *T. ceriodes* similar to *T. ceriodes angelini* morph A from the Upper Whitehouse Group (late Caradoc–early Ashgill) at Girvan, south-west Scotland (Ingham 1978, pp. 170, 171).

EXPLANATION OF PLATE 89

Figs. 1–12. *Tretaspis ceriodes* (Angelin) *angelini* Størmer. 1, 3, 5, morph D, PMO100826, dorsal, anterior, and lateral views of internal mould of cranidium, 5·3–5·4 m below top of Solvang Formation, Norderhov, Ringerike, × 4. 2, 4, morph D, PMO101552, dorsal and anterolateral views of external surface of cephalon, approximately 1·7 m below top of Upper Chasmops Limestone, East Raudskjer, Asker, × 6. 6, holotype, morph C, PMO H226, oblique anterolateral view of partially exfoliated cranidium, 2 m below top of Upper Chasmops Limestone, Terneholmen, Asker, × $6\frac{1}{2}$; also figured by Størmer (1930, pl. 9, fig. 5). 7, 10, morph A, PMO H593, posterolateral and frontal views of partially exfoliated cephalon, same horizon and locality as 6, × 5; also figured by Størmer (1930, pl. 9, fig. 10). 8, morph B, PMO H250, anterolateral view of partially exfoliated cephalon, same horizon and locality as 6, × 10. 9, PMO103952, dorsal view of pygidium, upper part of Solvang Formation, Lunner, Hadeland, × $4\frac{1}{2}$. 11, morph C, PMO81100, anterolateral view of partially exfoliated small cranidium, same horizon and locality as 2, × 20. 12, morph A, PMO H495, anterolateral view of partially exfoliated cephalon, 0·85–1·02 m above base of Lower Tretaspis Shale, Nakholmen, Oslo, × 4.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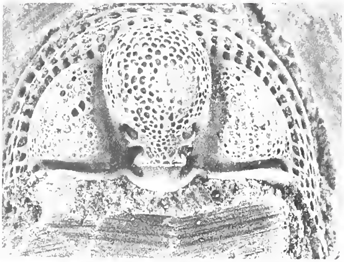
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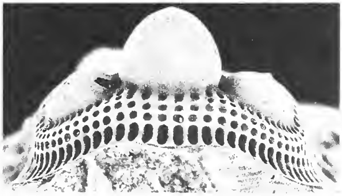
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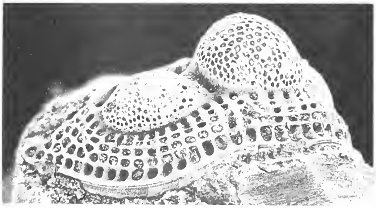
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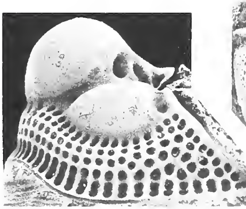
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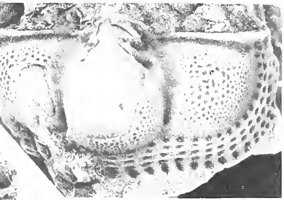
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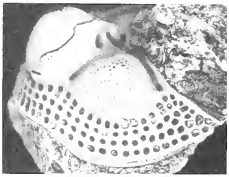
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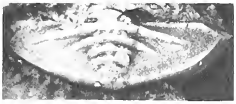
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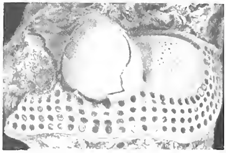
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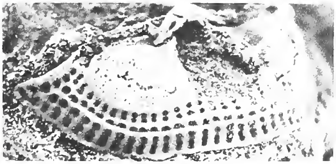
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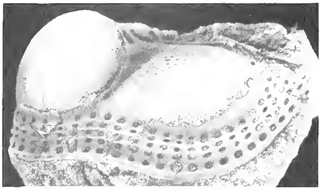
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OWEN, trilobite *Tretaspis*

Tretaspis seticornis group

Tretaspis seticornis (Hisinger, 1840)

Plate 90, figs. 1–4

1840 *Asaphus seticornis* Hisinger, p. 3, pl. 37, fig. 2.
1840 *Asaphus cyllarus* Hisinger, p. 3, pl. 37, fig. 3.
?1845 *Trinucleus seticornis* (Hisinger); Lovén, p. 107, pl. 2, fig. 2.
?1854 *Trinucleus seticornis* (Hisinger); Angelin, p. 84, pl. 40, fig. 19.
?1869 *Trinucleus seticornis* (Hisinger); Linnarsson, p. 79.
1883 *Trinucleus seticornis* (Hisinger); Törnquist, p. 43.
?1884 *Trinucleus seticornis* (Hisinger); Törnquist, pp. 84–87.
?1887 *Trinucleus seticornis* (Hisinger); Brøgger, p. 24.
1930 *Tretaspis seticornis* (Hisinger); Størmer (*pars*), pp. 55–67, ?pl. 7; ?pl. 8; ?pl. 11, fig. 4; text-figs. 27, 28 (*pars*), ?29, 33*a*, 34*b* (*pars*), 34*c*, ?36, ?37*a*, *b*, ?42.
1934 *Tretaspis seticornis*; Størmer (*pars*), p. 330.
1936 *Tretaspis seticornis* (Hisinger); Asklund (*pars*), p. 4, pl. 1, figs. 1–3, ?5, ?6, *non* 4.
?1959 *Tretaspis seticornis* (Hisinger); Whittington *in* Moore, text-fig. 323.2.
1979 *Tretaspis seticornis seticornis* (Hisinger); Owen, pp. 250, 251, 252, text-fig. 6.
1979 *Tretaspis seticornis seticornis* (Hisinger); Bruton and Owen, text-fig. 6.

This synonomy only includes references to material which actually, or very probably, belongs to *T. seticornis*. A more complete list, comprising forty-seven entries, was given by the writer (1977, pp. 243–245) in an unpublished thesis and includes reidentifications wherever possible.

Material, localities, and horizons. Hisinger's syntypes of *Asaphus seticornis* from the Fjäcka Shale in well diggings at Furudal in Dalarna, Sweden, have not been identified unequivocally in the collections of the Riksmuseum, Stockholm, and as noted by Törnquist (1883, p. 43) may not have been collected *in situ*. The species, as here defined, is known from the lower part of the Fjäcka Shale (J. K. Ingham, pers. comm. 1976), the lower part of the Lower Tretaspis Shale at Ole Deviks Vei (lowest 5·86 m), Åstaddammen (lowest 4·65 m at least), S. Gråkommen and between Føssung and Høgstad in Oslo-Asker, and from the Høgberg Member of the Solvang Formation on Frognøya, Ringerike.

Description. Most of the available material is crushed to some extent. Glabella and genal lobes similar to those of *T. ceriodes angelini* except that the pseudofrontal lobe is more elongate. External surface of glabella and genal lobes smooth or bearing a faint reticulation. Internal moulds smooth. Steeply declined fringe bears complete arcs E_1, I_1, I_2, and I_n, and an incomplete E_2 arc. Arcs I_1–E_{1-2} are out of phase with radii comprising the other two I arcs. Pits in I_1 and E_1 share sulci anteriorly and anterolaterally. There is insufficient material to assess the range of variation in pit distribution. Only one Norwegian specimen is sufficiently well preserved for the number in E_1 to be determined (18), and whilst one specimen clearly lacks E_2, others show minimum values of 4, 7, 9 (3 specimens), and 10 pits. I_n is seen completely in 4 specimens where it comprises 15, 17½, 18, and 18½ pits and there are 6 (3 specimens) or 7 (3 specimens) pits along the posterior margin of the fringe. Lists are not developed. One specimen (pl. 90, fig. 4) does not conform to the typical *T. seticornis* development in having a stronger reticulation and in having pits developed in I_3 on the lateral parts of the fringe at aR6, 7, 9, 11–17. Such a development is most unusual for any species of *Tretaspis* and may reflect hybridization with *T. hadelandica hadelandica* which includes morphs with this arc complete posteriorly.

Hypostoma unknown.

Thorax barrel-shaped, comprising six segments of which the third and fourth are slightly broader (tr.) than the rest. Rachis occupies 30% of the width of each segment and is bounded laterally by very weakly incised dorsal furrows. Rachial rings strongly convex in transverse view and each bears a small median tubercle on its anterior edge and is separated from its articulating half-ring by a transversely directed furrow which bears deep apodemal pits laterally. Pleurae parallel-sided proximally, tapering slightly over the distal 25% where they are deflected gently downwards and rearwards. Pleural furrows shallow, each directed transversely and broadening (exsag.) from near the anteromesial corner of the pleura such that the posterior band tapers abaxially and the anterior band expands a little.

Pygidium broadly similar to that of *T. ceriodes angelini*. Rachis composed of six, possibly seven rings and the pleural lobes bear up to three poorly defined ribs.

Discussion. Hisinger (1840) described two species of *Tretaspis*, '*Asaphus*' *seticornis* and '*A*'. *cyllarus*, from the Fjäcka Shale. His illustrations of both show the development of four complete arcs of pits and there is a well-developed list between the inner and the outer pairs of arcs on his drawings of *T. seticornis*. Dr. J. K. Ingham informs me (pers. comm. 1976) that in the probable syntypes of both species and all other available specimens from the Fjäcka Shale at Furudal which have the fringe preserved, arcs E_1, I_1, I_2, and I_n are complete and a short E_2 is developed posteriorly. Thus it seems reasonable to assume that this is indeed the case with the syntypes and, in order to stabilize the species, it is advocated that this be assumed to be the case. Dr. Ingham has examined material from Dalarna described by Angelin (1854) as *T. seticornis* and considers that this identification probably is correct. Angelin's originals of *T. affinis* have a complete I_3 arc developed and thus are excluded from *T. seticornis*.

Størmer (1930) assigned a large number of specimens to *T. seticornis* from the Fjäcka Shale and various horizons in Norway. Many of these are reassigned herein to *T. anderssoni* Størmer and *T. hisingeri* sp. nov. It is clear that at least three forms are present in the Fjäcka Shale and so references to *T. seticornis* in this unit by Linnarsson (1869) and Törnquist (1884) are only tentatively included in the above synonymy. Further discussion of material previously assigned to *T. seticornis* is given below in the discussions of *T. anderssoni* and *T. hadelandica*.

Tretaspis anderssoni Størmer, 1945

Plate 90, figs. 5–10; text-fig. 3

?*non*1894 *Trinucleus seticornis* (Hisinger); Andersson, p. 532, figs. 1–5.
1930 *Tretaspis seticornis* (Hisinger); Størmer (*pars*), pl. 11, figs. 2, 5; pl. 12, figs. 1–5; pl. 13, figs. 1, 2, 5–7; ?pl. 14, figs. 4, 5; text-figs. 33*b*, *c* (*pars*), *d*, 37*c*.
?1936 *Tretaspis seticornis* (Hisinger); Asklund (*pars*), p. 4, pl. 1, fig. 4.
1945 *Tretaspis seticornis* (Hisinger) var. *anderssoni* Størmer, p. 401, pl. 1, fig. 2.
1959 *Tretaspis seticornis* (Hisinger); Harrington *in* Moore, text-figs. 52, 67.
*non*1965 *T. seticornis anderssoni* Størmer; Cave, p. 296 [? = *T. hadelandica brachystichus* Ingham].
1975 *Tretaspis seticornis anderssoni* Størmer; Hughes *et al*., p. 563, pl. 4, figs. 52, 53.
1976 *Tretaspis seticornis* (Hisinger); Miller, text-fig. 2*h*.
1979 *Tretaspis seticornis anderssoni* Størmer; Owen p. 253 text-fig. 8.
?1979 [specimens resembling] *T. hadelandica* Størmer; Owen, p. 253.

Holotype. A cranidium (PMO65196) from the Frognøya Shale, on Frognøya, Ringerike.

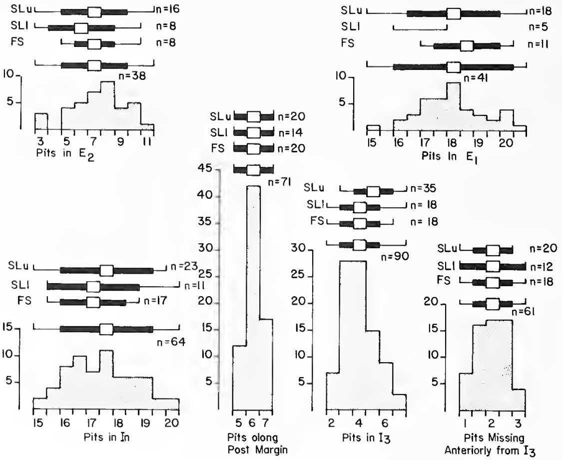
Material, localities, and horizons. Specimens from low in the Frognøya Shale tentatively compared with *T. hadelandica* by Owen (1979) probably belong in *T. anderssoni* in which case cephala, cranidia, lower lamellae, and pygidia are known from throughout the type unit on Frognøya and from the overlying Sørbakken Limestone (except the lowest 9 m and the uppermost 17 m) on Frognøya and at Norderhov, Ringerike. Two poorly preserved cranidia from the Venstøp Shale in Skien-Langesund may belong here also.

Description. Cephalic proportions similar to those of *T. ceriodes angelini*. The fine structure of the median glabellar tubercle in *T. anderssoni* was described by Størmer (1930, p. 87, text-fig. 37*c*; pl. 11, fig. 5; pl. 13, figs. 5–7) who noted that it bears four small pits arranged as at the corners of a square and a slightly larger central pit which may bear a fine canal opening. Størmer (1930, pl. 12, fig. 3; pl. 13, figs. 1, 2) also illustrated a lenticular body within the exoskeleton of the lateral tubercles of this species. On the external surface of the glabella and genal lobes there is a weakly developed fine reticulation which is seen faintly on a few internal moulds.

Fringe narrow, very steeply declined except laterally where a narrow brim is developed. A gentle anterior arch is present. The details of fringe pitting are given on text-fig. 3. Two distinct sets of radii are present, arcs E_1, I_1, I_2, and I_n are complete and in all specimens a short E_2 arc is developed posteriorly and I_3 is developed anterolaterally but never complete mesially. Arcs I_1–E_{1-2} share sulci which extend to between bR5 and bR14. The limited evidence available suggests that there is no significant difference in pit development between early and late populations of *T. anderssoni*.

Hypostoma and thorax unknown.

Pygidium similar to that of *T. ceriodes angelini*. Six rachial ring furrows, each with deep apodemal pits laterally, are seen on the external surface of the rachis. On internal moulds, a seventh pair of apodemal pits lies directly in front of the pygidial border. Pleural lobes bear four weakly developed pairs of ribs, the posterior two barely discernible.



TEXT-FIG. 3. Histograms showing the range of variation in fringe features of all available specimens of *Tretaspis anderssoni* with a comparison of samples from the Frognøya Shale (FS), from 9–28 m above the base of the overlying Sørbakken Limestone (SLl) and from 17 m below the top of this unit (SLu).

EXPLANATION OF PLATE 90

Figs. 1–4. *Tretaspis seticornis* (Hisinger). 1, PMO103953, dorsal view of internal mould of almost complete specimen, 4·65 m above base of Lower Tretaspis Shale, Åstaddammen, Asker, ×2½. 2, PMO101553, ventral view of part of cranidium, Høgberg Member of the Solvang Formation, Frognøya, Ringerike, ×4. 3, PMO103954, dorsal view of cast of almost complete specimen, Lower Tretaspis Shale, Ole Deviks Vei, Oslo, ×3. 4, PMO103955, anterolateral view of cast of cranidium showing I_3 developed laterally, 1·65 m above base of Lower Tretaspis Shale, same locality as 1, ×4¾.

Figs. 5–10. *Tretaspis anderssoni* Størmer. 5, PMO103956, dorsal view of internal mould of pygidium, 17 m below top of Sørbakken Limestone, Frognøya, Ringerike, ×7½. 6, 8, 9, holotype, PMO65196, dorsal, anterior, and lateral views of internal mould of cephalon, Frognøya Shale, Frognøya, Ringerike, ×3; also figured by Størmer (1945, pl. 1, fig. 2) and Hughes *et al.* (1975, pl. 4, figs. 52, 53). 7, PMO H103, posterolateral view of cephalon, same horizon and locality as 6, ×2½; also figured by Størmer (1930, pl. 11, fig. 5). 10, PMO80670, frontal view of cast of cranidium, Venstøp Shale, Friefjord, Skien-Langesund, ×7½.

Figs. 11–14. *Tretaspis hisingeri* sp. nov. 11, PMO H71, frontal view of partially exfoliated cephalon, 3·0–4·5 m below top of Frognøya Shale, same locality as 6, ×3½. 12–14, PMO H75, dorsal, lateral, and frontal views of partially exfoliated cranidium, Frognøya Shale, same locality as 6, ×3, ×3½, ×3½; also figured by Størmer (1930, pl. 11, fig. 3; 1945, text-fig. 4).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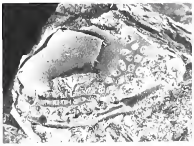
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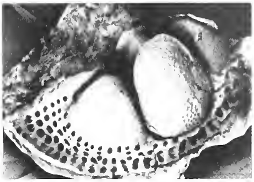
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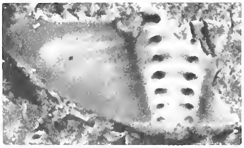
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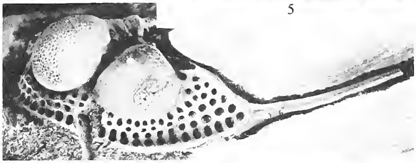
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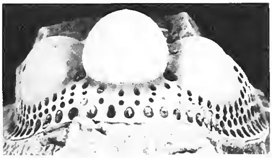
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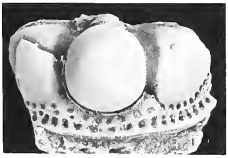
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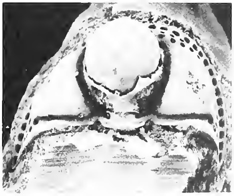
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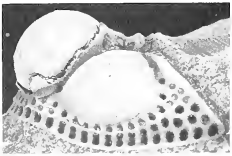
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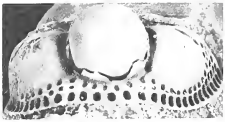
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OWEN, trilobite *Tretaspis*

Discussion. T. anderssoni differs from its probable ancestor, *T. seticornis* in having a short I_3 developed in all specimens. A broadly similar fringe development is seen in a number of described taxa and their interrelationships are discussed below under *T. hadelandica*.

Størmer (1945, p. 401) considered that specimens figured by Andersson (1894) as *T. seticornis* from the Lower Johnstorp Formation (Pusgillian–?Cautleyan) of Hulderstad, Öland, Sweden, probably belong to *T. anderssoni*. Examination of these specimens reveals that they have pit counts at the upper end of, or even beyond, the range of variation seen in *T. anderssoni* from Norway. The counts in these Riksmuseum, Stockholm, specimens Ar21551 and Ar21553 respectively are as follows: E_1 22, 20; E_2 9 (?10), ?8; I_n *c.* 17½, 18; I_3 5, 5. Without further specimens from Öland the affinities of this material must remain in doubt. Similarly, a specimen figured by Asklund (1936) from the Tretaspis Beds in Jemtland has a short I_3 but its affinities must await the description of further specimens.

Tretaspis hisingeri sp. nov.

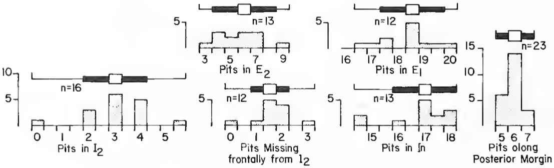
Plate 90, figs. 11–14; Plate 91, figs. 1–4; text-fig. 4

?1887 *Trinucleus seticornis* (Hisinger); Brøgger, p. 24.
1930 *Tretaspis seticornis* (Hisinger); Størmer (*pars*), pl. 11, figs. 1, 3, 6, 7; text-figs. 33*c* (*pars*), ?37*a*, *b*, 40, 47.
1934 *Tretaspis seticornis*; Størmer (*pars*), p. 330.
1945 *Tretaspis seticornis* (Hisinger) forma typica; Størmer, p. 401, text-fig. 4.
1970 *T.* sp. [?nov.]; Ingham, p. 41.
1975 *T.* sp. ?nov.; Hughes *et al.*, p. 563.
1979 *Tretaspis* sp. nov.; Owen, p. 253, text-fig. 8.

Holotype. An almost complete specimen (PMO H51) from 3·5–4·0 m below the top of the Frognøya Shale on Frognøya, Ringerike.

Material, localities, and horizons. The species has a limited stratigraphical distribution and is known from all but the lowest part of the Frognøya Shale on Frognøya and at Hole and Norderhov, and also between 9 and 14 m above the base of the overlying Sørbakken Limestone on Frognøya, Ringerike. The species is also known from the upper part of the Lower Tretaspis Shale at Ole Deviks Vei and on Bygdøy and Lindøya in Oslo, the Tretaspis Limestone at Nesbru, Asker, and the Venstøp Shale in Skien-Langesund.

Diagnosis. Very narrow fringe has E_1, I_1, and I_n complete, E_2 short and a short I_2 present in the vast majority of specimens but rarely continuous anteriorly, and in some instances asymmetrically distributed about the sagittal line. Two distinct sets of radii mesially and where I_2 is developed but laterally I_n is in phase with I_1–E_{1-2}.



TEXT-FIG. 4. Histograms showing the range of variation in all available specimens of *Tretaspis hisingeri* sp. nov. In the case of I_2, only specimens which are symmetrical about the sagittal line or which have only one side of the fringe visible are included. An additional five specimens are asymmetrical, and inclusion of the right or left counts with the data shown here does not change the mean value although the left counts increase the standard deviation to 1½. The number of pits missing from I_2 anteriorly from these specimens is the same for both right and left sides, and thus are incorporated in the histogram of this feature.

Description. The glabella and genal lobes of *T. hisingeri* differ from those of *T. ceriodes angelini* only in having the median node situated a little further forward, the lateral eye tubercles a little closer to the glabella, and in most of the larger holaspids lacking any reticulation on the external surface of the exoskeleton. A specimen of meraspis degree 4, however, has a very strong reticulation on both glabella and genae (pl. 91, fig. 4). Similar reduction in the extent and intensity of reticulation with growth in trinucleids is well documented (Čech 1975). Genal spines extending well beyond the pygidium. The fringe is very narrow with only E_1, I_1, and I_n complete. A short E_2 is developed posteriorly and nearly all specimens have a few pits in I_2 which is rarely continuous frontally (one specimen out of twelve). In some of the specimens where the development of I_2 can be seen on both sides of the glabella there are up to two pits less on one side than on the other. In an extreme case the arc is absent on the left side but contains two pits on the right (Pl. 90, fig. 11). The range of variation in fringe features is illustrated on text-fig. 4. Arcs I_n, I_1, E_1, and (where present) E_2 are arranged in a single set of radii laterally but I_1 and E_1 are out of phase with I_n mesially and with the inner two I arcs where I_2 is developed.

Hypostoma unknown.

Thorax of holaspis similar to that of *T. seticornis*. That of the meraspis degree 4 noted above has a narrower rachis which occupies 25% (cf. 30%) of the segment width.

Holaspid pygidium known only from the holotype in which it is incomplete. Rachis bears at least 6 pairs of apodemal pits. Meraspis degree 4 pygidium sub-semicircular in outline with a rachis of approximately 5 rings of which only the anterior 2 are distinct.

Discussion. The short I_2 development distinguishes *T. hisingeri* from all other named species. *T. hisingeri* succeeds *T. seticornis* without overlap and probably was derived from it by neoteny. A very similar form in which I_2 is incomplete but more extensive than in *T. hisingeri* occurs in the Fjäcka Shale in Sweden, and it too succeeds *T. seticornis* (J. K. Ingham, pers. comm. 1976).

Tretaspis hadelandica hadelandica Størmer, 1945

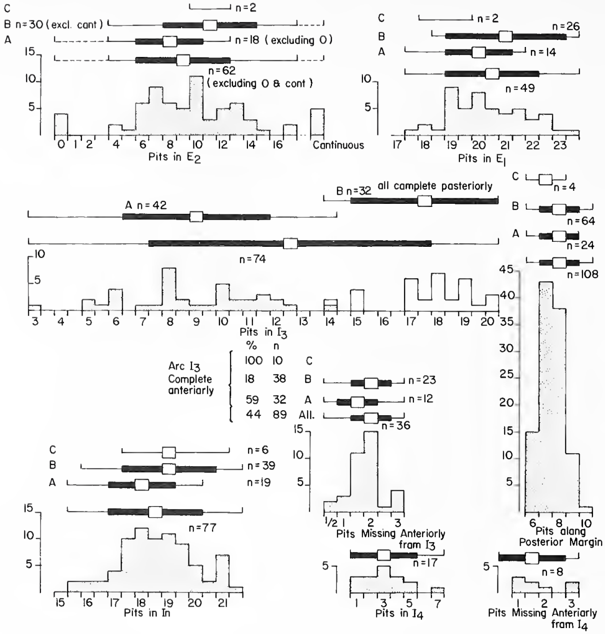
Plate 91, figs. 5–14; Plate 92, figs. 1, 2; text-fig. 5

1923 *Trinucleus* sp.; Holtedahl *in* Holtedahl and Schetelig, p. 22.
1945 *Tretaspis seticornis*; Størmer, p. 384.
1945 *Tretaspis seticornis* var. *hadelandica* Størmer, pp. 384, 388, 406–407, pl. 1, figs. 3, 4.
1945 *Tretaspis ceriodes* (Angelin); Størmer, pp. 387, 404–405, pl. 4, fig. 16.
1945 *Tretaspis kiaeri* Størmer; Størmer, pp. 387, 406, pl. 1, fig. 11.
1970 *Tretaspis hadelandica hadelandica* Størmer; Ingham, text-fig. 17.
1973 *Tretaspis seticornis*; Lauritzen, p. 29.
1978 *Tretaspis hadelandica hadelandica* Størmer; Owen, pp. 11, 13, 14, 17.

Holotype. An incomplete cranidium (PMO65187) probably from the Gagnum Limestone Formation south of Gagnum, Hadeland.

Material, localities, and horizons. A few complete specimens and a large number of disarticulated skeletal elements occur abundantly in the Gagnum Shale (except the lowest part in northern Hadeland) and Lunner Kirke members of the Lunner Formation, the shales of this formation around Lunner, and in the Gagnum Limestone and Kjørrven formations. The species is rare in the Grina Shale Member of the Lunner Formation. Fragmentary museum material from Nittedal (precise horizon unclear), between Oslo and Hadeland, may belong here also.

Description. Proportions of glabella and genal lobes very similar to those of *T. ceriodes angelini*. Specimens from the Gagnum Shale have a well-developed reticulation on the external surface and commonly on the internal mould, but most specimens from other units have only a subdued reticulation or are smooth. Fringe steeply declined with a slight brim developed laterally. Genal spines long, diverging rearwards very slightly. All specimens have two distinct sets of radii, and arcs E_1, I_1, I_2, and I_n are complete. Three morphs are recognized on the development of E_2, I_3, and I_4 (Table 1) and the distribution of pits in each arc is shown on text-fig. 5. Arc I_4 is absent from morphs A and B which respectively have I_3 incomplete and complete posteriorly. These morphs occur in all samples, whereas morph C, which has a short I_4 developed, is known only from a few populations from the lower part of the Gagnum Shale Member, the upper part of the Lunner Formation around Lunner, and from the Gagnum Limestone. In one specimen (Pl. 92, figs. 1, 2) I_3 is complete on the right side of the cranidium but not on the left, an asymmetry which encompasses both morph A and morph B. Samples are not large enough



TEXT-FIG. 5. Histograms showing the range of variation in fringe features of all available specimens of *Tretaspis hadelandica hadelandica* with a comparison of the range, mean, and sample standard deviation of the three morphs (A, B, and C) present in the subspecies.

to enable detailed unit by unit comparison of the variation in each morph but no obvious stratigraphical changes are apparent.

Hypostoma unknown. Thorax like that of *T. seticornis*.

Pygidium sub-semicircular in outline. Rachis crossed by 5–7 furrows each bearing apodemal pits laterally. On the ventral surface of the pygidium there are up to ten pairs of apodemes, the posterior three of which are situated on the steeply declined pygidial border. Pleural lobes bear three low ribs.

Discussion. When present, morph C occurs with morphs A and B which are always found together. Their great similarity in pit distribution in arcs E_1, I_n, and along the posterior margin argues strongly for these morphs being no more than broad phenotypes from the same gene pool. Their relative abundance, however, may be ecologically controlled. Table 2 gives the relative percentages of morphs present in the stratigraphical units in which they occur in measurable abundance.

3 × 2 and 2 × 2 contingency tests were carried out on the specimen numbers used to calculate these percentages. The latter test was used where morph C was absent from both samples under examination, or where expected frequencies of morph C were less than 5; Yates's Correction was applied in both instances. These tests show that the Gagnum Shale abundances are significantly different from all but those of the Kjørrven Formation at the 0·1% level. The Kjørrven Formation

TABLE 2. Percentages of each morph present in collections of *T. hadelandica hadelandica* from stratigraphical units in Hadeland

Morph	Gagnum Shale Member	Lunner Kirke Member	Lunner Formation above Lunner Kirke Member	Gagnum Limestone	Kjørrven Formation
A	55	17	18	13	47
B	31	83	75	77	53
C	14	0	7	10	0
Number of specimens	106	35	44	39	19

abundances differ from those of the Gagnum Shale near the 50% level which is not significant, and from those of the other three units at the 5% level which is considered significant. No significant differences are present between the remaining three units where, in fact, there is a high degree of correlation. The similarity between the Gagnum Shale and Kjørrven Formation abundances is the product of high proportions of morph A in these units. It may be noteworthy that both units have a much higher trilobite diversity (measured by the total number of known taxa) than the others, but speculation on the reasons for this similarity in morph composition would be very unreliable in view of the small sample size from the Kjørrven Formation.

T. hadelandica brachystichus Ingham, 1970, was based on samples from the Rawtheyan Stage (Ashgill Zones 5 and 6) in the Cautley area of northern England which have I_3 incomplete anteriorly and posteriorly. Ingham also tentatively included fragments from the mid-Cautleyan Stage (Zone 3) in this subspecies and suggested that specimens from the Gagnum Shale assigned to *T. seticornis* by Størmer may belong to the north of England form. These Gagnum Shale specimens are assigned to *T. hadelandica hadelandica* morph A herein. Ingham's material and specimens assigned to *T. hadelandica brachystichus* by Price (1973, 1977) and Cocks and Price (1975) from the uppermost part of the Sholeshook Limestone and lower part of the Slade and Redhill Mudstone (mid-Ashgill) in south Wales, have a range of variation which overlaps that seen in the Norwegian morph A (text-fig. 6). In the case of arcs E_2 and E_1 and the number of pits along the posterior margin, the range and, in the E arcs, the mean is higher than that of the Norwegian morph. The variation in number of pits in I_3, however, overlaps at the lower end of that seen in *T. hadelandica hadelandica* morph A and is closer to that of *T. anderssoni* which, in all these characters, has a range of variation which overlaps only at its upper end with that of *T. hadelandica hadelandica* morph A (text-fig. 6).

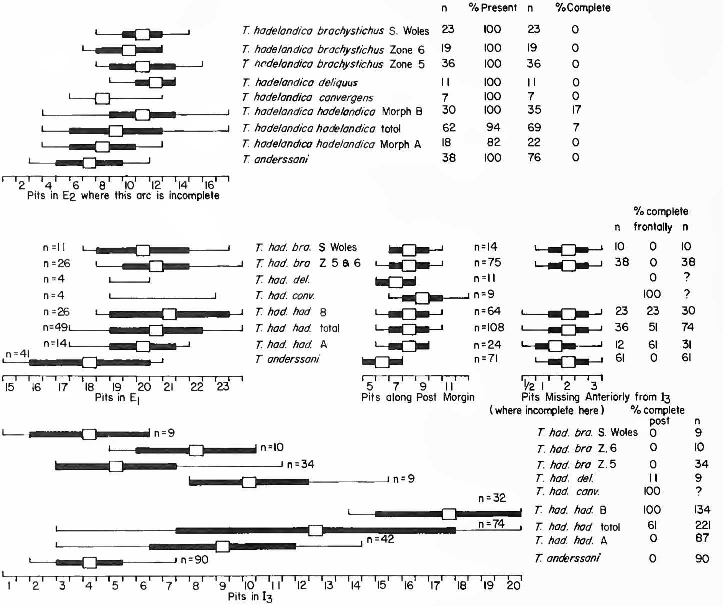
T. convergens Dean, 1961, was described originally from Pusgillian strata in the Cross Fell Inlier in northern England and subsequently by Ingham (1970) from Pusgillian and lower Cautleyan (Ashgill Zone 1) strata at Cautley and by McNamara (1979) from mid-Cautleyan (Zone 2 and lowest part of Zone 3) strata in the English Lake District. As noted by McNamara (1979, p. 62), the limited evidence available suggests that there is a progressive reduction in I pits with the Cross Fell specimens having a short (up to ten pits) I_4 arc, some specimens lacking this arc in the Cautley material, and in all the Lake District specimens this arc is not developed. This trend is continued in Ashgill Zone 3 in the Lake District with *T. convergens deliquus* McNamara, 1979; I_3 becoming incomplete anteriorly and then laterally. The earliest examples with *T. convergens deliquus* morphology occur with specimens with I_3 complete anteriorly (K. J. McNamara, pers. comm. 1979).

As text-fig. 6 shows, the over-all pit distribution and the broad range of variation seen in the subspecies of *T. convergens* is very similar to that of *T. hadelandica hadelandica* and consequently the English forms are regarded as subspecies of *T. hadelandica*. It seems reasonable to suggest that Ingham's indeterminate specimens from Zone 3 are, in fact, *T. hadelandica deliquus* and that the progressive decrease in pit number in I_3 documented by McNamara continued, giving rise to *T. hadelandica brachystichus*. Moreover, if the Zone 3 material from Cautley is indeed *T. hadelandica deliquus*, the restriction of *T. hadelandica brachystichus* to Zones 5 and 6 (i.e. lower Rawtheyan) in northern England would add weight to Ingham's suggestion (1977, p. 118) that the uppermost part of the Sholeshook Limestone is early Rawtheyan in age. *T. convergens* has been recorded from lower

Ashgill strata at Girvan, south-west Scotland (Ingham 1970, p. 46), but the affinities of this material are not known.

The succession of subspecies of *T. hadelandica* in northern England seems to represent a single local stock and the above revision is based on this. An alternative, but more contrived hypothesis would be the ecological replacement of *T. hadelandica hadelandica* morphs. Thus the Norwegian morph C resembles early *T. hadelandica convergens*, morph B resembles late *T. hadelandica convergens*, and early *T. hadelandica deliquus* and morph A resembles *T. hadelandica brachystichus*.

As far as morph A is concerned, the absence of E_2 in some specimens, the high percentage of individuals in which I_3 is continuous frontally, and the fairly limited overlap in number of pits in I_3 serves to distinguish it from *T. hadelandica brachystichus*. Chi-squared tests show that the ranges in I_3 pits and pits missing anteriorly from this arc are distinct at the 0·1% level, even when Ingham's samples from Zones 5 and 6 are considered together. There is only a limited amount of information on *T. hadelandica convergens* and *T. hadelandica hadelandica* morph C from the Gagnum Shale but this suggests that the English form commonly has more pits in E_1 ($19\frac{1}{2}$–$22\frac{1}{2}$ cf. 18–$19\frac{1}{2}$) and along the posterior margin (7–12 cf. 6–7), but fewer in E_2 (6–11 cf. 10–13) and in all cases I_3 is complete whereas it is incomplete posteriorly in 33% (of nine specimens) of the Norwegian morph C. The English form is also distinguished by its more swollen pseudofrontal lobe. Although later



TEXT-FIG. 6. Range, mean, and sample standard deviation of selected fringe characters of members of the *Tretaspis seticornis* group in which I_3 is incomplete in at least some individuals. Data for *T. hadelandica convergens*, *T. h. deliquus*, and *T. h. brachystichus* based on histograms given by Ingham (1970), McNamara (1979), and Price (1977).

populations of *T. hadelandica convergens* and early *T. hadelandica deliquus* lack I_4, they differ from *T. hadelandica hadelandica* morph B in always having I_3 complete frontally. It seems most likely, therefore, that *T. hadelandica hadelandica* with its broad range of variation (morphs A, B, and C) and the British series of subspecies with, at any one level, a much narrower range of variation were at most connected by a series of clines throughout much of the Ashgill.

T. clarkei Cooper (*in* Schuchert and Cooper, 1930) from Ashgill units in Quebec, Canada, has two distinct sets of radii and thus belongs to the *T. seticornis* group and is not a synonym of *T. ceriodes* (cf. Whittington 1941, p. 29; Lespérance 1968, p. 813; Bolton 1970, pp. 35–36). The holotype from the Whitehead Formation and specimens figured by Bolton (1970, pl. 6, figs. 12, 15, 17, 19) from the Vauréal Formation have I_3 incomplete posteriorly at least. Of the three specimens from the Whitehead Formation in the Hunterian Museum, two (HM A4319; 4320) have eight pits in I_3 which is incomplete anteriorly. A third specimen (HM A4321) has twelve pits in I_3 which is complete anteriorly and three pits in I_4. It is not known whether the specimens are from the same horizon but all fringe features fall within the range seen in *T. hadelandica.* Detailed sampling of *T. clarkei* populations is needed before its affinities can be fully determined.

As is noted in the discussion of *T. seticornis*, specimens of *Tretaspis* with arc I_3 developed are known from the Fjäcka Shale in Sweden. In addition to Angelin's material of *T. affinis*, which has this arc complete, other specimens in the Riksmuseum, Stockholm, have I_3 incomplete but, in some cases, extensive (J. K. Ingham, pers. comm. 1976). Dr. Ingham has also examined a specimen from the Slandrom Limestone (probably early Pusgillian) in the Siljan district (Jaanusson and Martna 1948, p. 187) which has a short I_3 and a coarsely reticulate glabella and genal lobes. Dr. P. J. Brenchley of Liverpool University has sent me a specimen resembling *T. hadelandica hadelandica* morph B from the flank facies of the Boda Limestone (Ashgill) in the Siljan district and this is the only specimen of *Tretaspis* known from these beds, and the genus is not known from the Boda Limestone itself. The Swedish species of *Tretaspis* are being revised by Dr. Ingham who has taken well-localized samples from the Fjäcka Shale.

There is a great deal of other material of the *T. seticornis* group with an incomplete I_3 and in need of modern study. This includes specimens from Ashgill units in Poland ascribed to *T. seticornis* by Kielan (1957, 1960) and Tomczyk (1962), and material from the Kràlův Dvůr Formation (mid-Ashgill) in Bohemia examined by the writer in the collections of the British Museum (Natural History). Specimens from this latter unit were referred to *T. seticornis* by Havlíček and Vaněk (1966) and Přibyl and Vaněk (1969). Ingham (1970, pp. 41, 49) noted that specimens which Lamont (1935, 1941) assigned to *T. seticornis* from the Lower Drummuck Group (Cautleyan) at Girvan has a short I_3 and was termed *T.* sp. by Hughes *et al.* (1975, p. 563). Price (1977, p. 786) noted a similarity between an unnamed form from low in the Slade and Redhill Mudstones and this species. Dr. Ingham informs me (pers. comm. 1976) that *T. seticornis* of Portlock (1843) and Fearnsides, Elles, and Smith (1907) from the Killey Bridge Beds (low Cautleyan) in Pomeroy, Ireland, may well prove synonymous with the broadly coeval Lower Drummuck Group form as both have a short I_3, a very extensive E_2, and large lateral eye tubercles quite close to the glabella. Moreover, *T.* sp. probably gave rise to *T. persulcatus* (Reed, 1935) from the Upper Drummuck Group (late Rawtheyan) in which E_2 is complete and the girder is indistinct posteriorly where an external pseudogirder is developed between E_1 and E_2 (see Ingham, 1970, p. 44).

Schmidt (1894) assigned specimens to *T. seticornis* from the Lykholm Group (late Caradoc to Ashgill) in Estonia, and Jaanusson (1956, pp. 379, 383) listed the species from the lower part of the group, the Nabala Formation (late Caradoc). It is not known whether the material referred to by Jaanusson is from the same beds as Schmidt's specimens, one of which (1894, pl. 5, fig. 22) is illustrated as having I_3 complete posteriorly, but it is not clear whether two sets of radii are developed. Assuming that existing correlations are correct, the Estonian specimens listed by Jaanusson would prove the oldest record of the *T. seticornis* group should they prove correctly ascribed to it.

Tretaspis latilimbus (Linnarsson, 1869) *norvegicus* subsp. nov.

Plate 92, figs. 3–7; text-fig. 7

1887 *Trinucleus seticornis* (Hisinger) (?) var.; Brøgger, p. 26.
1887 *Trinucleus* conf. *seticornis*; Brøgger, p. 29.
1887 *Trinucleus*; Brøgger, p. 30.
1887 *Trinucleus Wahlenbergi*; Brøgger, p. 31.
?1887 *Trinucleus Wahlenbergi* Rouault; Brøgger, p. 32.
1897 *Trinucleus Wahlenbergi* Rouault; Kiaer, p. 33 [Upper Isotelus Limestone, ?‘5a’].
1930 *Tretaspis latilimbus* (Linnarsson); Størmer (*pars*), pp. 67–69 [Tretaspis Limestone specimens only], pl. 11, figs. 8, ?9, 10, 11; text-figs. 33*f*, ?*g*, *non e* [= *T. anderssoni*], *non* 34*d* [= *T. latilimbus latilimbus*].
1934 *Tretaspis latilimbus*; Størmer, p. 330.
1945 *Tretaspis latilimbus* (Linnarsson); Størmer, p. 403, pl. 1, fig. 9.

Holotype. A cephalon (PMO11751) from the Tretaspis Limestone on Lindøya, Oslo.

Material, localities, and horizons. A great deal of very fragmentary material and rarer more complete specimens occur at various levels in Oslo-Asker: Tretaspis Limestone on Langåra, Lindøya, Ostøya, and Treneholmen; Upper Tretaspis Shale on Hovedøya and Nakholmen; Upper Isotelus Limestone on Hovedøya, Langøyene, Lindøya, and Skjaerholmen; all but the upper few metres of the Husbergøya Shale Formation on Hovedøya and possibly Husbergøya, Rambergøya, and Langøyene. A specimen in limestone (?Herøya Limestone) from the Skien–Langesund district probably belongs here also.

Diagnosis. Arcs E_1, I_{1-3}, and I_n complete. I_4 short to complete, E_2 present in 41% of thirty-four specimens. Reticulation on external surface of glabella and genae subdued.

Description. Proportions of glabella and genal lobes similar to those of *T. ceriodes angelini*. There is a fine, subdued reticulation on the external surface of the mesial part of the glabella and the adaxial parts of the genal lobes, but they are smooth on internal moulds. Arcs E_1, I_{1-3}, and I_n are complete, and I_4 is developed in all specimens, most having 3–11½ pits (twenty-four specimens) in this arc but one extreme specimen from the Tretaspis Limestone has this arc complete. Two morphs (A and B) are defined on the absence or presence

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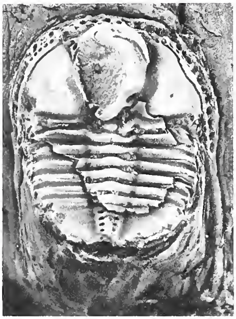
EXPLANATION OF PLATE 91

Figs. 1–4. *Tretaspis hisingeri* sp. nov. 1, 2, holotype, PMO H51, dorsal and lateral views of partially exfoliated almost complete specimen, 3·5–4·0 m below top of Frognøya Shale, Frognøya, Ringerike, ×2¾, ×2; also figured by Størmer (1930, text-fig. 47). 2, PMO80613, frontal view of partially exfoliated cranidium, Frognøya Shale, Ringsåsen, Norderhov, Ringerike, ×2. 4, PMO103957, dorsal view of cast of complete meraspis degree 4, 7·91–7·94 m above base of Lower Tretaspis Shale, Ole Deviks Vei, Oslo, ×12½.

Figs. 5–14. *Tretaspis hadelandica hadelandica* Størmer. 5, 8, 11, holotype, morph B, PMO65187, dorsal, frontal, and lateral views of partially exfoliated cephalon, probably from the Gagnum Limestone Formation, south of Gagnum, Hadeland, ×2; also figured by Størmer (1945, pl. 1, fig. 4). 6, morph B, PMO98489, dorsal view of lower lamella external to girder showing E_2 complete frontally, upper part of Lunner Formation, Kjevlingen, Hadeland, ×3½. 7, morph C, PMO103958, anterolateral view of partially exfoliated cranidium, Gagnum Limestone Formation, 500 m south-east of Lunner Bakken, Hadeland, ×4½. 9, morph A, PMO99537, oblique anterolateral view of cast of cranidium, 7·1–7·2 m below top of Gagnum Shale Member of the Lunner Formation, 75 m south of Roko, Hadeland, ×5. 10, PMO103959, dorsal view of unwhitened pygidium, lower part of Lunner Formation, 400 m east-south-east of Lunner Kirke, Hadeland, ×8. 12, PMO101483, dorsal view of internal mould of pygidium, Gagnum Limestone Formation, Ballangrud, Hadeland, ×4. 13, PMO103960, dorsal view of unwhitened thorax and pygidium, lower part of Lunner Formation, Haga, Hadeland, ×4. 14, morph A, PMO65193, dorsal view of partially exfoliated almost complete specimen, Gagnum Shale Member of the Lunner Formation, Gagnum, Hadeland, ×3½; also figured by Størmer (1945, pl. 4, fig. 16).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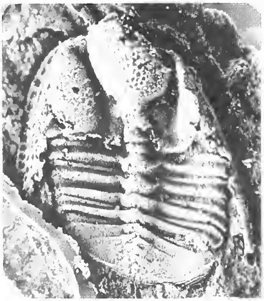
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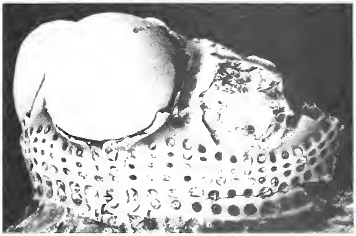
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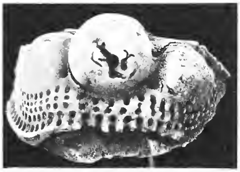
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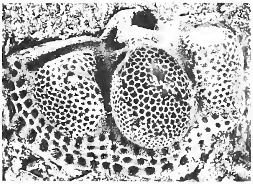
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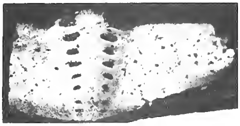
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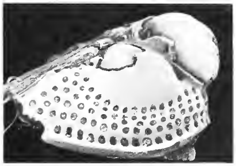
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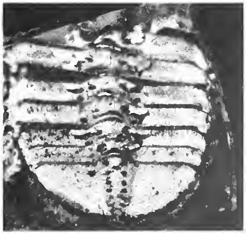
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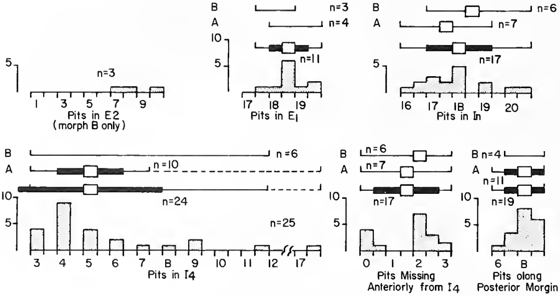
OWEN, trilobite *Tretaspis*

respectively of E_2 which occurs in 41% of the thirty-four specimens in which this feature could be determined (Table 1). As in all species of *Tretaspis* the most posterior one or two E_1 pits always lack equivalent E_2 pits. The range of variation in fringe pitting is illustrated on text-fig. 7. Arcs I_1, E_1, and, where present, E_2 are out of phase with the remaining I arcs and share sulci which extend to the anterolateral part of the fringe or even to the zone of complication. The available samples are too small to detect differences from rock unit to rock unit and both morphs are known from all but the lower part of the Husbergøya Formation. Personally collected material from the Upper Tretaspis Shale shows both morphs in the same bed.

Hypostoma unknown. Thorax similar to that of *T. seticornis*.

Pygidium only known with certainty from a few fragments. The one figured by Størmer (1930, pl. 11, fig. 9) may belong here or to *T. sortita broeggeri* (see below) as the precise horizon in the Husbergøya Formation is not known. This specimen has ten pairs of apodemal pits, the posterior three lying on the pygidial border.



TEXT-FIG. 7. Histograms showing range of variation in fringe features of all available specimens of *Tretaspis latilimbus norvegicus* with a comparison, where possible, of the range, mean, and sample standard deviation of the two morphs (A and B) present in the subspecies. In many instances the samples are too small for reliable standard deviations or even means to be calculated.

Discussion. Ingham (1970, p. 50, text-fig. 18*a*, *b*) chose a lectotype from Linnarsson's original material of *T. latilimbus* from the Upper Johnstorp Formation (Rawtheyan) of Västergötland, Sweden, and he figured a number of topotypes (1970, text-fig. 18*c*–*f*). Dr. Ingham has allowed me to collate some of his data on topotype material of the Swedish form in the collections of the Riksmuseum, Stockholm. All these specimens have an incomplete I_4 arc (2–11 pits in forty-two specimens) which is not continuous mesially. Where the E arc development is sufficiently well preserved, only one specimen out of thirty-five is seen to have pits in E_2 and thus the vast majority correspond to the development seen in *T. latilimbus norvegicus* morph A. The range of variation seen in the pit distribution of other arcs is similar to that of the Norwegian material and it is most likely that the Swedish form is simply a geographical subspecies of *T. latilimbus norvegicus* in which morph B has been virtually excluded. Fragments of *Tretaspis* from the Ulunda Formation (Rawtheyan) in Västergötland have a pit development similar to that of *T. latilimbus norvegicus* morph B (J. K. Ingham, pers. comm. 1976).

T. 'latilimbus' distichus Ingham (1970, p. 50, pl. 7, figs. 8–16, text-figs. 14*g*, 16) was based on material from the Rawtheyan Stage (Ashgill Zone 7) in the Cautley district of northern England and is characterized by the presence of a short I_4 and seven to ten pits in E_2. It thus resembles *T. latilimbus norvegicus* morph B and might be regarded as being a subspecies which developed in the same way as *T. latilimbus latilimbus*. However, Ingham (1970, p. 50) suggested that *T. 'latilimbus' distichus* may have been derived from *T. hadelandica brachystichus* with the completion of I_3 and the development of a short I_4. Indeed, one specimen of the latter was noted by Ingham to have a pit in I_4. When the ranges in variation in E_2 and I_3 in *T. hadelandica brachystichus* are considered for Zones 5 and 6 separately (text-fig. 6; Ingham 1970, text-fig. 16) there is a suggestion of a trend towards the condition seen in *T. 'latilimbus' distichus*. Moreover, McNamara (1979, p. 63) has noted the occurrence of specimens which he terms *T.* aff. *latilimbus distichus* from the White Limestone (top of Zone 6) in the Lake District which he considers to be intermediate between *T. hadelandica brachystichus* and *T. 'latilimbus' distichus*. Dr. McNamara informs me (pers. comm. 1979) that the White Limestone form has I_3 complete posteriorly and in some specimens there is a single pit in I_4. Thus it seems likely that the Zone 7 form is not directly related to *T. latilimbus* and ultimately may best be considered a stratigraphical subspecies of *T. hadelandica*.

The origins of *T. latilimbus* are not clear but *T. hadelandica hadelandica* seems to be the most likely ancestor.

Tretaspis sortita (Reed, 1935) *broeggeri* Størmer, 1945

Plate 92, figs. 8–11, 13, 14; text-fig. 8

?1887 *Trinucleus Wahlenbergi* Rouault; Brøgger, p. 32.
?1897 *Trinucleus Wahlenbergi* Rouault; Kiaer, pp. 32 (*pars*, '4dδ' specimens only), 73.
1945 *Tretaspis latilimba* (Linnarsson) var. *brøggeri* Størmer, p. 403, pl. 1, fig. 10.
1979 *Tretaspis sortita* (Reed) *broeggeri* Størmer; Owen, p. 257.

Holotype. An incomplete cephalon (PMO11957) from the upper part of the Husbergøya Shale Formation on Skjaerholmen, Oslo.

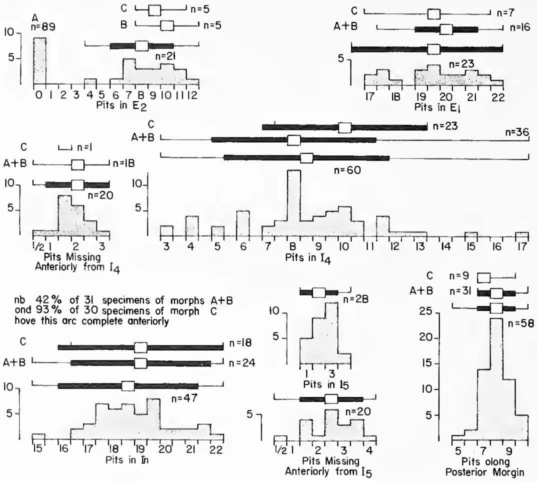
Material, localities, and horizons. Cephala, cranidia, and rare thoracic segments are known from the upper few metres of the Husbergøya Formation in Oslo, on the islands of Skjaerholmen, Husbergøya (upper 2 m), Hovedøya (upper 2·5 m), South Langøyene (upper 5 m), Lindøya, and Gressholmen.

Description. Glabella and genal lobes similar to those of *T. ceriodes angelini* but bear a variably developed, subdued, fine reticulation on the external surface (on the genal lobes this is restricted to the posterior parts) and are smooth on internal moulds. Fringe steeply declined with a well-developed anterior arch and a distinct brim laterally. Arcs E_1, I_{1-3}, and I_n are complete, I_4 is incomplete, and three morphs are recognized on the basis of the E_2 and I_5 development (Table 1) thus: morph A lacks E_2 and I_5, morph B lacks I_5 but has a short E_2, morph C has both E_2 and I_5 present but incomplete. The range of variation in pit development is shown on text-fig. 8. There are too few specimens to give meaningful comparisons of some of the parameters in the three morphs separately, and in some instances morphs A and B are considered together on text-fig. 8. Arc E_2 is irregularly developed in a few specimens (e.g. Pl. 92, figs. 8, 10) but in most cases where it is present it is restricted to the posterior part of the fringe. In all morphs, arcs I_1–E_1 share sulci to bR2–8 (mean bR5, sample standard deviation 1, eighteen specimens) and distinct lists are developed between most arcs over the whole fringe except E_1–I_1, where they share sulci and between E_1 and E_2 and also I_5 and I_n. Two sets of radii are developed.

Hypostoma not known. Thorax and pygidium known only from a few poorly preserved fragments.

Discussion. The holotype of *T. sortita broeggeri* has eleven pits in E_2 and one in I_5, and thus is of morph C type. Morphs A and B are indistinguishable from the two morphs constituting *T. latilimbus norvegicus* although their relative abundances are very different with E_2 being developed much more commonly in *T. sortita broeggeri*. Størmer's subspecies probably was derived from *T. latilimbus norvegicus* with the development of I_5 in some individuals and replaces the earlier form quite abruptly in the Husbergøya Formation, although it is not possible to assign unequivocally isolated specimens of morphs A and B to either form.

T. sortita sortita (Reed, 1935, pp. 3–6, pl. 1, figs. 4–10; see also Begg 1944, pp. 114, 115, pl. 5, figs. 2–7) was based on material from the Upper Drummuck Group (late Rawtheyan) at Girvan, south-west Scotland. A complete topotype specimen was figured by Ingham (1970, pl. 8, fig. 1) who noted (1970, p. 50) that the Scottish form has an incomplete E_2, an extensive but incomplete I_4, and a few pits in I_5. Dr. Ingham has informed me (pers. comm. 1976) that the vast majority of specimens from



TEXT-FIG. 8. Histograms showing the range of variation in fringe features of all available specimens of *Tretaspis sortita broeggeri* with a comparison of the range, mean, and sample standard deviation of the three morphs (A, B, and C) present in the subspecies. Owing to the limited amount of data for morphs A and B, these are considered together in most instances.

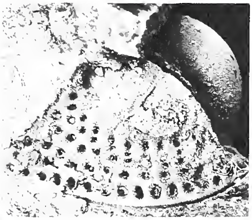
EXPLANATION OF PLATE 92

Figs. 1, 2. *Tretaspis hadelandica hadelandica* Størmer. PMO103961, right and left lateral views of internal mould of cranidium showing asymmetrical I_3 development, lower part of Gagnum Shale Member of the Lunner Formation, 200 m north of Åslund, Hadeland, ×8.

Figs. 3–7. *Tretaspis latilimbus* (Linnarsson) *norvegicus* subsp. nov. 3, holotype, ?morph A, PMO11751, anterolateral view of incomplete cephalon, Tretaspis Limestone, Lindøya, Oslo, ×4; also figured by Størmer (1945, pl. 1, fig. 9). 4, morph B, PMO101551, anterolateral view of partially exfoliated cranidium, same horizon as 3, west Rambergøya, Oslo, ×3. 5, morph A, PMO80518, oblique anterolateral view of internal mould of cephalon, Husbergøya Shale Formation, North Langøyene, Oslo, ×3. 6, morph A, PMO103962, dorsal view of internal mould of cephalon and part of thorax, Upper Tretaspis Shale, north Hovedøya, Oslo. 7, morph B, PMO80573, oblique posterolateral view of cephalon, same horizon as 3, Ostøya, Baerum, ×3.

Figs. 8–11, 13, 14. *Tretaspis sortita* (Reed) *broeggeri* Størmer. 8, morph B, PMO31010, anterolateral view of internal mould of incomplete cephalon showing irregular E_2 development, upper part of Husbergøya Shale Formation, South Langøyene, Oslo, ×2½. 9, holotype, morph C, PMO11957, lateral view of internal mould of incomplete cephalon, same horizon as 8, Skjaerholmen, Oslo, ×4½; also figured by Størmer (1945, pl. 1, fig. 10). 10, PMO100720, ventral view of cast of lower lamella, pygidium, and thorax, top of Husbergøya Shale Formation, Rambergøya, Oslo, ×2½. 11, 14, morph C, PMO103963, frontal and anterolateral views of cast of cephalon, same horizon as 8, Hovedøya, Oslo, ×3. 13, morph C, PMO103964, posterior view of cast of crushed cephalon and incomplete thorax, note weak reticulation on posteromesial parts of genal lobe, upper 2 m of Husbergøya Shale Formation, Husbergøya, Oslo, ×4.

Figs. 12, 15. *Tretaspis askerensis* sp. nov. 12, PMO64649, frontal view of cast of crushed cranidium, middle part of Grina Shale Member of the Lunner Formation, Grina, Hadeland, ×4; also figured by Størmer (1945, pl. 1, fig. 1). 15, PMO6376, posterolateral view of cast of incomplete cephalon, from either the lower part of the Langåra Limestone-Shale Formation or the Husbergøya Shale Formation, Hvalstad, Asker, ×6.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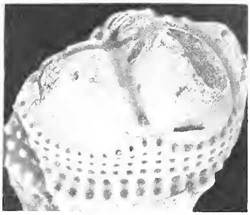
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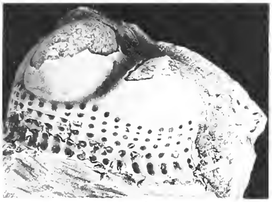
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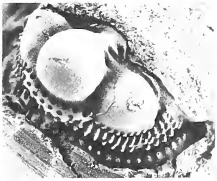
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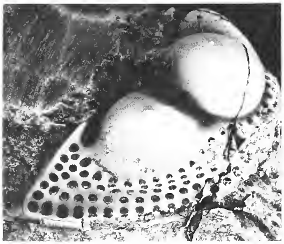
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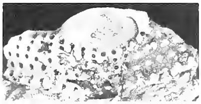
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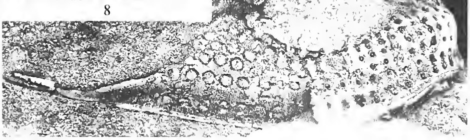
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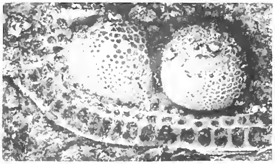
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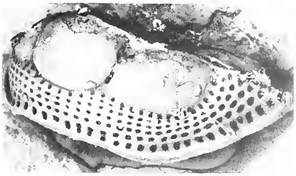
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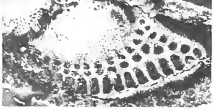
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OWEN, trilobite *Tretaspis*

Girvan are of this type and are very similar, if not identical, to the Norwegian morph C. Thus *T. sortita broeggeri* differs from the Scottish form only in the proportions of constituent morphs.

Price (1977, pp. 784–785, pl. 103, figs. 1–7; text-fig. 2) assigned material to *T. sortita* from late Ashgill mudstones in the Meiford area and commented on other Welsh material probably belonging to this species. The specimens which he described have E_2 developed and only one out of seven lacks pits in I_5. Unlike both the Norwegian and Scottish forms, the genal lobes are completely smooth, arcs I_1–E_1 share short sulci in only a few specimens and lists are less well developed.

Dr. Ingham informs me (pers. comm. 1976) that one specimen of *Tretaspis* from the type unit and locality of *T. latilimbus latilimbus*, the Upper Johnstorp Formation in Västergötland, has a short I_5 developed (four pits). The E pits are not preserved but the specimen may well be of *T. sortita* type and further, well-localized, collections may enable greater correlation between the Swedish, Norwegian, and British upper Ashgill sequences.

Tretaspis askerensis sp. nov.

Plate 92, figs. 12, 15; Plate 93, figs. 1–5.

1902 *Trinucleus Wahlenbergi* Rouault; Kiaer, p. 78.
1945 *Tretaspis seticornis* (Hisinger) forma typica; Størmer, p. 406, pl. 1, fig. 6.
1978 *Tretaspis* aff. *seticornis seticornis* (Hisinger); Owen, p. 15.

Holotype. A cranidium (PMO100657) from either the Husbergøya Shale Formation or the lower part of the Langåra Limestone-Shale Formation (i.e. '5a' of Brenchley and Newall 1975) Holmenskjaeret, Holmen, Asker.

Material, localities, and horizons. Four incomplete cranidia from the type horizon and locality, a cephalon probably from '5a' at Øvre Nes badestrand, a cranidium possibly from this unit at Hvalstad, three cranidial fragments from 2–3 m above the base of the Husbergøya Formation on Brønnøya and 1–4 m above the base of this unit on Langåra, all Asker. Two cranidia from the lowest 13 m of the Husbergøya Formation on Kalvøya, Baerum. Three fragmentary cranidia from a channel conglomerate in the upper part of the Langåra Formation on Ostøya, Baerum (indicating transport from the west), and one external mould of a cephalon from the Grina Shale Member of the Lunner Formation at Grina Hadeland.

Diagnosis. Pseudofrontal lobe strongly swollen, almost circular in dorsal view. Arcs E_1, I_1, I_2, and I_n complete. A short I_3 is present in a few specimens. I_1–E_1 sulci deep. E_2 short or absent.

Description. Most specimens of this form are noticeably smaller than those of other Norwegian species but the material is too incomplete to quantify this adequately. Pseudofrontal lobe strongly swollen, almost circular in dorsal view but otherwise the proportions of the glabella and genae very similar to those of *T. ceriodes angelini*. The external surface of the glabella and genae bears a well-developed reticulation which is very fine except on the posteromesial parts of the genal lobes where it is coarser. Some internal moulds fairly strongly reticulate. Fringe steeply declined. Arcs E_1, I_1, I_2, and I_n complete. E_2 developed in two specimens (of four) where it comprises up to six pits. I_3 present in two specimens (of seven) where it contains two or three pits, beginning at about aR3. There are eight pits along the posterior margin of the fringe in three specimens. There are nineteen pits in I_n in one topotype specimen and the Grina Shale cephalon and $16\frac{1}{2}$ in a specimen from Kalvøya. Arcs E_1 and I_1 share deep sulci over all but the posterior part of the fringe and are out of phase with the remaining I arcs.

Remainder of exoskeleton unknown.

Discussion. The fringe development of *T. askerensis* resembles that of *T. seticornis* and the Grina Shale specimen was assigned to this species by Størmer (1945) and Owen (1978). *T. askerensis* differs in its deep I_1–E_1 sulci, in having I_3 developed in a few specimens, in having eight (cf. six or seven) pits along the posterior margin, and the number of pits in I_n extends beyond the maximum recorded for *T. seticornis*. Clearly the very limited number of specimens of both species makes objective comparison very difficult. The more circular outline of the pseudofrontal lobe and much stronger reticulation also distinguish the younger species although the latter character may have little taxonomic value (see Price 1977, p. 781). *T. seticornis* has a very short stratigraphical range, being restricted to low Pusgillian strata in both Norway and Sweden. *T. askerensis* occurs in Rawtheyan units and probably was derived from, for example, *T. hadelandica hadelandica* or *T. latilimbus norvegicus*. The relatively small size, well-developed reticulation (see Størmer 1930, p. 65) and simple fringe morphology suggest a neotenous origin for the species.

Tretaspis sagenosus group?

Tretaspis kiaeri Størmer, 1930

Plate 93, figs. 6–15; text-fig. 9

1921 *Trinucleus*; Kiaer, p. 500.
1930 *Tretaspis kiaeri* Størmer, pp. 50–55, pl. 10, figs. 1–6; pl. 11, fig. 12; pl. 13, fig. 13; pl. 14, figs. 1–3; text-figs. 21*c*, 23–26, 38.
1945 *Tretaspis kiaeri* Størmer; Størmer (*pars*), p. 403, pl. 1, fig. 12; *non* pp. 387, 406, pl. 1, fig. 11 [= *T. hadelandica hadelandica*].
1953 *Tretaspis kiaeri*; Størmer, p. 87.
1959 *Tretaspis kiaeri* Størmer; Harrington *in* Moore, text-fig. 70*c*.
non 1966 *Tretaspis kiaeri* Størmer; Whittington, pp. 90–92, pl. 28, figs. 1, 6–12, 14.
non 1968 *Tretaspis kiaeri* Størmer; Whittington, p. 93, pl. 29, figs. 1, 2, 4.
1975 *T. kiaeri* Størmer; Hughes *et al.*, p. 563.
non 1975 *T.* aff. *kiaeri*; Hughes *et al.*, p. 563.
1979 *Tretaspis kiaeri* Størmer; Owen, pp. 250, 251, 252, text-fig. 6.
1979 *Tretaspis kiaeri* Størmer; Bruton and Owen, text-fig. 6.

Holotype. An almost complete internal mould of a cephalon (PMO H197) from the Høgberg Member of the Solvang Formation, Frognøya, Ringerike.

Material, locality, and horizon. The species is known only from the type horizon and locality from which many hundreds of disarticulated skeletal elements are known.

Description. Proportions of glabella and genal lobes similar to those of *T. ceriodes angelini* except that the glabella is a little more inflated and overhangs the fringe a little. Reticulation variable. On the glabella it is coarsest around the median node and extends to a transverse line at the maximum width (tr.) of the occiput. The reticulation of the genal lobes is finer and more subdued than that of the mesial part of the glabella and becomes finer abaxially. On some internal moulds there is a faint reticulation on the genal lobes and, less commonly, the glabella. Fringe steeply declined laterally, less so across I_n mesially, in front of which it is vertical. Arcs E_{1-2}, I_{1-3}, and I_n complete mesially and posteriorly. I_4 is continuous mesially but extends to the posterior margin in only 5% of sixty-one specimens. Two morphs are defined on the absence (A) or presence (B) of I_5 which occurs in 35% of eighty-one specimens and extends mesially in 22% of the twenty-three specimens in which its frontal extent can be determined (Table 1). The range of variation in selected fringe characters is shown on text-fig. 9. Two sets of radii are developed and pits in the outer set, I_1, E_{1-2}, share sulci to the posterior part of the fringe in some specimens but in a few this sulcation is less extensive and I_1 becomes discrete as far forwards as bR5. Very fine lists are developed between all I arcs except I_4 and I_5.

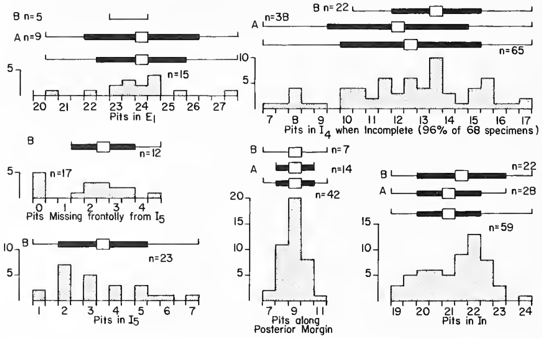
Hypostoma unknown. Thorax similar to that of *T. seticornis*, although it is not known whether or not median tubercles are present. The pygidial rachis commonly has up to six transversely directed furrows bearing deep apodemal pits distally. These furrows are progressively less well incised rearwards along the rachis and on well-preserved specimens (Pl. 93, fig. 9; Størmer 1930, pl. 10, fig. 4) a further three to five pairs of apodemal markings are seen, the posterior two or three pairs being situated on the anterior part of the border. Three pairs of weakly developed pleural ribs present.

Discussion. Whittington (1966, 1968) ascribed specimens from the Ashgill of Wales to *T. kiaeri*. One of these (1966, pl. 28, fig. 13) was referred to *Nankinolithus* Lu by Hughes *et al.* (1975, p. 559). The remainder comprise at least three distinct forms of *Tretaspis* and have been reassessed by Price (1977, pp. 786–787) who considered specimens from the Rhiwlas Limestone (probably Rawtheyan) figured by Whittington (1968, pl. 28, figs. 12, 16) to be similar to *T. calcaria* Dean, 1971, a form described originally from the Chair of Kildare Limestone (probably Rawtheyan) in Eire. *T. calcaria* is almost certainly related to *T. kiaeri* but differs in having I_4 always complete posteriorly, I_5 more extensive, and all complete arcs have a higher pit count (e.g. 30–31 cf. $20\frac{1}{2}$–$27\frac{1}{2}$ in E_1). As noted by Price, the poorly preserved Rhiwlas Limestone material is difficult to compare with Dean's species but differences in fringe pitting seem slight.

Other British and Irish forms previously assigned to *T. kiaeri* have been reassessed by Ingham (1970, pp. 44–57) and Price (1974, pp. 844–847; 1977, pp. 766–778). Most are clearly members of the *T. moeldenensis* group and thus are distinguished from *T. kiaeri* primarily in having complete radial alignment of the fringe pits. A few are *T. seticornis* group members and have E_2 incomplete mesially.

EVOLUTION OF THE *TRETASPIS SETICORNIS* GROUP

The study of populations of *Tretaspis* from Norway indicates that the phylogenetic relationships are more complex than was thought previously and that a purely typological approach to their taxonomy is not possible. Nevertheless, the broad evolutionary history of the *T. seticornis* group is becoming clear (text-fig. 1).

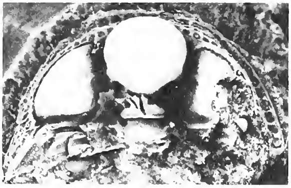


TEXT-FIG. 9. Histograms showing the range of variation in fringe features seen in all available specimens of *Tretaspis kiaeri* with a comparison of the range, mean, and sample standard deviation of the two morphs (A and B) present in the species.

EXPLANATION OF PLATE 93

Figs. 1–5. *Tretaspis askerensis* sp. nov. 1–3, holotype, PMO100657, dorsal, lateral, and anterolateral views of partially exfoliated cranidium, Husbergøya Shale Formation, or lower part of Langåra Limestone-Shale Formation, Holmenskjaeret, Holmen, Asker, × 7. 4, PMO80463, anterolateral view of partially exfoliated cranidium, same horizon and locality as 1–3, × 10. 5, PMO100878, cast of flattened incomplete cephalon, probably from the type unit, Øvre Nes badestrand, Nesbru, Asker, × 6.

Figs. 6–15. *Tretaspis kiaeri* Størmer, Høgberg Member of the Solvang Formation, Frognøya, Ringerike. 6, 10, holotype, morph B, PMO H197, dorsal and frontal views of internal mould of cephalon, × $3\frac{1}{2}$; also figured by Størmer (1930, pl. 10, fig. 1). 7, morph B, PMO H338, lateral view of internal mould of cephalon, × 3; also figured by Størmer (1930, pl. 10, fig. 3). 8, PMO103965, dorsal view of cast of pygidium and incomplete thorax, × $4\frac{1}{2}$. 9, PMO103966, dorsal view of internal mould of pygidium, × $4\frac{1}{2}$. 11, morph A, PMO103967, anterolateral view of internal mould of incomplete cephalon, × 2. 12, morph A, PMO H208, posterolateral view of incomplete partially exfoliated cranidium showing pitting along the marginal band, × 4; also figured by Størmer (1930, pl. 11, fig. 12). 13, PMO103968, slightly oblique dorsal view of cast of glabella and left genal lobe, note glabellar reticulation, × $4\frac{1}{2}$. 14, morph B, PMO103969, dorsal view of internal mould of cephalon and part of thorax, same specimen as 8, × 4. 15, morph B, PMO354, oblique anterolateral view of cephalon, × 3; also figured by Størmer (1945, pl. 1, fig. 12).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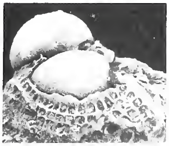
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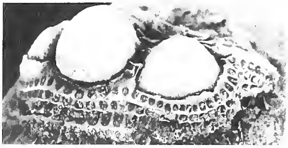
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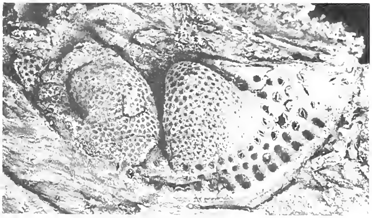
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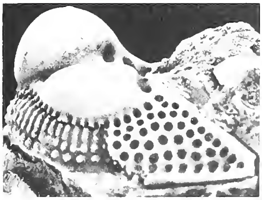
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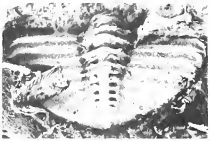
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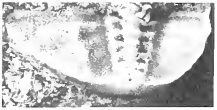
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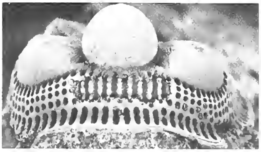
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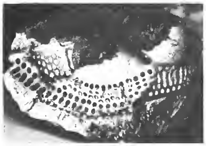
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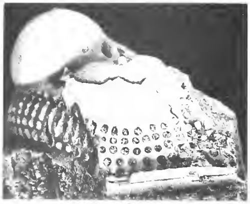
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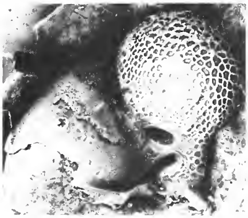
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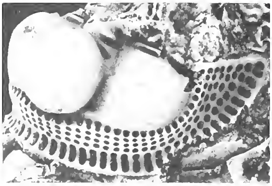
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OWEN, trilobite *Tretaspis*

The earliest known species of *Tretaspis* from the Anglo-Welsh and Scandinavian areas is *T. ceriodes* which is restricted to latest Caradoc units in all these areas. The species is polymorphic in Norway and almost certainly gave rise to the *T. seticornis* group, the replacement of the former by the latter being geologically instantaneous and an excellent tool in recognizing the Caradoc-Ashgill boundary (Owen 1979, p. 251). The earliest representatives of this group are distinct in different areas with *T. hadelandica* in England and Hadeland and *T. seticornis* in Oslo-Asker, Ringerike, and Sweden. This rapid speciation involved the development of two sets of pit radii and, with the exception of some members of early *T. hadelandica* populations, the restriction of E_2 to the lateral parts of the fringe. The polymorphic nature of the ancestral *T. ceriodes* populations accounts for all other fringe features of the early *T. seticornis* group forms. Local populations of *T. hadelandica* became isolated very early on, giving rise to what are interpreted as geographical subspecies. The *T. moeldenensis* group persisted into the Ashgill in Britain but not in Scandinavia.

In Britain, *T. hadelandica* is now interpreted as ranging from earliest Pusgillian to mid/late Rawtheyan with a series of stratigraphical subspecies showing a progressive simplification of fringe characters (*T. h. convergens*—*T. h. deliquus*—*T. h. brachystichus*) followed by a slight reversal of this trend within *T. h. brachystichus* which may have been continued with the development of *T. 'latilimbus' distichus*. This reinterpretation strengthens the stratigraphical usefulness of the British forms especially in view of the long-ranging homeomorphs present in Norway. The origins of the Irish and Scottish *T.* sp. from which *T. persulcatus* were descended are unclear.

In Hadeland, *T. hadelandica hadelandica* persisted from early Pusgillian to Rawtheyan times, and although there are differences in the percentages of constituent morphs in different units, these are considered to reflect ecological rather than temporal controls. *T. hadelandica* may have given rise to a homeomorph of *T. seticornis*, *T. askerensis* which occurs in Hadeland and Asker.

In Oslo-Asker, Ringerike, and Sweden, *T. seticornis* has a short stratigraphical range and gave rise to another short ranging form, *T. hisingeri*. In Ringerike, *T. seticornis* also gave rise to *T. anderssoni*, a form which has a very narrow range of variation throughout its range from mid-Pusgillian to early Rawtheyan. In Oslo-Asker, *T. hisingeri* is replaced by *T. latilimbus norvegicus*, a polymorphic form of uncertain origin which extends well into the Rawtheyan and which almost certainly gave rise to *T. sortita broeggeri*. One of the morphs constituting *T. latilimbus norvegicus* is by far the dominant form in the nominate subspecies which is a Swedish taxon developed during the Rawtheyan. Populations of *T. sortita sortita* from the late Rawtheyan of Scotland differ from *T. sortita broeggeri* in the proportions of constituent morphs.

There is still very little information on bed-by-bed changes in populations of *Tretaspis*, and the Norwegian material is not sufficiently abundant for such a study. There is a suggestion that the development of phenotypes in *T. ceriodes angelini* is to some extent progressive but as far as morphs B, C, and D are concerned this represents no more than an increase in the upper limit of the range of variation. Many forms have long stratigraphical ranges within which there is no directional change. The only likely example of evolutionary trends are the zigzag evolution seen in the British *T. hadelandica* subspecies and the introduction of a third morph to produce *T. sortita broeggeri* from *T. latilimbus norvegicus*. The latter change was fairly abrupt as was the development of the *T. seticornis* group itself. There is insufficient evidence to say whether or not the changes in the British subspecies of *T. hadelandica* are gradual. Neoteny is thought to have produced two species, *T. hisingeri* and *T. askerensis* and probably also *T. ceriodes* from the *T. sagenosus* group.

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A TECHNIQUE FOR REVEALING THE STEREOM STRUCTURE OF FOSSIL CRINOIDS

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Abstract. The stereom of fossil crinoid ossicles preserved in an argillaceous matrix can be revealed by treating them with hydrofluoric acid. The clay filling the stereom pores is dissolved and the skeletal calcite is faithfully replaced by fluorite. Features discovered in selected Lower Carboniferous crinoid ossicles prepared by this method include the following: large canals penetrating the areola in the columnals of a particular inadunate crinoid; triple aboral nerve canals, and labyrinthic stereom in the muscle fossae of distinctive inadunate brachials; and a regular arrangement of trabeculae forming a cubic structure in the stereom of flexible crinoid brachials.

Over the last decade, there have been a number of studies of the detailed morphology of recent echinoderm ossicles, using scanning electron microscopy. Of these, we pick out the surveys of crinoid microstructure by Macurda and Meyer (1975, 1976) and the extensive investigations of the crinoid stem by Roux (1970, 1971, 1974*a*, 1974*b*, 1975) as having particular significance for fossil crinoid studies. In all of these studies the architecture of the stereom has been shown to have a functional significance. Unfortunately the details of the stereom are difficult to discern in most fossil material, because carbonate cements precipitated epitaxially on the skeletal calcite occlude the stereom pore spaces. In some examples, however, the stereom is clearly visible in thin section. The most common cases of this are when the stereom pores are filled by an iron-rich carbonate cement (which can be differentiated by staining), or by micritic sediment or cement, or by iron sulphides or oxides, or by clay minerals. When such mineralogical or textural differences are exploited by natural weathering or by controlled acid etching, the three-dimensional stereom architecture may be revealed: Lane and Macurda (1975) established the presence of muscular articulation in naturally weathered brachials of the Pennsylvanian cladid crinoid, *Aesiocrinus*; and Lapham, Ausich, and Lane (1976) have illustrated the structure of the stereom of Mississippian crinoid ossicles which had been etched in weak formic acid.

Whilst trying to recover miopores from a Carboniferous marine shale, we accidentally discovered that some crinoid ossicles treated with hydrofluoric acid (HF) showed surprisingly detailed microstructure: clay filling the stereom pores was dissolved and the calcite of the ossicles was faithfully replaced by fluorite, a process which has been named fluoridization by Upshaw, Todd, and Allen (1957, p. 793). The use of hydrofluoric acid in the preparation of calcareous fossils has been independently (and often accidentally) discovered several times (Cookson and Singleton 1954; Grayson 1956; Wetzel 1921). Most stress has been laid on the translucent nature of fluoridized fossils when they are immersed in liquid. Sohn (1956) was able to make visible ostracode muscle scars by treating the valves with HF, and Upshaw *et al.* (1957) illustrated the internal structures of fluoridized foraminifers. Sprinkle and Gutschick (1967) used HF to prepare blastoids preserved in a fine-grained sandstone.

We have applied the fluoridization technique to Carboniferous crinoid material preserved in a variety of rock types, ranging from plastic clays of the mid-western United States to indurated silty mudstones from Ireland. Examples of the results obtained are shown in Plates 94 and 95.

[Palaeontology, Vol. 23, Part 4, 1980, pp. 749–756, pls. 94–95.]

METHODS

The material for which the fluoridization technique is most effective is that preserved in clay mudstones or shales where the clay has penetrated deeply into the stereom pores. We have generally used bulk samples rather than attempting to fluoridize particular individual specimens, because of the risk of damage. However, most of the microcrinoids described by Lane and Sevastopulo (in press) were first picked from washed clays and then fluoridized.

It is worth while to remove as much matrix from the sample as possible. Soft clays may be disaggregated by being air-dried, soaked in paint thinner or paraffin, and then vigorously boiled in water with soda ash. More indurated mudstones and shales may require simmering in Quaternary 'O' (Zingula 1968), but since that detergent is weakly acid, prolonged treatment results in some etching of skeletal calcite; we prefer to treat particularly intractable samples directly with HF.

The partially cleaned fossil material is reacted with HF; the optimum strength of the acid and length of the reaction time vary from sample to sample. We have used 48% HF and reaction times of between 5 minutes and 1 hour for small specimens; for larger specimens weaker acid (approximately 6%) and longer reaction times (up to 24 hours) as advocated by Grayson (1956, p. 78) lead to better results. The fluoridization can be judged to have proceeded far enough when the surfaces of the ossicles appear bleached; it is not necessary to convert whole ossicles to fluorite.

Two adverse effects can occur during fluoridization. Firstly, the ossicles may crack and pieces may spall off. This can be largely avoided by reducing the reaction time to a minimum and by diluting the acid. Secondly, a glaze-like precipitate of fluorite may form on the surface of the ossicles. This can be prevented by using a large enough quantity of acid (we have found five times the volume of material being fluoridized a suitable amount). When the specimens have been fluoridized, they should be thoroughly washed and dried. Specimens for study under the scanning electron microscope should be transferred to stubs immediately, because their delicate surfaces can be easily damaged by abrasion.

Although we have been interested principally in the preparation of crinoid material, our bulk samples have contained many other fossils, most of which appear perfectly preserved after fluoridization. We believe that the technique may have general application in cleaning small fossils for study under the scanning electron microscope.

Because hydrofluoric acid is extremely dangerous, the fluoridization process should always be carried out in a properly designed fume cupboard with an efficient extraction system, by an operator wearing protective clothing, rubber gloves, and a face-mask. The reaction between the sample and the acid may be very vigorous, and large amounts of carbon dioxide may be generated rapidly. It is important, therefore, to treat the sample in an adequately large polythene vessel to prevent froth from forming and spilling out. We fluoridize approximately 10 g of bulk sample in an 80 mm-diameter 400 ml polythene beaker.

COMMENTS ON THE SPECIMENS ILLUSTRATED

The four ossicles illustrated in Plates 94 and 95 were obtained from a bulk sample of the soft clay shale above the Charlestown Main Limestone, collected near the bathing pool, St. Monance, Fife, Scotland (National Grid Reference NO 536 020). The shale is of Lower Carboniferous (Brigantian) age and has been correlated with the Neilson Shell Band (George *et al.* 1976, fig. 14, p. 53). The sample was partly disaggregated by being soaked in paraffin, and then boiled in water with soda ash. Small amounts of the disaggregated material were reacted with 48% HF for 1 hour. The fluoridized ossicles were mounted on stubs and coated with carbon and a gold palladium mixture, and were examined using an ETEC Autoscan, Model H-1, scanning electron microscope. The diameters of stereom pores were measured on enlarged scanning electron micrographs and the surface porosity by point counting along two mutually perpendicular axes as suggested by Macurda and Meyer (1975, p. 2). The terminology used is from Ubaghs (1978, T. 58 et seq.). The illustrated specimens and other representative material are reposited in the palaeontological collections of Trinity College, Dublin (catalogue numbers prefixed TCD).

Pentagonal columnals (TCD 19861-3) (Pl. 94, figs. 1, 3)

Columnals of this kind are moderately abundant in the sample. The longest pluricolumnal found consists of a nodal between two pairs of internodals. The nodal is cirrus-bearing and approximately

0·8 times as long as wide; the internodals are of two orders with length to width ratios of 0·4 and 0·6. The sides of the columnals are straight, or have a ridge or swelling around the equator, a feature particularly well developed on the nodals. Each nodal has one or two cirral sockets positioned between the equator and the joint surface. The sockets are comparable in some respects to cirral facets of Mesozoic crinoids illustrated by Ubaghs (1978, T. 85, fig. 61). They are gently concave and slope towards the joint face. The lumen of the axial canal is a vertical slit. The half of the socket closest to the equator of the columnal is furnished with short culmina; the half closest to the joint face is smooth. The sides of the columnal are formed of dense stereom with a surface ornament of slightly raised granules approximately 15 μm in diameter.

In facetal view (Pl. 94, fig. 1) the following regions of the articulum can be differentiated:

1. The lumen, approximately 20–25% of the width of the articulum, which appears faintly five- or ten-lobed in well-preserved specimens.
2. An adaxially sloping concave area surrounding the lumen (the floor of the spatium), approximately 10–12% of the width of the articulum. The degree to which this region is depressed is variable; it is very shallow in the specimen illustrated. It is floored by open stereom (round to ovoid pores, with diameters from 6 to 14 μm, mostly about 12 μm) which in broken specimens can be seen to form a thin layer overlying denser paraxial galleried stereom like that flooring the areola.
3. In some specimens (but not the figured example) the outer margin of the floor of the spatium is raised to form a narrow perilumen constructed of denser stereom.
4. The areola (approximately 10–15% of the width of the articulum) which is flat and floored by paraxial galleried stereom (pore diameter 6–9 μm; surface porosity approximately 44%). Most pores are subrounded and bounded by four trabeculae and many are arranged in long slightly arcuate rows.
5. The crenularium (approximately 10–15% of the width of the articulum) consisting of steep-sided culmina and crenellae (Pl. 94, fig. 3). The top of the culmina and base of the crenellae are approximately equidistant from the level of the areola. The surfaces of the culmina are dense with conspicuously thickened trabecular intersections (pore diameters are 2·5–5·0 μm; surface porosity 30% or less), but are underlain by paraxial galleried stereom. The crenellae are mostly floored by galleried stereom similar to that of the areola (pore diameters 7–10 μm), but in some the stereom is much more open and labyrinthic.

A conspicuous feature of the articulum is the set of large tunnel-like pores (up to 35 μm in diameter) which in several specimens can be seen to completely penetrate the columnal. They are crudely arranged in ten lines and extend to the outer part of the areola.

In most respects the microstructure of these Carboniferous columnals is comparable with that of Recent and Mesozoic columnals described by Macurda and Meyer (1975, 1976) and Roux (1971). The galleried stereom of the areola probably housed ligament fibres. The denser stereom of the perilumen and of the crenularium served as bearing surfaces. The large pores penetrating the columnals may have contained nerves, as suggested by Macurda and Meyer (1975, p. 3) for similar pores in the columnals of the Recent species *Isocrinus blakei*. The pore diameters of the columnals described here are consistently smaller than those reported for most Recent and Mesozoic forms.

The taxonomic affinity of the specimens is not known. They almost certainly belonged to a cladid inadunate, possibly an ampelocrinid in view of the pentagonal stem and cirrus-bearing nodals.

Elliptical columnal of Platycrinites (TCD 19864–6) (Pl. 94, figs. 2, 4)

Columnals with elliptical articular surfaces are moderately common in the sample. They vary considerably in shape. The majority, mainly smaller specimens, are longer than wide and have a distinct equatorial waist. Most of them bear scattered nodes or blunt spines. A few specimens are wider than long, and some of these, possibly nodals, have conspicuous equatorial spine-bearing flanges. The articular surfaces are also variable although a basic pattern can be observed in all of them: a raised fulcral region along the major axis of the face separates two gently concave fields. The lumen is small and elliptical and is surrounded by open paraxial galleried stereom (pore diameters up to 13 μm; porosity approximately 37%). The central parts of the bifascial fields are floored by paraxial galleried stereom with pore diameters typically 6–10 μm and porosity approximately 32%. The peripheries of the faces are slightly raised above the bifascial fields and are formed of denser stereom (pore diameter 3–5 μm; porosity less than 30%). The long axis of the articular surface is occupied by a fulcral region which in many specimens consists of a broad slightly raised ridge of dense stereom (pore diameter typically 4 μm; surface porosity approximately 20%). In some specimens the surface of the fulcral region is crossed by low, dense, vermiform ridges. At each end of the major axis of the articular surface are raised culmina, generally three in number, which rise above the level of the fulcral region (Pl. 94, fig. 4). They interlock with crenellae of adjacent columnals. The culmina are formed of dense stereom (pore diameters typically less than 4 μm; porosity less than 20%) and the crenellae are floored by galleried stereom (pore diameter typically 9 μm). The major axes of opposing faces of many of the columnals are set at 90° to each other.

The ossicles are easily identified as belonging to *Platycrinites* but their specific identity is not known. In many respects their structure is comparable with that of the columnals of the Recent millericrinid *Democrinus* (Macurda and Meyer 1975, pp. 4, 5) which also has synarthrial articulation. In the Scottish *Platycrinites*, however, the fulcral ridge is much less dense than in *Democrinus*, and the elaborate keying mechanisms of that genus are not developed. Instead, limited symplectial articulation occurred at both ends of the fulcral ridge.

Inadunate brachial (TCD 19867–9) (Pl. 95, figs. 1, 3)

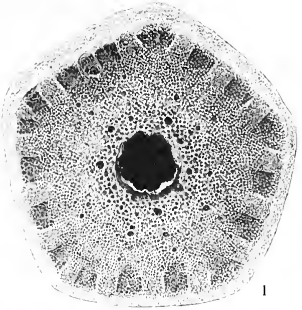
This kind of brachial is the most common in the sample. All examples that have been found are cuneate, pinnule-bearing, higher than long, and most have nodes or blunt spines on the aboral surface, particularly along the distal margins. All the brachials were joined by oblique muscular articulations; the fulcral ridges on the two faces of a brachial may diverge by as much as 60°. The following regions may be differentiated on the articular surfaces (Pl. 95, fig. 1):

1. The fulcral ridge, which is narrow at its mid-point and widens slightly at both ends to approximately 75 μm in typical specimens. The ridge is constructed of dense stereom (pore diameters typically 4 μm or less; porosity approximately 20%).
2. A slightly depressed area less than 30 μm deep bounded by the fulcral ridge and the aboral margin. By analogy with Recent crinoids, this area in Palaeozoic inadunates has been identified as the aboral ligament fossa which housed the extensor ligament bundles. It is floored by galleried stereom (pore diameters typically 7 μm; porosity approximately 35%). The pores are subrounded and arranged in a crude rectilinear pattern. In most specimens (but not the figured example) a distinct small deeper ligament pit occurs just aborally of the mid-point of the fulcral ridge.
3. Two wide subequal depressions, typically less than 30 μm deep, adoral of the fulcral ridge and on either side of its mid-point, which have been identified as interarticular ligament fossae. They are floored by galleried stereom in which the trabeculae and pores are conspicuously wider than elsewhere on the articular surface. Pore diameters generally range from 10 to 15 μm; the porosity is approximately 40%.

EXPLANATION OF PLATE 94

Figs. 1, 3. Fluoridized pentagonal columnal (TCD 19861), from the shale above the Charlestown Main Limestone, St. Monance, Fife (Lower Carboniferous; Brigantian age). 1, slightly oblique view of the articular surface, ×45. 3, stereopair of the crenularium and outer part of the areola, located at about 7 o'clock on fig. 1, ×230.

Figs. 2, 4. Fluoridized *Platycrinites* columnal (TCD 19864), from the shale above the Charlestown Main Limestone, St. Monance, Fife (Lower Carboniferous; Brigantian age). 2, oblique view of columnal, ×38. 4, stereopair of part of the fulcral ridge and culmina, from the left side of fig. 2, ×150.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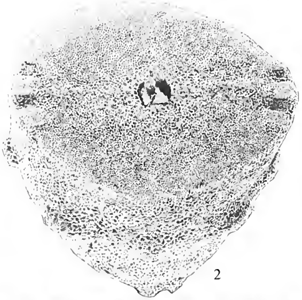
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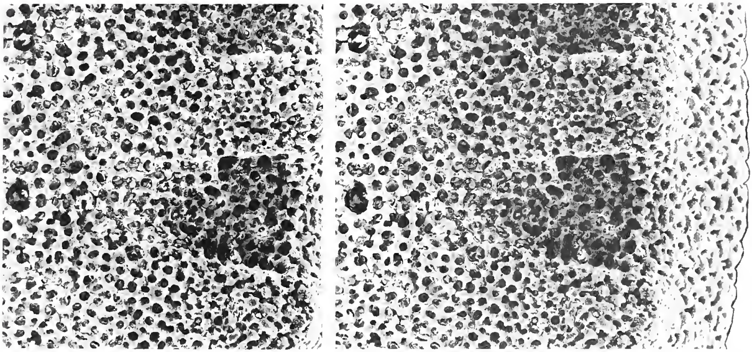
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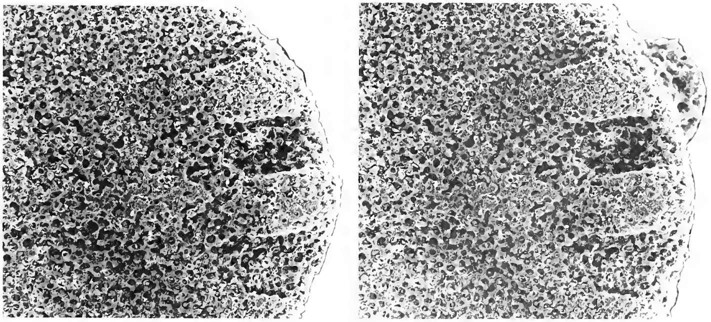
4

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4. A slightly raised area extending from the adoral groove to the mid-point of the fulcral ridge and separating the interarticular ligament fossae. This area bears a very weak medial groove which ends short of the fulcral ridge. The stereom of the raised area is galleried (pore diameter 6–8 μm) along the margins and more open (pore diameter 10–15 μm) and less regular along the median groove.

5. Well-marked, unequal, 'rabbit-ear'-shaped depressions on either side of the ambulacral groove, which have been interpreted as flexor muscle scars. They are floored by distinctive dense labyrinthic stereom (pore diameters mostly less than 4 μm; porosity approximately 20%). The surfaces of the fossae are formed by blunt-ended trabecular rods projecting upwards (Pl. 95, fig. 3).

All well-preserved specimens can be seen to have three pores 20–30 μm in diameter adoral of the fulcral ridge on both articular surfaces. Two of them lie along a line normal to the bisectrix of the angle of the adoral groove; the third is between the other two, closer to the fulcral ridge.

Many of the features observed are similar to those reported by Lane and Macurda (1975) for the Pennsylvanian cladid inadunate *Aesiocrinus magnificus*. The upward projecting trabecular rods of the 'rabbit ear' fossae were probably sheathed with a thin connective tissue layer to which the muscle fibres were attached, as illustrated for the Recent crinoid *Annacrinus* by Roux (1974*b*, pl. 1, figs. 6–7). An unusual feature of the Scottish brachials is the presence of the three canals interpreted here as aboral nerve canals. In Recent crinoids there is only one canal in the brachials; Lane and Macurda (1975) showed that in *Aesiocrinus* a 'double-barelled' nerve canal was present. We have found the 'double-barelled' arrangement in a number of different inadunate brachials, but the triple canal has only been found in the ossicles described here. We are unable to identify the brachials. They clearly were from a cladid inadunate. We have recovered axillary brachials, which show that the rays were branched and that the first dichotomy was above the first primibrachial.

Flexible brachial (TCD 19870–3) (Pl. 95, figs. 2, 4)

Brachials of this kind are moderately abundant in the sample, but there is considerable variation in the ratio of width to height; possibly more than one crinoid species is represented. The proximal articular surfaces are extended aborally into patelloid processes and the distal surfaces each have a fossa into which the process fits. In the specimen illustrated (Pl. 95, fig. 2), the lateral margins of the articular surface are crenulate with steep-sided culmina approximately 100 μm high. There is no fulcral ridge, but a fulcral ridge is present on some larger specimens. The stereom of the articular surface occurs in three different arrays. Over most of the surface, excluding the area around the patelloid process and a narrow median area extending aborally from the adoral groove, the pores are quadrangular to round, the diameters of 13–20 μm, and the porosity is approximately 45%. The trabeculae on either side of the aboral/adoral axis of the brachial are oriented at similar angles to the median line and produce a markedly rectilinear pore pattern. The stereom pores visible in side view are approximately the same dimensions as on the articular surfaces, so that the trabeculae form a regular cubic framework. In the median region, aboral of the adoral groove, the pores are slightly reduced in size and the regular arrangement of the pores is lost. On the aboral part of the articular surface around the patelloid process, the stereom is much denser (pore diameter 5–8 μm; porosity less than 30%) and less regularly arranged.

EXPLANATION OF PLATE 95

Figs. 1, 3. Fluoridized inadunate crinoid brachial (TCD 19867), from the shale above the Charlestown Main Limestone, St. Monance, Fife (Lower Carboniferous; Brigantian age). 1, slightly oblique view of proximal articular surface, with pinnule facet to the left, ×48. 3, stereopair of the left side 'rabbit ear' fossa and adjoining interarticular ligament fossa, ×300.

Figs. 2, 4. Fluoridized flexible brachial (TCD 19870), from the shale above the Charlestown Main Limestone, St. Monance, Fife (Lower Carboniferous; Brigantian age). 2, view of the proximal articular surface, ×48. 4, stereopair of culmina, located near the middle of the left margin in fig. 1, ×180.

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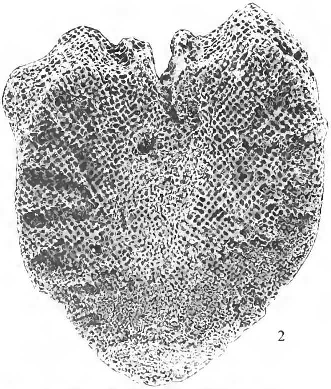

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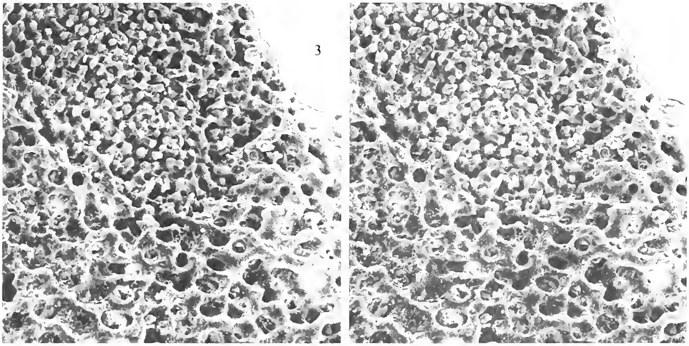

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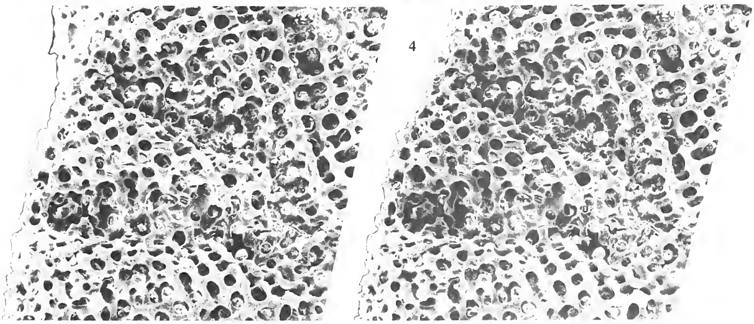

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These flexible brachials cannot be more closely identified; all the Carboniferous flexible ossicles encountered in this study have had remarkably similar microstructure.

Most authors (for instance, Van Sant and Lane 1964, p. 51) have suggested that flexible crinoids had only ligamentary articulations. Whether ligament fibres penetrated all the 'cubic' structured stereom or were restricted to certain areas is not certain, but the former arrangement seems more likely.

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THE VALUE OF OUTLINE PROCESSING IN THE BIOMETRY AND SYSTEMATICS OF FOSSILS

by G. H. SCOTT

Abstract. Widespread use of gross dimensions and similar point-to-point measurements in biometric studies of fossils is probably due more to instrumental limitations and the influence of preceding studies than to theoretical considerations. Are such data suitable for classificatory studies which are heavily dependent on visual assessment of morphology? Theory suggests that the outlines of objects are particularly significant in visual recognition because of their high information content. They provide a parsimonious description of form. Biometry can best supplement qualitative visual processes in taxonomic studies by treating outline data in ways that replace the information lost due to the short-term, degradable nature of visual data stored in the human memory. Variation in the axial outlines of the foraminifer *Globorotalia puncticulata* (Deshayes) is examined as an example.

Data collection is fundamental to biometry. Nevertheless, textbooks concentrate on techniques of data reduction and analysis, and offer little guidance about the collection of data. Such limited reference is understandable. Organisms are exceedingly diverse in form and organization. Guidelines for the collection of quantitative data can be cited (e.g. Simpson, Roe, and Lewontin 1960) but concepts such as 'character' and 'variable' are so context-dependent that most writers seem to concede, at least implicitly, that their selection in biometric studies should be left to the discretion of the student. While the literature indicates that there is considerable accord among researchers on protozoans to vertebrates on the types of data to be collected, this does not necessarily signify adherence to a common rationale of data collection. Precedents and instrumental constraints exert powerful influences on the data collected in a project. Here I consider the role of biometry in classificatory studies (broadly, recognition of taxa and allocation of specimens) in the light of theory on the mechanisms of visual perception. It is advocated that biometry should supplement these mechanisms by processing comparable data so that there is a parallel between qualitative and quantitative treatments of specimens. In this way biometry can contribute to resolving the problems of the systematist that arise from deficiencies in visual recognition.

TYPICAL PRACTICE

While it is not claimed that the measurements illustrated in text-fig. 1 portray all aspects of modern practice in variate selection, they are sufficiently representative to indicate that biometric studies primarily use data on the gross dimensions of structures. Point-to-point measurements of maximum dimensions of skeletal parts form the vast majority of the data reported in the literature, and the example of the measurement of the length of a curve (text-fig. 1c) is unusual.

Instrumentation, operational convenience, and the precedents set by previous studies account for the preference for gross dimensions. The first two, in conjunction, are fundamental. Operationally, gross dimensions offer considerable advantages in variate selection. Much of the form of skeletal structures consists of smooth, continuously curved surfaces. In such regions well-defined, relocatable loci for measurement may be few, and the obvious 'landmarks' for the biometrician are the extremities of the structure. Usually these are homologous within the population sampled. The simple scales and calipers which are the stock in trade of the palaeontologist are well suited to measurements of gross dimensions, whereas they are unsuited to determining the lengths of vectors or curves, for example. Indeed, the widespread use of gross dimensions and of measurements between

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well-defined 'landmarks' in biometry is probably due as much to the limitations of instruments as to their value on purely biological grounds in morphological description and analysis.

Precedent is an ancillary influence that tends to stabilize the set of characters measured and perhaps inhibits fresh consideration of what should be measured. Moreover, pioneering works that use point-to-point measurements have an advantage in the selection of precedents because of the general availability of comparable measurement devices. The measurements (partly shown in text-fig. 1A) on trilobites made by Shaw (1957) are a good example of the influence on later workers (Temple 1975) of a pioneering study.

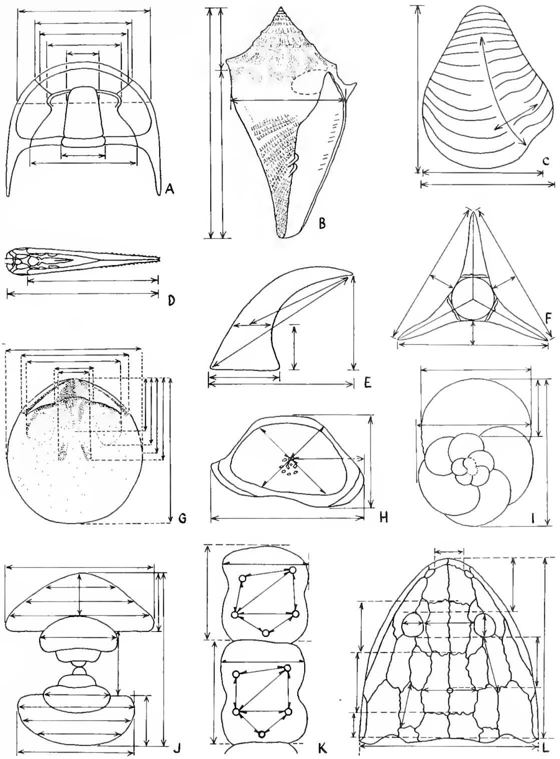
A BASIS FOR BIOMETRY

There is very little evidence in the literature that theoretical considerations have influenced the choice of characters for measurement. In an introduction to a major biometric study of Ostracoda, Reyment (1963) asserted that statistical analysis would provide a comprehensive representation of variation but made no comment on the adequacy of the measurements (carapace length, height, and breadth) that formed the great majority of his data. It is conjectural whether the claim by Hallam and Gould (1975, p. 517) that their nine measurements on the left valve of *Gryphaea* are 'adequate to express overall features of valve shape and the character of the sulcus' can be substantiated. Most workers (myself included) can be easily pilloried on the grounds of *ad hoc* selection of data without justification. A relevant example is Melville's (1978) critique of a biometric study of leaf shape in *Ulmus*. Which features should be selected for measurement?

The choice of measurements and their analysis should relate to the aims and methods of the investigation. This is self-evident in an application of biometry to a study of functional morphology, for example, where mechanical hypotheses are presented for testing. But it is a useful point of departure when considering the role of biometry in the generally less-structured tasks of classification. Here the primary activities concern the establishment of classes and the allocation of specimens. The principal problems concern the estimation of intra-group variation and inter-group separation or distance. Where do class limits fall? Modern evolutionary theory and research provide a cogent account of the mechanisms of variation. The systematist, however, is presented with the end products of various genetic, phenotypic, ontogenetic, and diagenetic processes. In a particular instance there may be very strong reasons, *a priori*, to suppose that the specimens under systematic scrutiny are samples from discrete populations. The problem is that of recognition.

Although data on distribution and ecology are significant, the primary information in the systematics of fossils is morphological, obtained by qualitative visual examination. The immense production of illustrations of fossils over the last two centuries attests the fundamental importance of visual representation in systematics. Certainly, the initial phase of simple qualitative visual assessment is followed by analysis, sometimes using quantitative data, that leads to diagnoses of taxa. But the latter is a conscious refinement of the initial phase. The brain is an immensely fast and powerful processor of visual imagery. Visual data are rapidly assembled, images reconstructed and interpreted. Messages about the identity of specimens are produced almost involuntarily and are the basis of classificatory work. The process is that used in other visual recognition tasks in day-to-day experience, although a higher standard of recognition and discrimination is desirable. Form variation in biological materials is often complex, with major ontogenetic and environmental sources to be allowed for in taxonomic recognition.

What is the role of biometry in such studies? Should it supplant or supplement qualitative perception? If only for reasons of instrumentation, the present role must be supplementary. In many aspects the human visual system is more advanced than any similar device. It is in inter-image discrimination that the human system is least effective, especially when sample sizes are large, variation multidimensional, and groups ill defined. Objects are scanned and features of others recalled in attempts to reach classificatory decisions. Here the static, long-term memories of digital devices seem to have marked advantages over the human system. Re-recording of image information to refresh the memory is made unnecessary. Once stored, it remains available for recall and



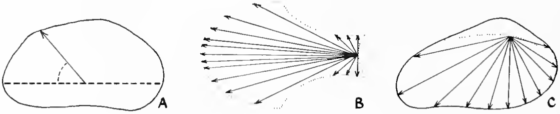
TEXT-FIG. 1. Measurements of structures commonly preserved as fossils. Variate identifications and scales are omitted in the adaptations. A, non-agnostidean trilobite cephalon after Shaw (1957, text-fig. 11). B, gastropod, *Athleta petrosa* (Conrad), after Fisher, Rodda, and Dietrich (1964, text-fig. 1). C, bivalve, *Gryphaea*, after Hallam and Gould (1975, fig. 1). D, pterosaur skull, *Pterodactylus*, after Mateer (1976, fig. 1). E, conodont, after Sergeyeva *et al.* (1975, fig. 5). F, acritarch, after Sellberg and Kjellstrom (1975, fig. 1). G, brachiopod, *Linnarssonella girtyi* Walcott, after Rowell (1966, table 4). H, ostracod, *Bairdia victrix* Brady, after Cadot and Kaesler (1973, fig. 2). I, foraminifer, *Globorotalia miozea miozea* Finlay, after Scott (1972, text-fig. 2). J, ammonite, *Vascoceras*, after Berthou, Brower, and Reyment (1975, fig. c). K, molar teeth of condylarth mammal, after Olson and Miller (1958, fig. 61). L, amphibian skull, *Trimerorhachis*, after Olson (1953, fig. 1).

reprocessing without degradation. If biometry is to supplement the 'weak' points of visual perception, it follows that it should process the same sort of data. The problem with *ad hoc* characters is that they may record aspects of the object that are insignificant in visual processing. How does the human system function?

Visual perception. Once the preserve of the psychologist, the mechanics of visual perception have become an interdisciplinary subject because of their relevance in automatic pattern recognition and allied studies. A comprehensive survey is not attempted, but there is general agreement about the significance of the outline in object recognition. Gestalt psychologists (e.g. Koffka 1935) concentrated on those properties of figures that facilitated their recognition or isolation from background data. One of their laws of organization drew attention to the importance of closure. Closed figures tend to be perceived as units more readily than unclosed. From quite different premises, information theorists showed that much visual data is redundant in recognition processes because of high correlation among the data received by adjacent visual receptors. Attneave (1954) gave a simple, convincing, example of this and suggested that early visual processing filters out much redundant information, leaving a reduced, more economic, description of the data. Redundancy is high in regions of an object that are homogeneous in some visual property (e.g. colour, texture, curvature) and low in regions where such properties change rapidly. The margins of an object are regions where redundancy is particularly low, although zones of uniform slope or curvature along the margin have higher redundancy than those in which there are rapid changes in direction or slope. Attneave showed that an object can be recognized readily from a simplified sketch consisting of the points of maximum curvature of the outline linked by straight lines. Such a result is an explanation of the verisimilitude achieved so effortlessly by the competent cartoonist or street artist. But it is also highly suggestive to the biometrician. Marr (1976) suggested that a major element in early visual processing is the construction of a 'primal sketch' from grey-level changes in the receptor data array. Intensity changes are isolated and used to construct a description of the array. Edges are major elements in the description.

Commentary. The review indicates the prime importance of outline data in visual recognition. There will be many examples in which data, highly significant for recognition, lie within the outline. But, in general, treatment of the outline is a suitable commencement for biometry in classificatory studies. Measurement loci, as shown in text-fig. 1, show various degrees of compatibility with Attneave's interpretation of visual perception. Some are located on outline segments of low curvature to which the eye gives little attention (e.g. text-fig. 1H, I). Others (e.g. text-fig. 1F) are on outline segments of high curvature that are probably significant in object recognition. However, the use made of measurement loci in most biometrical practice differs considerably from that suggested by the foregoing theory. Biometricians have recorded distances between loci, whereas theory suggests that it is the position of loci as well as interloci distances that is important in perception. A vectorial approach is indicated.

Vectorial data have been collected in previous studies (text-fig. 2), although not as implementations of the rationale developed above. Examples are Anstey and Delmet (1973) and Cheetham and Lorenz (1976) on bryozoans, Christopher and Waters (1974) on miospores, Gevirtz (1976) and Pastiels (1953) on bivalves, Kaesler and Waters (1972) and Margerie (1977) on ostracods, Scott



TEXT-FIG. 2. Examples of outline recording. A, ostracod, *Eucypris*, after Margerie (1971, fig. d). B, cheilostome bryozoan, after Cheetham and Lorenz (1976, fig. 4). C, bivalve, *Carbonicola*, after Pastiels (1953, fig. 4).

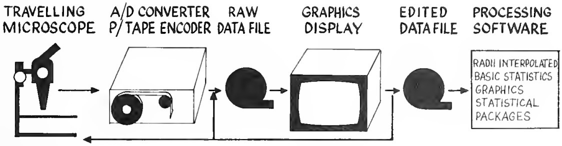
(1976) on foraminifera, and Waters (1977) on blastoids. A common aim has been to describe accurately the form of the specimen outline. Although representative outlines were presented in several studies, data have not usually been presented in ways that assist in the resolution of taxonomic problems. For example, assemblies of outlines (pictograms) have, in the light of the previous discussion, good theoretical support as effective presentations of intra-sample variation. The problem of specimen organization within the pictogram can be readily resolved if outline coordinates are available.

TECHNIQUE AND AN EXAMPLE

This section gives some simple representations of outline data that are useful in classificatory studies.

Data capture. Text-fig. 3 summarizes the data logging and processing system. The digitizer attached to the stereomicroscope (Scott 1975) was built to specification and is suitable for fossils with greatest diameters between 0·05 mm and 40 mm. It is manually guided (by movement of the travelling head) and the x, y coordinates of loci selected by the operator are recorded in units of $5{\cdot}3\ \mu$m on paper tape.

Specimens are digitized in a standard orientation. Errors in orientation are minimized when specimens have two or more structures that are small in relation to the accuracy of the measurement system and occur in invariant positions. Such structures are seldom available. In the example, the axial profiles of the shell were recorded with the coiling axis aligned east–west with reference to a cross-line in the ocular lens. The coiling axis in foraminifera and similar shells is not a physical structure, but its position can be estimated from the location of the proloculus (initial chamber) and umbilicus.

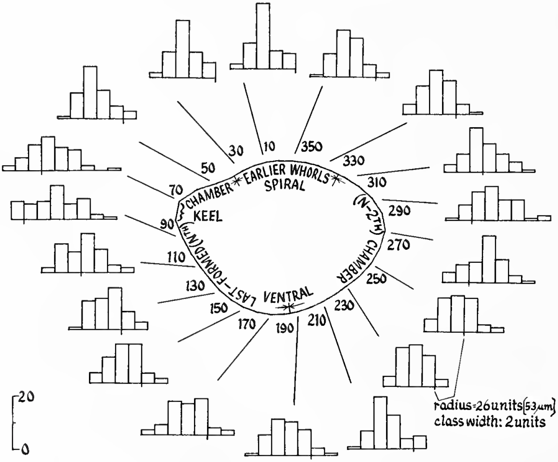


TEXT-FIG. 3. Flow diagram of data capture, editing, and processing system. The equipment includes a custom-built digitizer, Tektronix 4006 graphics display, Hewlett Packard 7202A graphics plotter, and Hewlett Packard 2100, Burroughs B6700, and IBM 370/168 processors.

Editing. Errors due to mis-positioning (backlash, parallax, involuntary movement) increase in importance as the size of the specimen or structure decreases. Graphical editing of the recorded x, y data is highly desirable. With batch processing much can be done using lineprinter plots and editing runs, but interactive editing with a graphics terminal is preferable. My equipment displays x, y coordinates in order of recording and joined by straight lines (the specimen is represented as a polygon). Coordinates may be inserted or deleted and the figure redisplayed.

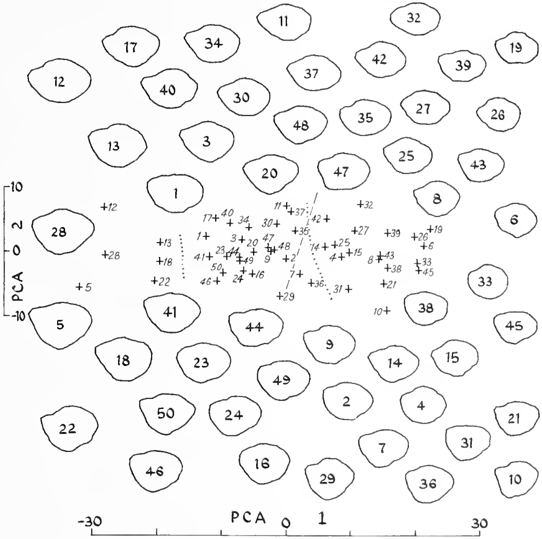
Reconstruction. I record about fifty loci approximately equidistant about the periphery of the specimen. There is no quantitative control over their position relative to the starting-point. Thus the *ith* point on one specimen is not necessarily positionally equivalent to the *ith* point on another. Another consideration is that only the obviously spurious coordinates can be removed by editing. A residual of small-scale errors in positioning remains in the data. Smoothing of the data and interpolation of points at fixed positions about the periphery are performed by fitting a Fourier Series curve to each specimen. An angular expansion of the radius about the specimen centroid is applied (Ehrlich and Weinberg 1970). Radii are interpolated at 10° intervals using 15 harmonics. This produces mild smoothing. Note that this expansion is suitable only for generally convex figures in which radii are single-valued. All subsequent processing uses the file of interpolated radii.

Variation in Globorotalia puncticulata sphericomiozea. Referred to this upper Miocene-lower Pliocene planktonic foraminiferal taxon are New Zealand populations that are intermediate in morphology and stratigraphic position between *Globorotalia miozea conoidea* Walters and *G. puncticulata puncticulata* (Deshayes). In axial orientation *G. miozea conoidea* is weakly conical with the base formed by the flattish spiral of the early whorls and the cone by the ventrally extended chambers of the last whorl (for terminology see text-fig. 4). The keel at the shell margin is well defined on the last-formed chamber but is usually buried by secondary calcification on earlier chambers. The form of the shell in *G. puncticulata puncticulata* is globose, rather than conical. This is produced by moderate inflation of chambers. Straight-line segments of the chamber outline are replaced by gentle curves. There is no keel. At some horizons, some specimens of *G. puncticulata sphericomiozea* have the axial form of the ancestral *G. miozea conoidea* (and its variant *G. conomiozea* Kennett). Others anticipate the shape of *G. puncticulata puncticulata.* Blow (1969 p. 361) suggested that such samples represented a mixture of two taxa on the hypothesis that keels, once evolved, are thereafter retained in phylogeny. He rejected the idea of populations in which some specimens possessed a keel and others did not. Although there is no theoretical support for the permanency of a structure, Blow's suggestion about mixed samples warrants study because Kennett (1977) showed that there was marked deterioration in climate in the New Zealand region in the uppermost Miocene, about the stratigraphic position of *G. puncticulata sphericomiozea.* Changes in the distribution of planktonic taxa in response to shifts in watermasses and the appearance of migrants are to be expected in such a regime. To assess Blow's idea, the systematist needs to examine intra-sample variation. Is it continuous? Can sub-sample clusters be detected? Here, the axial outline of the shell is examined. This profile provides information on the shape of chambers near the location of the keel at the shell periphery. The topics considered are the construction of a typical outline, and the pictorial representation of within-sample variation.



TEXT-FIG. 4. Histograms show distributions of radii at 20° intervals about centroids of fifty specimens of *Globorotalia puncticulata sphericomiozea* Walters from P29/f55, Blind River, New Zealand. The polygonal outline is formed from the mean lengths of radii spaced at 10° intervals.

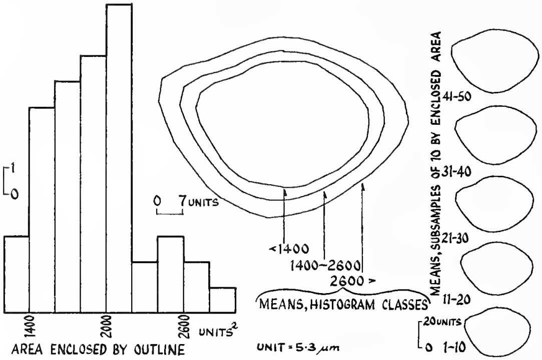
Outline representations. The distributions of radii (text-fig. 4) about the centroid of the axial outline of fifty specimens from P29/f55 Blind River (close to sample 32 in Kennett and Watkins 1974), show some variation in kurtosis but tend to be unimodal. The outline in the centre of text-fig. 4 is drawn from mean values of the thirty-six radii and reflects common features in the sample outlines shown in text-fig. 5. Gentle doming in the vicinity of the spire, rapid change in curvature of the outline of the *n*th chamber at the site of the keel, and ventral extension of chambers are features of most of the outlines in text-fig. 5 that are also apparent in the sample mean outline.



TEXT-FIG. 5. Plot of sample from P29/f55 (fifty individuals) on two largest principal component axes (dispersion matrix, thirty-six radii as deviations from means). PCA 1 and PCA 2 represent 81% and 6% of sample variance. Location of axial outlines of specimens is related to their position in the plot (objectively defined pictogram). Dotted lines show three-cluster division of sample using the non-hierarchical clustering algorithm (sum of squares criterion) in GENSTAT (statistical package produced by Rothamsted Experimental Station) and dashed line is the two-cluster partition. This algorithm transfers specimens between clusters to improve the criterion but a global optimum is not necessarily reached.

However, use of the sample mean outline as a representative form in comparisons among taxa is contingent on negligible shape change within the sample size range. If allometry is marked, the sample mean outline may be quite unrepresentative, not corresponding with the shape of any specimen. Size-related changes in shape complicate taxonomic recognition and may require special study. Brower and Veinus (1978) discussed an approach suitable for vectorial data. In the example, mean outlines for five size-defined subsamples (text-fig. 6) are similar, and even specimens from the extreme size classes show close resemblance, although there is a modest radial extension of the outline in the vicinity of the (n–2)th chamber of the largest specimens (text-fig. 6 centre). I conclude that size-related shape changes within the material do not greatly affect the use of the sample mean outline as a representative form.

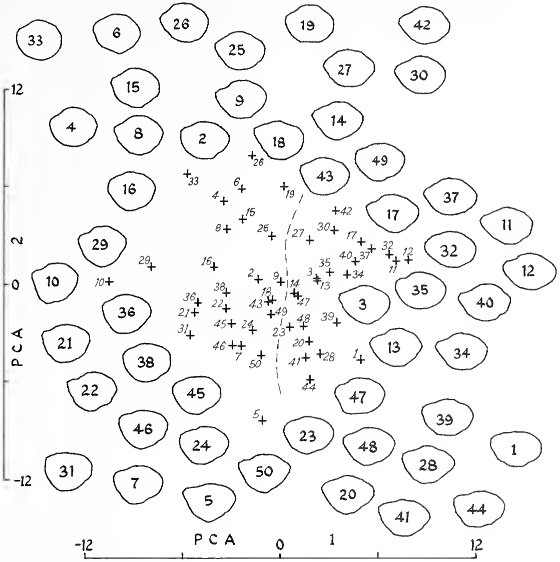
There is a minority of specimens (e.g. 16, 23, 33 in text-fig. 5) in which spiral and ventral segments of the outline of the nth chamber form a rounded rather than an angular junction (70–90° radii in text-fig. 4). In this respect they resemble *G. puncticulata puncticulata.* Do they form an identifiable subsample? A quantitative or metric version of the pictogram (text-fig. 5), in which outlines are referred to specimen positions on a principal component plot, shows that such specimens are scattered through the sample. Thus specimens 12 and 45 lie at opposite ends of the distribution along PCA 1 which represents much of the intra-sample variation in outline size. PCA 2 reflects variation in the degree of ventral inflation of the outline. Again, there are specimens (e.g. 12, 16) that show considerable difference in ventral inflation yet have rounded peripheries.



TEXT-FIG. 6. Histogram shows distribution of area enclosed by outlines (axial profile) of fifty specimens from P29/f55. Area is taken as a natural measure of size. The superimposed outlines used subsamples based on the histogram intervals. Outlines at right were formed by ranking the fifty specimens by area and dividing them into five equal subsamples.

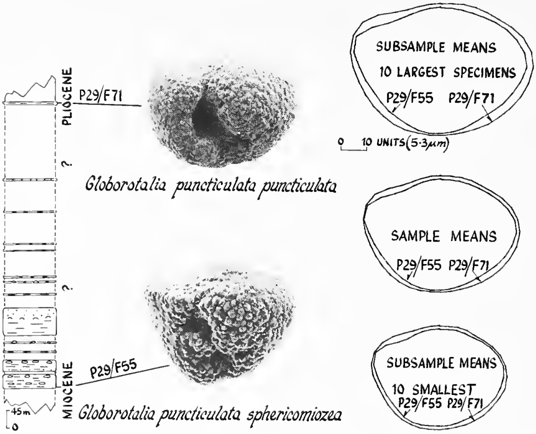
If size can be neglected in a taxonomic judgement it is useful to examine a representation in which it is held constant (text-fig. 7). Much of the arrangement of text-fig. 5 is preserved but there are several displacements that clarify shape similarities. For example, specimen 1 (low spire, weak axial inflation) lies on the periphery of the scatter in text-fig. 7 whereas in text-fig. 5 it lies between specimens 3 and 13. Specimens 33 and 45 are dissimilar in shape but their common size causes their close proximity in text-fig. 5. They are widely separated in text-fig. 7. A group of specimens with weak axial inflation and a slight dome representing the early chambers (e.g. specimens 11, 12, 17, 32, 37, 40) are in closer proximity in text-fig. 7 than in text-fig. 5.

Distinct clusters are not obvious in text-figs. 5 and 7. This impression is supported by the intra-sample divisions produced by a non-hierarchical clustering algorithm in GENSTAT. Large specimens are isolated by the procedure using raw data (text-fig. 5, 3-cluster partition) but 2-cluster partitions using either raw or size-standardized data separate specimens that are similar in shape and in close proximity in the principal component plots. The partitions are placed in a central location in the scatter. This results from the fairly uniform distribution of specimens in the hyperspace.



TEXT-FIG. 7. Principal component plot of the sample from P29/f55 using thirty-six radii (as deviations from means) after areas of outlines were standardized. Radii were incremented/decremented iteratively until the area of each polygonal outline fell within 5% of an arbitrary constant, close to the mean of the enclosed area distribution using raw data. Axes PCA 1 and PCA 2 represent 30% and 24% of sample variance (dispersion matrix). The dashed line is the location of the two-cluster partition produced by the non-hierarchical clustering algorithm in GENSTAT (sum of squares criterion). Axial outlines of specimens using standardized data are arranged according to their locations in the plot.

The data in text-figs. 4–7 indicate that a variable population was sampled, even when size is eliminated. But the representations show gradations in form and the absence of well-defined disjunctions in specimen distributions. A connection is not observed between the form of the periphery of the *n*th chamber and the gross axial shape of the shell. These results assist the taxonomist to assess the validity of *G. puncticulata sphericomiozea* in the light of Blow's hypothesis. Inter-sample comparisons may also be useful. Text-fig. 8, for example, indicates the changes in axial form between *G. puncticulata sphericomiozea* and *G. puncticulata puncticulata* much more explicitly than do direct comparisons of specimen suites. In the latter the outline of the *n*th chamber about the 30–70° segment (see text-fig. 4 for locations) is raised relative to the equivalent segment in *G. puncticulata sphericomiozea*. This occurs throughout the size range sampled. But in the 110–150° segment of the *n*th chamber, inflation relative to *G. puncticulata sphericomiozea* is marked only in larger specimens. The study of the transformation in shape between the taxa leads to techniques reviewed by Bookstein (1977).



TEXT-FIG. 8. Inter-sample comparisons of outlines. Location of samples P29/f55 and P29/f71 in the Blind River sequence, scanning electron micrographs of random specimens of *Globorotalia puncticulata puncticulata* (Deshayes) and *G. puncticulata sphericomiozea* Walters, and superimposed outlines from the samples.

CONCLUSION

I do not contend that biometric studies using *ad hoc* variates should be abandoned. Rather, I suggest that analyses with these variates usually do not integrate easily with qualitative assessment of form. Generally, they provide an inadequate representation of the outline and may include measurement loci not significant in visual recognition. Vector relationships between measurements are entirely omitted yet are essential in object identification. By processing the coordinates of outlines, a quantitative study provides information that is easily and directly related to the material posing a classificatory problem, and amenable to statistical testing. Of course, outline data may also contain significant functional information. For example, the form of the shell of an infaunal burrower is likely to show adaptations to the mechanism of movement.

Representation of outlines by polar coordinates requires large sets of data that may cause housekeeping problems on small computers. There is commonly some redundancy in the variate set (dispersion matrices less than full rank) and a more parsimonious set is possible. However, the set provides directly a polygonal representation of form which is easy to manipulate (magnification, rotation, reflection) and from which image descriptors (Rink 1976) and *ad hoc* variates can be derived readily. The verbal descriptors of Riedel (1978) are less exact and less suitable for simple graphical reconstructions and manipulations. The techniques of numerical taxonomy and automated identification (Sneath 1979) usually operate with character states, selected by the investigator, and do not provide shape representations at the basic population level.

Outlines are rich in information for the taxonomist. That is why they should be used in biometry. Nevertheless, they are only a point of departure. Systems that process all pictorial information from a specimen suite in various orientations offer the prospect of much more sophisticated assistance to the taxonomist.

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HIATELLA—A JURASSIC BIVALVE SQUATTER?

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ABSTRACT. English late Jurassic (Middle Volgian) *Hiatella* occur in two habitats; firstly, as simple byssal nestlers on local hard substrates and, secondly, within *Gastrochaenolites*-type borings penetrating hard substrates. Most *Hiatella* occupy borings that they did not originally construct themselves, although ancestors as well as other bivalve genera could have been responsible. The morphology of the Mesozoic *Hiatella* is compared briefly with modern species which occur around the British Isles and which include both boring and nestling forms. A sequence of events is postulated for the formation of the Basal phosphatized Nodule Bed of the Spilsby Sandstone in Lincolnshire, and a palaeoenvironmental model is suggested for the East Midlands Shelf in Middle Volgian times.

THE borings made by bivalves into hard substrates have been the subject of considerable attention from both zoologists and palaeontologists and there are many important articles in the publications edited by Clapp and Kenk (1963), Crimes and Harper (1970, 1977), and Frey (1975). Unlike most trace fossils, borings of bivalves may commonly contain the skeletal remains of their occupants. However, caution is necessary in recognizing whether the occupant is primary, i.e. the organism which originally constructed the boring, or whether it is secondary and is effectively a squatter in the vacated domicile. There is ample evidence of modern bivalves reoccupying vacant borings, largely those of pholads, but including (updated names) *Tresus*, *Petricola*, *Macoma*, and *Irus* (Evans 1967); *Kellia* and *Notirus* (Stevenson 1946); *Tapes*, *Cumingia*, *Kellia*, *Diplodonta*, *Eudodesma*, and *Mytilus* (Barrows 1917); *Modiola*, *Scaphula*, and *Corbula* in *Martesia* borings in brickwork (Annandale 1923); *Idasola* in borings of *Teredo* in wood (Jensen 1912). Kühnelt (1933, 1951) recorded *Ungulina*, *Montacuta*, *Lepton*, *Coralliophaga*, *Trapezium*, *Venerupis*, *Sphenia*, *Perna*, *Lyonsia*, *Petricola*, and *Hiatella*, all of which are deformed to some degree to fit the borings in which they occur. Some bivalves like *Hiatella* and *Petricola* (Yonge 1958; Hunter 1949) may either bore into hard substrates or nestle epibyssally. Bivalve borings in turn may be reinfested by other phyla, e.g. hydroids and bryozoa described by Evans (1949), surviving in the wet microenvironments of the vacant borings in the intertidal zone. Warme (1970) noted that abandoned borings may be modified and deepened by nestling bivalves, gastropods, polychaetes, arthropods, etc.

Records of fossil bivalves reoccupying vacant borings are much less common. Masuda (1968) noted *Barbatia*, *Irus*, and *Phlyctiderma* in partially eroded Miocene borings. Itoigawa (1963) recorded the borings of Miocene *Parapholas* which were subsequently infilled by sediment, and then burrowed by *Lutraria* before consolidation. Kennedy and Klinger (1972) discussed a number of encrusting and nestling organisms occupying borings constructed by a Cretaceous mytilid; these include serpulids, a bryozoan, ostreids, and *Barbatia*. Jurassic *Hiatella* has been recognized only rarely. Eudes-Deslonchamps (1838) ascribed two species from the Middle Jurassic of Normandy to *Saxicava* (a junior synonym of *Hiatella*), and Chavan (1952) introduced the genus *Pseudosaxicava* for a Lower Kimmeridgian species from the same area, and this name is placed as a subgenus of *Hiatella* by Keen (*in* Moore 1969). From England, Cox (1929) described '*Arca*' *foetida* from the Portland Sand and Hartwell Clay (Middle Volgian). This latter species is conspecific with other material described here from the Middle Volgian. The updated name of this species is *Hiatella* (*Pseudosaxicava*) *foetida* (Cox 1929).

There has been little ecological information associated with these early records, though Eudes-Deslongchamps noted that his Middle Jurassic examples were associated with borings into corals and bivalve shells. The description here of specimens from the English Middle Volgian adds significantly

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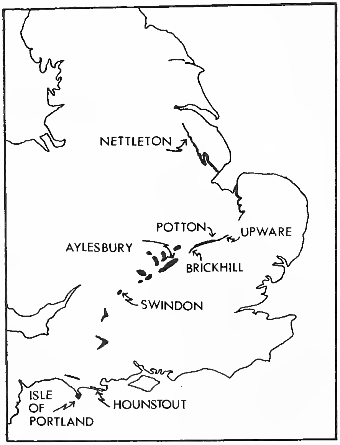
to the paleoecology of *Hiatella*. There is evidence that the shell shape is strongly controlled by the substrate to which it is attached. There is little positive evidence for English Upper Jurassic *Hiatella* having been capable of boring, while there is plenty of evidence which indicates that vacant bivalve borings were commonly infested by *Hiatella* spat. Modern British *Hiatella* have been studied by Hunter (1949), who described considerable variation in shell shape which is closely paralleled by the late Jurassic forms, depending largely on whether they are boring or nestling. Strauch (1968) suggested that the shell length of Recent *Hiatella* was inversely related to the winter minimum water temperature and consequently was useful in estimation of Cenozoic palaeotemperatures. However, this is partially doubted by Rowland and Hopkins (1971) who believe that there is a more complex situation and that size is controlled more by mode of life in each population.

STRATIGRAPHY

The specimens used in this study are all from the Middle Volgian (equivalent to the upper part of the Upper Kimmeridgian and the lower part of the Portlandian of England). Extensive collecting was carried out in the Basal Spilsby Nodule Bed in a sand pit, now bulldozed, on Nettleton Hill, Lincolnshire (TF 108989) (see text-fig. 1 for localities). Although *in situ* collecting is no longer possible at this site, the hillside about 200 m to the north provides much weathered-out loose material from the same horizon. The collections made from this horizon have been deposited with the Institute of Geological Sciences, London (IGS). Casey (1973) referred this bed to the *Titanites giganteus* Zone. The status of this zone in Lincolnshire is not clear since Wimbledon and Cope (1978) have completely revised the zonal sequence in southern England. However, it is possible that the fauna of this bed may represent several zones as repeated phases of phosphatization can be recognized and the ammonites (all phosphatized) belong to the genera *Crendonites*, *Epilaugeites*, *Kerberites*, and *Pavlovia* (R. Casey pers. comm.). The Basal Spilsby Nodule Bed rests upon eroded, plastic blue-grey Kimmeridge Clay with occasional cementstones up to 0·2 m thick and containing *Pectinatites* of Lower Volgian age. The nodule bed itself is about 0·2 m thick and is composed of brown and blackened phosphatized concretions up to 0·2 m in diameter, but commonly 10–30 mm, together with small lyditic pebbles set in a dark, glauconitic silty sand. Many of the concretions show compound structure and are commonly abraded, showing signs of bioerosion, e.g. flask-shaped borings attributable to bivalves



TEXT-FIG. 1. Sketch map of the distribution of Middle Volgian strata in England, with locations of sites where *Hiatella* has been obtained.

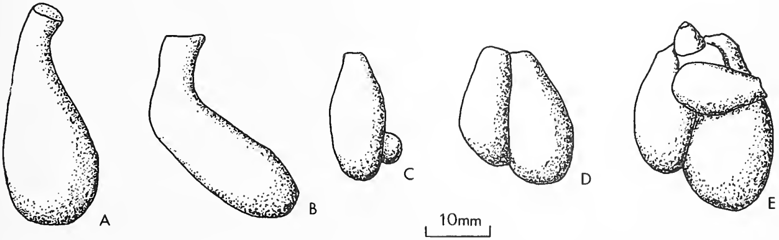
and grazing trails probably caused by gastropods. A rich fauna, especially of bivalves, has been obtained from this bed (Kelly 1977). The preservation of the fauna is normally as hollow phosphatized moulds, with internal moulds of bivalves and of parts of ammonites making up a high proportion of the nodules of the bed. Above the nodule bed lies 0·6 m of poorly consolidated glauconitic silty sand, the base of which is pale coloured, becoming brown (ferruginous) near the centre and grey at the top, and which contains unidentified, partly phosphatized, ammonites.

Similar phosphatized material with *Hiatella* occurs in the base of the Lower Greensand at Upware, Potton, and Brickhill, and is preserved in the Sedgwick Museum, Cambridge. Although these specimens are mixed with other phosphatized material ranging from Oxfordian to Aptian in age, they occur with ammonites, a large proportion of which are of Middle Volgian age and they are undoubtedly of the same age. Unphosphatized *Hiatella* occur in the Hartwell Clay of Buckinghamshire and the Swindon Clay of Wiltshire (both of *Pavlovia pallasioides* Zone) and are preserved in the British Museum (Natural History), the Institute of Geological Sciences, and the Sedgwick Museum, Cambridge (e.g. Pl. 96, figs. 15, 16). From an unspecified horizon in the Portland Sand of Hounstout, Dorset (Waddington Collection, untraced), two specimens were figured as '*Arca*' *foetida* sp. nov. by Cox (1929, pl. 1, figs. 2, 3). These specimens are likely to have come from the horizons recorded by Arkell (1935, p. 310), who listed *Parallelodon* (*Beshausenia*) *foetidum* from the White Cementstone and Bed 11 of the Emmit Hill Marls. In the latter horizon Arkell noted that another more elongate species of the genus was also present. *Hiatella* has also been collected recently from borings in the upper part of the Portland Limestone on the Isle of Portland. It is interesting to note that Woodward (1851–1856) recorded modern *Hiatella* actively attacking the Portland Stone breakwater at Plymouth, which perhaps even makes possible the reoccupation of Jurassic borings after some 135 million years.

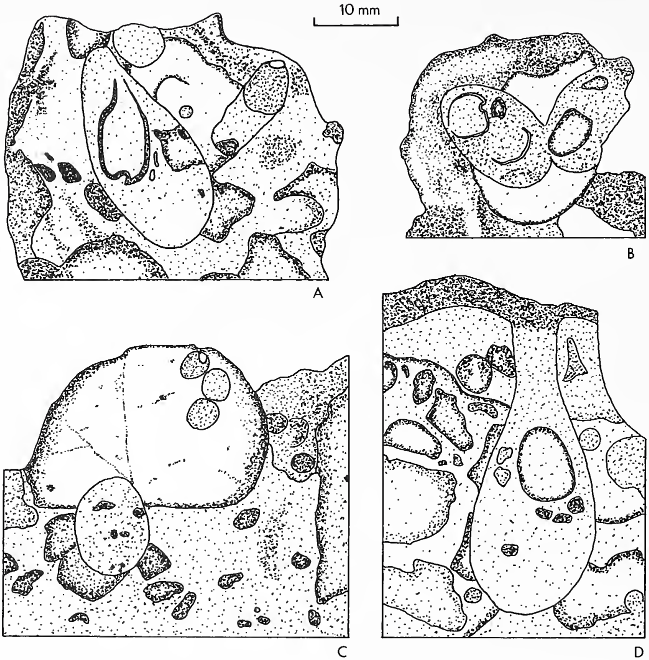
DESCRIPTION OF BORINGS AND THE *HIATELLA*

In the Basal Spilsby Nodule Bed, *Hiatella* was collected both from within flask-shaped borings and independently of the borings. These two types appear to be morphologically distinct and are therefore described separately, although it is possible to find intermediate forms. As much of the discussion in this paper centres around the occurrence of *Hiatella* in the borings, these structures are described first, followed by details of the shell shape in both the boring and the non-boring habitat.

The borings. The Basal Spilsby nodules contain several types of borings of which the most conspicuous are flask-shaped cavities or their phosphatized infillings, commonly up to 30 mm in length (text-fig. 2*a–c*). The flask is circular in cross-section (text-fig. 3*c*) with a maximum diameter of 13 mm. The constricted neck reaches 5 mm diameter and is circular except near the aperture, where it becomes slightly oval and weakly flared (Pl. 96, fig. 23). Oblique sections through the flask may be



TEXT-FIG. 2. Camera lucida drawings of phosphatized infillings of *Gastrochaenolites* borings in Basal Spilsby Nodule Bed, Nettleton, Lincolnshire, S. R. A. Kelly Collection IGS: A, Zu2229; B, Zu2230; C, Zu2228; D, Zu2231; E, Zu2232.



TEXT-FIG. 3. Camera lucida drawings of polished sections through phosphatized compound nodules of the Basal Spilsby Nodule Bed showing *Gastrochaenolites* borings; some (figs. A and B) show *Hiatella* in sites within the borings. Nettleton, Lincolnshire. S. R. A. Kelly Collection, IGS: A, Zu2237; B, Zu2223; C, Zu2238; D, Zu2236.

pear-shaped (text-fig. 3*a*). A complete longitudinal section through an infilled boring is shown in text-fig. 3*d*. The borings are preserved as hollows penetrating the already phosphatized nodules. They may penetrate both nodules and phosphatized matrix alike without break, which indicates that the substrate was evenly lithified despite an apparent heterogeneous nature. Each phase of phosphatization can be distinguished by a darkened outer margin. Absence of crushed or distorted borings also shows that the substrate was completely lithified. Borings may not be perfectly straight but may have bent necks (text-fig. 2*b*). These are presumably due to the original boring organism modifying the direction of boring because of unsuitable substrate or of crowding by other individuals. Interpenetrating borings also occur (text-figs. 2*c*, *e*). The first-formed boring appears to be infilled and phosphatized before being cut across by a second boring.

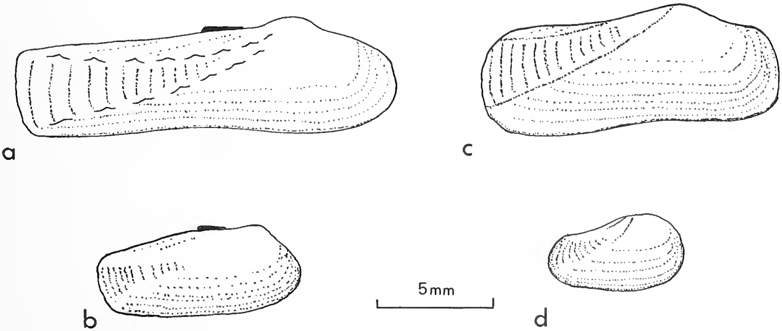
Although the substrate of these borings is normally a phosphatized nodule, one particular example shows a large piece of reptilian bone which has been attacked. The upper surface of the bone (Pl. 96, fig. 23) shows that little erosion has taken place since the original construction of the borings as the openings are still oval. The whole flasks can be seen in Plate 96, fig. 24, together with a specimen of

Hiatella in situ in one of them. The bone must have been buried before abrasion destroyed the oval necks of the borings. Another specimen, not figured, shows a boring penetrating an icthyosaurian vertebra. In contrast, Plate 96, fig. 18 shows part of a phosphatized nodule that has been bored and subsequently abraded so deeply prior to final burial that only rounded bases of the deepest part of the borings remain visible. The borings are normally found penetrating nodules; however, during phases of reworking the nodules may become broken and the lithified boring infillings become loose. Such infillings may be found reworked into the sediment as clasts in the manner described by Radwanski (1977).

These borings correspond closely to the ichnogenus *Gastrochaenolites* Leymerie (1842), originally described from the Calcaire à Spatangues, Neocomian, Aube, France. This name was not included in the *Treatise* (Häntzschel 1975). Leymerie clearly described *Gastrochaenolites* as a boring in rock which was found in association with *Gastrochaena dilatata* Deshayes. It is distinguished from *Teredolites* Leymerie (1842) which penetrated wood and is more evenly tapered along its length. Bromley (1972) placed both *Gastrochaenolites* and *Teredolites* with the more recent ichnotaxon *Trypanites* Magdefrau (1932), which Häntzschel (1975) restricted to straight-sided tunnels of 1–2 mm width. The ichnogenus *Gastrochaenolites* is retained here for the Basal Spilsby Nodule Bed borings until the taxonomy of these ichnogenera is clarified.

Evans (1970) showed that with increasing rock hardness the ratio of the valve length to valve depth decreased for *Penitella*, and the weight of a valve of given size increased. As a consequence, the shape of the boring also changed, becoming shorter and broader with increased hardness. It has not yet been possible to compare in detail the borings containing *Hiatella* from the Portland Stone in southern England, and therefore varied substrates cannot be compared to show whether the hardness of the substrate affected the shape of the boring. There is also the problem of establishing without doubt the original constructor of the boring and if several different bivalves are constructing the borings they may each have distinctive sized and shaped borings.

Hiatella in the borings. Specimens of *Hiatella* found inside *Gastrochaenolites* borings in the Basal Spilsby Nodule Bed range up to 12 mm in length. They are preserved as internal and external moulds in phosphorite. The specimens illustrated on Plate 96 are largely casts made from silicone rubber. The distinctive features of these specimens are: the tendency of the two carinae bounding the dorsal and



TEXT-FIG. 4. Sketches of Recent and Jurassic *Hiatella* valves to illustrate shell form in boring and non-boring habit. *a*, *Hiatella* (*Hiatella*) *arctica* (Linné), non-boring habitat, Recent (after Hunter 1949); *b*, *H.* (*H.*) *gallicana* (Lamarck), boring habitat, Recent (after Hunter 1949); *c*, *H.* (*Pseudosaxicava*) *foetida* (Cox), non-boring habitat, Middle Volgian; *d*, *H.* (*P.*) *foetida* (Cox), boring habitat, Middle Volgian.

ventral margins of the posterior area to be distinct only close to the umbo and to disappear gradually towards the posterior margin (Pl. 96, figs. 1–6, 19; text-fig. 4*d*); the posterior area tends to be weakly inflated and the comarginal ornament is normally suppressed; the umbones are usually low; the growth-lines may become crowded towards the commissure and there is little trace of median sulcus on the ventral margin. All these features suggest that the shell may be becoming confined by the shape of the boring in which it lived. Some specimens, however, are clearly too small to have constructed the boring (text-fig. 3*a*, *b*; Plate 96, fig. 20) and also two individuals have been found in the same boring (Pl. 96, fig. 22); such specimens lack features which indicate confining by the boring and tend to have fully developed ornament. These features in general indicate that the *Hiatella* is infesting borings which are not of its own making.

Gastrochaena *in borings*. About 150 specimens of *Hiatella* have been found in *Gastrochaenolites* borings in the Basal Spilsby Nodule Bed. However, one rock specimen has two *Gastrochaenolites* borings containing the bivalve *Gastrochaena* itself (Pl. 96, fig. 17) and a single external mould of a right valve of *Gastrochaena* shown as a cast in Plate 96, fig. 21. Recent *Gastrochaena sensu stricto* is well known as a borer into calcareous substrates in temperate and tropical regions. It is distinguished from *Hiatella* by its large anterior pedal gape and its lack of external ornament like carinae and lamellae. The borings associated with the Spilsby *Gastrochaena* fit tightly around the shells and show weak traces of the calcareous extension tubes, which are not actually seen on any borings associated with *Hiatella*. It is not clear whether *Gastrochaena* was a precursor to the *Hiatella* in the borings of the Basal Spilsby Nodule Bed, or whether the two were contemporaneous.

Hiatella *independent of borings*. The best-preserved examples of *Hiatella* found independently of the borings are the aragonitic examples from the Hartwell and Swindon Clays (Pl. 96, figs. 15, 16). Such specimens are normally found as disarticulated valves, while those from the Basal Spilsby Nodule Bed are normally complete internal phosphatized moulds with valves in occlusion (steinkerns) (Pl. 96, figs. 7, 8, 11–14). The independent shells commonly range up to a larger size (30 mm) than those from the borings. Although the upper length limit of 30 mm is identical to the maximum length of the borings, the maximum expected size of a *Hiatella* in a boring would be about 20 mm, because of the constricted neck area. Presumably the destruction of further large *Gastrochaenolites* specimens would provide larger *Hiatella* than the 12 mm recorded above. The shell is more oval in cross-section;

EXPLANATION OF PLATE 96

Figs. 1–14, 19, 20, 22. *Hiatella* (*Pseudosaxicava*) *foetida* (Cox). 1, 2, cast of complete individual, IGS Zu2216, 2217, ×1. 3, 4, cast of complete individual, IGS Zu2219, ×1. 5, 6, cast of incomplete individual, IGS Zu2222, ×1. 7, 8, phosphatized steinkern, IGS Zu2241, ×1. 9, 10, cast of complete individual, IGS Zu2218, 2219, 2220, ×1. 11, 12, phosphatized steinkern with cast of some adhering shell, IGS Zu2242, ×1. 13, 14, phosphatized steinkern, IGS Zu2243, ×1. 19, phosphatized internal mould completely fitting within boring, IGS Zu2225, ×1. 20, cast within boring that is too small to have been made by this occupant, IGS Zu2234, 2235, ×1·5. 22, two phosphatized internal moulds of right valves representing two individuals within the same boring; Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincolnshire.

Figs. 15, 16. *H.* (*P.*) *foetida* (Cox). Right valve exterior, IGS Y709, Hudleston Collection, ×1; Upper Kimmeridge Clay, *Pavlovia pallasioides* Zone, Middle Volgian, Swindon, Wiltshire.

Figs. 17, 21. *Gastrochaena* sp. 17, individuals with *Gastrochaenolites*-type borings, ×1·5. 21, cast (seen as mould on fig. 17) of left valve, ×2. IGS Zu2224. Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincolnshire.

Figs. 18, 23, 24. *Gastrochaenolites* ichnosp. 18, eroded flask bases, IGS Zu2226, ×1·5. 23, reptilian bone showing oval apertures to flask-shaped borings. 24, same specimen in broken section showing opened flasks and an individual *Hiatella* steinkern *in situ* in one, IGS Zu2227, ×2. Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincolnshire.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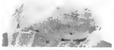
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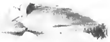
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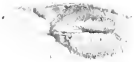
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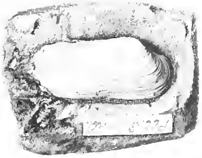
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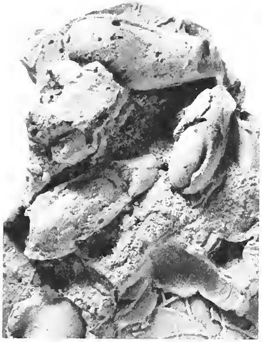
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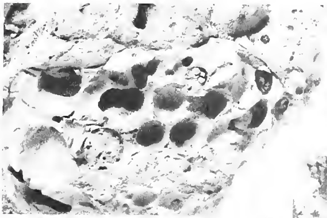
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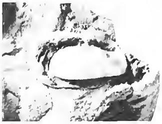
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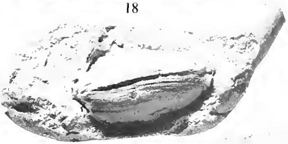
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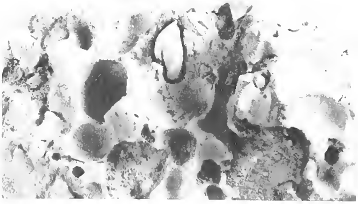
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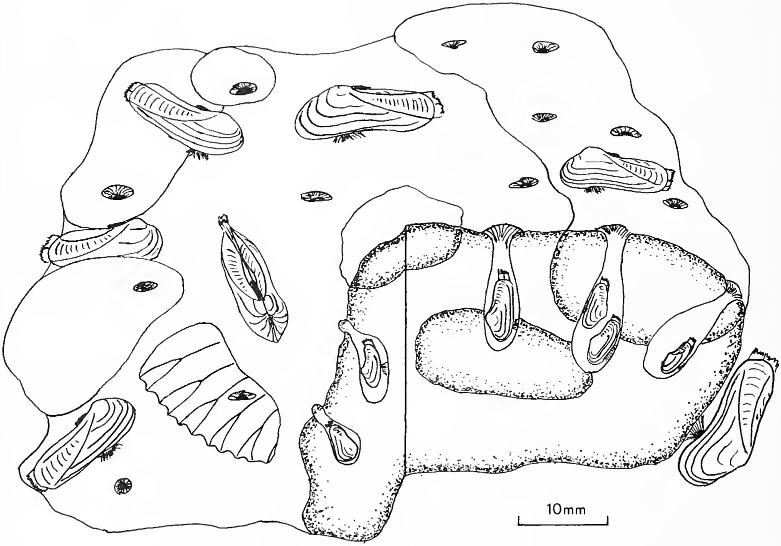
KELLY, Jurassic boring bivalves

the posterior carinae are distinct throughout their length; the posterior area is gently concave; comarginal lamellae are well developed on the posterior area, and the ventral margin is usually gently sulcate, the latter feature giving the byssate shell greater stability in currents (Pl. 96, figs. 9, 10; text-fig. 4*c*). Unfortunately Oates (1974), in his palaeoecological study of the Hartwell Clay, did not recognize *Hiatella*, although the collections he examined do contain them, but they tend to be confused with species of *Grammatodon*. I believe that in the Hartwell and Swindon clays both the *Hiatella* and *Grammatodon* are byssate nestlers and not shallow infauna as Oates suggested. Both these taxa may show a weak byssal gape.

The non-boring *Hiatella* are believed to have been byssally attached to the exterior of local hard substrates such as shells of ammonites and phosphatized nodules. Uninhibited growth allowed the shells to grow to a greater size than in the borings. The large number of complete internal moulds in the Basal Spilsby Nodule Bed, as opposed to isolated valves, probably reflects rapid burial, with the shells still attached to the substrate. Early diagenetic phosphatization took place within the reduced zone defined by the valves. Subsequent winnowing and destruction of the shell concentrated the internal moulds together with other phosphatized debris. A reconstruction of a Basal Spilsby Nodule infested with boring and non-boring *Hiatella* is shown in text-fig. 5.



TEXT-FIG. 5. Reconstruction of a Basal Spilsby Sandstone phosphatized nodule, partially cut away to illustrate *Hiatella* (*Pseudosaxicava*) *foetida* (Cox) in its two ecological niches. The smaller, more constricted shelled specimens occupy the borings, while the larger, more fully developed examples are epibyssally attached to the exterior of the nodule. For simplification the abundant and varied associated fauna of bivalves, gastropods, brachiopods, serpulids, etc. are omitted.

DISCUSSION

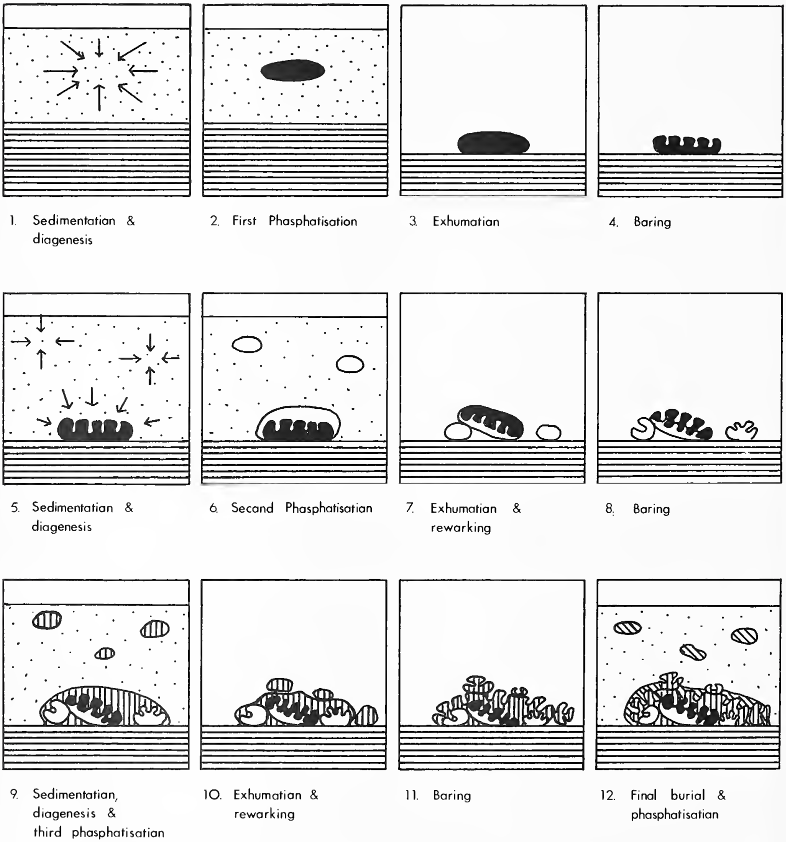
Recent *Hiatella* are byssally attached to the substrate of their choice, whether living epifaunally on hard substrates or infaunally in borings. The range in shape of the Jurassic shells is very similar to that of the recent British species (discussed by Hunter 1949), and there is little reason to suspect that they lived in different ways.

Hunter (1949) recognized two recent species; the first, *H. gallicana* (Lamarck) (text-fig. 4*b*) is normally found inhabiting borings in calcareous substrates. The shell shows features akin to *Hiatella* from borings in the Basal Spilsby Nodule Bed, in particular the suppression of the umbo, posterior carinae, and lamellae. The species is accepted as a rock borer and is believed to bore with the foot using sand grains and mucus as an abrasive. There is as yet no positive evidence for any chemical secretion being used as in the calcium complexing compound discovered in *Lithophaga* by Jaccarini, Bannister, and Micallef (1968). There is, however, one significant difference between the Jurassic and recent species. The Jurassic species had no posterior gape, while the modern species does. *H. gallicana* may frequently start its byssal life attached in the opening of an annelid boring (Parfitt 1871), which is then enlarged and deepened into the substrate. The second species, *H. arctica* (Linné) (text-fig. 4*a*) is a byssal nestler which is not normally associated with borings, but which may fortuitously occur there. It is commonly found single in association with masses of byssate bivalves like *Mytilus*, although Ockelmann (1958) records it occurring as monotypic clusters in Greenland. This species is similar to the non-boring Jurassic forms described above, but is slightly more elongate and the posterior carinae have more lamellose tuberculate ornament. *H. arctica* and *H. gallicana* are readily distinguished in the larval stage, but the adult morphologies intergrade because of overlap in habitat, and it is not always possible to separate them perfectly on features of the hard-part anatomy. There is therefore little reason to attempt to separate the Volgian ecomorphs into different species.

Bivalve borings in phosphatized hardgrounds. Although bivalves are commonly found associated with calcareous substrates, there appear to be relatively few recorded examples of them penetrating phosphatized hardgrounds. It is clear that the Spilsby nodules were already phosphatized at the time of attack; any doubts that could be raised can be dispelled by the occurrence of the borings into fossil bone, which is a primary phosphate. Carcelles (1944) recorded *Lithophaga* (*Diberus*) penetrating the plates of *Glyptodon* and Boreske, Goldberg, and Cameron (1972) reported the occurrence of Miocene bivalve borings in the bone of *Squalodon* and attributed them to *Parapholas*. They also recorded the occurrence of such borings in mammoth tusks. If these borings in phosphatized substrates are constructed by mechanical processes there are no problems. However, if chemical techniques are to be invoked, further research along the lines of Jaccarini *et al.* (1968) should be investigated.

Environment of deposition of Basal Spilsby Nodule Bed. The Basal Spilsby Nodule Bed formed a hardground not of a continuous type (e.g. type 2 of Goldring and Kazmierczak (1974, p. 957)), but of isolated nodules surrounded by glauconitic silty matrix. The nodules show a complex depositional history and correspond partly to the hiatus concretions of Voigt (1968), whose observations were based on Liassic calcareous concretions. These calcareous concretions were formed by coalcscence of concretions of different age. The younger concretions envelope the older, the concretions themselves being of early diagenetic origin. Voigt recognized the following cyclic sequence of events: 1, formation of concretion; 2, washout; 3, corrosion, boring, and encrustation; 4, burial. The Cenomanian phosphatized nodules described by Kennedy and Garrison (1975) correspond more closely to the Spilsby nodules. For discussion of earlier studies on phosphatized horizons of condensation see Brückner (1977). Kennedy and Garrison (1975) propose the following sequence for the formation of nodules that are largely composed of fossil moulds: 1, infilling of shell by sediment; 2, burial; 3, mould cementation (probably by high-magnesian calcite); 4, dissolution of aragonitic shell; 5, disinterment; and 6, phosphatization, boring, and encrusting. The Basal Spilsby Nodules appear to have formed under similar conditions, although it is believed here that phosphatization probably took place at depth in the sediment and not on the surface of the sea floor as Kennedy and Garrison (1975, p. 357) suggest. It is not possible to see deep burrowing bivalves like *Pleuromya* and

Lucina in life position in the Basal Spilsby Nodule Bed, although they are particularly common as heavily darkened phosphatized internal moulds. However, in the Speeton Clay of the Yorkshire coast (Lower Cretaceous), deep burrowers such as *Thracia* and *Pleuromya* are commonly preserved in life position as weakly phosphatized, pink or pale-brown internal moulds with some original shell attached. These have clearly never been exposed on the sea floor; those that have become exposed and occur in the reworked nodule beds are usually blackened on the exterior and may show signs of erosion.



TEXT-FIG. 6. Simplified diagrammatic representation of the sequence of events leading to the formation of the Basal Spilsby Nodule Bed.

The preservation of many fossils in the Basal Spilsby Nodule Bed as phosphatized internal moulds suggests that the confining shell walls have provided a reduced zone within the sediment. The phosphatization occurred within this zone and appears first in deep recesses such as the umbonal infilling in bivalves, and may appear weaker towards the commissure, especially so in forms with commissural gapes. During a phase of winnowing these moulds would have been condensed and concentrated in the manner described by Fürsich (1978, p. 247). Once the nodules were exposed on the sea floor they would have been open to attack by boring bivalves and grazing gastropods, etc., and available for encrustation by ostreids and *Plicatula*. During the next phase of burial, the first-formed concretions would have been bound together by further phosphatization. Repetition of this sequence would have increased the complexity of formation of these hiatus concretions. So far at least three phases of phosphatization have been recognized in the Basal Spilsby Nodule Bed, as illustrated in text-fig. 3*a–d*. All these figures show light-coloured but phosphatized areas with blackened exteriors. These are surrounded by glauconitic sand which in turn is phosphatized. Both these earlier phases of phosphatization are cut across by borings which have then been filled with sediment and phosphatized again. The number of phases of boring and phosphatization are likely to be a conservative estimate, as the largest pieces of the nodule bed are small, with a maximum diameter of 20 cm. The reconstructed series of events leading to the formation of the Basal Spilsby Nodule Bed is shown diagrammatically in text-fig. 6.

In modern sediments phosphate formation has been described by Parker (1975) and Mannheim, Rowe, and Jipa (1975). Parker, working on the Agulas Bank on the south coast of South Africa, concluded that the area of phosphate formation was estuarine and undergoing regression. Phosphatization was replacing lime mud matrix of packestones and wackestones, and sometimes cementing conglomerates of similar reworked sediments. Deeper-water phosphate appeared to be redeposited from shallow areas. Mannheim *et al.*, working on Holocene sediments from the coast of Peru, recognized that the calcareous tests of foraminifera were being replaced by phosphate. The sediments were rich in organic debris, but occurred in an area with a low rate of terrigenous sedimentation which allowed concentration of the phosphate. The depth at which high-concentration phosphate occurred is between the shelf break and 1000 m. But the highest concentration was recorded from a submarine hillock at 144 m.

The Basal Spilsby Nodule Bed is a shelf deposit; although it would be dangerous to suggest an absolute depth, it appears to be a shallower-water deposit than the preceding Kimmeridge Clay, and contains a much more diverse benthic macrofauna. There is no evidence for the environment being estuarine, although it would appear that it occurs in a marine strait that crossed the East Midlands Shelf in Middle Volgian times. To the south-east it was bounded by the Anglo-Brabant Massif, and to the north-west by the Pennine Anticline. Despite penecontemporaneous uplift the land must have had low water runoff and therefore low sedimentation rates in the adjacent sea. Cold currents from the northern connection to Boreal seas could have provided the high organic content and source of phosphate. Uplift has probably been caused by movements of axes such as the Market Weighton structure. The Basal Spilsby Nodule Bed, which is well developed in the north of Lincolnshire, probably represents a winnowed local topographic high on the East Midlands Shelf. Contemporaneous sediments like the glauconitic Hartwell Clay in Buckinghamshire probably represent what the Basal Spilsby sediment would have been like during a phase of deposition. The Hartwell Clay-type sediment was probably originally widespread over most of the East Midlands Shelf and central England, from Swindon to Lincolnshire, at least in early Middle Volgian times. The bulk of it was destroyed during phases of condensation, leaving only the phosphatized nodules.

CONCLUSIONS

Although it is clear that *Hiatella* is largely a squatter, reoccupying vacant *Gastrochaenolites*-type borings in the Basal Spilsby Nodule Bed, it is still not established that the original borings were made by *Hiatella* itself. *Gastrochaena* was responsible at least for some of the borings, but it seems unlikely that these were the ones subsequently occupied by *Hiatella*. Certainly the necks of borings containing

Hiatella do not show traces of a calcareous extension tube, nor do they have figure-of-eight apertures which are both features of *Gastrochaena* borings.

British Middle Volgian *Hiatella* has two distinctive morphological varieties. One occurs in borings where shell features are suppressed due to the enclosure of the boring, which it was possibly unable to modify. A larger, more elongate and fully ornamented form occurs which is not associated with borings and was probably a simple byssate nestler. As both forms intergrade they probably represent the same species.

The Basal Spilsby Nodule Bed represents a highly condensed and phosphatized unit once composed of a Hartwell Clay-type sediment. It probably formed on a topographic high on the East Midlands Shelf from which fine unlithified sediment was winnowed.

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EVOLUTION OF THE SILURIAN TRILOBITE *TAPINOCALYMENE* FROM THE WENLOCK OF THE WELSH BORDERLANDS

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ABSTRACT. Some calymenid trilobites from the Wenlock Series of the Welsh Borderland are described and assigned to a new genus *Tapinocalymene*, type species *T. nodulosa* (Shirley 1933). An evolutionary lineage from *T. volsoriforma* sp. nov. (early Wenlock) through *T. vulpecula* sp. nov. (late Wenlock) to *T. nodulosa* (late Wenlock) is proposed, involving an increase in the length and area of the preglabellar furrow. *Tapinocalymene* was probably benthic in habit, and occurs in somewhat offshore, generally deepish water, clastics. *Calymene diademata* Barrande, 1846 (Wenlock, Bohemia), *C. nasuta* Ulrich, 1879 (Llandovery, United States) and *C. blumenbachii* Brongniart, 1822 (Wenlock, England), respectively the type species of the calymenines *Diacalymene* Kegel, 1927, *Spathacalymene* Tillman, 1960, and *Calymene* Brongniart, 1822 are figured and compared with members of *Tapinocalymene*. *S. nasuta* and *T. nodulosa* both have a particularly long preglabellar area, but each differs in its form and derivation. Several Ordovician and Silurian calymenid genera, some only distantly related, evolved a long preglabellar area, the taxonomic value of which should be treated with caution.

SINCE the pioneer revisions made by Shirley (1933, 1936) on British Silurian calymenid trilobites, they have occasionally been discussed in studies on non-British faunas (Campbell 1967; Haas 1968; Schrank 1970; Whittington 1971*b*), but except for the work of Temple (1969, 1970, 1975) on Llandovery species, no direct attention has been paid to them. This paper is part of a wider project undertaken by the present author to investigate north-west European Silurian (and Ordovician) calymenids. The terminology, measurement, photographic and preparation techniques are those of Siveter (1977, 1979), except that surface sculptural terms are now used in the sense of Miller (1975, pp. 341, 343). Specimens used in this work are housed in the following museums: British Museum (Natural History), London (BM); Geological Museum, Institute of Geological Sciences, London (GSM); National Museum of Wales, Cardiff (NMW); Ludlow Museum, Salop (LM); Hunterian Museum, Glasgow (HM); Naturhistoriska Riksmuseet, Stockholm (RM); National Museum of Natural History, Smithsonian Institution, Washington (USNM).

SYSTEMATIC PALAEONTOLOGY

Family CALYMENIDAE Milne Edwards, 1840
Subfamily CALYMENINAE Milne Edwards, 1840

Discussion. I have advocated (Siveter 1977, p. 353) that this subfamily should contain only those genera possessing the papillate-buttress structure, but future work may provide exceptions to this general rule, with the possibility of buttressed forms giving rise to non-buttressed forms through the arrested development of this feature during ontogeny (Siveter 1979, p. 373).

Genus TAPINOCALYMENE gen. nov.

Type species. *Calymene nodulosa* Shirley, 1933; Wenlock Series, Coalbrookdale Formation, Burrington, Hereford, and Worcester.

Derivation of name. Greek, *tapeinos*, humble, alluding to the glabella which is fairly low and short relative to the fixed cheeks.

[Palaeontology, Vol. 23, Part 4, pp. 783–802, pls. 97–101.]

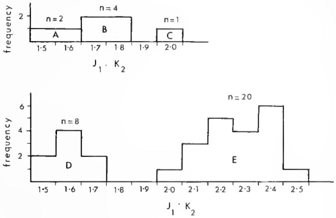
Other species. *T. volsoriforma* sp. nov., *T. vulpecula* sp. nov.

Diagnosis. A calymenine genus which combines the following characters: Preglabellar area relatively long, variably formed. Anterior glabellar margin normally lies behind anterior margin of fixed cheek, exceptionally both margins are in line (tr.); dorsal glabellar surface stands just above, or anteriorly is sometimes slightly below, fixed cheek. Glabellar lobe 2p is bridged across axial furrow to a genal buttress. Palpebral lobes are from twice to 2·5 times as wide (tr.) apart as glabellar width at 2p lobes. Hypostoma has ventral protuberance on middle of anterior lobe; maculae well developed. Pygidial axis almost flat (tr.); inner pleural region slopes gently abaxially; interpleural furrows are weak or obsolete. Numerous small to medium-sized granules uniformly and closely distributed on glabella; anterior adaxial part of fixed cheek, and often anterior border, coarsely granulate.

Discussion. Shirley (1936) advocated that calymenids showing a 'ridged' (or 'thickened') preglabellar area and a papillate 2p glabellar lobe joined to a genal buttress should be placed in his amended concept of *Diacalymene*; those species with this bridge across the axial furrow but without the 'ridged' preglabellar area should be placed in *Calymene*. The separation of *Diacalymene* on this basis has recently been questioned (Temple 1975; Ingham 1977; McNamara 1979) and certain British Ashgill and Llandovery species which Shirley placed in that genus are now held in abeyance in *Calymene* (*sensu lato*). At present I prefer to consider the type species of *Diacalymene*, *C. diademata* Barrande, 1846 (late Wenlock age), and also several other related taxa such as *D. horbingeri* (Šnajdr, 1975) (Llandovery of Bohemia), as generically distinct from *C. blumenbachii* Brongniart, 1822 and related species. Nevertheless, assigning species to either *Diacalymene* or *Calymene* according to the nature of the preglabellar area was impracticable in the case of *Tapinocalymene nodulosa* (Shirley, 1933), *T. volsoriforma* sp. nov. and *T. vulpecula* sp. nov. These species all have the 2p lobe joined to a genal buttress, but whereas *T. volsoriforma* and *T. vulpecula* show a fairly distinct break in slope in the preglabellar area, where the anterior side of the preglabellar furrow meets the posterior edge of the less steeply sloping anterior border (Pl. 99, fig. 2; Pl. 100, fig. 2), similar to that in certain species variously referred to *Diacalymene* and *Calymene* (s.l.), *T. nodulosa* (Pl. 97, fig. 11) has a preglabellar area similar to, though very much longer than, most *Calymene* species. All three species share characters which unite them as a genus distinct from other calymenines. The preglabellar area in *Tapinocalymene* is believed to have evolved quite rapidly and is useful for specific discrimination, though not for diagnosing the genus. None of the generic characters is completely exclusive, but in particular the low glabella which fails to protrude anteriorly beyond the fixed cheeks (Pl. 98, figs. 2, 3; Pl. 99, figs. 1, 2; Pl. 100, figs. 1, 2), the widely separated palpebral lobes (Pl. 98, fig. 6; Pl. 99, fig. 13; Pl. 100, fig. 4), and the style of cranidial sculpture (Pl. 97, fig. 9; Pl. 99, fig. 14) all combine to distinguish *Tapinocalymene*. Other characteristic features include the axis, interpleural furrows, and inner pleural region of the pygidium. All *Tapinocalymene* species are closely associated in time and space.

Compared with *Tapinocalymene*, *Diacalymene* has a more raised, forwardly protruding glabella, narrowly separated palpebral lobes, and a more pointed inner, anterior corner to the fixed cheek (cf. Pl. 98, figs. 9–11; Pl. 101, figs. 5, 6, 10). Furthermore, *Diacalymene* lacks coarse granules on the inner part of the fixed cheek, though both genera have small, close-set glabellar granules. '*C*.' *allportiana* Salter, 1865 (Much Wenlock Limestone Formation, Dudley) has the same type of cranidial sculpture and pygidial axis as *Tapinocalymene* (Shirley 1933, pp. 58, 59, pl. 1, figs. 12–14); also the separation of its palpebral lobes falls just within the range of variation of the new genus (text-fig. 1). '*C*.' *allportiana* is certainly more closely related to *Tapinocalymene* and *D. diademata* than to *C. blumenbachii*, but is excluded from *Tapinocalymene* as presently defined because of its more anteriorly, and (to a lesser extent) dorsally, projecting glabella. When *Diacalymene* is fully reassessed the generic position of '*C*.' *allportiana* will become clearer. Most *Calymene* species differ from those of *Tapinocalymene* in the following features: a more dorsally and anteriorly projecting glabella having more variably sized, often larger, granules; less widely separated palpebral lobes; a steeper slope to the inner pleural region of the pygidium; a more convex (tr.) pygidial axis; better defined interpleural furrows, particularly distally. These differences are most obvious in the late Wenlock species *C. aspera* Shirley, 1936 and *C. blumenbachii* (cf. Pl. 97, figs. 1, 3, 10, 11; Pl. 100, figs. 9–12, 14, 16; text-fig. 1). Features characteristic of *Tapinocalymene* are occasionally exhibited, or closely approached, by *Calymene* species. For example, *C. tuberculosa* Dalman, 1827, from the Wenlock of Gotland (and Wenlock Edge) has a gently convex pygidial axis, and *C. tenera* Barrande, 1852 from the Kopanina Formation (Ludlow) of Bohemia has very weak interpleural furrows. The Ludlow species *C. neointermedia* R. and E. Richter, 1954 has been allied with *T. nodulosa*, as both have similar scoop-like preglabellar areas (Schrank 1970, p. 122; Whittington 1971*b*, p. 463); the same character is present in *C. puellaris* Reed, 1920, also of Ludlow age. *C. neointermedia* and *C. puellaris* clearly belong within *Calymene*. The similarity in the preglabellar area of the three species is believed due to adaptive convergence.

Tomczykowa (1970) referred *Tapinocalymene nodulosa* to the monotypic genus *Spathacalymene* from the Osgood Formation (upper Llandovery; Berry and Boucot 1970), Indiana, an assignment made mainly because *S. nasuta* and *T. nodulosa* both have a long preglabellar area. However, it is not unusual for calymenid genera to independently develop a long preglabellar area and, in each genus, for it to be morphologically different. Compare, for example, that in *Thelecalymene mammillata* (Hall, 1861; Whittington 1971*a*, pl. 1, figs. 4, 5; pl. 2, fig. 1) from the upper Ordovician of the United States, *Prionocheilus foveolatus* (Törnquist, 1884; Warburg 1925, pl. 4, figs. 13, 16) from the middle Ordovician of Sweden, *Reedocalymene expansa* (Yi, 1957; Lu 1975, pl. 46, fig. 4) from the middle Ordovician of China, and *Calymenesun tingi* (Sun, 1931; Lu 1975, pl. 46, figs. 9–11) from the middle Ordovician of China. There is no resemblance in the preglabellar area of *Spathacalymene nasuta* and *Tapinocalymene nodulosa* apart from their uncommon length (see below and Pl. 98, figs. 6, 9, 12; Pl. 101, figs. 1, 4, 8). The former differs from the latter in its very convex (sag. and tr.), more dorsally and anteriorly projecting glabella, narrowly separated palpebral lobes (text-fig. 1), V-shaped rostral suture, subconical inner anterior corner to the fixed cheek, narrower thoracic and pygidial pleural region, and the lack of coarse granules on the inner, anterior part of the fixed cheek. I have no doubt that these species are not congeneric. The three calymenids with a spatulate preglabellar area from the Ludlow of Poland, which have been named *S. flexuosa*, *S. brevis*, and *S. linguata* by Tomczykowa (1970), should also be excluded from *Spathacalymene*. I agree with Whittington (1971*b*, p. 459) that these species represent a quite separate lineage (non-calymenine; but see Siveter 1979, p. 373). *Papillicalymene* Shirley, 1936 from the Ludlow of Gotland and Podolia, and Downton age glacial erratics of the north German plain, has a very advanced type of genal buttressing (Whittington 1971*b*, pls. 85, 86) which easily distinguishes it from *Tapinocalymene*.



TEXT-FIG. 1. Histogram of ratio of width between palpebral lobes to width of glabella at lobe 2p (=variates J_1 and K_2 of Siveter 1977, p. 338, fig. 1). A. *Spathacalymene nasuta*. B. *Diacalymene diademata*. C. '*Calymene*' *allportiana*. D. *Calymene blumenbachii*. E. *Tapinocalymene*: *T. volsoriforma*, n = 6; *T. vulpecula*, n = 4; *T. nodulosa*, n = 10.

Occurrence. *Tapinocalymene* has a stratigraphic range of early to late Wenlock; that is Sheinwoodian, probably *Cyrtograptus centrifugus* or *C. murchisoni* biozones, to Homerian, Gleedon Chronozone, *G. nassa* Biozone. It is limited to the main Wenlock outcrop of the Welsh Borderland from Rushbury, Ape Dale, through the core of the Ludlow anticline and the Wigmore Rolls area, to Dolyhir, Powys.

Tapinocalymene nodulosa (Shirley, 1933)

Plate 97, figs. 1–6, 8, 9, 11; Plate 98; text-fig. 2A–F

non *1827* *Calymene blumenbachii* var α, *tuberculosa*; Dalman, p. 227.
v. 1839 *Calymene blumenbachii* Brongniart; Murchison (*pars*), p. 653, pl. 7, fig. 5 (GSM 6588), *non* figs. 6, 7.
v. 1848 *Calymene tuberculosa*, Salter; Salter, *in* Phillips and Salter, p. 342, pl. 12, figs. 1, 1*a* (GSM 19642), 2, 3, 5, ?fig. 4.
v. 1849 *Calymene tuberculosa* Salter; Salter, p. 1, pl. 8, figs. 1, 2 (GSM 19642), 1*, 3–5, 7, ?fig. 6, *non* figs. 8*, 8 (= *C. puellaris* Reed; GSM 19690).
non *1851* *Calymene tuberculosa* (Salter); McCoy, *in* Sedgwick and McCoy, p. 167.
v. *1859* *Calymene tuberculosa*, Salter; Murchison, pl. 18, fig. 11 (GSM 6588).
v. 1865 *Calymene tuberculosa*, Salter; Salter, p. 91, pl. 8, figs. 1, 2, 3 (GSM 19642), 4, 5 (GSM 19646), 6.
. *1873* *Calymene tuberculosa*, Salter; Salter (*pars*), p. 133, *non* p. 166.
v. *1884* *Calymene tuberculosa*; La Touche, p. 66, pl. 10, fig. 243 (GSM 6588).
1885 *Calymene tuberculosa* Salter *non* Dalman; Lindström, p. 66.
. *1888* *Calymene tuberculosa* Salter; Etheridge (*pars*), p. 46.
v. *1919* *Calymene blumenbachii* Brongniart; Reed, *in* Garwood and Goodyear, p. 20.
. *1925* *Calymene tuberculosa* Salter; Warburg, p. 158.
1927 *Calymene* (*Diacalymene*) *tuberculosa* Salter; Kegel, pp. 618, 620, text-fig. 2*f*.
v* *1933* *Calymene nodulosa* nom. nov.; Shirley, p. 53, pl. 1, figs. 6–11.
. 1936 *Calymene nodulosa* Shirley; Shirley, pp. 388, 390, 393, 399, 400, text-figs. 1, 2 (*pars*).
. *1938* *Calymene nodulosa* Shirley 1933; Stubblefield, pp. 37, 38.
? *1953* *Calymene nodulosa* Shirley; Williams, pp. 199, 200 (specimens not seen).
v? *1968* *Calymene nodulosa* Shirley; Greig, Wright, Hains, and Mitchell, p. 354 (specimens inadequate).
. *1970* *Calymene nodulosa* Shirley, 1933; Schrank, pp. 115, 122, 123.
. 1970 *Spathacalymene nodulosa* (Shirley); Tomczykowa, pp. 63, 70, 72, text-figs. 4*k*, 5*f*.
. *1971b* *Calymene nodulosa* Shirley 1933; Whittington, p. 463.

Holotype. Nearly complete specimen lacking preglabellar area, with cuticle removed from abaxial part of cheeks and abaxial pleural region of thorax, GSM 19642; figured Salter 1848, pl. 12, figs. 1, la; 1849, pl. 8, figs. 1, 2; 1865, pl. 8, figs. 2, 3; Shirley 1933, pl. 1, figs. 6–10; pl. 98, figs. 1–3.

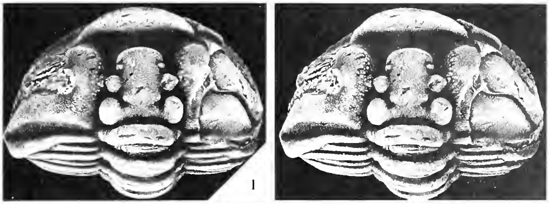
EXPLANATION OF PLATE 97

Figs. 1–6, 8, 9, 11. *Tapinocalymene nodulosa* (Shirley, 1933). All specimens are from the Wenlock Series, Homerian Stage, Coalbrookdale Formation, vicinity of Burrington, Hereford and Worcester; 2, 5, 8, 9 come from *C. lundgreni* Biozone strata, sunken lane south of Burrington (SO 442 718). 1, 3, 11, enrolled specimen lacking left, and most of the right, free cheeks, HM A212/1, dorsal stereo-pair, frontal view, ×$1\frac{1}{2}$, left lateral view, ×2. 2, slightly distorted cranidium, LM 4885, dorsal view, ×2. 4, incomplete thorax and pygidium, NMW 75.35G.400, posterior view, ×1·5. 5, incomplete cranidium and rostral plate, NMW 77.31G.10, ventral view, ×2. 6, hypostoma and rostral plate, RM Ar38841, ventral stereo-pair, ×3·5. 8, pygidium, NMW 77.31G.9, posterior view, ×5. 9, cranidium, LM 4902, dorsal view, ×4.

Fig. 7. *Tapinocalymene nodulosa*? (Shirley, 1933). Pygidium, NMW 77.31G.11, Wenlock Series, Homerian Stage, Coalbrookdale Formation, base of Farley Member, *G. nassa* Biozone, track section 252 m at 82° from St. Edith's Church, Eaton, Ape Dale, Salop (SO 5023 9002; Bassett *et al.* 1975, loc. 25, p. 16); posterior view, ×1·5.

Fig. 10. *Calymene blumenbachii blumenbachii* Brongniart, 1822. Complete enrolled specimen, GSM 19668, Wenlock Series, Homerian Stage, Much Wenlock Limestone Formation, Dudley, West Midlands; dorsal view, ×2 figured Shirley 1933, pl. 1, figs. 4, 5.

PLATE 97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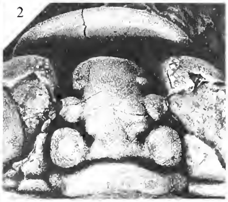
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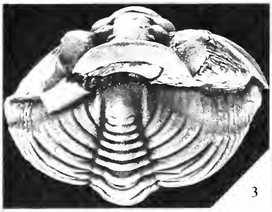
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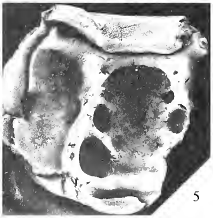
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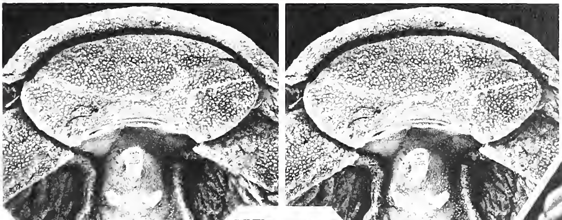
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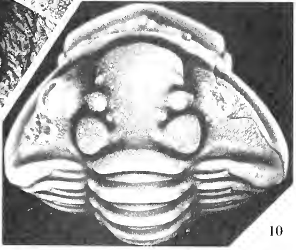
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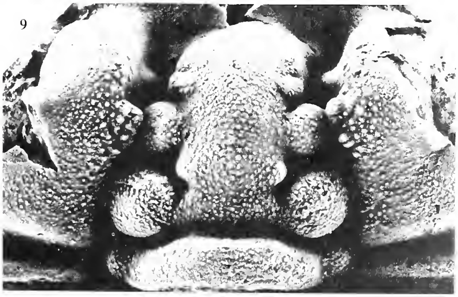
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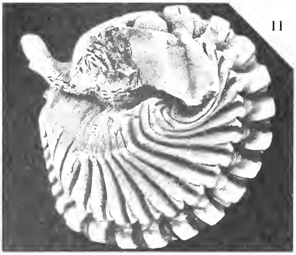
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SIVETER, Calymenid trilobites

Type locality. Wenlock Series, Homerian Stage, Coalbrookdale Formation, Burrington, Hereford and Worcester. The Coalbrookdale Formation in the vicinity of Burrington includes strata of the *Cyrtograptus lundgreni*, *G. nassa*, and *Monograptus ludensis* biozones (Holland, Rickards, and Warren 1969). It is perhaps most likely that *lundgreni* Biozone strata yielded the holotype, and I have collected *T. nodulosa* from this horizon in the sunken lanes south of Burrington church.

Additional material and occurrences. At least 6 nearly complete individuals, 20 cranidia, 20 pygidia, 5 hypostomata. I have noted material in the British Museum (Natural History); Museum of the Institute of Geological Sciences, London; National Museum of Wales, Cardiff; Hunterian Museum, Glasgow; Ludlow Museum; Naturhistoriska Riksmuseet, Stockholm. The species occurs in the Coalbrookdale Formation of the following localities: Calcareous concretions within the small faulted patch of shales (=within the *C. rigidus* to *C. lundgreni* biozones; Bassett 1974, p. 759) above the Dolyhir Limestone, quarry 'D' of Garwood and Goodyear (1919, pl. 5, fig. 1, pl. 7), Dolyhir, Powys (SO 2412 5805); Birtley Lane, 6·5 km south-south-west of Leintwardine, Hereford and Worcester (SO 3687 6888); Homerian Stage, *C. lundgreni* Biozone, track section at St. Edith's Church, Eaton, Ape Dale, Salop (SO 5001 9002). A pygidium of *Tapinocalymene* (Pl. 97, fig. 7) from the base of the Farley Member, Coalbrookdale Formation, the track section at Eaton (SO 5023 9002), may also belong to *T. nodulosa.* Greig *et al.* (1968, p. 354) list the species from nearby Rushbury, Ape Dale (*C. lundgreni* Biozone; Bassett *et al.* 1975, p. 16, fig. 2); these specimens belong to *Tapinocalymene* but a specific assignment cannot be made with certainty. I cannot confirm Shirley's (1933, p. 56) record of Wenlock-age specimens from a quarry beside Nant Tresglen, behind Halfway Inn, 8 km east of Llandovery (SN 828 328). Williams (1953, pp. 199, 200) cited *T. nodulosa* from his 'Lower' and 'Upper' Wenlock groups of the Llandeilo district. This material has not been seen but the *C.* cf. *nodulosa* figured (White, *in* Squirrell and White 1978, pl. 3, figs. 3, 4) from the Wenlock of the Cennen Valley near Llandeilo is not close to *T. nodulosa* and does not appear to be congeneric.

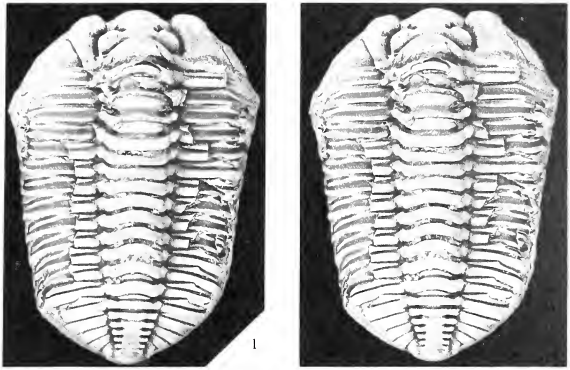
Diagnosis. Preglabellar area is from about two-fifths to almost one-half as long as glabella, directed forward, and curving progressively more steeply upward. Preglabellar furrow about three-fifths to three-quarters as long as preglabellar area; transition in slope between steep anterior side of this furrow and relatively short (sag. and exsag.), convex anterior border is gradual.

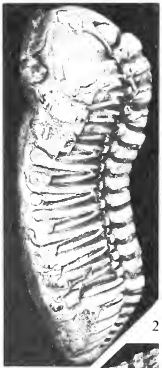
Description. Cranidium about twice as wide as long. Glabella slightly longer than wide with a subtrapezoidal to bell-shaped outline; in lateral profile dorsal surface is above fixed cheek at lobe 1p, is equal to or below fixed cheek at about furrow 2p (Pl. 97, fig. 11; Pl. 98, figs. 11, 12). Occipital ring about one-quarter as long (sag.) as wide, slightly wider than glabella at lobe 1p, is longest medially then shortens and swings forward laterally towards axial furrow where it is swollen. Occipital furrow longest and shallowest medially, shortens and deepens towards axial furrow, has a more steeply inclined posterior than anterior slope. Lobe 1p about one-third as wide as glabella. Abaxial part of 1p furrow deep, divides adaxially into two branches; posterior branch runs inward and obliquely backward, shallows before finally turning inward towards median line; weaker anterior branch directed forward and inward, not reaching as far adaxially as posterior branch. Shallow extension of posterior branch connects with occipital furrow to separate 1p lobe from frontomedian lobe. Small intermediate lobe within fork of furrow 1p (Pl. 97, fig. 9). Lobe 2p is papillate, joined to adaxially directed genal buttress. Furrow 2p directed inward and slightly backward, is continued as sharply flexed shallow depression which meets anterior branch of furrow 1p, thus semi-isolating lobe 2p. Lobe 3p much smaller than 2p, slightly elongate (tr.), sited on

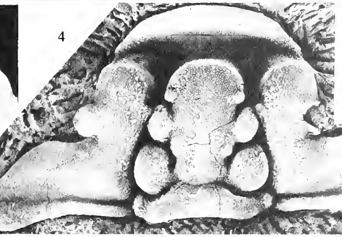
EXPLANATION OF PLATE 98

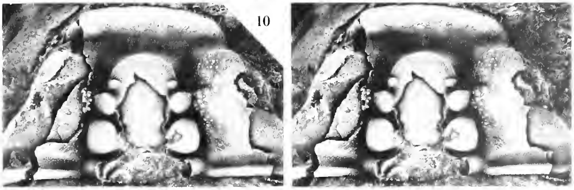
Figs. 1–11. *Tapinocalymene nodulosa* (Shirley, 1933). 1–4 are from the Wenlock Series, Homerian Stage, Coalbrookdale Formation, vicinity of Burrington, Hereford and Worcester; 4 is from *C. lundgreni* Biozone strata, sunken lane south of Burrington (SO 442 718). 1–3, holotype, partial internal mould specimen lacking preglabellar area, GSM 19642, dorsal stereo-pair, left lateral view, × 1·5, dorsal view (cephalon), × 2; figured Salter 1848, pl. 12, figs. 1, 1*a*; 1849, pl. 8, figs. 1, 2; 1865, pl. 8, figs. 2, 3; also Shirley 1933, pl. 1, figs. 6–10. 4, cranidium, NMW 77.31G. 8, dorsal view, × 2. 5–12 are from calcareous concretions within faulted patch of Coalbrookdale Formation, Dolyhir, Powys (SO 2412 5808). 5, 7, 8, partial internal mould pygidium, NMW 53.288.G1, right lateral, posterior views, × 1·5, oblique view, × 2. 6, 12, cranidium, GSM Zs195, dorsal, right lateral views, × 2. 9–11, partial internal mould cranidium, GSM Zs183, oblique view, × 6, dorsal stereo-pair, right lateral view, × 2.

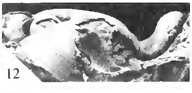
PLATE 98











SIVETER, *Tapinocalymene*

dorsolateral glabellar surface. Furrow 3p directed at about right angles to median line. Possible 4p furrow (not observed dorsally) expressed ventrally as a ridge joined to outer, posterior end of ridge which represents furrow 3p (Pl. 97, fig. 5). Frontal lobe bluntly rounded in outline, falls steeply to preglabellar furrow.

Axial furrow deep, steep-sided and narrowest around lobe 1p, is at least two to three times wider anterior to bridge of 2p lobe and genal buttress (Pl. 97, fig. 9). Anterior pit deep, situated very low down on adaxial side of axial furrow just anterior to furrow 3p; it is represented ventrally by a boss, the inner anterior slope of which is hollowed for reception of anterior wing process of hypostoma (Pl. 97, fig. 5). Some specimens show vestige of eye ridge running down abaxial side and across base of axial furrow opposite furrow 3p (Pl. 97, fig. 9; Pl. 98, fig. 9). In dorsal view anterior margin of preglabellar area is moderately (Pl. 98, fig. 10) to strongly (Pl. 97, fig. 2) convex forward, in lateral profile it is raised just above frontal glabellar lobe (Pl. 97, fig. 11), in frontal view it is sometimes slightly swollen upward opposite axial furrow. Long (sag. and exsag.) preglabellar furrow passes smoothly forward and progressively more upward on its anterior slope into short, convex (sag.) anterior border. Outer part of anterior border slopes downward and slightly backward to rostral suture (Pl. 97, figs. 6, 11).

Posterior border of cranidium lengthens (exsag.) very slightly from axial furrow to fulcrum, abaxially from which it expands more quickly until shortening slightly and becoming less convex (exsag.) near facial suture. Posterior border furrow has a less steeply inclined anterior than posterior slope, both slopes become more gently inclined abaxially. Postocular part of fixed cheek slopes moderately downward to border furrow; convex preocular part projects beyond frontal glabellar lobe, is vertical or slightly overhangs abaxial continuation of preglabellar furrow (Pl. 97, fig. 11). Mid-length of palpebral lobe is opposite some part or anterior margin of lateral lobe 2p, initially it continues slope of fixed cheek then abaxially has a more horizontal attitude (Pl. 98, fig. 4). Posterior branch of facial suture runs outward and slightly backward then swings in broad curve to lateral border, finally turning more posteriorly to posterior margin (Pl. 98, fig. 6); anterior branches are abaxially convex, slightly convergent. Free cheek incompletely known, slopes steeply to open U-shaped lateral border furrow, doublure is sharply reflexed upward and outward from lateral border.

Border sector of rostral plate just greater than one-third to just less than one-half as long as wide, slightly more than three times as long (sag.) as outer part of anterior border (Pl. 97, fig. 6). Rostral suture moderately arched. Connective sutures gently convex outwards, converge posteriorly towards angular junction of border and doublure sectors. Inner arc of border sector about parallel to rostral suture, marked by a slight ridge (Pl. 97, fig. 6). Hypostoma 1·1 to 1·2 times as wide across anterior wings than long (sag.). Anterior margin broadly convex forward. Anterior border flexed ventrally; border furrow shallow. Anterior wing with deep pit. Lateral margin slightly convex abaxially between anterior wing and lateral shoulder; lateral border narrows (tr.) posteriorly; border furrow most distinct opposite (tr.) median protuberance of anterior lobe. Posterior border flattened, projecting into two broad spines. Faint median furrow connects two conspicuous, ovate maculae. Anterior lobe of median body about 2·25 to 2·5 times as long as posterior lobe; a spur-like protuberance is directed ventrally from centre of anterior lobe. Posterior lobe is crescent-shaped.

Thorax characteristically wide (tr.); anterior part of axis less wide than pleural region. Axis has thirteen rings, each of about constant length (sag. and exsag.) and flat to gently convex in lateral profile, flexed forward abaxially and swollen at axial furrow. Posterior band of each pleura higher than anterior, moderately convex (exsag.), forms posterior rim to articulating facet (Pl. 97, fig. 11; Pl. 98, fig. 2). Pleural furrow moderately deep and U-shaped at fulcrum, less well marked abaxially, dies out on articulating facet. Many specimens have slightly sinuous course to the distal, posterior margins of thoracic pleurae due to enrolment contact of free cheek; point of contact more dorsally positioned on posterior pleurae, becomes progressively lower on anterior pleurae, is continued posteriorly as a cincture on the pygidium (Pl. 97, figs. 4, 11).

Pygidial axis very gently convex (tr.), has six distinct and one indistinct axial rings and terminal axial piece. Each ring is almost flat (sag.); anterior rings slightly inflated at axial furrow. Ring furrows shallowest medially, become deeper towards axial furrow which becomes weaker posteriorly and scarcely present around terminal axial piece. Inner pleural region slopes gently (tr.) to cincture, thereafter much more steeply to lateral margin. Pleural region usually has five distinct pleural furrows to the cincture (Pl. 97, figs. 3, 8), one specimen (Pl. 98, figs. 5, 7, 8) has trace of a sixth. Interpleural furrows very faint. On outer pleural region pleural and interpleural furrows very weak (Pl. 97, fig. 8) or absent (Pl. 98, fig. 8), leaving smooth border. Postaxial sector falls almost vertically from terminal axial piece.

Small to medium-sized granules are evenly distributed on glabella; much larger ones on genal buttress, anterior adaxial part of fixed cheek, and sometimes anterior border (Pl. 97, fig. 9; Pl. 98, fig. 9). Abaxial inflations of occipital and axial rings have concentration of small granules. Small, closely spaced granules on border sector of rostral plate and lateral border of cheek (Pl. 97, fig. 6). Scattered fine granules on hypostoma, thorax, and pygidium. Maculae and deepest part of preglabellar, pleural, axial, and articulating furrows lack granules.

Discussion. Variation is present in the degree of upward curving of the preglabellar area and impression of cincture and interpleural furrows on the pygidium, though the latter are never strongly developed and may be almost completely absent. The largest cranidium (Pl. 98, fig. 4; ?gerontic specimen) is the only one to have the anterior glabellar margin transversely in line with the fixed cheek.

Cranidia from Dolyhir (Pl. 98, figs. 6, 9–12) have a more swollen anterior border, and thus a relatively shorter preglabellar furrow, than in typical Burrington specimens (cf. Pl. 97, fig. 2); in this character, therefore, they approach *T. vulpecula.* They are placed with *T. nodulosa* because they lack the more distinct break in slope between preglabellar furrow and anterior border that is diagnostic of the new species (cf. Pl. 98, figs. 6, 12; Pl. 100, figs. 1, 2), and because the anterior border of other specimens from Burrington is very similar to that in the Dolyhir material (cf. Pl. 97, figs. 1, 11; Pl. 98, figs. 10, 11).

Tapinocalymene volsoriforma sp. nov.

Plate 99, figs. 1–15; text-fig. 2I, J

1919 *Calymene blumenbachii* Brongniart; Reed, *in* Garwood and Goodyear, p. 19.

Derivation of name. Latin, *volsorium*, a curved archstone, referring to the cranidial anterior border outline in dorsal view.

Holotype. Almost complete cranidium, GSM Zs63, Garwood Collection; Pl. 99, figs. 1–4.

Type locality. Wenlock Series, Sheinwoodian Stage, shale band included within the Dolyhir and Nash Scar Limestone Formation near its base, Dolyhir Quarries near Old Radnor, Powys (see Garwood and Goodyear 1919, p. 18, pl. 7). There are no specific horizon data given for *T. volsoriforma* specimens in the Institute of Geological Sciences Garwood Collection. Apart from the Pre-Cambrian, only the Dolyhir and Nash Scar Limestone Formation and a small faulted patch of Coalbrookdale Formation outcrop in this area. The lithology of the Coalbrookdale Formation here is different to the matrix surrounding the *T. volsoriforma* specimens and this patch yields instead *T. nodulosa.* The matrix is also unlike the mass of pure, crystalline Dolyhir Limestone, though Garwood and Goodyear's (1919, p. 18) description of a shale band included in the limestone near its base fits the IGS material. I have collected a *T. volsoriforma* cranidium from this shale band on the north side of the disused railway track, Dolyhir (SO 2410 5823). The exact location of the type locality amongst the Dolyhir Quarries is unknown. The Dolyhir and Nash Scar Limestone Formation is considered to span the *Cyrtograptus centrifugus*, *C. murchisoni* and part of the *Monograptus riccartonensis* biozones of the Sheinwoodian (Bassett 1974, p. 759).

Additional material and occurrences. At least three incomplete cranidia, GSM Zs62, GSM Z19983, LM 2850; one incomplete cephalon, GSM Zs65; one incomplete cephalon plus rostral plate GSM Zs58; one incomplete hypostoma GSM Z19696; seven incomplete pygidia GSM Zs22, GSM Zs24, GSM Zs57, GSM Zs59–61, GSM Zs64. Numerous other fragments of cranidia, pygidia, and thoracic segments are present in the Garwood Collection, Institute of Geological Sciences Museum.

Only recorded with certainty *in situ* from the type area, but it may also be present in the Coalbrookdale Formation of Salop (Pl. 99, fig. 16). One transported specimen (Pl. 99, fig. 5) was collected from a stream bed near English Bridge, Shrewsbury.

Diagnosis. Preglabellar area about one-third as long as glabella. Preglabellar furrow about one-sixth as long (sag.) as preglabellar area. Anterior border relatively long, it slopes fairly gently upward and forward from the more steeply inclined anterior side of preglabellar furrow. Axial furrow anterior to lobe 2p only slightly wider than around 1p lobe. Hypostoma with only moderately inflated subcircular protuberance on anterior lobe.

Description. Glabella essentially as in *T. nodulosa* but inflation within fork of 1p furrow generally weaker. Axial furrow deep and fairly narrow around lobe 1p, slightly wider beside lobe 3p and frontal lobe. Anterior pit is anterior to furrow 3p. Preglabellar furrow short and moderately deep medially, lengthens (exsag.) at anterolateral corner of frontal lobe, continues forward and outward between fixed cheek and anterior border into deep, narrow, lateral border furrow; steeply sloping anterior side of preglabellar furrow meets anterior border at change of slope. Anterior border about one-quarter (Pl. 99, fig. 5) to three-tenths (Pl. 99, fig. 1) as long as glabella, dorsal surface very gently convex (sag.), slopes forward and slightly upward. In lateral profile anterior margin rises above anterior part of frontal lobe. Fixed cheek, palpebral lobe, and facial suture as in *T. nodulosa*. Free cheek has narrow eye socle (Pl. 99, figs. 7, 13), convex inner part of cheek falls steeply to U-shaped lateral border furrow; junction of border furrow with lateral border is more angular (tr.) than with inner part of cheek. Lateral border rolled under ventrally. Rostral plate (Pl. 99, fig. 11) imperfectly preserved but apparently similar to *T. nodulosa*. Hypostoma has moderate, subcircular inflation on anterior lobe (Pl. 99, fig. 8). Oval macula smooth; median furrow very faint. Posterior border expanded into two spines.

Thoracic segments (fragmentary) have axial rings inflated near axial furrow. Pygidium like that of *T. nodulosa*. Axis very weakly convex (tr.), has at least seven rings plus terminal piece. Axial rings longest (sag.) and ring furrows shallowest medially. Seventh ring furrow lacking abaxially; very faint trace medially of eighth furrow (Pl. 99, fig. 6). Inner pleural region descends gently abaxially, outer part falls more strongly. Five (possibly six) pleural furrows are best marked on inner pleural region; interpleural furrows much weaker.

Glabella, outer part of fixed cheek and free cheek have numerous small to medium-sized granules. Inner part of fixed cheek (especially anteriorly), genal buttress and anterior border are coarsely granulate (Pl. 99, fig. 14). Deepest parts of glabellar and preglabellar furrows lack granules; lateral and posterior border furrows have scattered small granules. Pygidium and hypostoma are finely granulate.

Discussion. Compared to the holotype (Pl. 99, fig. 1), a cranidium from outside the type area (Pl. 99, fig. 5) has a more rounded outline to the anterolateral corner of the frontal lobe, a shallower preglabellar furrow, a much weaker break in slope between preglabellar furrow and anterior border, and a relatively shorter anterior border (to the glabella). This variation is considered to be intraspecific as Dolyhir specimens vary in a like manner (for example, Pl. 99, fig. 13 in the first three of these characters).

Two other *Tapinocalymene* cranidia from Salop (Pl. 99, fig. 16; NMW 77.31G.13) may belong to *T. volsoriforma*, but are indifferently preserved. They are associated with *Monograptus flemingii* (identified by Dr. I. Strachan; pers. comm. Dr. C. N. Rodgers), indicating a post *M. riccartonensis* to *C. lundgreni* Biozone age. Apparently *T. volsoriforma*, or a species close to it, existed outside the type area at a later date.

Tapinocalymene vulpecula sp. nov.

Plate 100, figs. 1–8, 13, 15; text-fig. 2G, H

Derivation of name. Latin, diminutive of *vulpes*, fox, alluding to the appearence of the hypostoma.

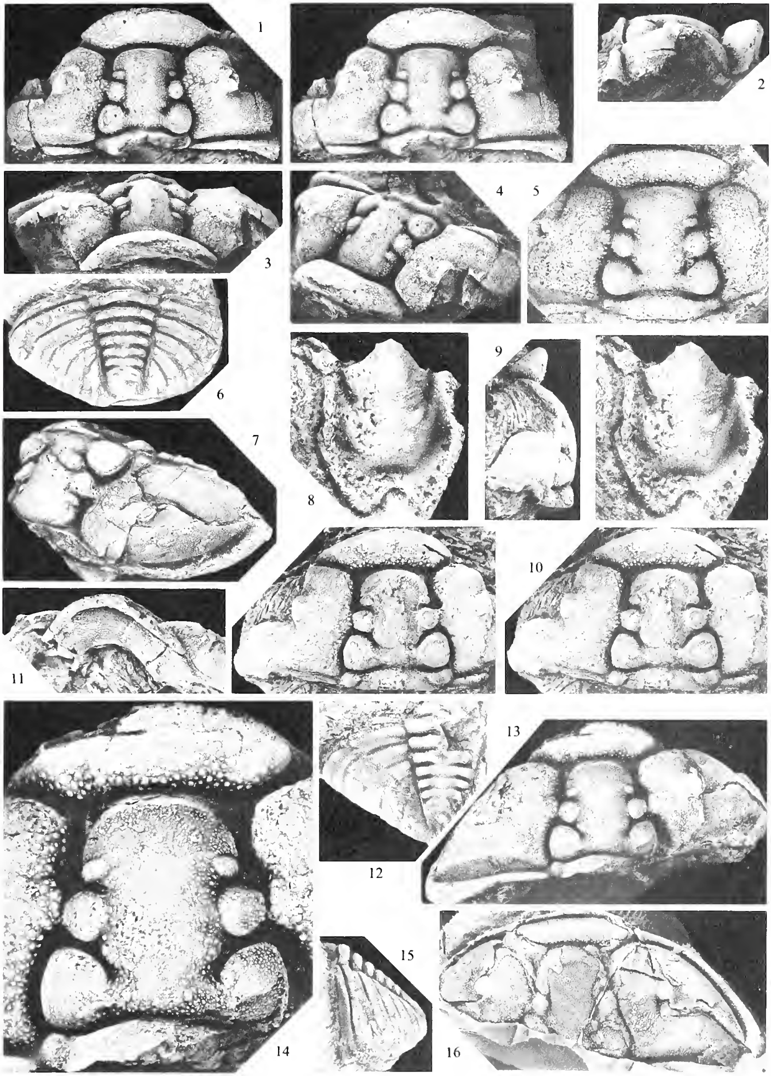
Holotype. Incomplete cranidium, NMW 77.31G.1, collected D. J. Siveter 1971; Pl. 100, figs. 1, 2.

Type locality. Wenlock Series, small disused quarry on the west side of the road from Letton to Walford, ½ km north of Letton, Hereford and Worcester (SO 3790 7080). Graptolites (SM A80317–21, SM A80387–91) from this locality have been assigned to *M. flemingii*, and probably belong to the *lundgreni* Biozone (pers. comm. Dr. R. B. Rickards).

EXPLANATION OF PLATE 99

Figs. 1–15. *Tapinocalymene volsoriforma* gen. et sp. nov. All specimens except fig. 5 are from the Wenlock Series, Sheinwoodian Stage, included shale band in Dolyhir and Nash Scar Limestone Formation, Dolyhir, Powys. 1–4, holotype cranidium, GSM Zs63, dorsal stereo-pair, frontal, left oblique views, × 2, right lateral view, × 2·25. 5, cranidium, silicone-rubber cast of external mould, LM 2850b, specimen from a water-transported pebble, found near English Bridge, Shrewsbury, Salop; dorsal view, × 2. 6, 15, pygidium, GSM Zs61, dorsal, left lateral views, × 2·25. 7, cranidium and left free cheek, GSM Zs65, left oblique view, × 2. 8, hypostoma, GSM Z19696, ventral stereo-pair, × 5. 9, 10, cranidium, GSM Z19983, left lateral view, dorsal stereo-pair, × 2. 11, 13, 14, cephalon, GSM Zs58, ventral (rostral plate), dorsal views, × 2, dorsal view, × 4. 12, pygidium, GSM Zs64, dorsal view, × 2·25.

Fig. 16. *Tapinocalymene* cf. *T. volsoriforma* gen. et sp. nov. Cephalon, silicone-rubber cast of external mould, NMW 77.31G.12b, Wenlock Series, Coalbrookdale Formation, road cutting on A489 between Horderley and Plowden, south side of Long Mynd, Salop (SO 402 875); dorsal view, × 2.



SIVETER, *Tapinocalymene*

Additional material. Only from type locality; three incomplete cranidia, NMW 77.31G.2–4; two pygidia, one with cuticle, NMW 77.31G.6, the other an internal mould, NMW 77.31G.7; one hypostoma, internal mould plus counterpart, NMW 77.31G.5a,b. Numerous other fragmentary cranidia, pygidia, and thoracic segments.

Diagnosis. Preglabellar area about two-fifths to one-third as long as glabella. Preglabellar furrow about as long (sag.) as anterior border and half as long as preglabellar area. Marked break in slope where anterior side of furrow meets posterior margin of border.

Description. Glabella similar to that of *T. nodulosa.* Axial furrow at least twice as wide at lobe 3p and frontal lobe than around lobe 1p. Anterior pit situated in axial furrow below lateral glabellar furrow 3p. Preglabellar furrow deep, U-shaped (sag.), about as long as anterior border medially, shortens (exsag.) abaxially where fixed cheek approaches anterior border; anterior side of furrow is about vertical and meets posterior part of anterior border in a sharp break of slope, border then continues less steeply forward and upward (Pl. 100, fig. 2). Anterior border is of about constant length abaxially from median line to opposite axial furrow, thereafter shortening (exsag.) towards facial suture. In lateral profile anterior margin is about level with or just above height of frontal lobe. Fixed cheek, palpebral lobe, facial suture, and hypostoma essentially like that of *T. nodulosa.* Free cheek and rostral plate unknown. Pygidium, showing no differences to that of *T. nodulosa*, has six complete, one incomplete, very gently convex (tr. and sag.) axial rings. Anterior six ring furrows shallowest at and just either side median line, deepen quickly abaxially; very faint seventh ring furrow does not reach axial furrow which is weakest around terminal axial piece. Pleural region slopes very gently to cincture, more steeply abaxially. Five pleural furrows run outward and backward to cincture, apparently absent from here to lateral margin though this part of pygidium is imperfectly preserved. Interpleural furrows extremely faint, best seen near axial furrow, not marked on internal mould (cf. Pl. 100, figs. 8, 13). Sculpture like that of *T. nodulosa* and *T. volsoriforma.*

Distinctions between Tapinocalymene *species*

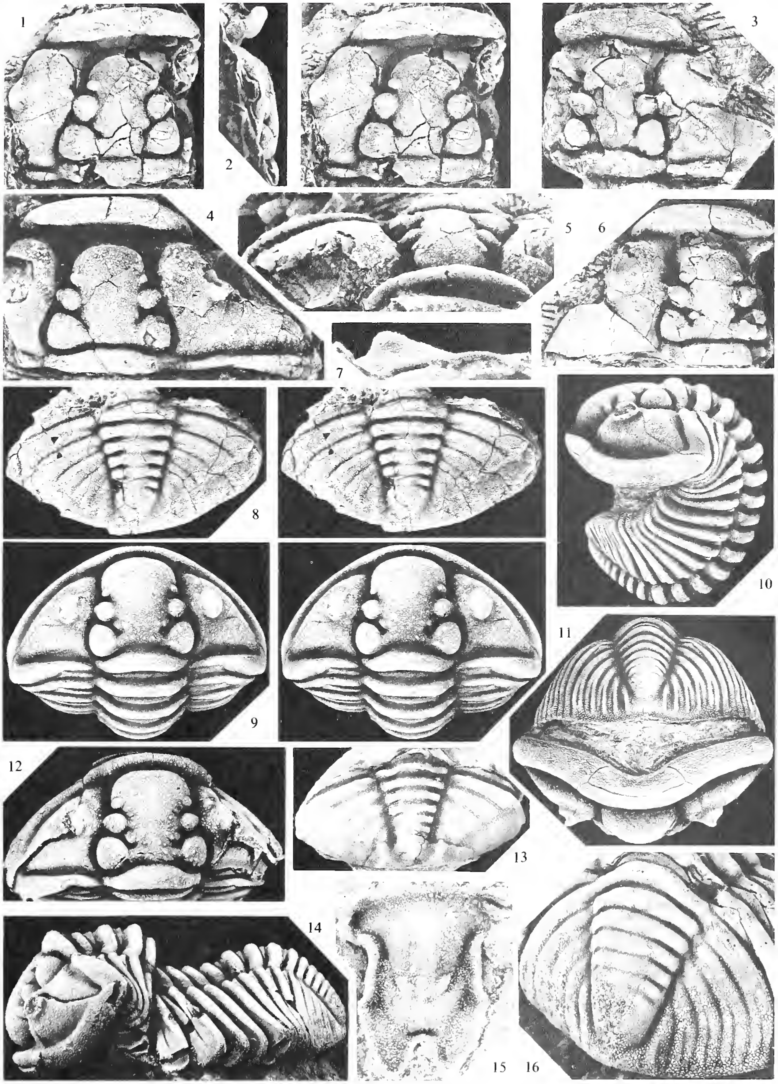
T. volsoriforma differs most obviously from *T. vulpecula* and *T. nodulosa* by its much shorter preglabellar furrow and longer anterior border (cf. Pl. 97, fig. 2; Pl. 99, fig. 1; Pl. 100, fig. 1). Further, *T. volsoriforma* has a narrower axial furrow anterior to glabellar lobe 2p (cf. Pl. 97, fig. 9; Pl. 99, figs. 13, 14; Pl. 100, fig. 1), and a ventral protuberance on the anterior lobe of the hypostoma which seems less well developed than that in the other two species (cf. Pl. 97, fig. 6; Pl. 99, fig. 8; Pl. 100, figs. 7, 15). *T. vulpecula* is best distinguished from *T. nodulosa* by its relatively shorter preglabellar furrow, longer anterior border, and sharper break in slope between these two features. In the change from *T. volsoriforma* to *T. nodulosa* through the Wenlock, in addition to a very marked change in the preglabellar area, the axial furrow anterior to lobe 2p becomes wider, the hypostomal protuberance seemingly becomes better developed (there is only one incomplete hypostoma of *volsoriforma*), and the inflation within the adaxial fork of furrow 1p becomes generally stronger (cf. Pl. 97, fig. 9; Pl. 99, fig. 14).

EXPLANATION OF PLATE 100

Figs. 1–8, 13, 15. *Tapinocalymene vulpecula* gen. et sp. nov. All specimens are from Wenlock Series, Coalbrookdale Formation, probably *Cyrtograptus lundgreni* Biozone, Homerian Stage, small old quarry on west side of road from Letton to Walford, ½ km north of Letton, Hereford and Worcester (SO 3790 7080). 1, 2, holotype cranidium, NMW 77.31G.1, dorsal stereo-pair, left lateral view, × 2. 3, partial internal mould cranidium, NMW 77.31G.2, dorsal view, × 2. 4, 5, cranidium, NMW 77.31G.4, dorsal, frontal views, × 4. 6, cranidium, NMW 77.31G.3, dorsal view, × 2. 7, 15, hypostoma, silicone-rubber cast of external mould, NMW 77.31G.5b, lateral, ventral views, × 8. 8, pygidium, NMW 77.31G.6, dorsal stereo-pair, × 2·25. 13, internal mould pygidium, NMW 77.31G.7, dorsal view, × 2·25.

Figs. 9–11. *Calymene blumenbachii blumenbachii* Brongniart, 1822. Complete enrolled specimen, BM 44213, Wenlock Series, Homerian Stage, Much Wenlock Limestone Formation, Dudley, West Midlands; dorsal stereo-pair, left lateral, posterior views, × 2.

Figs. 12, 14, 16. *Calymene blumenbachii* subsp. nov. Complete specimen, NMW 73.28G.3a, Wenlock Series, Sheinwoodian Stage, Woolhope Limestone Formation, temporary trench just north of church, Woolhope, Hereford and Worcester; dorsal, left lateral views, × 2, posterior oblique view, × 4.



SIVETER, Calymenid trilobites

ORIGIN OF THE GENERA *TAPINOCALYMENE* AND *SPATHACALYMENE*

Tapinocalymene

T. volsoriforma and *T. nodulosa* show the two morphological extremes in the preglabellar area of *Tapinocalymene*, that of *T. vulpecula* being intermediate in form. *T. volsoriforma* is from the lower Wenlock; *T. nodulosa* is from the upper Wenlock (*C. lundgreni* and ?*G. nassa* biozones), *T. vulpecula* being of probable *lundgreni* Biozone age. An evolutionary sequence involving an increase in the length and area of the preglabellar furrow through the Wenlock is postulated, from the sagitally short furrow in *T. volsoriforma* (text-fig. 2I, J), through the moderately long furrow of *T. vulpecula* (text-fig. 2G, H), to the scoop-like furrow and preglabellar area of *T. nodulosa* (text-fig. 2A, B). This trend is accompanied by a loss of the angular break in slope in the preglabellar area; the intraspecific variation attributed to *T. nodulosa* in the anterior border (Dolyhir specimens, text-fig. 2E, F) is taken as further evidence of the proposed phyletic series.

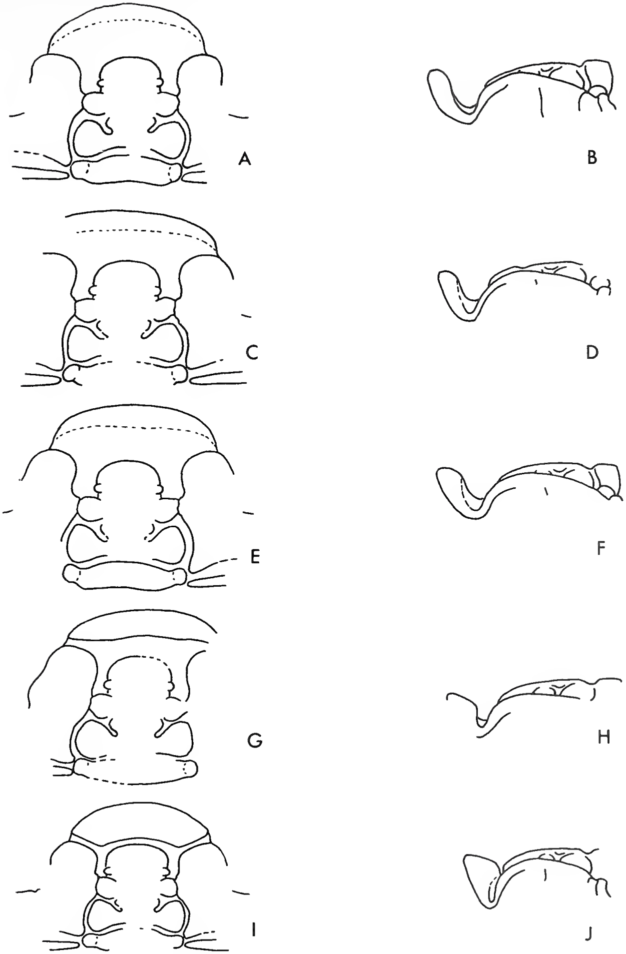
The exoskeleton of *T. nodulosa* is wide and rather depressed suggesting a benthic habit (cf. Fortey and Barnes 1977, p. 304 for broadly analagous conditions in certain olenids). Though the function of the distinctive preglabellar area is problematic, it may have been used in shallow burrowing, or to disturb superficial sediment in search of food. It may have been adapted to the carbonate mud facies of the Coalbrookdale Formation. *T. nodulosa* and *T. vulpecula* both occur in the same Wenlock calcareous shale facies, deposits interpreted (Bassett 1974, pp. 770–773, text-figs. 7, 8) as somewhat offshore, deepish-water clastics; in this context my own collections show that graptolites and small brachiopods invariably accompany these two species. The main mass of algal-rich Dolyhir and Nash Scar Limestone Formation was formed in shallow water deposited on a local offshore topographic high of faulted Pre-Cambrian rocks (Bassett 1974, p. 772, text-fig. 7; Hurst, Hancock, and McKerrow 1978, p. 204); the included shale band, which yields *T. volsoriforma*, suggests there may have been a temporary incursion of deeper water.

Tapinocalymene originated from *Diacalymene*, possibly from a stock broadly ancestral to *D. diademata*, rather than from *D.*? *crassa* Shirley, 1936 and allied species. It is not related to *Calymene sensu stricto*. Specimens provisionally assigned to a new subspecies of *C. blumenbachii* are known from the Woolhope Limestone Formation of low Wenlock age (*C. centrifugus* and *C. murchisoni* biozones). These (Pl. 100, figs. 12, 14, 16) are approximately coeval with *T. volsoriforma*, yet are morphologically quite distinct (see differences between *Tapinocalymene* and *Calymene* in generic discussion). The *C. blumenbachii* species group, in contrast to *Tapinocalymene*, is characteristic of more onshore, generally shallower-water environments.

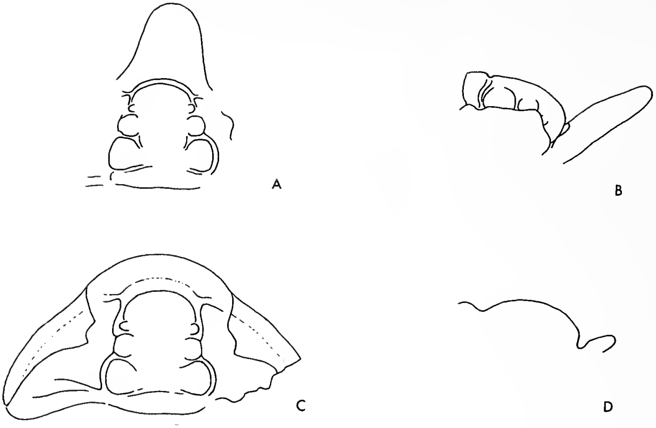
Spathacalymene

The preglabellar area of *Spathacalymene nasuta* has an inverted U-shaped, posteriorly divergent outline in dorsal view, with a long, dorsally flattened anterior border sloping moderately steeply posteriorly to meet a short, more steeply inclined preglabellar furrow. Apart from its length, this form is similar to the preglabellar area of certain calymenids assigned to *Diacalymene* by Shirley (1936); also similar is the pointed, forwardly and inwardly directed, anterior part of the fixed cheek. Both similarities apply to *D.*? *crassa* from the early Llandovery (Rhuddanian) of Wales which, moreover, has a strongly convex (sag. and tr.), high glabella (relative to the fixed cheeks), as in *S. nasuta* (cf. Temple 1975, pl. 25, figs. 3, 4; Pl. 101, figs. 1, 4, 8 herein). The unrevised *C. vogdesi* Foerste (1887, p. 95, pl. 8, figs. 12, 13; 1893, p. 526, pl. 25, fig. 25; pl. 27, figs. 12, 13; 1919, pl. 19, fig. 5) from the lower Silurian of Ohio is a possible senior synonym of *crassa*, and it is also recorded (Foerste 1893, p. 527) from Indiana, where the upper Llandovery *S. nasuta* occurs. Foerste (1919, p. 393) regarded *vogdesi* as a 'typical Brassfield species'; his use of the term Brassfield included strata of middle to upper Llandovery age (Berry and Boucot 1970, p. 127).

The evolution of the preglabellar area of *S. nasuta* from that of '*C*'. *vogdesi* or a similar species requires only the lengthening of the anterior border. This involves much less change in morphology from ancestor to descendant than in that proposed for *Tapinocalymene* (cf. text-figs. 2, 3).



TEXT-FIG. 2. Proposed evolutionary lineage in *Tapinocalymene* gen. nov. Dorsal and lateral outlines of cranidia, all × 2. A, B. *T. nodulosa*, HM A212/1, pl. 97, figs. 1, 11. C, D. *T. nodulosa*, GSM Zs183, pl. 98, figs. 10, 11. E, F. *T. nodulosa* GSM Zs195, pl. 98, figs. 6, 12. G, H. *T. vulpecula*, holotype, NMW 77.31G.1, pl. 100, figs. 1, 2. I, J. *T. volsoriforma*, holotype, GSM Zs63, pl. 99, figs. 1, 2.



TEXT-FIG. 3. Possible origin of *Spathacalymene* Tillman, 1960. A, B. *Spathacalymene nasuta*, USNM 170363, dorsal and right lateral cranidial outlines, × 1, pl. 101, figs. 1, 8. C, D. '*Calymene*' *vogdesi*, holotype, lower Silurian, Centreville, Ohio, U.S.A., dorsal and sagittal cranidial outlines; magnification unknown, but equal to Foerste's (1887, pl. 8, figs. 12, 13) original illustrations.

EXPLANATION OF PLATE 101

Figs. 1, 3, 4, 7–9. *Spathacalymene nasuta* (Ulrich, 1879). 1, 4, 8, 9, complete specimen, USNM 170363, Osgood Limestone (late Llandovery), quarry 1·3 km east of Napoleon, Ripley County, Indiana, U.S.A.; dorsal stereo-pair, right lateral view, × 1, right oblique view, × 2, posterior oblique view, × 3·3; figured Tillman 1960, pl. 116, figs. 1, 4, 5, 8, 9. 3, 7, paralectotype, cephalon, rostral plate and two thoracic segments, Osgood Formation (late Llandovery), Osgood, Indiana, U.S.A.; dorsal, ventral views, × 1·5; figured Tillman 1960, pl. 116, figs. 10–12.

Figs. 2, 5, 6, 10. *Diacalymene diademata* (Barrande, 1846). Cranidium, largely internal mould, NMW 71.8G.377, upper part of the Liteň Formation, *Cyrtograptus radians–Monograptus testis* biozones (late Wenlock), above path leading from Svatý Jan pod Skalou to Vraz, south-west of Prague, Czechoslovakia; frontal, right lateral views, dorsal stereo-pair, × 2, right oblique view, × 2·5.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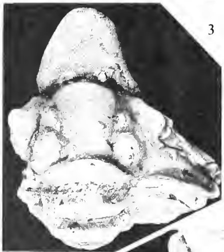
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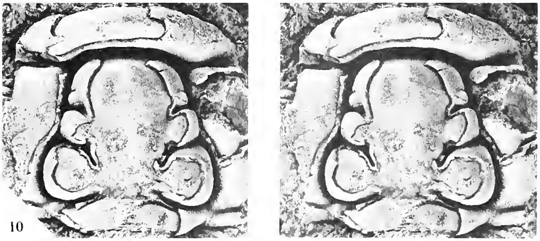
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SIVETER, Calymenid trilobites

CONCLUSIONS

1. *C. nodulosa* Shirley, 1933, *T. volsoriforma* sp. nov. and *T. vulpecula* sp. nov. from the Wenlock Series of the Welsh Borderland belong to a new genus, *Tapinocalymene*.

2. *Tapinocalymene* shows plasticity in the form of its preglabellar area, which links the phyletic series *T. volsoriforma*, *T. vulpecula*, *T. nodulosa*.

3. *Tapinocalymene* was probably benthic and occurs throughout its stratigraphic range in somewhat offshore carbonate muds. The scoop-like preglabellar area of *T. nodulosa* developed in response to this mode of life and bottom conditions.

4. The possession of a long, conspicuous preglabellar area provides no basis for considering *T. nodulosa* and *S. nasuta* congeneric; details of its morphology and origin are distinctive in both taxa, and it is a feature that species of different calymenid lineages occasionally develop.

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SPICULE PSEUDOMORPHS IN A NEW PALAEOZOIC CHAETETID, AND ITS SCLEROSPONGE AFFINITIES

by DAVID I. GRAY

ABSTRACT. A Palaeozoic chaetetid, bearing intramural spicule pseudomorphs, *Chaetetes* (*Boswellia*) *mortoni* sp. nov., is described from the British Dinantian. Spicules are preserved as calcite, pyrite, and silica pseudomorphs. Only silica pseudomorphs retain detail of their tylostyle form. Neomorphism locally obliterates the spicular fabric. A primary mineralogy is suggested consisting of an aragonitic calcareous skeleton, with entrapped opal 'A' spicules. Comparison of morphology and microstructure with extant and fossil sclerosponges indicates a close relationship between this chaetetid and the Ceratoporellida, and supports the sclerosponge nature of some Palaeozoic chaetetids.

THE Class Sclerospongiae Hartman and Goreau, 1972, was proposed following the rediscovery of coralline sponges among the Jamaican coral-reef ahermatypic cryptofauna (Hartman 1969; Hartman and Goreau 1970). Sclerosponges were defined by Hartman and Goreau (1972, p. 144) as 'sponges secreting a compound skeleton of siliceous spicules, proteinaceous fibres and calcium carbonate, the latter laid down as a basal mass in which the siliceous spicules may or may not be entrapped'. The similarity of fossil chaetetids to some sclerosponges (briefly discussed by Kirkpatrick (1909, 1912*a*, 1912*b*) along with the monticuliporans), led Hartman and Goreau (1972) to remove the Chaetetida Okulitch, 1936, from the Anthozoa or Hydrozoa to the Sclerospongiae. They also erected the Order Ceratoporellida Hartman and Goreau, 1972, to include four extant sclerosponge genera, and added a third Order, the Tabulospongida Hartman and Goreau, 1975, following the discovery of a tabula-bearing form from the Pacific (Hartman and Goreau 1975), of which two more extant species have subsequently been described (Mori 1976, 1977) and a record traced back into the Mesozoic. Stearn (1972, 1975) discussed the sclerosponge affinities of the stromatoporoids.

The recognition of the Sclerospongiae as a Class has been questioned by a number of authors. Lévi (1973) considered the sclerosponges as a Subclass of the Demospongiae, subsequently followed by Vacelet, Vasseur, and Levi (1976) and Vacelet (1977). This classification takes into account the organization of living sclerosponge tissue which is 'basically similar to that of the Class Demospongiae except that it is divided into units each of which extends down into the upper layer of the basal calcareous skeleton' (Hartman and Goreau 1972, pp. 144–145).

The variability in spicule form and distribution (see Table 1) suggests that some sclerosponges may be related even more closely to other groups of demosponges. For example, Vacelet (1977, p. 347) mentions that the spicule character of *Tabulospongia wellsi* is similar to that displayed by the Spirastrellidae. Vacelet (1977, p. 347) also states that a basal calcareous skeleton may be a convergent structure in many groups of demosponges. This would account for the great variability of calcareous skeletal morphology and microstructure (see Table 1) observed in those forms classified as sclerosponges, and would imply that 'sclerosponge' is a convenience term for considering groups with a similar homeomorphic tendency.

In this paper the sclerosponges are considered as a Subclass of the Class Demospongiae Sollas, 1875.

The fossil history of sclerosponges that entrap spicules in their calcareous skeleton is represented by a limited assortment of forms including a few ceratoporellids, one species (Kaźmierczak 1974) of

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the Order Muranida Kaźmierczak and Hillmer, 1974, a few problematical records of stromatoporoids and, until now, only two species of Mesozoic chaetetids. Table 1 summarizes their distribution and variation and allows comparisons to be made with extant forms.

Chaetetids are a diverse group with separate Palaeozoic and Mesozoic histories. Differences exist in the skeletal architecture of Palaeozoic and Mesozoic forms (Fischer 1970), and their phylogenetic relationships are not completely understood. Scrutton (1979, p. 169) reviewed briefly their relationships, and whilst supporting their sclerosponge affinities he emphasized the lack of convincing spicules associated with chaetetids as 'a major source of doubt for some workers' to their classification within the Porifera. Dieci, Russo, Russo, and Marchi (1977) were the first to report a spicule-bearing 'chaetetid', *Atrochaetetes medius* Cuif and Fischer, 1974, from the Upper Triassic of Italy, with intramural acanthostyle spicules, replaced by calcite. *Atrochaetetes* Cuif and Fischer, 1974, is characterized by a discontinuous backfill of fascicular fibrous carbonate extending into the lumen (Cuif and Fischer, 1974, p. 8) rather than complete tabulae typical of the chaetetids *s.s.* Continuous fascicular fibrous backfills are typical of ceratoporellids (see below). Since *A. medius* also has a ceratoporellid-like spicular fabric, the genus *Atrochaetetes* should be regarded as an aberrant member of the Ceratoporellida, and removed from the Chaetetida.

Kaźmierczak (1979) reported intramural monaxon spicules, replaced by pyrite, within a Lower Cretaceous (Barremian) chaetetid, *Chaetetopsis favrei* (Deninger 1906) from the Crimea. Like many Mesozoic chaetetids, *C. favrei* increases both by intramural offset and longitudinal (pseudoseptal) fission. The former is not known to occur in Palaeozoic chaetetids (Sokolov 1962, p. 262). The walls of *C. favrei* are anhedral calcite miscospar that is possibly a neomorphic overprint (Kaźmierczak 1979, p. 101), and is dissimilar from the typical fascicular fibrous microstructure of Palaeozoic chaetetids.

This is the first report of convincing intramural spicule pseudomorphs in a Palaeozoic chaetetid, *Chaetetes* (*Boswellia*) *mortoni* sp. nov., from the Lower Carboniferous of north Wales, northern England, and southern Scotland. Comparison is made with other chaetetids and sclerosponges, and a model is developed for the mode of spicule preservation. Classification of the Chaetetida within the Sclerospongidea is supported.

OCCURRENCE AND PRESERVATION OF MATERIAL

Eight colonies of this new species have recently been collected from the Lower Asbian (Upper Dinantian), Tynant Limestone (Somerville, 1979) (Lower Brown Limestone of Morton, 1879) of the Llangollen area, north Wales. Although this sclerosponge is a rare element in the brachiopod-dominated macrofauna, it has been collected from a 20-m range of cyclic strata at sites over 4 km of outcrop, and from the underlying scree. It occurs towards minor cycle bases, in subtidally deposited argillaceous algal-foraminiferal packstones and grainstones. The colonies were rolled and some were fragmented prior to burial. One colony has a pronounced micritic (?endolithic algal) rim on part of its

TABLE 1. Table of extant and fossil sclerosponges with associated spicules showing their spicule form and relationship to the basal calcareous skeleton. Mesozoic stromatoporoids of Schnorf (1960) and Yabe and Sugiyama (1935) are omitted owing to their uncertain spicular nature. Species of *Leiospongia* d'Orbigny, 1850, and *Hartmanina* Dieci *et al.* 1974, described by Dieci, Russo, and Russo (1974*b*) are ommitted owing to the absence of associated spicules.

Order symbols, Cer = Ceratoporellida, Tab = Tabulospongida, Unas = Unassigned, Mur = Muranida, Ch = Chaetetida, Stp = Stromatoporoidea; calcareous microstructure symbols, Fascic. fib. = fascicular fibrous, Agg. spher. = aggregated spherules, Microgran. = microgranular; original mineralogy symbols, A = aragonite, Mg-cc. = high magnesian-calcite; spicule distribution symbols, I. = intramural, E. = extramural, m. = subparallel to microstructure fibres, s. = subparallel to growth axis of skeleton, d. = embedded only within the distal portion of the calcareous skeleton, r. = random; spicule type symbols, * = megasclere, ** = microsclere; spicule mineralogy symbols, cc. = calcite, pyr. = pyrite, Fe ox. = iron oxide.

AGE	ORDER	SCLEROSPONGE	SOURCE OF DATA	CALCAREOUS SKELETON		SPICULE DATA				
				MICRO-STRUCTURE	ORIGINAL MINERALOGY	DISTRI-BUTION	TYPE	SIZE RANGE Length (µm)	Diam. (µm)	PRESENT MINERALOGY
EXTANT	Cer	*Ceratoporella nicholsoni*	Hartman & Goreau 1970	Fascic.fib.	A	I.m.	Acanthostyle*	206 - 298	3.1 - 4.0	Opal'A'
		Stromatospongia vermicola	"	"	"	"	"	165 - 187	6.2 - 8.0	"
		Stromatospongia norae	"	"	"	"	"	195 - 215	5.5 - 6.1	"
		Hispidopetra miniana	"	"	"	"	Style*	269 - 301	5.4 - 7.4	"
		Goreauiella auriculata	"	"	"	"	Acanthostrongyle*	60 - 68	2.3 - 2.7	"
	Tab	*Tabulospongia wellsi*	Hartman & Goreau 1975	Stacked lamellar	Mg-cc	E.	Tylostyle* Spiraster**	c.290 Highly variable	c.3.5	" "
		Tabulospongia horiguchii	Mori 1976	"	"	"	Fusiform oxea* Sphaeraster form**	300 - 350	5.7 - 14.0 20 - 25	" "
		Tabulospongia japonica	Mori 1977	"	"	"	Dichotriaene*	300 - 355	140 - 190	"
	Unas	*Merlia normani*	Kirkpatrick 1909	Fascic.fib.	A	"	Tylostyle* Clavidisc** Raphide**	c.140 c. 45 c. 80	c.1.8 c. 30 slender	" " "
		Merlia sp.	Hartman & Goreau 1970	"	"	"	Tylostyle* Clavidisc**	160 35	1.8 26	" "
		Astrosclera willeyana	Kirkpatrick 1910	Agg.spher.	"	"	Acanthostyle*	c. 70	c. 8	"
MESOZOIC L.Cretaceous	Mur	*Murania lefeldi*	Kazmierczak 1974	Microgran. & fib.	?	I.m.	Style or Acanthostyle*	200	30	cc.
	Ch	*Chaetetopsis favrei*	Kazmierczak 1979	Microgran.	?	I.s.	"	c.400	c.28	pyr.
	Cer	*Neuropora pustulosa*	Kazmierczak & Hillmer 1974	Fibro-normal	?A	"	?Acanthostyle*	128 - 141	6.6 - 7.6	cc.
U.Jur	Unas	*Ptychochaetetes* sp.	Termier & Termier 1976	"Lepidoporoid" (Scaly,porous)	?	I.d.	Monaxon*	?90	?10	Fe ox.
U. Triassic	Cer	*Keriocoelia conica*	Dieci *et al*.1977	Fascic.fib.	?	I.m.	Style*	190 ± 40	5.2 ± 1.8	cc.
		Meandripetra zardinii	"	"	?	"	"	390 ± 140	27 ± 7	pyr.
		Sclerocoelia hispida	"	"	?	"	Acanthostyle*	61 ± 16	2.3 ± 0.7	cc.
		Sclerocoelia fasciculata	"	"	?	"	"	43 ± 12	2.3 ± 0.7	cc.
	?Cer	*Atrochaetetes medius*	"	"	?	"	"	74 ± 20	3.9 ± 0.9	cc.
PALAEOZOIC U.Carb	?Stp	*Parallelopora mira*	Newell 1935	Granular	?	I.s.	?Monaxon* (?Microscleres transverse to megascleres)	c. 250	c.10	"
L.Carb	Ch	*Chaetetes* (*Boswellia*) *mortoni* sp.nov.	This paper	Fascic.fib.	?A	I.m.	Tylostyle* ?Raphide**	275 ± 50 c. 70	6.9 ± 0.9 c.3	Silica;cc.; pyr.
Dev	Stp	*Stromatopora centrotum*	Twitchell 1929	?	?	I.r.	"Spinose rod"*	c.100	c.7	cc.

surface (Pl. 102, fig. 6). These colonies are calcitic, with a variable degree of microstructure alteration and compaction distortion. Spicule pseudomorphs have been observed in five of these colonies.

Comparison with material in the British Museum (Natural History) (repository prefix BMNH), Royal Scottish Museum (repository prefix R.S.M.) and Merseyside County Museum (repository prefix LIV.C.M.), led to the discovery of a further five spicule-bearing specimens of the same species. Two of these are partly silicified with intramural spicules locally replaced by silica.

SYSTEMATIC PALAEONTOLOGY

Class DEMOSPONGIAE Sollas, 1875
Sub-Class SCLEROSPONGIDEA Hartman and Goreau, 1972
Order CHAETETIDA Okulitch, 1936
Family CHAETETIDAE Milne-Edwards and Haime, 1850
Subfamily CHAETETINAE Milne-Edwards and Haime, 1850
Genus *CHAETETES* Fischer von Waldheim, 1830
Subgenus *BOSWELLIA* Sokolov, 1939

Type species. Chaetetes (*Boswellia*) *boswelli* Heritsch, 1932, 'Upper *Dibunophyllum* Zone (D_2)' of Ivovik, Serbia, U.S.S.R.

Diagnosis. Chaetetids with thickened irregular walls and rounded corners to lumina that may be either irregular or subpolygonal. Increase by pseudoseptal and basal fission. Incomplete fission and separation of pseudosepta into isolated columns occurs locally. Fascicular fibrous walls. Complete tabulae, variable in distribution. Intramural spicules (originally siliceous) present in some.

Remarks. Palaeozoic chaetetids have been subdivided generically on gross calicle morphology (Sokolov 1939, 1962). Sokolov (1939, p. 411) erected the subgenus *Chaetetes* (*Boswellia*) to include chaetetids with 'thickened irregular' calicle walls and 'undulate rounded' lumina, also stating that *C.* (*Boswellia*) 'occupies an intermediate position between . . .' *Chaetetes* and the meandrine genus *Chaetetipora* Struve, 1898. Species of *C.* (*Boswellia*) show this intermediate relationship very clearly, from the more prismatic thick-walled *C.* (*B.*) *uniformis*, Spiro 1961, and *C.* (*B.*) *heritschi* Sokolov, 1950, to the irregular calicles of *C.* (*B.*) *torquis* Spiro, 1961, which is very similar to some of the less meandrine chaetetiporinids, e.g. *Chaetetipora agonia* Sokolov, 1950. Although this classification is accepted provisionally here the division of the Chaetetidae at a generic level requires further clarification, that must now be based on an understanding of poriferan growth and variation.

EXPLANATION OF PLATE 102

Chaetetes (*Boswellia*) *mortoni* sp. nov., Lower Asbian (Lower Carboniferous, Eglwyseg Escarpment, Llangollen (Clwyd, North Wales).

Fig. 1. Paratype BMNH R49965. Compaction-fractured colony with laminar overgrowth. Negative of longitudinal section, ×2·3.

Fig. 2. Detail of a compaction-fractured thin-wall growth zone, BMNH R44965. Longitudinal section, ×45.

Fig. 3. Holotype BMNH R49964. Transverse section illustrating the subpolygonal to slightly irregular calicle pattern, ×12.

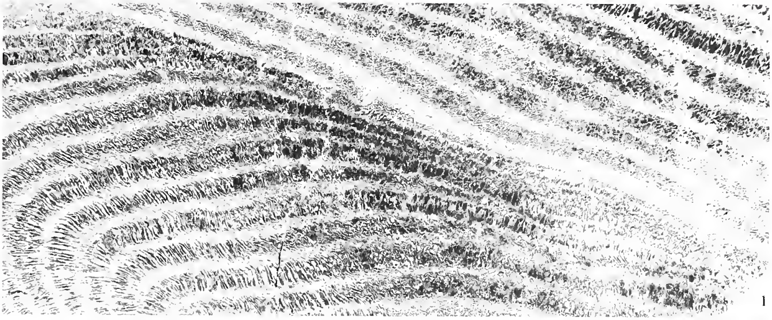
Fig. 4. Transverse section illustrating an irregular calicle pattern, with many pseudosepta, scalloped margins to lumina, and isolated trabecular column (Tr), BMNH R49965, ×35.

Fig. 5. Transverse section illustrating pseudoseptal fission in the corner of a calicle, BMNH R49964, ×40 (D = Daughter calicle).

Fig. 6. Transverse section illustrating mosaic neomorphic fabric to calicle walls with a micritic rim. Outer margin of BMNH R49964, ×70.

Fig. 7. Fractured tabula extending into lumen, longitudinal section, BMNH R49964, ×150.

Fig. 8. Sub-spherical 'vacuole' (V) within the calicle wall of BMNH R50133, ×100.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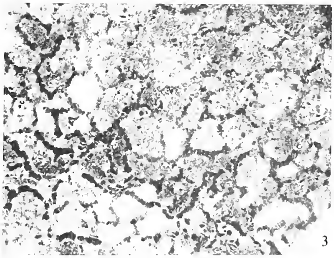
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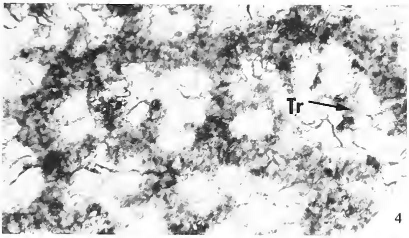

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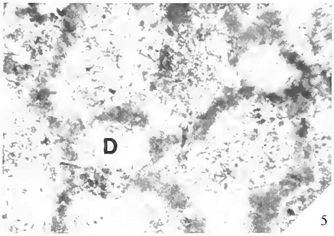

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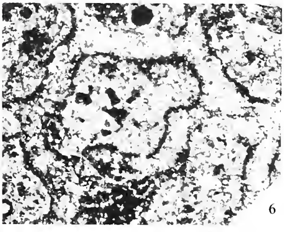
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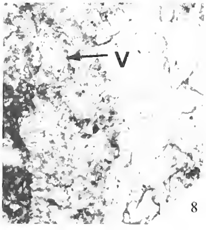

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GRAY, Palaeozoic chaetetid

Chaetetes (*Boswellia*) *mortoni* sp. nov.

Plates 102, 103; text figs. 1–4; Table 2

Derivation of species name. After G. H. Morton who devoted many years of research to the Carboniferous of north Wales in the latter part of the nineteenth century.

Holotype. BMNH R49964, Tynant Limestone (Lower Asbian), quarried face, 400 m north of Tynant Ravine, 4 km north of Llangollen, Clwyd (National Grid Ref. SJ 21964573)

Paratypes. BMNH R4429 (Morton Collection), Lower Brown Limestone (in part equivalent to Tynant Limestone), Llangollen, Clwyd (partly silicified); BMNH R49965, Tynant Limestone (Lower Asbian), quarried face 500 m north of Tynant Ravine (SJ 21974582).

Other material. BMNH R50134, Tynant Limestone (Lower Asbian), World's End, 6 km north of Llangollen, Clwyd (SJ 23314789); BMNH R50133, BMNH R50135, and BMNH R50136 loose on scree slopes near Tynant Ravine, near the base of the Eglwyseg escarpment; BMNH R50188 and BMNH R50189, Tynant Limestone, 300 m north of Llwyn Hên-parc Gulley, Eglwyseg escarpment (SJ 22152638); LIV.C.M. 1974. 57, Eglwyseg Escarpment, Llangollen (in scree, partly silicified); BMNH R45851, Lower Carboniferous, Ravenstonedale, Cumbria; BMNH R46144, J. S. Baker Collection, Carboniferous Limestone (Blue Quarries), Ashfell Edge, Ravenstonedale, Cumbria; R.S.M. 1967.66.86–89 Nicholson Collection (thin sections only; all probably from one colony), Carboniferous Limestone, Archer Beck, Dumfriesshire.

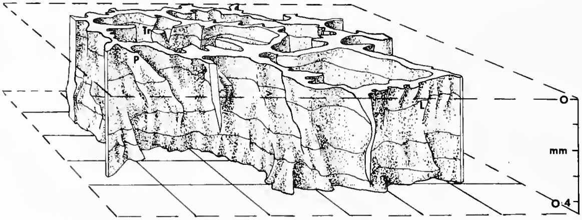
Range. ?Holkerian (BMNH R46144 from ?Ashfell Limestone) to Lower Asbian.

Diagnosis. *Chaetetes* (*Boswellia*) with irregular to subpolygonal (intracolonially variable) calicles. Fascicular fibrous walls with pseudosepta and irregular longitudinal ridges. Isolated pseudoseptal columns locally. Lumen diameter av. *c*. 500 μm; wall thickness av. *c*. 110 μm. Intramural spicules (monaxon tylostyle megascleres) subparallel the fibres, diverging distally, with their pointed (oxeote) ends directed distally. Spicule diameter *c*. 7 μm; spicule length variable *c*. 275 μm in well-preserved specimens. Tabulae well spaced. Basal and pseudoseptal fission only.

Description

Colony form. The colonies are laminar or bulbous, rarely greater than 12 cm diameter by 8 cm high. They display distinct growth bands in rhythms 2 to 5 mm thick, with zones of thinner calicle walls preferentially compaction fractured (Pl. 102, figs. 1, 2). On weathered and polished surfaces the thick-wall bands stand prominent, being a paler shade of brown-grey than the compaction fractured zones. Neither epitheca, astrorhizae, nor surface mamelons have been observed on any colony.

Calicle morphology. The calicles are irregular to subpolygonal (Pl. 102, figs. 3, 4), with the mean diameter of more polygonal lumina between 420 μm and 535 μm (see Table 2). The walls vary greatly in mean thickness, from *c*. 90 μm to *c*. 140 μm (measurements taken between ridges and pseudosepta). Pseudosepta are common, occasionally separating from the calicle walls as isolated columns. Both pseudosepta and ridges (undeveloped pseudosepta) longitudinally ornament the calicle walls (text-fig. 1) imparting a scalloped appearance to the lumina in



TEXT-FIG. 1. Block diagram of *Chaetetes* (*Boswellia*) *mortoni* sp. nov. to illustrate the development of longitudinal ridges (L), pseudosepta (P), and isolated trabecular columns (Tr) off the calicle walls. Diagram constructed from serial acetate peels of BMNH R50133.

transverse section (Pl. 102, fig. 4). Increase is by both pseudoseptal and basal fission. Pseudoseptal fission commonly occurs in calicle corners (Pl. 102, fig. 5). Incomplete pseudoseptal fission locally forms an irregular calicle pattern. Tabulae are rarely visible, appearing well spaced ($\leqslant$ 2 per mm), although this may in part be due to the degree of compaction fracture (Pl. 102, fig. 7).

Microstructure. The walls are fascicular fibrous penicillate calcite or chalcedonic silica, with a brown 'dusty' appearance in thin section due to submicroscopic to micrometre-sized inclusions of ?organic material. In the calcitic specimens these inclusions vaguely define the wall fibres and cause a variable pseudopleochroism (between paler and darker brown) cf. Hudson (1962). One specimen, BMNH R50133 has rare subspherical 'vacuoles', *c.* 50-μm diameter, within the calicle walls, of uncertain origin (Pl. 102, fig. 8). Neomorphism has destroyed details of the microstructure to varying degrees (Pl. 102, fig. 6; text-fig. 5), resulting in inclusion-poor areas lacking spicule relicts (especially the thin-wall growth bands). The walls rarely show a coarser fibrous fabric, with each fibre surrounded by thin brown pellicles that are probably the remnants of the ?organic inclusions.

Spicule form. In the calcitic specimens, spicule pseudomorphs occur within the walls subparallel to the fascicular fibres, diverging distally as straight or slightly curved elongate rods of clearer, inclusion-deficient calcite (Pl. 103, fig. 3) up to 300 μm long. In transverse section they appear as clear calcite circles or ellipses with a range of mean diameters between 6·6 μm and 8·2 μm (Pl. 103, fig. 4). Rarely they may exceed 20 μm diameter. Although surface detail is not visible on these pseudomorphs, their clarity varies from prominent to indistinct, reflecting variation in neomorphism. Rarely the spicules may be preserved as pyrite pseudomorphs with aggregates of pyrite crystals along their length (text-fig. 4*c*), similar to those described by Kaźmierczak (1979). In contrast some calicles of BMNH R4429 and LIV.C.M. 1974.57 are partially replaced by chalcedonic silica (Pl. 103, figs. 1, 2), with perfect intramural silica spicule pseudomorphs occurring adjacent to more vague calcitic ones. These pseudomorphs are low-relief colourless to high-relief red-brown translucent tylostyles, with circular cross-sections (Pl. 103, fig. 6), distinct bosses at their proximal ends and distally tapering points (Pl. 103, figs. 2, 8, 9, 10). As with the totally calcitic specimens these spicules diverge distally in the calicle walls (Pl. 103, fig. 2), subparalleling the fascicular fibres, but occasionally cross-cutting the wall-fibre trend at a high angle. Fossilized early corrosion features are seen on many spicule pseudomorphs (Pl. 103, figs. 7, 8, 10, 11).

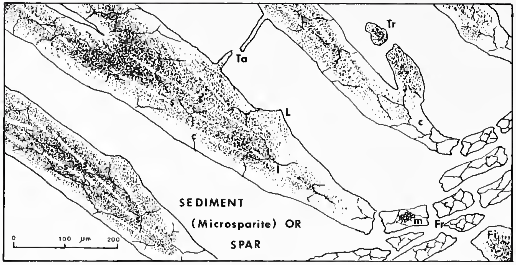
Seldom, and within BMNH R4429 only, ?raphide microsclere pseudomorphs occur (Pl. 103, fig. 7), as thin rods, pointed at both ends, *c.* 70 μm by 3 μm. These are only discernible in the chalcedonic regions, and would be too small to distinguish within the microstructure of calcitic calicle walls.

Spicule distribution. Spicule pseudomorphs have a variable distribution within the colonies. In the calcitic specimens they are only discernible within some of the ?organic-inclusion-rich areas associated with the less-fractured thick-wall growth bands where neomorphism has most perfectly replaced the primary fabric (see text-fig. 2). Specimens BMNH R4429 and LIV.C.M. 1974.57 also have a variable spicule distribution (see text-fig. 3) dependent on the replacement mineralogy. In BMNH R4429 totally and partly calcitic calicles rarely have visible calcitic spicule pseudomorphs. Here the microstructure is masked by a dense inclusion distribution. Siliceous spicules occur where the outer zone of these calicle walls is silicified. Only two growth bands are completely silicified (text-fig. 3), in which the best examples of a dense spicule distribution are visible (Pl. 103, figs. 1, 2).

TABLE 2. Variation in calicle and spicule size in six specimens of *Chaetetes* (*Boswellia*) *mortoni*

	Average lumen diameter in μm			Average wall thickness in μm			Average spicule length in μm			Average spicule width in μm		
SPECIMEN	mean	s.d.	n.	mean	s.d.	n.	mean	s.d.	n.	mean	s.d.	n.
*BMNH R49964	455	130	15	115	35	15	170	70	12	6.6	1.0	20
**BMNH R4429	420	140	10	94	29	10	275	50	10	6.9	0.9	10
**BMNH R49965	485	160	25	130	40	50	155	45	15	7.5	4.0	50
BMNH R50133	520	150	15	117	23	12	154	65	10	7.2	1.8	15
BMNH R50134	423	140	10	141	34	10	207	60	10	8.2	1.1	10
BMNH R50135	535	110	10	116	28	15	(Strongly neomorphosed microstructure)					

* = Holotype; ** = Paratype; s.d. = standard deviation; n. = sample number.



TEXT-FIG. 2. Sketch showing the relationships of the microstructural fabrics in calcitic specimens of *Chaetetes* (*Boswellia*) *mortoni* sp. nov. in longitudinal section. Symbols: Ta = fractured tabula; Tr = isolated trabecular column; L = longitudinal ridge or pseudoseptum; s = calcitic spicule pseudomorph; Fr = fracture zone of thin-wall growth bands; I = transition from ?organic-inclusion-dense thick-wall bands to inclusion-poor compaction-fractured zone; c = neomorphic crystal mosaic, with varying degrees of undulose and sweeping extinction often not discernible in the ?organic-inclusion poor regions; m = localized neomorphic fabric of vaguely fibrous microspar-size crystals, with thin brown pelicles.

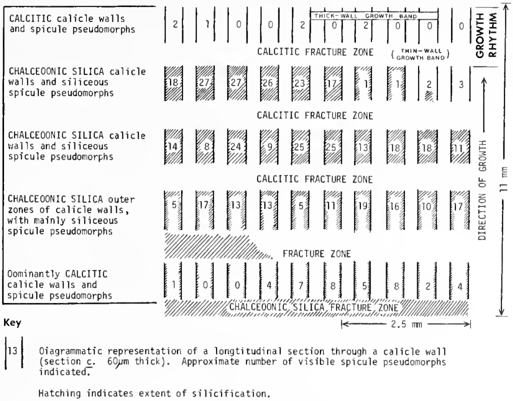
Discussion

The over-all similarity in colony, calicle, and microstructure form confirm that the calcitic and siliceous specimens are conspecific (see Table 2).

Species of *Chaetetes* are poorly defined. The size and degree of variation in calicle form, wall thickness, and tabula density are used as species-dependent characters. Many or all of these characters may, however, be controlled by environmental influences (e.g. Weyer 1967), and therefore where possible care must be taken to sample as large a population as possible. Variation within the specimens of *C.* (*B.*) *mortoni* described here is mostly intracolonial. Some similarities exist between this and previously described species. The calicle morphology is locally (Pl. 102, fig. 3) similar to *C.* (*B.*) *uniformis* Spiro, 1961 from the 'Visean' of the Moscow region, but differs by having a higher density of pseudosepta and slightly smaller calicles. Other closely comparable species are *C.* (*B.*) *torquis* Spiro, 1961, a densely tabulate form that displays many ridge swellings on its calicle walls (Spiro 1961, pl. 3, fig. 1*a*) in a similar manner to *C.* (*B.*) *mortoni*, *Chaetetipora agonia* Sokolov, 1950 and the larger-calicled *C. dubjanskyi* Sokolov, 1950. The latter two both show pseudoseptal fission in calicle corners (Sokolov 1950, pl. 15), but differ from *Chatetes* (*B.*) *mortoni* with their indistinctly meandrine form and dense tabula distribution. Compaction-fracture of *C.* (*B.*) *mortoni* colonies, however, imparts a superficial meandrine calicle pattern which may obscure the true calicle shape.

Chaetetipora etheridgeii (Thomson, 1881) is a variably meandrine species, characterized by a variable calicle shape, some arranged in 'sub-stellate groups radiating irregularly around a large central . . .' calicle (Thomson 1881, p. 208). It is densely tabulate, with calicles commonly from 0·5 to 2·0 mm diameter, and with thin calicle walls. *Chatetes* (*B.*) *mortoni* may be readily distinguished from this chaetetid by its lack of sub-stellate calicle-groups and its rare tabulae.

Whether the presence of intramural spicule pseudomorphs is a species-dependent factor is open to question. Extant sclerosponges have growth-variable spicule distributions (Hartman and Goreau 1972, p. 213) and Stearn (1972), remarked on a whole population of the extant *Astrosclera* Lister, 1900 (unassigned sclerosponge), from the Pacific without spicules. The problem is further complicated by the variable preservation of the spicules as pseudomorphs. In three calcitic specimens



TEXT-FIG. 3. Schematic diagram illustrating the spicule distribution within the calicle walls of the partly silicified BMNH R4429. Note that the higher numbers of visible spicule pseudomorphs per section of calicle wall occur in the chalcedonic silica zones, which are themselves in part controlled by the growth and fracture banding within the colony.

of *C.* (*B.*) *mortoni* they are undetected (BMNH R50135, BMNH R50136, and BMNH R50189). Therefore, although the spicular character is of great significance in understanding the phylogeny and histology of chaetetids, it must only be used with caution as a specific character in fossil forms.

MINERALOGY AND DIAGENESIS OF C. (*B.*) *MORTONI*

Basal calcareous skeleton. Extant sclerosponges secrete both aragonite (e.g. ceratoporellids) and high-magnesian calcite (e.g. tabulosponges) in their basal skeletons. Both are possible original mineralogies for Palaeozoic chaetetids. Fossil ceratoporellids (Viezer and Wendt 1976), probable sclerosponges (Dieci, Russo, and Russo 1974*a*), and stromatoporoids (Wendt 1975), that have retained their original aragonitic mineralogy, and have suffered little diagenetic alteration (Scherer 1977), have all been recorded from the Upper Triassic.

The *in situ* transformation of aragonite to calcite (Bathurst 1964; Dodd 1966), observed in Pleistocene scleractinian corals and molluscs (James 1974; Pingitore 1976; Wardlaw, Oldershaw, and Stout 1978), produces a secondary fabric which retains some detail of the primary microstructure. This transformation apparently occurs via a thin solution film less than 15 nm wide (Wardlaw *et al.* 1978, p. 1864) or a chalky solution zone (James 1974; Pingitore 1976). In this polymorphic transformation, relict detail of microstructure is defined by organic, and rarely aragonite, inclusions enclosed within a coarse mosaic of brown neomorphic calcite. Each of these coarse mosaic crystals exhibits straight (James 1974, p. 793) or undulose (Schneidermann, Sandberg, and Wunder, 1972, p. 88) extinction under crossed polars.

The transformation of high to low-magnesian calcite involves a paramorphic incongruent dissolution process (Plummer and Mackenzie 1974, p. 79). Fine detail is preserved in skeletal components during this transformation (e.g. Towe and Hemleben 1976), although ultrastructural changes may be noted (e.g. Sandberg 1975). In comparison, Lohmann and Meyers (1977, p. 1086) described milky skeletal calcite rich in microdolomite inclusions as evidence of an original high-magnesian calcite mineralogy, apparently caused by an 'incongruent dissolution or solid-stage exsolution' process re-equilibrating the magnesium within coarse crystals that acted as closed or semi-closed systems (Meyers and Lohmann 1978) during the mineralogical transformation. Richter and Fuchtbauer (1978) used the preservation of primary structures by ferroan calcite as a criterion for recognition of primary, high-magnesian calcite.

In calcitic specimens of *C.* (*B.*) *mortoni* a relationship between the crystal form and ?organic-inclusion distribution is observed. The paler-brown calicle walls of specimens with less included material comprise 50 μm to 300 μm mosaic crystals with irregular margins, and either straight or slightly undulose extinction under crossed-polars. Most inclusion-rich areas have sweeping or undulose extinction and some lack a crystal mosaic. Often the wall crystals are continuous with the clear lumen-filling spar. No distinct wall-fibre boundaries are visible but vague fibre boundaries are defined by trains of inclusions. Similarly, the margins of calcitic spicule pseudomorphs are indistinct and often masked by these inclusions. Compaction fractured zones lack a dense inclusion distribution and have a neomorphic mosaic which suggests that the transformation to calcite locally destroyed much of the original microstructure. Larger surface areas of fractured calicle walls, exposed to the calcifying pore waters, may have induced a more rapid and destructive mineralogical transformation.

In partly silicified specimens, the chalcedonic silica cementation and replacement occurred after compaction fracture, as indicated by the preferential silicification of their fracture zones. According to Meyers (1977), such compaction fracture could occur as a result of overburden pressure after burial to metres or tens of metres.

The ?organic-inclusions within the calicle walls appear to have provided a template retaining some detail of the original microstructure. The inclusion distribution may be partly related to the diagenetic history of the calicle walls as they are invariably less dense in compaction-fractured zones, and partly primary, caused by a variable secretion of organic matrix within the basal calcareous skeleton. This reliance on inclusions to define the primary microstructure, and the presence of neomorphic crystals with irregular margins, that often continue into the lumina as clear spar suggests an *in situ* transformation from primary aragonite to calcite. Schneidermann *et al.* (1972, p. 89) stated that continuity of neomorphic crystal fabrics from skeletal components into surrounding spar indicated an early aragonite void-cementation that could be 'expected to appear only in association

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EXPLANATION OF PLATE 103

Chaetetes (*Boswellia*) *mortoni* sp. nov., Lower Asbian (Lower Carboniferous), Eglwyseg Escarpment, Llangollen (Clwyd, North Wales).

Fig. 1. Paratype BMNH R4429 (Morton Collection). Longitudinal section of calicle walls replaced by chalcedonic (length fast) silica, and zoned dolomite lumen infills. Micrgranular silica spicule pseudomorphs visible as dark streaks within the calicle walls, ×50.

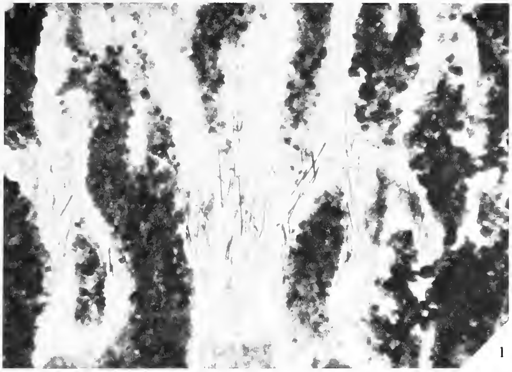
Fig. 2. BMNH R4429. Detail of chalcedonic silica calicle wall in longitudinal section, showing the spicule pseudomorphs diverging distally, ×150.

Fig. 3. Holotype BMNH R49964. Longitudinal section of calicle wall illustrating well-preserved calcitic spicule pseudomorphs, diverging distally and subparalleling the fascicular fibres, defined by trains of inclusions, ×120.

Fig. 4. BMNH R50134. Transverse section of calicle, with distinct and vague transverse sections through calcitic spicule pseudomorphs (S), ×150.

Fig. 5. BMNH R4429. Microgranular silica spicule pseudomorph extending to lumen void (L) calicle wall (W) junction, indicating original extension of distal portion of spicule into the lumen, and its subsequent dissolution, ×200.

Figs. 6–11. Microgranular silica spicule pseudomorphs of BMNH R4429. 6, transverse section, × 1000. 7, slight surface corrosion on tylostyle (C), with adjacent ?raphide-microsclere (Mi), ×200. 8, tylostyle with discontinuity and replacement by dolomite rhomb (R), ×200. 9, perfect tylostyle pseudomorph. Note proximal boss and distal point, ×200. 10, discontinuous tylostyle pseudomorph (probably a dissolution feature), ×200. 11, detail of a highly corroded tylostyle pseudomorph (C), ×600.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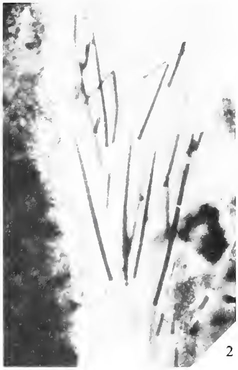
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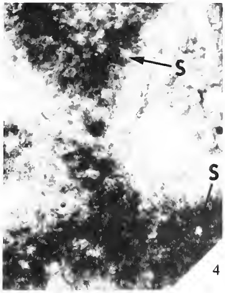

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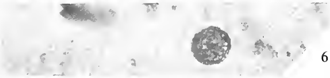
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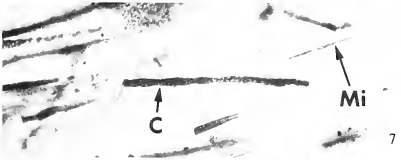

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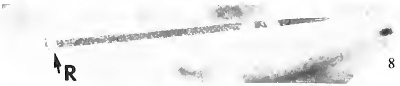

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GRAY, Palaeozoic chaetetid

with previously aragonitic skeletons'. Conversely, in silicified specimens rare microdolomite inclusions occur (Pl. 103, fig. 8) within the calicle walls suggesting a high-magnesian calcite original mineralogy. However, intense dolomitization of the lumina of these colonies, the lack of microdolomite inclusions within calcitic specimens, and the common association of dolomite with chert nodules in the Tynant Limestone indicates that the magnesium may have an external source. Staining has not revealed any obviously 'ferroan' calcitic specimens. It would therefore appear that aragonite is the most probable original mineralogy of *C.* (*B.*) *mortoni.*

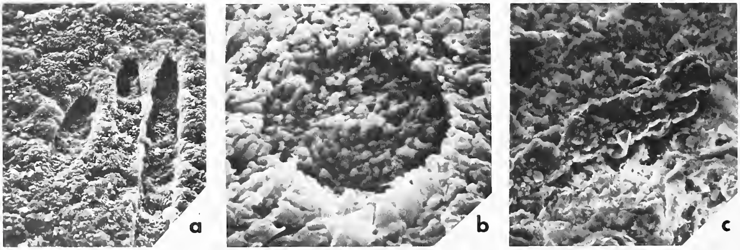
Spicule preservation. There are significant variations in the mode of preservation of the intramural spicules. Extant sclerosponges secrete siliceous spicules of various types (see Table 1) within or external to a calcareous skeleton. Hartman and Goreau (1970, pp. 210, 213) and Land (1976) described live colonies of ceratoporellans in which the opaline silica spicules (Opal 'A' of Jones and Segnit (1971)) were dissolving within the basal calcareous mass.

In *C.* (*B.*) *mortoni* spicules are preserved as calcite, silica, and pyrite pseudomorphs. Most specimens contain calcitic pseudomorphs. No spicule pseudomorphs convincingly extend into the lumina, although many spicules would have originally done so, as shown by extrapolation of spicule microstructure where it terminates abruptly against the calicle wall edge (Pl. 103, fig. 5).

The siliceous spicule pseudomorphs of BMNH R4429 and LIV.C.M. 1974.57 show dissolution features (Pl. 103, figs. 7, 11) from slight surface pitting to deep corrosion. Often the spicule pseudomorphs are discontinuous (Pl. 103, figs. 8, 10). The origin of this last feature is uncertain, but may be a severe localized corrosion effect. Dissolved parts of spicules have been replaced by clear chalcedonic silica indicating that a degree of dissolution occurred prior to the silicification of calicle walls. A later diagenetic event is indicated by dolomite rhombs replacing both spicule pseudomorphs (Pl. 103, fig. 8) and chalcedonic-silica walls.

In specimen BMNH R4429 neither axial canals nor axial filaments are visible, even with scanning electron microscopy of HF etched specimens (text-fig. 4*b*) (cf. Schwab and Shore 1971), indicating that an internal alteration of the spicule mineralogy has occurred. This is further confirmed by the presence of sub-microscopic microgranules which impart a red-brown hue and high relief to the spicule pseudomorphs. Deeper coloration corresponds to a more dense microgranule distribution. They give the spicule surface a smooth but frosted appearance in transmitted light. S.E.M. with E.D.A.X. shows that the micrognanules are siliceous, and indistinguishable from the surrounding chalcedonic-silica walls. HF etched surfaces reveal the micrognanule's form (text-fig. 4*b*). They vary between 0·2 μm and 0·5 μm diameter, and have sharp edges implying an internal structural ordering.

At an early or intermediate stage of diagenesis, biogenic opal 'A' is either converted *in situ* to opal



TEXT-FIG. 4. S.E.M. photomicrographs of spicule pseudomorphs in *C.* (*B.*) *mortoni*: 4*a*, longitudinal section of calicle wall with siliceous spicule pseudomorphs preferentially etched (10% HF for 3 minutes), BMNH R4429, × 1000; 4*b*, transverse section of a micrognanular silica spicule pseudomorph (etched in 10% HF for 3 minutes), BMNH R4429, × 5000; 4*c*, pyritic spicule pseudomorph, composed of pyrite crystal aggregates (HCl etch), BMNH R46144, × 1000.

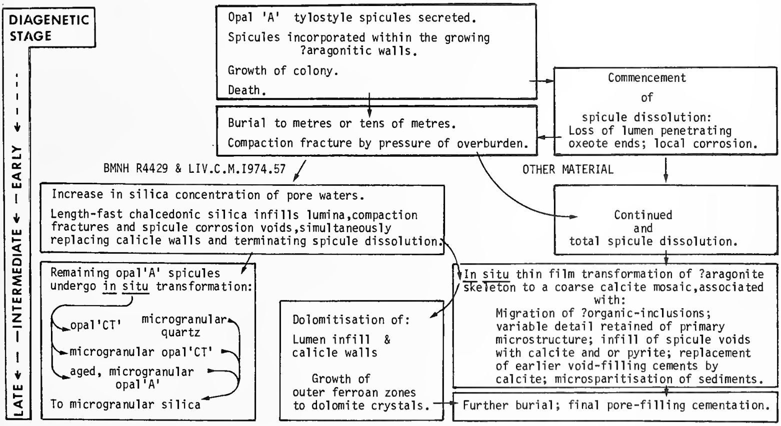
'CT' (Ernst and Calvert 1969; Wise and Weaver 1974, p. 305), a disordered cristobalite-tridymite silica polymorph (Jones and Segnit 1971), or dissolved and subsequently reprecipitated as opal 'CT' or quartz, filling voids and replacing carbonate grains (von Rad, Riech, and Rösch 1978). With increasing diagenetic maturity (depth of burial; time; temperature controls) opal 'CT' is eventually converted to quartz (Reich 1979). There are few records of opal 'CT' from pre-Cretaceous sediments.

The mineralogical composition of the spicule pseudomorphs in *C.* (*B.*) *mortoni* invites discussion. Are the spicules not pseudomorphs but diagenetically aged opal 'A' relic spicules? Reich (1979, pp. 754–755, pl. 1, fig. 4) reported Eocene opal 'A' sponge spicules with a pronounced microgranular texture similar to that observed on HF etched spicules in BMNH R4429.

Opal 'CT' normally occurs as bladed microspherules or lepispheres, 3 μm to 15 μm diameter. Siliceous sponge spicules have been recorded replaced by lepispheres that subsequently have been inverted to quartz (Reich 1979, p. 742) leaving visible relics of the precursor lepisphere. Von Rad *et al.* (1978, p. 903, pl. 3, figs. 2, 3) figured lepispheres replaced by microgranular quartz, also with a similar texture to that observed in spicule pseudomorphs of BMNH R4429 (text-fig. 4*b*). No lepisphere relics are visible in these spicules. Robertson (1978, p. 25) suggested that 'domains' of opal 'CT' would 'presumably appear' within opal 'A' 'which had escaped early diagenetic dissolution, becoming increasingly numerous as solid state ordering proceeds'. These 'domains' may be analogous to the microgranules within the spicule pseudomorphs (i.e. opal 'CT' without a lepisphere stage) or they may be a microgranular quartz replacement of opal 'CT' microgranules.

Opal 'CT' is generally recognized to have a higher relief than opal 'A', but exceptions are known. The high relief of microgranule-dense spicules in BMNH R4429 and LIV.C.M. 1974.57 may be caused by internal reflections on the surfaces of the microgranules. The spicules dissolve in HF far more readily than the surrounding chalcedonic silica (text. fig. 4*a*). This may be due to their fine granular nature, but Robertson (1978, p. 22) found that opal 'CT' dissolved preferentially in HF with respect to chalcedonic silica.

Thus the origin of the microgranular silica within the spicule pseudomorphs is unclear. It may be diagenetically aged opal 'A'; microgranular quartz replacement of opal 'CT' or relic microgranular opal 'CT' that has not gone through a lepisphere stage (see text-fig. 5). The nature of the silica matrix



TEXT-FIG. 5. Chart illustrating the sequence of events in the diagenetic history of *Chaetetes* (*Boswellia*) *mortoni* sp. nov. in relation to the preservation of microstructures and spicule pseudomorphs.

to the microgranules is unknown. In spicule pseudomorphs with few microgranules the matrix is optically similar to the surrounding chalcedonic silica. The occurrence of this microgranular silica fabric within the spicule pseudomorphs and not within the surrounding chalcedonic silica walls, and the retention of delicate spicule corrosion features suggest that the spicules were not originally calcareous, but probably opal 'A', as in extant sclerosponges.

In specimens BMNH R46144, BMNH R50188, and BMNH R45851 pyritic spicule pseudomorphs occur, similar to those described by Kaźmierczak (1979). The pyrite replacement is imperfect, with microcrystalline pyrite (text-fig. 4*c*) forming discontinuous chains or aggregates of 1 μm to 7 μm crystals along the pseudomorph length. The non-pyritic parts of the pseudomorphs are replaced by calcite. In BMNH R45851 the spicules are pseudomorphed by pyrite only towards the outer edges of calicle walls, where they merge with highly pyritic lumen-filling sediment. In contrast, BMNH R50188 has void-filling spar in the lumina, with pyritic spicule pseudomorphs terminating abruptly at the calicle wall margins, indicating that pyritization occurred after at least partial spicule dissolution. Rickard (1970) suggested that framboidal pyrite may replace organic globules or infill gaseous vacuoles. The calcitic spicule pseudomorphs often contain ?organic-inclusions, which may play a role in the pyrite formation.

AFFINITIES OF *C.* (*B.*) *MORTONI* WITH CERATOPORELLIDS

Ceratoporellids secrete a basal calcareous skeleton of fascicular fibrous aragonite calicles. These are subsequently infilled with fibrous aragonite by the upward-growing basal pinacoderm (Hartman and Goreau 1970, 1972). The calicles of *Ceratoporella nicholsoni* are regular, rounded to polygonal, rarely with a meandrine form (Hartman and Goreau 1972, fig. 17) similar to that of *Stromatospongia* Hartman, 1969, another extant ceratoporellid genus. Unlike chaetetids, ceratoporellids do not secrete tabulae. However, as Hartman and Goreau (1972, p. 142) point out, 'the difference is one of degree', with the growth of tabulae representing periodic rather than continuous carbonate secretion from the basal pinacoderm of the sponge animal. *Atrochaetetes*, a Mesozoic ceratoporellid (see above), lacks a continuous calicle infill (Cuif and Fischer 1974) and exhibits intramural spicule pseudomorphs in at least one species (Dieci, Russo, and Russo 1977). Its backfill may have formed by periodic secretion, or by periodic distally directed movement of the living tissues, and may be a character intermediate between solid backfills and tabulae.

The calicle surfaces of ceratoporellids are often ornamented with arborescent processes, rounded knobs, and spines of aragonite. No detailed calicle surface is available on *Chaetetes* (*B.*) *mortoni* for comparison; however, longitudinal sections show the distal edges of the calicles as rounded, although pre-burial erosion may have enhanced this. Isolated aragonitic trabeculae grow within the soft tissue of *Ceratoporella*, and are subsequently incorporated within the calcareous walls (Hartman and Goreau 1972, p. 135). These may be compared to the trabecular columns within *C.* (*B.*) *mortoni* which remain isolated during growth. Surface mamelons and astrorhizae, evident in some specimens of ceratoporellids as a result of differential growth-rates beneath excurrent canal systems (Stearn 1975), are not present on studied specimens of *C.* (*B.*) *mortoni*.

Ceratoporellids increase by pseudoseptal division, and Palaeozoic chaetetids by both pseudoseptal and basal fission. Mesozoic chaetetids in contrast also increase by intramural offset, as do tabulosponges.

Opal 'A' spicules are secreted from scleroblast cells within the living tissue of ceratoporellids and are incorporated within the skeleton as the colony grows. Hartman and Goreau (1972, p. 134) state that the spicules of *Ceratoporella nicholsoni* 'entrapped in the aragonite tend to follow the orientation of the calcareous crystalline units that surround them'. This is very like *C.* (*B.*) *mortoni*. The proximal (basal) spicule heads in living ceratoporellids are embedded within an organic matrix (Hartman and Goreau 1970). Although there is no direct evidence for organic fibres surrounding the head of spicules in *Chaetetes* (*B.*) *mortoni* the presence of ?organic-inclusions indicates an intimate relationship between the organic, calcareous, and siliceous components of the skeleton. Hartman and Goreau (1970, p. 213) also note that there are regions of the calcareous skeleton of *Ceratoporella* *nicholsoni* devoid of siliceous spicules. Although spicule preservation is variable throughout the colonies of *Chaetetes* (*B.*) *mortoni*, the local variation in spicule distribution may in part be primary. Ceratoporellids secrete monaxons of various forms, although they are neither known with tylostyles, nor with microscleres. The size of *C.* (*B.*) *mortoni* tylostyles does, however, fall within the size range of known ceratoporellid spicules.

The ecology of extant sclerosponges is fundamentally different from that of fossil chaetetids. Extant ceratoporellids are commonly found in a complex association with serpulid worms in submarine caves and at depth on fore-reef slopes (Hartman and Goreau 1970), whereas Palaeozoic chaetetids are common open-shelf dwellers, often associated with shallow-water carbonates.

There are significant similarities between *C.* (*B.*) *mortoni* and ceratoporellids in colony, calicle, microstructure form, and spicule character, indicating a close phylogenetic relationship. One notable difference is the presence of true tabulae in *C.* (*B.*) *mortoni* and the solid calcareous calicle infill characteristic of extant ceratoporellids.

AFFINITIES OF *C.* (*B.*) *MORTONI* WITH OTHER SCLEROSPONGES

Tabulospongids (Hartman and Goreau 1975; Mori 1976, 1977) secrete a calicular basal skeleton of high-magnesian calcite with a lamellar microstructure. The calicles are partitioned by horizontal tabulae, and spiny processes project into the lumina. The distribution of organic fibrils within the skeleton of tabulospongids is documented by Hartman and Goreau (1975, p. 167). These nanometre-sized fibrils act both as a matrix for the calcitic skeleton, and are present within the soft tissues. In *Tabulospongia horiguchii*, Mori (1976, pl. 3, fig. 3) shows that calicle wall centres are richest in organic matrix, resembling the distribution of probable organic matter now visible in calcitic specimens of *C.* (*B.*) *mortoni*. This may be a relict primary texture in the latter.

Tabulospongids secrete siliceous spicules that are not incorporated within their basal calcareous skeleton, but remain within the surface tissues. These spicules have a very low fossilization potential. The spicules are a variety of complex forms, with both megascleres and microscleres secreted by the same colony (see Table 1).

Although the calcareous skeleton is similar in design to many chaetetids, the marked differences in microstructure and spicule form and distribution readily distinguish tabulospongids from such Palaeozoic chaetetids as *C.* (*B.*) *mortoni*.

Merlia is an unassigned extant sclerosponge that secretes a prismatic tabular basal aragonitic skeleton, partitioned horizontally by incomplete tabulae. A variety of siliceous spicules are secreted within the living tissue, but not incorporated within the skeleton. Each prismatic calicle is formed by the outgrowth and interlocking of flanges, set at 120°, off stout fibre fascicles which form the calicle corners (see Stearn 1975). The architecture of Merlia therefore is subtly different from that of chaetetids. In contrast the types of spicules secreted by Merlia are similar to those of *C.* (*B.*) *mortoni* (see Table 1) (tylostyles and raphides) indicating some histologic similarities between these sponge animals.

Some Mesozoic stromatoporoids also have similarities with *C.* (*B.*) *mortoni*. Schnorf (1960) and Yabe and Sugiyama (1935) described Lower Cretaceous and Upper Jurassic forms with clear areas within the walls which may be sites of intramural spicules (Hartman and Goreau 1970), or part of the primary calcareous microstructure (Fenninger and Flajs 1974). The calcareous skeleton of these sclerosponges resembles chaetetids in as much as they also possess calicles with tabulae and hollow lumina. They are a diverse group, however, and show many characters atypical of Palaeozoic chaetetids.

In addition Table 1 lists the other known forms of spicule-bearing sclerosponges. These are not closely comparable with the present material but indicate the variety of microstructural and morphological patterns thus far encountered within the Sclerospongidea.

CONCLUSIONS

C. (*B.*) *mortoni* sp. nov. is a Palaeozoic (Upper Dinantian) chaetetid. The calicle morphology of this chaetetid is variable between slightly irregular (chaetetiporinid) and subpolygonal, having irregularly thick fascicular fibrous walls, ornamented with longitudinal ridges and pseudosepta. These factors place it within the subgenus *Boswellia* Sokolov, 1949, a typical Palaeozoic chaetetid.

Comparison of the basal calcareous skeleton with extant and fossil sclerosponges, the presence of a neomorphic mosaic, and the dependence on ?organic-inclusions to define the primary microstructure which is variably preserved, suggest that the original calcareous mineralogy was aragonite. Text-fig. 5 summarizes the approximate sequence of diagenetic events related to the preservation of microstructures in the skeletons of *C.* (*B.*) *mortoni.*

Spicule pseudomorphs occur within the fascicular fibrous walls as long thin tylostyles, with distally diverging oxeote ends that often would have penetrated the lumen of the sponge animal. They occur now as calcite, pyrite, or silica pseudomorphs, their mineralogy dependent on the diagenetic history of the basal skeleton.

In calcitic specimens, the spicule pseudomorphs are preserved as clear calcite rods in regions of the calicle walls with a dense ?organic-inclusion distribution. They are absent from compaction-fractured zones and are more common in thick-wall zones of growth rhythms. More rarely, the spicules are defined by trains or aggregates of pyrite crystals.

Chalcedonic silica locally replaces the calicle walls, enveloping spicule pseudomorphs that retain detail of their tylostyle form. Early dissolution features are fossilized within these spicules. Voids formed by spicule dissolution are infilled with clear chalcedonic silica. Remaining spicules have undergone alteration to microgranular silica of three possible forms, either diagenetically aged opal 'A', microgranular quartz replacement of opal 'CT', or relic microgranular opal 'CT' that has not gone through a lepisphere stage.

The presence of intramural spicule pseudomorphs within an otherwise typical member of the Palaeozoic Chaetetida further supports the sclerosponge affinities of at least some members of this group. Comparison of this chaetetid with other sclerosponges indicates that the spicular character and calcareous microstructure is very similar to that of the Ceratoporellida. The secretion of tabulae in chaetetids, rather than the backfill of ceratoporellids, remains the distinguishing microstructural feature. Of the two previously described intramural spicule pseudomorph bearing Mesozoic 'chaetetids' *Atrochaetetes* Cuif and Fischer, 1974, may be regarded as an aberrant member of the Ceratoporellida rather than a chaetetid *s.s.*, on account of its discontinuous backfill.

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ORIGIN, EVOLUTION AND SYSTEMATICS OF THE CRETACEOUS AMMONITE *SPATHITES*

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ABSTRACT. *Spathites* Kummel and Decker, 1954, a predominantly early to mid-Turonian genus common in Tethyan regions of both the Old and New Worlds, is a key genus in the early radiation of the Mammitinae (of which the Metoicoceratinae and Fallotitinae are shown to be synonyms). *Spathitoides* Wiedmann, 1960 is a strict synonym and *Jeanrogericeras* Wiedmann, 1960 (of which *Fallotites* Wiedmann, 1960 is a synonym) no more than subgenerically distinct. The genus evolved from *Metoicoceras*; a succession is demonstrated from *S.* (*Jeanrogericeras*) to *S.* (*Spathites*). *Mammites* is an early offshoot from the former subgenus, whilst the Coniacian *Buchiceras*, previously referred to the Tissotiidae, is a direct descendant of the *S.* (*S.*) *rioensis* Powell to *S.* (*S.*) *chispaensis* Kummel and Decker to *S.* (*S.*) *puercoensis* (Herrick and Johnson) lineage.

LOWER Turonian successions, especially those of Tethyan regions, have yielded great numbers of ammonites with a reduced acanthoceratid ornament, currently referred to *Spathites* and *Spathitoides* of the Vascoceratinae, *Fallotites* of the Fallotitinae, and *Jeanrogericeras* of the Mammitinae. The type specimens of the type species are mostly distinct enough, but it has proved difficult to allocate a number of other species to one or other genus.

This is particularly true where large subsequent collections have shown that the range of intraspecific variation in some forms spans currently accepted generic limits.

Study of the earliest described species of the group, *Ammonites reveliereanus* Courtiller, 1860, as part of our over-all revision of the ammonite fauna of the Turonian stratotype, provides a basis for the discussion of all the above genera, which are regarded as members of the subfamily Mammitinae, in direct lineal descent from the late Cenomanian *Metoicoceras*.

SYSTEMATIC PALAEONTOLOGY

Repositories of material. These are indicated as follows: OUM, University Museum, Oxford; MNHP, Muséum d'Histoire Naturelle, Paris; SP, Sorbonne Collection, now housed in the Université Paris VI; FSR, Faculté des Sciences, Rennes; AM, Muséum d'Histoire Naturelle, Angers; CS, Château de Saumur; UT, Texas Memorial Museum, Austin; WW, C. W. Wright coll.

Suture terminology. The suture terminology of Wedekind (1916) (see Kullman and Wiedmann 1970 for a recent review) is followed here: I = Internal lobe, U = Umbilical lobe, L = Lateral lobe, E = External lobe.

Dimensions. All dimensions are given in millimetres, figures in parentheses being the percentage of the total diameter. D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilicus.

Superfamily ACANTHOCERATACEAE Grossouvre, 1894
Family ACANTHOCERATIDAE Grossouvre, 1894
Subfamily MAMMITINAE Hyatt, 1900

(= Metoicoceratinae Hyatt, 1903; Fallotitinae Wiedmann, 1960)

Discussion. The systematics of the latest Cenomanian and Turonian Acanthoceratidae are in a state of flux, but a classification at subfamily level is emerging that will accord with phylogeny. The earliest Acanthoceratidae known are *Mantelliceras*, subfamily Mantelliceratinae, which are directly descended caenogenetically from species of *Stoliczkaia* (Lyelliceratidae, Stoliczkaiinae) with bituberculate venter on the inner whorls. Mantelliceratinae, characterized by dominant, more or less

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sharp ribs, appear to have persisted through the Cenomanian and seem to have produced forms with trituberculate venters. Acanthoceratinae characterized by trituberculate venter and a tendency to coarse rounded ribbing and tuberculation, first appeared early in the Lower Cenomanian, but later than *Mantelliceras*, with *Acompsoceras*, whose origin is uncertain. Its strong ventrolateral and weak siphonal tubercles, the latter normally present on the inner whorls only, suggest that its most probable source lies in Mantelliceratinae, but trituberculate-ventered *Stoliczkaia*, *S.* (*Lamnayella*) Wright and Kennedy, persist into the Lower Cenomanian and it is conceivable that here lies the origin of Acanthoceratinae.

During the mid Cenomanian the subfamily gave rise to the Euomphaloceratinae (Cooper 1978; Kennedy, Wright, and Hancock 1980*a*), a line which ended with *Romaniceras* in the late Turonian. Both Acanthoceratinae and Euomphaloceratinae are characterized by, amongst other features, a row of siphonal tubercles. Late in the Cenomanian, *Thomelites*, itself probably derived from some siphonally tuberculate member of the Mantelliceratinae, began to lose its siphonal tubercles and gave rise to *Metoicoceras*, in which the venter is bituberculate in all but the early stages of early species such as *M. praecox* Haas and *M. latoventer* Stephenson.

Hyatt (1903, p. 115) erected a family Metoicoceratidae for this genus (and placed it in his superfamily Mantelliceratida), but he had previously (1900, p. 588) established a family Mammitidae (in his superfamily Mammitida) for another stock with bituberculate venters. The two families were reduced to subfamily status within the Acanthoceratidae by Wright and Wright (1951, p. 24). Re-examination of the Lower Turonian acanthoceratids with bituberculate venters suggests an even simpler situation with a lineal phyletic succession *Thomelites* → *Metoicoceras* → *Spathites* (*Jeanrogericeras*) [= *Fallotites*] → *S.* (*Spathites*) → *Buchiceras* and an offshoot branch *Spathites* (*Jeanrogericeras*) → *Mammites* → *Metasigaloceras*. All these genera are closely related morphologically and we consider that they should all be placed in one subfamily Mammitinae. We maintain Mammitinae within the Acanthoceratidae because there are no sufficiently important distinguishing features present throughout ontogeny to separate it further from the other subfamilies.

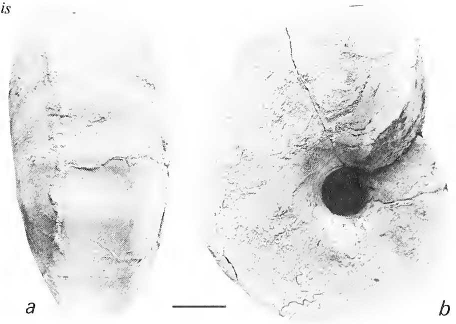
Genus SPATHITES Kummel and Decker, 1954
[= *Spathitoides* Wiedmann, 1960]

Type species. *Spathites chispaensis* Kummel and Decker, 1954, by original designation.

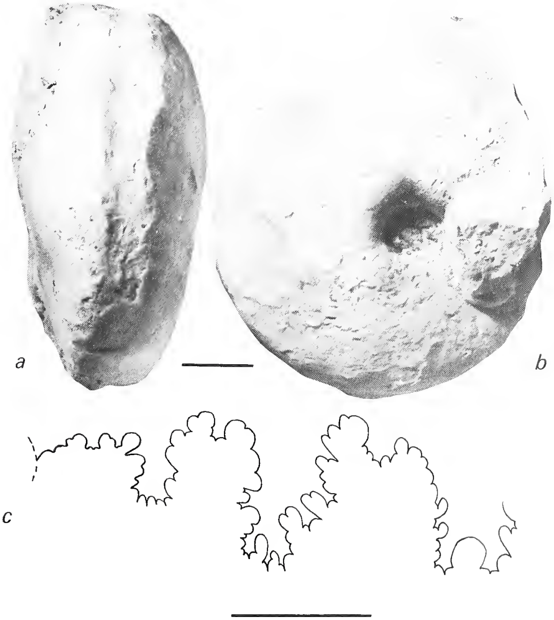
Diagnosis. Medium sized, involute ammonites with compressed to depressed whorl sections, trapezoidal when young, but tending to the subquadrate when mature. During early to middle growth there are strong to weak umbilical bullae giving rise to from one to three ribs, with additional shorter, intercalated ribs, each of which bears clavate inner and outer ventrolateral tubercles on either side of a flat or concave venter. When adult, the ornament commonly declines, leaving shells which either have blunt bullae and low ribs bearing low ventral clavi, or are smooth with sharp ventral shoulders with or without low clavi and a concave venter crossed by low, broad ribs corresponding to the clavi.

Suture simple with broad, asymmetrically bifid saddles and narrow lobes, pseudoceratitic in some species.

Discussion. The type species of *Spathites*, *S. chispaensis* Kummel and Decker, 1954 (p. 311, pl. 30, figs. 1, 2; pl. 31, figs. 1–15; text-fig. 1. Text-fig. 1 herein) was originally described on the basis of large collections from the early mid-Turonian Chispa Summit Formation of northern Chihuahua, Mexico, and Chispa Summit, Jeff Davis County, Texas. We have re-examined this material, in the collections of the Texas Memorial Museum, Austin, Texas, and confirm the very wide intraspecific variation described by Kummel and Decker, which is also demonstrated by new material before us (OUM KT. 859, 895, 943, etc.). There is every transition from compressed, feebly ornamented nuclei (Kummel and Decker 1954, pl. 31, figs. 7–9) to depressed ones with strong tubercles and ribs (Kummel and Decker 1954, pl. 31, figs. 10–12). In all forms, however, these decorated inner whorls are followed by a virtually smooth adult stage, where ribbing is restricted to low transverse undulations across the venter (text-fig. 1), corresponding to long low clavi at the shoulder. These adults are close to the holotype of *Neoptychites* (*Spathitoides*) *sulcatus* Wiedmann (1960, p. 756, pl. 7, figs. 7, 8, text-figs. 11, 12). This (text-fig. 2) comes from a somewhat lower horizon in the Turonian of northern Spain, and



TEXT-FIG. 1*a*, *b*. *Spathites* (*Spathites*) *chispaensis* Kummel and Decker. The holotype UT 20811, from the mid-Turonian Ojinaga Formation of the Placer de Guadalupe district, Sabaco (San José de Cocahuatá). Bar scale is 2 cm.



TEXT-FIG. 2*a*, *b*, *c*. The holotype of *Spathitoides sulcatus* Wiedmann, Geol. Pal. Inst. Tübingen Collection no. 1162/4 from the early Turonian south of Pedrosa, Burgos, Spain. Bar scales are 2 cm.

was regarded by Wiedmann as a derivative of *Neoptychites*, characterized by being completely smooth with a trapezoidal whorl section, a narrow umbilicus, and a truncated, concave siphonal region with periodic constrictions. The suture (text-fig. 2) is much subdivided, with the lateral lobe deeper than the external, and asymmetric. The umbilical lobe is short, the incisions on the lobes are sharp, the terminations of the saddles are rounded, and the umbilical saddle is much enlarged. As can be seen from comparing text-fig. 1 and text-fig. 2 the species is identical with the feebly ornamented variants of *S. chispaensis*, the 'constrictions' on the venter noted by Wiedmann corresponding to the interspaces between the ribs on the venter of *S. chispaensis*. The sutures are indeed more incised than those of *S. chispaensis* but no more so than *S. rioensis* Powell (1963, p. 1228, pl. 169, fig. 2; pl. 170, figs. 1-3, 6-7; text-figs. 5*j*, 6*c*-*e*), as can be seen from comparing text-figs. 1*b* and 8*c*. We would, therefore, regard *Spathitoides* as a synonym of *Spathites*.

Jeanrogericeras Wiedmann, 1960, is shown, by study at all growth stages of its type species, *Ammonites reveliereanus* Courtiller, 1860, to differ from *Spathites* only in the shape and ornament of the mature last whorl; no more than subgeneric separation is appropriate. Moreover, *Jeanrogericeras*, with its unspecialized last whorl, intermediate between that of *Metoicoceras* and typical *Spathites*, is clearly more primitive, and, in Europe at least, occurs earlier than *S.* (*Spathites*).

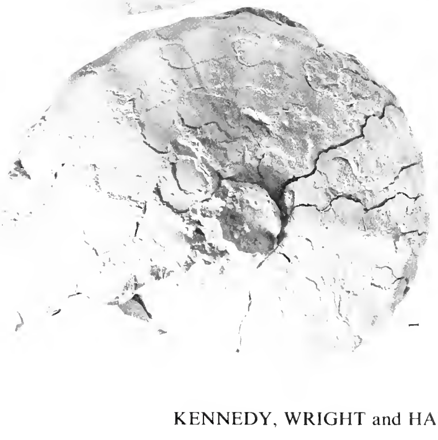
Wiedmann (1960, p. 741) established a genus *Fallotites*, with type species *Vascoceras subconciliatum* Choffat (1898, p. 64), in a new subfamily Fallotitinae. The genus was characterized by inner whorls with subquadrate or trapezoidal section, flat sides and venter and large umbilical tubercles each giving rise to two or three weak ribs, each of which bears weakly clavate inner and outer ventrolateral tubercles; the body chamber looses all ornament except large rounded umbilical tubercles, becomes rounded in section and tends to uncoil. His species of *Fallotites* include both depressed forms and those with a whorl section slightly higher than wide. Moreover, some of his figures show that the body chamber retains very low coarse ribs as well as the umbilical tubercles (Wiedmann 1960, pl. 3, figs. 4-7; pl. 4, figs. 2, 3). The characters of the inner whorl are exactly those of *S.* (*Jeanrogericeras*) *reveliereanus* at the corresponding stage (compare Pl. 104, figs. 6-8; Pl. 105, figs. 13-15 with Pl. 105, figs. 1-12), whilst those of the outer whorl are only slightly more extreme than those of some specimens of *reveliereanus* (compare Pl. 106, figs. 4-5 and text-figs. 2 and 5). There is thus a continuum that includes the variable populations of *reveliereanus* and *Fallotites* spp; indeed, Stankievich and Pojarkova (1969) include in *Fallotites* species with much stronger ribbing on the body chamber than occurs in *Jeanrogericeras*. We see no good reason for separating these two taxa and regard *Fallotites* as a synonym of *S.* (*Jeanrogericeras*). *Fallotites* (*Ingridella*) Wiedmann, 1960, includes species with outer whorls that resemble some *Vascoceras*, but they have inner whorls with distinct but subdued inner and outer ventrolateral tubercles, very feeble ribs, and sparse, very large rounded umbilical tubercles that persist to the outer whorl, where other ornament disappears, leaving a depressed rounded whorl section. We would therefore regard *Ingridella* as a further, specialized, subgenus of *Spathites*.

Occurrence. Highest Cenomanian (Wright and Kennedy, in press) to mid-Turonian of western Europe—England; Touraine, Aquitaine, and Provence in France; Spain, Portugal, Czechoslovakia, the U.S.S.R. (Kirgisia and the Tadzhiksian depression); southern India, north Africa; Texas, New Mexico, and northern Mexico.

EXPLANATION OF PLATE 104

Figs. 1-5. *Spathites* (*Spathites*) *puercoensis* (Herrick and Johnson). Specimens are from the mid-Turonian part of the Mancos Shale at USGS Mesozoic Locality D4020 1·1 miles south-west of Ojito Springs, San Ysidro Quadrangle, Sandoval County, New Mexico. USGS Coll., Denver.

Figs. 6-8. *Spathites* (*Jeanrogericeras*) *robustus robustus* (Wiedmann). Inner whorls of the holotype Geol. Pal. Inst. Tübingen Collections, Ce 1162/12. Early Turonian of Picofrentes (Soria), Spain.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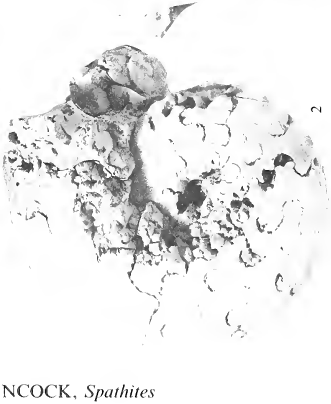
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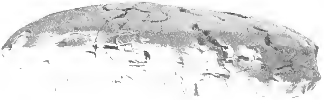
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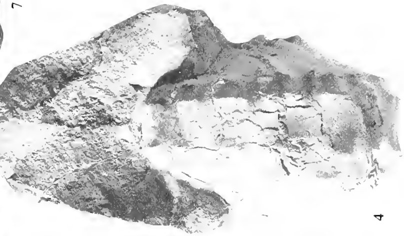
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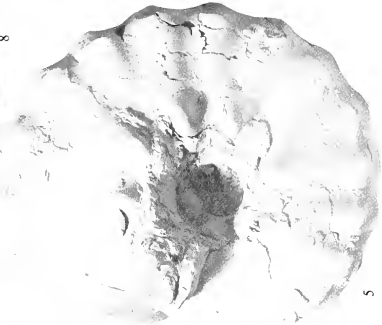
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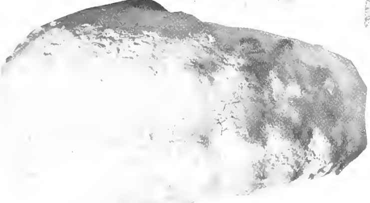
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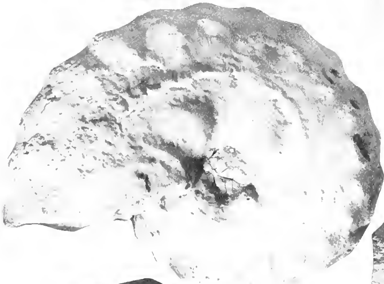
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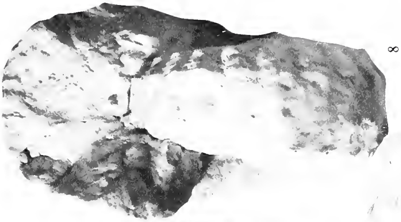
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KENNEDY, WRIGHT and HANCOCK, *Spathites*

Subgenus *Jeanrogericeras* Wiedmann, 1960
[=*Fallotites* Wiedmann, 1960]

Type species. Ammonites reveliereanus Courtiller, 1860, by original designation.

Name of type species. In 1860 Courtiller spelt the name *revelieranus* on p. 249 and *Reveliereanus* in the explanation of plate 2, fig. 5. Where two different spellings of a name appear in the first publication, Art. 32(*b*) of the *Rules of Zoological Nomenclature* provides that the spelling adopted by the first reviser is to be accepted as the correct original spelling. Courtiller himself was the first reviser and in 1867 consistently spelt the name '*Reveliereanus*'.

Diagnosis. Spathites in which the outer whorls retain ribs and tubercles.

Spathites (*Jeanrogericeras*) *reveliereanus* (Courtiller)

Plate 105, figs. 1–12; Plate 106, figs. 1–2; text-figs. 3–6

1860 *Ammonites revelieranus/Reveliereanus* Courtiller, p. 249, pl. 2, figs. 5–8.
1867 *Ammonites Reveliereanus* Courtiller; Courtiller, p. 4, pl. 3, figs. 1–4.
1894 *Mammites Revellieri* (Courtiller); de Grossouvre, p. 28.

TEXT-FIG. 3, *a*, *b*. *Spathites* (*Jeanrogericeras*) *reveliereanus* (Courtiller). Adult specimen from the mid-Turonian of Loudon, France, in the Sorbonne Collections (ex de Grossouvre Collection).

1896 *Ammonites/Mammites rochebruni* Coquand; Peron, p. 23.
1902 *Mammites binicostatus* Petrascheck, p. 145, pl. 7, fig. 6*a–b*; pl. 8, figs. 1*a–b*, 3*a–b*.
1903 *Ammonites Revelieranus* (Courtiller); Pervinquière, fiche 7, 7*a*, 7*b*.
1907 *Mammites Revelіereanus* Courtiller; Pervinquière, p. 311.
1912 *Mammites Revelieri* Courtiller; de Grossouvre, p. 18.
1912 *Mammites Reveliereanus* Courtiller; Roman, p. 12, pl. 1, fig. 1, 1*a*.
1928 *Mammites revelierei* Courtiller; Douvillé, p. 11.
1935 *Mammites revelierei* Courtiller; Faraud, p. 18, fig. 3.
1935 *Mammites revelieranus* Courtiller; Karrenberg, p. 131, pl. 30, figs. 2–4; pl. 33, figs. 2–3; text-fig. 2 (including vars. *quadrata*, *globosa*, and *lata*).
1940 *Mammites revelieranus* Courtiller sp.; Fabre, p. 278, pl. 10, figs. 5–6.
1960 *Jeanrogericeras revelieranum* (Courtiller); Wiedmann, p. 740.
1960 *Jeanrogericeras binicostatum* (Petrascheck); Wiedmann, p. 741, pl. 2, figs. 7–9; text-fig. 5.
1964 *Jeanrogericeras revelieranum* (Courtiller); Wiedmann, p. 127.
1964 *Jeanrogericeras binicostatum* (Petrascheck); Wiedmann, p. 126, figs. 10*a–c*, 11.
1967 *Metoicoceras stoliczkai* Sastry and Matsumoto, p. 2, pl. 1, figs. 1*a–f*.
1977 *Jeanrogericeras reveliereanum* (Courtiller); Hancock, Kennedy, and Wright, p. 156.

Lectotype. Here designated, the original of Courtiller 1860, pl. 2, figs. 5–6, refigured by Pervinquière 1903, figs. T1–T2. It was originally in the Museum of the Château de Saumur, but we were unable to locate it with the rest of Courtiller's types.

Other specimens. The original of Courtiller 1867, pl. 3, figs. 1–2, survives and is figured here as text-fig. 5; it is probably from the Saumur region. MNHP 6777 (d'Orbigny Collection) from Saumur, one of the syntypes of *A. fleuriausianus* d'Orbigny. A further individual with this number is also a *J. revelieranus*, but is labelled 'Rochefort' on the specimen. MNHP unregistered, from 'Taillenbourg, Charente, Ligérien E', bearing an old label '*Ammonites rochebruni* Coquand' (Pl. 106, figs. 1–2). SP, unregistered, de Grossouvre Collection, Loudon (text-fig. 3). OUM KZ767–771 from the St. Cyr-en-Bourg Fossil Bed of the Champignonnière Les Rochains, 7 km south of Saumur and north-east of Montreuil-Bellay (Pl. 105, figs. 1–12). FSR 1700, from Taillenbourg; OUM KZ779–783 from the Calcaire à Céphalopodes, Cimentièrie Lafarge, east of Route N10, 5 km south-west of Angôuleme. Geol. Pal. Inst. Tübingen CE 1162/6, the original of Wiedmann 1960, pl. 2, figs. 7–9, from Ollogoyen, Navarra, Spain. A cast of the holotype of *Metoicoceras stoliczkai* Sastry and Matsumoto, Geological Survey of India Collections no. 18170, from north of Mungilpadi, Perambalur Taluk, Tiruchinapalli (Trichinopoly) district, Madras (text-fig. 4).

Dimensions.

	D	*Wb*	*Wh*	*Wb*:*Wh*	*U*
GPIT Ce 1162/6	132·0 (100)	50·0 (380)	61·0 (46)	0·82	24·0 (18)
SP, Loudon	105·5 (100)	37·5 (36)	43·2 (41)	0·87	23·9 (23)
S5	102·5 (100)	43·5 (42)	50 (49)	0·87	18·2 (17·8)
MNHP Taillenbourg	95·5 (100)	45·0 (47)	40·0 (42)	1·13	18·2 (19)
GSI. 18170	77·6 (100)	32·2 (41)	38·7 (50)	0·83	17·0 (22)
OUM KZ767	44·0 (100)	19·8 (45)	22·1 (50)	0·89	7·8 (17)
	— (—)	14·8 (—)	16·5 (—)	0·89	— (—)
OUM KZ770	42·8 (100)	26·4 (62)	19·7 (46)	1·34	7·6 (18)
OUM KZ771	32·7 (100)	18·6 (61)	15·7 (48)	1·18	5·3 (16)
OUM KZ768	— (—)	8·0 (—)	12·3 (—)	0·65	— (—)

Description. Juveniles up to 50 mm are very variable. Coiling is involute, with a small umbilicus (usually around 16% of the diameter). Our most compressed individual is OUM KZ768 (Pl. 105, figs. 10–12), with a whorl breadth to height ratio of 0·65. The whorls are high, with the greatest breadth low on the flanks, the inner flanks being gently inflated, the outer flanks flattened, converging to the narrow, tabulate venter. Weak umbilical bullae give rise to pairs of low flexuous ribs, which bear faint inner and well-developed outer ventrolateral clavi on either side of the flattened venter. As inflation increases (Pl. 105, figs. 7–9; text-fig. 5), the whorl section become trapezoidal, with the greatest breadth at the umbilical bullae. In OUM KZ770 (Pl. 105, figs. 4–6), with a whorl breadth to height ratio of 1·18, the umbilicus is deep, with a high subvertical wall and abruptly rounded shoulder, gently swollen inner and convergent outer flanks, and a narrow, flattened venter. There are six or seven strong conical umbilical bullae; these give rise to groups of two or three broad, strong, straight prorsiradiate ribs,

TEXT-FIG. 4*a*, *b*, *c*, *d*. The holotype of *Metoicoceras stoliczkai* Sastry and Matsumoto, Geological Survey of India Collections no. 18170, from north of Mungilpadi, Perambalur Taluk, Tiruchinapalli district, Madras, India.

with additional intercalated ribs arising below mid-flank to give a total rib-density of 23 or 24 per whorl. Each rib bears a conical to feebly clavate inner and a strong clavate outer ventrolateral tubercle. Rib strength varies even in individuals showing this degree of inflation, as does rib direction, from prorsiradiate to rursiradiate, as in OUM KZ771. The most inflated individuals, including the lectotype, have swollen sides, with a whorl breadth to height ratio of up to 1·4. Here the bullae are coarse, conical, and crowded, 6 to 8 per whorl, giving rise to groups of ribs with inner and outer ventrolateral tubercles as before (Pl. 105, figs. 1–3).

EXPLANATION OF PLATE 105

Figs. 1–12. *Spathites* (*Jeanrogericeras*) *reveliereanus* (Courtiller). 1–3, OUM KZ769; 4–6, OUM KZ770; 7–9, OUM KZ767; 10–12, OUM KZ768. All specimens are from the mid-Turonian St. Cyr-en-Bourg Fossil Bed of the Champignonnière Les Rochains, 7 km south of Saumur and north-east of Montreuil-Bellay, France.

Figs. 13–15. *Spathites* (*Jeanrogericeras*) *subconciliatus hispanicus* (Wiedmann). OUM Collections, early Turonian of Pedrosa, Burgos, Spain.


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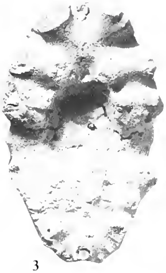
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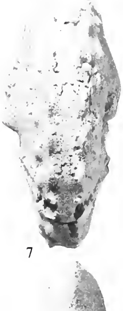
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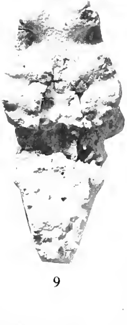
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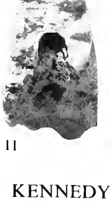
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KENNEDY, WRIGHT and HANCOCK, *Spathites*

Adult specimens before us show a similar range of whorl inflation from compressed, as in the Loudon example (text-fig. 3), to inflated, as in OUM KZ769. Most individuals, however, have whorl breadth to height ratios of between 0·9 and 1·1. The whorl section is trapezoidal, with the greatest breadth at the umbilical bullae, the flanks convex and the venter narrow and flattened or even sulcate. Five to seven coarse, blunt umbilical bullae each give rise to two or three low, broad, commonly rursiradiate ribs which may bear a trace of an inner ventrolateral tubercle (although this commonly disappears by 70–80 mm diameter), together with long, low, outer ventrolateral clavi, linked by a broad swelling across the flattened to concave venter, giving an undulose lateral profile (Pl. 106, figs. 1, 2) to the shell. Between clavi the ventrolateral shoulders are markedly angular. The last part of the adult body chamber may show a decline in ornament, especially of the ribs and clavi, and may contract (text-fig. 3), so that the coiling becomes scaphitoid and the umbilicus expands to 23% of the diameter.

The sutures are moderately subdivided, with rounded incisions. E/L is massive and asymmetrically bifid; L is deep and narrow; L/U_2 small and bifid, as is U_2 and the first auxiliary element (text-fig. 6).

Discussion. Courtiller introduced the name *A. reveliereanus* in 1860 with both a description and figure; he illustrated additional material in 1867. Pervinquière (1903) refigured some of these specimens photographically. Coquand had introduced the name *A. rochebruni* in 1858 and de Grossouvre (1894) regarded *rochebruni* as having priority over *reveliereanus*; Peron used this name in 1896 for material from Charente, Touraine, Les Jeannots, and Revest in Provence. Coquand gave no illustrations of *rochebruni* and we have been unable to locate the type specimens in the Collections of the Muséum d'Histoire Naturelle or the School of Mines (now at Lyon) which contains the other ammonite types from this work. Coquand's description could well be of a *Jeanrogericeras*, but significant specific features mentioned by Coquand differentiate it from *reveliereanus*: the presence of 12/13 ventral tubercles per whorl on inner whorls, fewer tubercles on the outer, the umbilical now becoming larger and conical and the ventral tubercles disappearing altogether. Now *J. reveliereanus* has far more ventrolateral tubercles per whorl when young (18–22) and the umbilical bullae tend to weaken with age. It thus seems unlikely, if Coquand's description is accurate, that the two species are the same. *A. rochebruni* might be a *Paramammites* or belong to some other genus. We would therefore continue to use the name *reveliereanus*, at least until the types of *rochebruni* are discovered and illustrated.

Courtiller (1860) was clearly aware that individuals of his species varied greatly, describing the 'females' as 'beacoup plus renflées, surtout vers l'ombilic, que les mâles. Leurs tubercles sont aussi beaucoup plus développés'. Karrenberg (1935, p. 32, text-fig. 2, pl. 30, figs. 2–4; pl. 33, figs. 2–3) discussed this variation at length, naming three forms: (*a*) Typical form: the whorl section is trapezoidal, with a variable whorl height to whorl breadth ratio. The flanks are rather flat and are clearly differentiated from the flattened venter. The greatest breadth is at the umbilical edge. (*b*) Var. *quadrata*. The juveniles have the whorl section of the typical form up to a diameter of 30 mm. Later, the flanks become parallel, giving an almost quadrate section. (*c*) Var. *globosa*. The whorl section is almost circular, with the greatest breadth at approximately mid-flank. It differs from the typical form even when young because of the distinctive section. (*d*) Var. *lata*. Flanks and venter are evenly rounded, with the whorl section significantly wider than high. The inner whorls show the typical cross-section.

EXPLANATION OF PLATE 106

Figs. 1–2. *Spathites* (*Jeanrogericeras*) *reveliereanus* (Courtiller). Unregistered specimen in the Collections of the Muséum d'Histoire Naturelle, Paris, from Taillenbourg, Charente, France.

Fig. 3. *Spathites* (*Spathites*) *puercoensis* (Herrick and Johnson). Ventral view of the specimen illustrated as Plate 104, fig. 1.

Figs. 4–5. *Spathites* (*Jeanrogericeras*) *subconciliatus hispanicus* (Wiedmann). OUM Collections, early Turonian of Pedrosa, Burgos, Spain.

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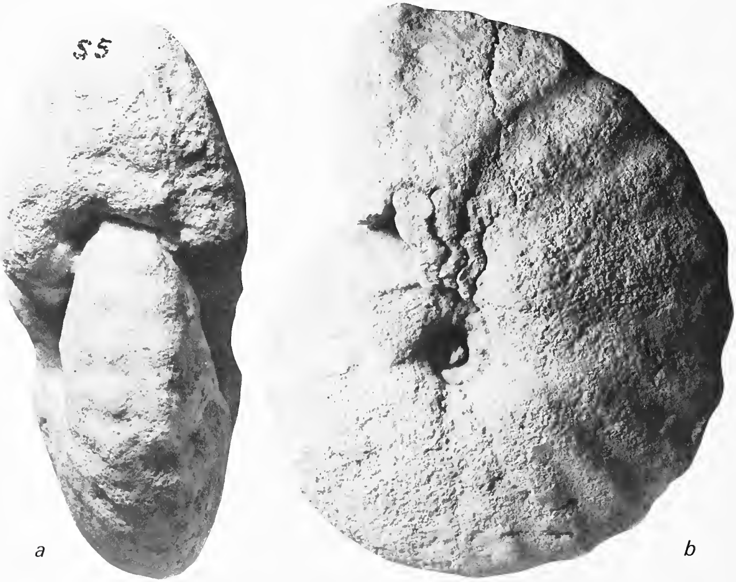
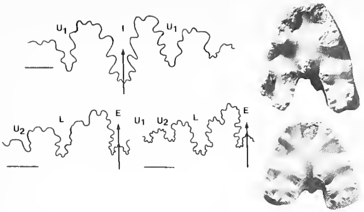
KENNEDY, WRIGHT and HANCOCK, *Spathites*

The Touraine material shows even wider variation, as discussed above, the breadth to height ratio ranging from 0·69 to 1·4, with typical covariance of ornament: the compressed individuals have weak bullae, low, flexuous ribs and scarcely detectable inner ventrolateral tubercles; the depressed individuals have massive conical bullae, coarse ribs, and well-differentiated inner and outer ventrolateral tubercles.

S. (*Jeanrogericeras*) *binicostatum* (Petrascheck) (1902, p. 145, pl. 7, fig. 6*a–b*; pl. 8, figs. 1*a–b*, 3*a–b*; see also Wiedmann 1960, p. 741, pl. 2, figs. 7–9; text-fig. 5; 1964, p. 126, figs. 10*a–c*, 11) shows considerable variation, according to Petrascheck's illustrations; Wiedmann (1960, 1964) distinguished it from *S.* (*J.*) *reveliereanus* on the basis of the absence of intercalated ribs, eight rather than four umbilical tubercles, sharper ventrolateral shoulders, a more marked, excavated siphonal region, a larger umbilicus and more massive, less asymmetric lobes in the suture line. The lectotype closely matches the individual from Loudon illustrated here as text-fig. 3, whilst sharpness of ventrolateral shoulders appears to be in part a matter of preservation, the Bohemian material being distorted by compaction in our experience. The alleged difference in numbers of umbilical bullae cannot be supported: the small lectotype of *J. reveliereanus* very clearly has at least seven in Pervinquière's figure; other specimens have eight or nine, matching the smaller specimen figured by Petrascheck (1920, pl. 7, fig. 6*a–b*). Wiedmann's large Spanish specimen (1960, pl. 2, figs. 7–8; 1964, fig. 10*a–c*) has eight massive bullae, the original of Courtiller (1867, pl. 3, figs. 1–2) has seven. In many specimens before us it is a matter of opinion whether ribs are grouped and attached to bullae or



TEXT-FIG. 5*a*, *b*. The surviving Courtiller specimen of *Spathites* (*Jeanrogericeras*) *reveliereanus* (Courtiller). CS5, from the Saumur region, Touraine, France.



TEXT-FIG. 6. Suture lines and whorl sections of juvenile *Spathites* (*Jeanrogericeras*) *reveliereanus* (Courtiller), from OUM KZ767 and 769 from the mid-Turonian St. Cyr en-Bourg Fossil Bed of the Champignonnière Les Rochains, 7 km south of Saumur and north-east of Montreuil-Bellay, France. Bar scale is 1 cm.

intercalated in some cases. None of these criteria seems sufficient to justify specific separation of two taxa.

Metoicoceras stoliczkai Sastry and Matsumoto (1967, p. 2, pl. 1, fig. 1*a–f*) (text-fig. 4) is also a synonym of *J. reveliereanus*, closely resembling the lectotype of *J. binicostatum*. The suture line is clearly that of a *Jeanrogericeras*, rather than a *Metoicoceras*.

Occurrence. *S.* (*Jeanrogericeras*) *reveliereanus* has a restricted range in the mid-Turonian, where it occurs with early *Collignoniceras woollgari* (Mantell), *Kamerunoceras turoniense* (d'Orbigny), and other ammonites in Touraine, and at this and slightly lower levels in Aquitaine, Provence, Spain, and Czechoslovakia. The Indian occurrence is not accurately dated.

MAMMITINE PHYLOGENY

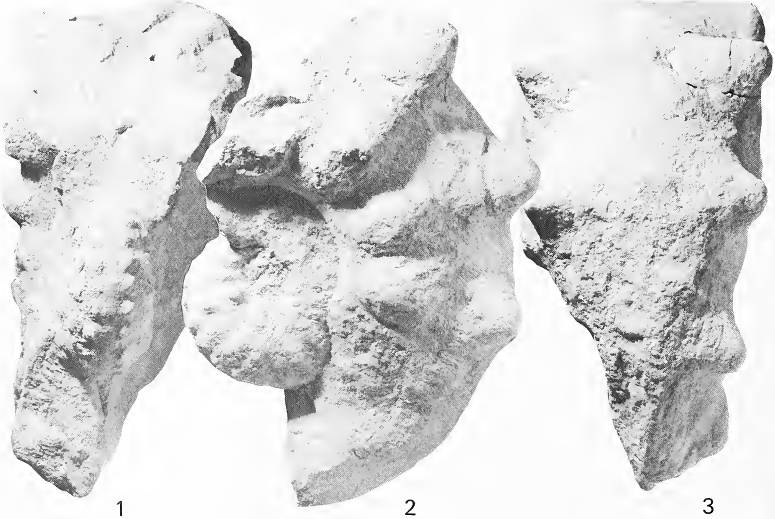
The inferred position of *S.* (*Spathites*) and *S.* (*Jeanrogericeras*) in mammitine phylogeny is shown in text-fig. 9. Rather than duplicate existing descriptions we refer the reader to Kennedy, Juignet and Hancock (in press) for an account of the late Cenomanian *Metoicoceras* species and to Kummel and Decker (1954) and Powell (1963) for descriptions of *S.* (*Spathites*). More extensive accounts of the late Cenomanian *Thomelites* and Turonian *Mammites* and *Metasigaloceras* will appear elsewhere (Wright and Kennedy, in press).

Thomelites first appears at the base of the Upper Cenomanian, and is represented by an undescribed form from the Chalk Basement Bed of Askerswell, Dorset (Kennedy 1970, p. 644; OUM Collections). By the middle of the Upper Cenomanian, the genus is known from Britain, France, the Middle East, Brazil and elsewhere, and overlaps in time the first *Metoicoceras*, which evolved in the western interior and Texas regions of the United States. As already noted, the earliest species of this genus have a siphonal tubercle when young, but later forms such as *M. defordi* Young (1957), *M. mosbyense* Cobban and *M. muelleri* Cobban (1953), although endemic to this area, show a bituberculate venter throughout. Towards the close of the Cenomanian in the American *S. gracile* Zone *Metoicoceras* spread to the Old World and *M. geslinianum* (d'Orbigny) occurs in England just below the level of the first *S.* (*Jeanrogericeras*) in Devon, which yields *S.* (*Jeanrogericeras*) cf. *subconciliatus* (Choffat) (Wright's Collection no. 25310). This occurrence can be correlated firmly with Zone III of Wiedmann's Iberian sequence (1960, 1964) which clearly demonstrates the succession with *S.* (*Jeanrogericeras*) ['*Fallotites*'] in his Zones III–V and *S.* (*Spathites*) ['*Spathitoides*'] occurring only in Zone V. In Europe *S.* (*Jeanrogericeras*) extends upwards to overlap early *C. woollgari*, *R.* (*Romaniceras*) *kallesi* Zàzvòrka, *Neoptychites cephalotus* (Courtiller), and other species in France and Spain and a somewhat impoverished but contemporaneous assemblage in Czechoslovakia.

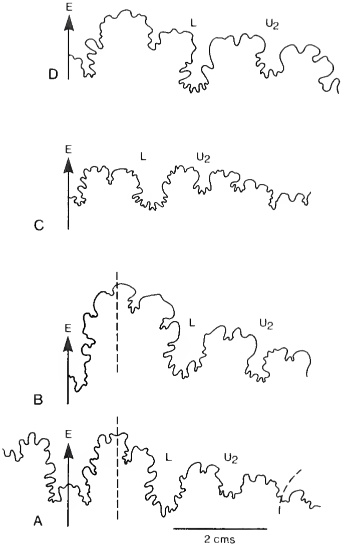
This association can in turn be related to the first well-documented occurrences of *S.* (*Spathites*) in the New World, where the early *C. woollgari* Zone fauna of northern Mexico documented by Powell (1963) yields *S.* (*Spathites*) *rioensis* in association with *C. woollgari* (= *Selwynoceras mexicanum* (Böse) of Powell), *Kamerunoceras isovokyense* (Collignon), *Neoptychites xetriformis* Pervinquière and *Mammites depressus* Powell. Our present state of knowledge suggests that this occurrence is a little below that of the Touraine assemblages. Above this a sequence can be traced through *Spathites*

(*S.*) *chispaensis* Kummel and Decker (which occurs with *Romaniceras* (*Yubariceras*) *ornatissimum* (Stoliczka)) at a higher level in the *woollgari* Zone to *S.* (*S.*) *puercoensis* Herrick and Johnson (1900), which occurs in the succeeding North American *Prionocyclus hyatti* Zone. Detailed discussion of these American species is beyond the scope of this contribution, but we note that all species show as wide a range of intraspecific variation as is shown by *S.* (*J.*) *reveliereanum*, as can be seen from Pl. 104, figs. 1–5; Pl. 106, fig. 3.

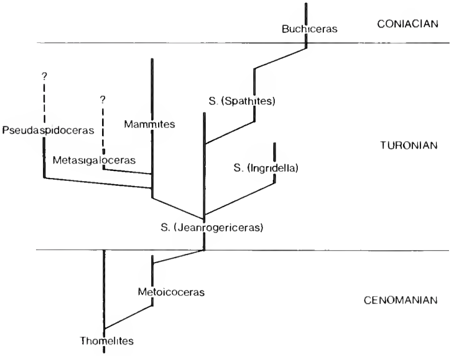
Of especial interest is the progressive change in sutural complexity in the *rioensis* → *chispaensis* → *puercoensis* lineage, shown here in text-fig. 8. This reduction in incisions and trend towards a pseudoceratitic form provides a clue to the evolutionary origin of the Coniacian *Buchiceras* Hyatt, 1875, currently classed as a tissotiid. In our view, sutural pattern, gross shell form, and ornament all point to *Buchiceras* as the last member of the Mammitinae. Its evolute quadrate whorls with ribs branching from umbilical bullae and terminating in ventral tubercles are mammitine and distinct from Tissotiidae with siphonal keel or row of tubercles, which we now regard as an offshoot of the Barroisiceratinae via *Tissotioides*. This view is confirmed by a most important specimen, now housed at the U.S. Geological Survey at Denver, collected from the *Prinocyclus hyatti* Zone of Bells, Grayson County, Texas, by the late James Conlin of Fort Worth. This has a more compressed body chamber than typical *S.* (*Spathites*) but still shows a slight facet representing the outer flank between the two rows of ventrolateral tubercles; its suture is identical with that of *Buchiceras* and it is clearly intermediate between *S.* (*S.*) *chispaensis* and *B. bilobatum*. We would also argue that the early, robust *S.* (*Jeanrogericeras*) of the *subconciliatus*/*quadratus* group (e.g. Pl. 104, figs. 6–8) are the origin of *Mammites*. The early whorls of these species and early forms of *Mammites* occurring immediately above them in southern England are identical in their general plan of decoration (text-fig. 7);



TEXT-FIG. 7. 1–3. *Mammites* sp. WW 19898, from the lower part of the *Inoceramus labiatus* Zone of White Cliff, Seaton, Devon. The outer whorls are those of a true *Mammites*, the inner strongly reminiscent of *Spathites* (*Jeanrogericeras*), ×0·56.



TEXT-FIG. 8. Progressive modification of sutures in the *Spathites* (*Spathites*) to *Buchiceras* sequence: A: *Spathites rioensis* Powell, OUM KT1244, low *Collignoniceras woollgari* Zone, Cannonball Hill, Chihuahua, northern Mexico. B: *S. chispaensis* Kummel and Decker, OUM KT943 high *C. woollgari* Zone, Chispa Summit, Texas. C: *S. puercoensis* (Herrick and Johnson), USGS 15947-20, *Prionocyclus hyatti* Zone, USGS Mesozoic locality D4020, 1·1 miles south-west of Ojito Springs, San Ysidro Quadrangle, Sandoval County, New Mexico (kindly supplied by W. A. Cobban). D: *Buchiceras bilobatum* Hyatt, Coniacian of Otusco, Peru. Copy of Brüggen 1910, fig. 9D. A and C are from middle-aged specimens; B and D from adults. Bar scale is 2 cm.



TEXT-FIG. 9. Inferred phylogy of *Buchiceras*, *Spathites*, and other early Mammitinae.

Mammites has developed by an increase in size and strengthening rather than weakening of ornament during ontogeny.

These last observations fully confirm our initial observations on the relationships of this array of early Turonian acanthoceratids with quadrate or trapezoidal whorls, umbilical and inner and outer ventrolateral tubercles, and simple ribs: they are a homogeneous close-knit group. Refinements in correlation between England, France, Spain, Portugal, and the United States permit the construction of a detailed phylogeny and show this group to be monophyletic rather than heterochronous homoeomorphs.

Acknowledgements. We thank J. Sornay (Muséum d'Histoire Naturelle, Paris), D. Pajaud (Université Paris VI), J. Louail (Rennes), M. Maury (Angers), and our other French colleagues for their help on the revision of the stratotype Turonian. Professor T. Matsumoto (Kyushu), C. Duerdon and K. Young (Austin), D. Reaser (Arlington, Texas), W. A. Cobban and J. D. Powell (Denver), E. G. Kauffman and N. F. Sohl (Washington) assisted with work on U.S. faunas. M. R. Cooper (Salisbury, Zimbabwe), and J. Wiedmann (Tübingen) provided additional help and discussion. Dr. S. C. Hook of the New Mexico Bureau of Mines and Mineral Resources, Socorro, New Mexico, kindly gave us specimens of *Spathites puercoensis* for study.

The technical assistance of the staff of the Geological Collections, University Museum, Oxford, is acknowledged, as is financial assistance from the Natural Environment Research Council, Wolfson College, Oxford, the Lindemann Trust, and the Royal Society.

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THE ORDOVICIAN TRILOBITE FAUNA OF THE SHOLESHOOK LIMESTONE FORMATION SOUTH WALES

by DAVID PRICE

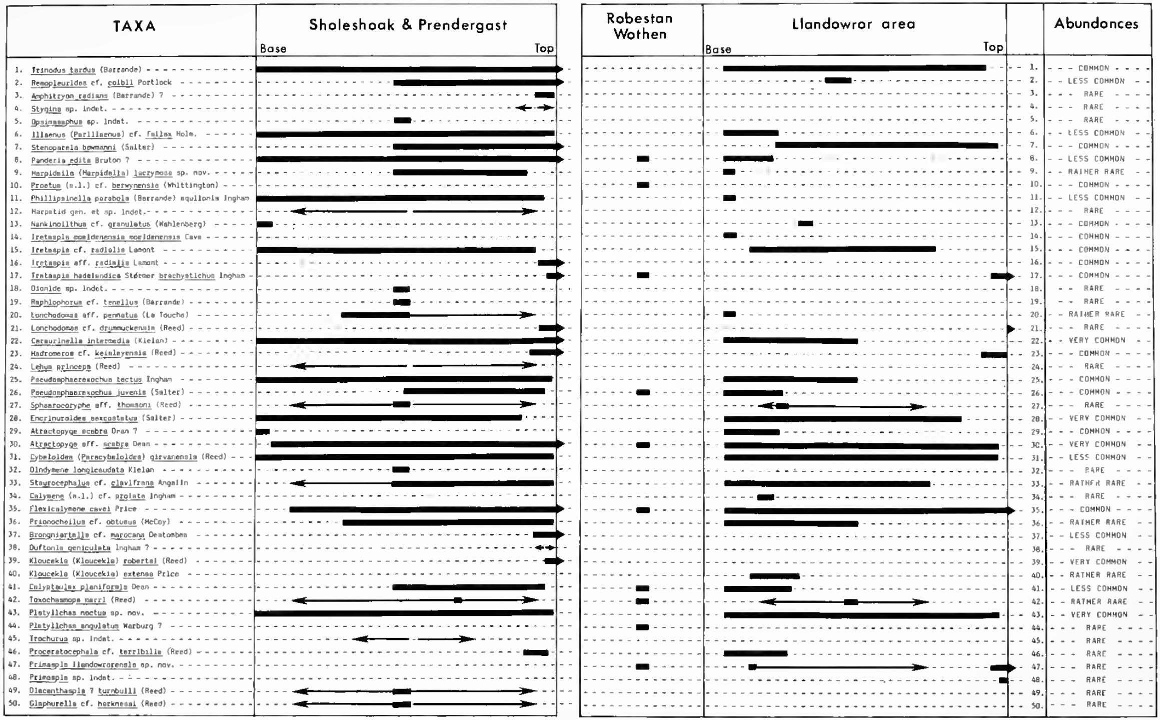
ABSTRACT. This paper gives a complete account of the historically important trilobite fauna of the Sholeshook Limestone; it comprises 50 species here placed in 40 genera and representing 23 families. Three new species, *Harpidella* (*H.*) *lacrymosa*, *Platylichas noctua*, and *Primaspis llandowrorensis* are included. Species of *Liocnemis* and *Whittingtonia* occur in laterally equivalent parts of the Slade and Redhill Mudstone Formation; the former genus is described for the first time from British strata. *Proceratocephala* is described for the first time from Wales. The rostral plate of *Stenopareia bowmanni* (Salter) is described, and a free cheek figured. A pygidium is described for a form tentatively referred to *Panderia edita* Bruton. Well-preserved topotype specimens of *Pseudosphaerexochus juvenis* (Salter) give a better characterization of the species than Salter's original syntypes. A thorax is illustrated for *Duftonia geniculata* Ingham, and a distinctive hypostoma is described for a form tentatively referred to *Platylichas angulatus* Warburg. Ranges and abundances are charted. The Sholeshook Limestone was deposited in an environment intermediate between deep-slope mudstones and shelf-edge carbonates, and has elements of its trilobite fauna in common with both facies types.

THE Sholeshook Limestone Formation is a lithologically variable thickness of mudstones, sandstones and (predominantly) siltstones of calcareous type developed between the Mydrim Shale Formation and the Slade and Redhill Mudstone Formation at Sholeshook and Prendergast, Haverfordwest, south-west Dyfed (type development), and in the area around Llandowror about 30 km further east. It is present between the type Robeston Wathen Limestone and the Slade and Redhill Mudstones at Robeston Wathen, about 13 km east of Haverfordwest. Further details of stratigraphy were given in an earlier account (Price 1973*a*) which showed the formation to have a diachronous base and to overlie the Mydrim Shales unconformably. The base of the normally succeeding Slade and Redhill Mudstones was also diachronous, so that to the north and west of Haverfordwest this formation contains strata laterally equivalent to the type Sholeshook Limestone. At that time the age of the Sholeshook Limestone was considered to range from the upper part of Zone 1 to probably Zone 3 of the Cautleyan Stage. Since then, largely as a result of re-examining the trilobite fauna during the preparation of this paper, aided by recent descriptions of Ashgill trilobites by other authors, it has been found necessary to revise the younger of these age limits and the formation is now considered to range upwards into Zone 5 of the Rawtheyan Stage (Price 1980).

Both the Sholeshook Limestone and its trilobite fauna have played an important part in the development of knowledge and concepts concerning upper Ordovician stratigraphy (see Price 1973*a*, p. 226; 1973*b*, p. 535; 1974, p. 841). The present paper deals with the trilobite fauna as a whole. The trilobites of the basal Slade and Redhill Mudstones are also mentioned since these beds are partly correlatives of the Sholeshook Limestone and, with the exception of two forms, all their species are common to both formations. Occurrences of Sholeshook species in the higher Slade and Redhill Mudstones are also noted.

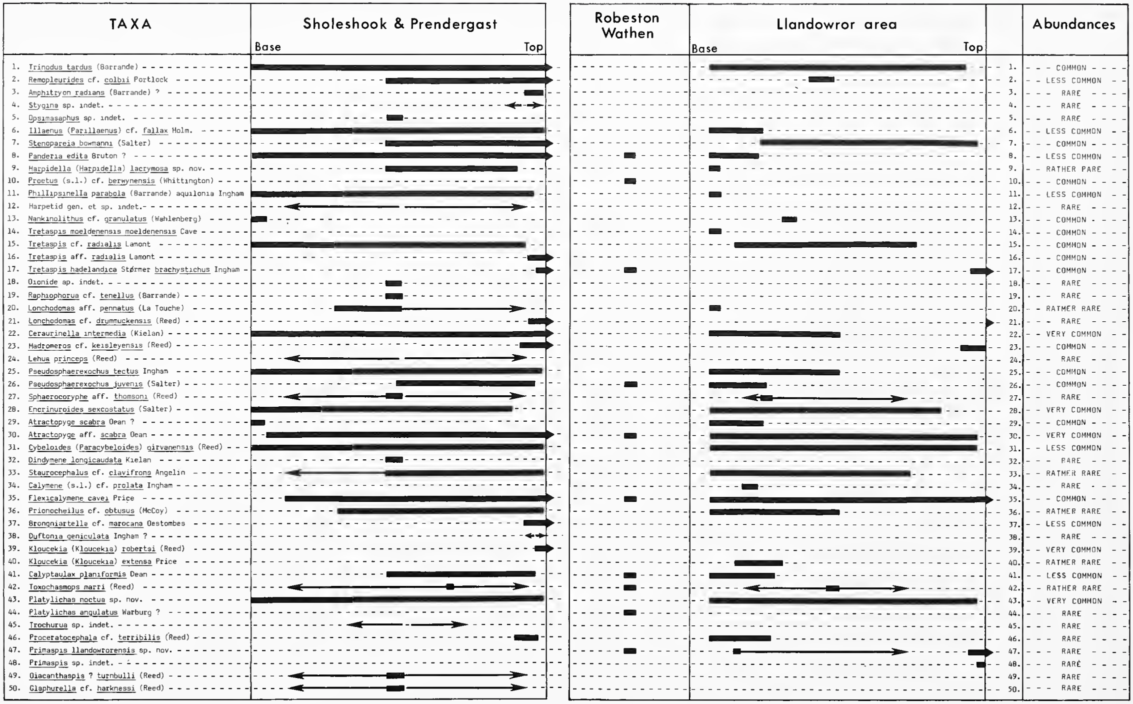
The trilobite fauna of these horizons is a rich and varied one, comprising some 52 species representing 42 genera and 23 families. Its treatment within a single relatively short paper is possible because some of its elements have already been described in detail elsewhere (e.g. Price 1974, 1977), and because recent descriptions of Ashgill trilobites have been given by such workers as Kielan (1960), Whittington (1962–8), Ingham (1970–7), Dean (1971–8), and McNamara (1979*a*).

[Palaeontology, Vol. 23, Part 4, 1980, pp. 839–887, pls. 107–114.]



	TAXA	Abundonces
1.	*Trinodus tardus* (Barrande)	COMMON
2.	*Remopleurides* cf. *colbii* Portlock	LESS COMMON
3.	*Amphitryon radians* (Barrande) ?	RARE
4.	*Stygina* sp. indet.	RARE
5.	*Opsimasaphus* sp. indet.	RARE
6.	*Illaenus* (*Parillaenus*) cf. *fallax* Holm.	LESS COMMON
7.	*Stenopareia bowmanni* (Salter)	COMMON
8.	*Panderia edita* Bruton ?	LESS COMMON
9.	*Harpidella* (*Harpidella*) *lacrymosa* sp. nov.	RATHER RARE
10.	*Proetus* (s.l.) cf. *berwynensis* (Whittington)	COMMON
11.	*Phillipsinella parabola* (Barrande) aquilonia Ingham	LESS COMMON
12.	Harpetid gen. et sp. indet.	RARE
13.	*Nankinolithus* cf. *granulatus* (Wahlenberg)	COMMON
14.	*Tretaspis moeldenensis moeldenensis* Cave	COMMON
15.	*Tretaspis* cf. *radialis* Lamont	COMMON
16.	*Tretaspis* aff. *radialis* Lamont	COMMON
17.	*Tretaspis hadelandica* Størmer *brachystichus* Ingham	COMMON
18.	*Dionide* sp. indet.	RARE
19.	*Raphiophorus* cf. *tenellus* (Barrande)	RARE
20.	*Lonchodomas* aff. *pennatus* (La Touche)	RATHER RARE
21.	*Lonchodomas* cf. *drummuckensis* (Reed)	RARE
22.	*Ceraurinella intermedia* (Kielan)	VERY COMMON
23.	*Hadromeros* cf. *keisleyensis* (Reed)	COMMON
24.	*Lehua princeps* (Reed)	RARE
25.	*Pseudosphaerexochus tectus* Ingham	COMMON
26.	*Pseudosphaerexochus juvenis* (Salter)	COMMON
27.	*Sphaerocoryphe* aff. *thomsoni* (Reed)	RARE
28.	*Encrinuroides sexcostatus* (Salter)	VERY COMMON
29.	*Atractopyge scabra* Dean ?	COMMON
30.	*Atractopyge* aff. *scabra* Dean	VERY COMMON
31.	*Cybeloides* (*Paracybeloides*) *girvanensis* (Reed)	LESS COMMON
32.	*Dindymene longicaudata* Kielan	RARE
33.	*Staurocephalus* cf. *clavifrons* Angelin	RATHER RARE
34.	*Calymene* (s.l.) cf. *prolata* Ingham	RARE
35.	*Flexicalymene cavei* Price	COMMON
36.	*Prionocheilus* cf. *obtusus* (McCoy)	RATHER RARE
37.	*Brongniartella* cf. *marocana* Destombes	LESS COMMON
38.	*Duftonia geniculata* Ingham ?	RARE
39.	*Kloucekia* (*Kloucekia*) *robertsi* (Reed)	VERY COMMON
40.	*Kloucekia* (*Kloucekia*) *extensa* Price	RATHER RARE
41.	*Calyptaulax planiformis* Dean	LESS COMMON
42.	*Toxochasmops marri* (Reed)	RATHER RARE
43.	*Platylichas noctua* sp. nov.	VERY COMMON
44.	*Platylichas angulatus* Warburg ?	RARE
45.	*Trochurus* sp. indet.	RARE
46.	*Proceratocephala* cf. *terribilis* (Reed)	RARE
47.	*Primaspis llandowrorensis* sp. nov.	RARE
48.	*Primaspis* sp. indet.	RARE
49.	*Diacanthaspis* ? *turnbulli* (Reed)	RARE
50.	*Glaphurella* cf. *harknessi* (Reed)	RARE

TABLE 1. Ranges and abundances of trilobite species in the Sholeshook Limestone Formation. Bold solid bars where short indicate actual occurrences, where longer show known ranges. Solid black arrow-heads show which forms range up into the overlying Slade and Redhill Mudstones at Haverfordwest and Llandowror. Lighter bars with arrow-heads indicate the possible range of occurrence of ill-localized material.



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2.	Remopleurides cf. colbii Portlock	LESS COMMON
3.	Amphitryon radians (Barrande) ?	RARE
4.	Stygina sp. indet.	RARE
5.	Opsimasaphus sp. indet.	RARE
6.	Illaenus (Parillaenus) cf. fallax Holm.	LESS COMMON
7.	Stenopareia bowmanni (Salter)	COMMON
8.	Panderia edita Bruton ?	LESS COMMON
9.	Harpidella (Harpidella) lacrymosa sp. nov.	RATHER RARE
10.	Proetus (s.l.) cf. berwynensis (Whittington)	COMMON
11.	Phillipsinella parabola (Barrande) aquilonia Ingham	LESS COMMON
12.	Harpetid gen. et sp. indet.	RARE
13.	Nankinolithus cf. granulatus (Wahlenberg)	COMMON
14.	Tretaspis moeldenensis moeldenensis Cave	COMMON
15.	Tretaspis cf. radialis Lamont	COMMON
16.	Tretaspis aff. radialis Lamont	COMMON
17.	Tretaspis hadelandica Størmer brachystichus Ingham	COMMON
18.	Dionide sp. indet.	RARE
19.	Raphiophorus cf. tenellus (Barrande)	RARE
20.	Lonchodomas aff. pennatus (La Touche)	RATHER RARE
21.	Lonchodomas cf. drummuckensis (Reed)	RARE
22.	Ceraurinella intermedia (Kielan)	VERY COMMON
23.	Madromeros cf. keisleyensis (Reed)	COMMON
24.	Lehua princeps (Reed)	RARE
25.	Pseudosphaerexochus tectus Ingham	COMMON
26.	Pseudosphaerexochus juvenis (Salter)	COMMON
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34.	Calymene (s.l.) cf. prolata Ingham	RARE
35.	Flexicalymene caveі Price	COMMON
36.	Prionocheilus cf. obtusus (McCoy)	RATHER RARE
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40.	Kloucekia (Kloucekia) extensa Price	RATHER RARE
41.	Calyptaulax planiformis Dean	LESS COMMON
42.	Toxochasmops marri (Reed)	RATHER RARE
43.	Platylichas noctua sp. nov.	VERY COMMON
44.	Platylichas angulatus Warburg ?	RARE
45.	Trochurus sp. indet.	RARE
46.	Proceratocephala cf. terribilis (Reed)	RARE
47.	Primaspis llandowrorensis sp. nov.	RARE
48.	Primaspis sp. indet.	RARE
49.	Diacanthaspis ? turnbulli (Reed)	RARE
50.	Glaphurella cf. harknessi (Reed)	RARE

TABLE 1. Ranges and abundances of trilobite species in the Sholeshook Limestone Formation. Bold solid bars where short indicate actual occurrences, where longer show known ranges. Solid black arrow-heads show which forms range up into the overlying Slade and Redhill Mudstones at Haverfordwest and Llandowror. Lighter bars with arrow-heads indicate the possible range of occurrence of ill-localized material.

Accordingly, the complete fauna is given in an annotated list below and only forms meriting further comment are given systematic descriptions. The composition of the fauna is discussed in a final section. The trilobites dealt with here largely come from outcrops of naturally decalcified rock and are normally preserved as internal and external moulds; material representing the exoskeleton is only rarely present. The vast majority of specimens are disarticulated exoskeletal parts of which a high proportion are fragmentary or incomplete. Nevertheless a few complete or partly articulated specimens are known, and seventeen of the Sholeshook species are represented by at least one such specimen. Most material is somewhat distorted.

Terminology. For the purposes of description, measurement, and illustration, specimens have been viewed in the standard orientations described by Temple (1975); for isolated exoskeletal parts the horizontal plane is generally defined by the (maximized) sagittal length. An exception is made in the case of trinucleid cephala which, following Hughes, Ingham, and Addison (1975) are oriented with the anterior and posterior fossulae in the horizontal plane. All references to shape and proportions, unless otherwise stated, refer to dorsal views. The term glabella is used to include the occipital ring and glabellar lobes and furrows are numbered from the rear. The term 'bullar lobes' (Temple 1972) is used for the structures formerly designated 'composite' or 'bicomposite' lobes in the lichid genus *Trochurus*. Several of the forms described here have lengthy synonomies; where these are available in earlier references they are not repeated herein.

Repositories and localities. Material is housed in the following museums: British Museum (Natural History) (BM), Hunterian Museum, Glasgow (HM), Institute of Geological Sciences (GSM), National Museum of Wales (NMW), and the Sedgwick Museum, Cambridge (SM). The determinations and descriptions in this paper are based on all available material in these collections which for most forms is too numerous to be listed separately. Maps and tables showing precise localities for specimens collected by the author and for other well-localized material have been given previously (Price 1973*a*) and it is to these that locality numbers cited in the text refer. Occurrences within the Sholeshook Limestone are shown graphically in Table 1.

ANNOTATED LIST OF COMPLETE TRILOBITE FAUNA

The forms marked with an asterisk are treated in the Systematic Account. Those based on type material from the Sholeshook Limestone or basal Slade and Redhill Mudstones are marked thus †

Trinodus tardus (Barrande). Pl. 107, figs. 1–3. See also Dean's illustrations (1971, pl. 1, figs. 1, 2) of the syntypes of *Agnostus tardus*, var. *β convexus* Salter, 1848 from the Sholeshook Limestone

Remopleurides cf. *colbii* Portlock*

Amphitryon radians (Barrande)? Pl. 107, fig. 9; Pl. 108, fig. 9. Rare; 2 cranidia from basal Slade and Redhill Mudstones (locs. 3, 4), 2 from high Sholeshook Limestone (locs. 8b, 8c) of Prendergast

Stygina sp. indet.*

Opsimasaphus sp. indet.*

Illaenus (*Parillaenus*) cf. *fallax* Holm*

Stenopareia bowmanni (Salter)†. Pl. 107, fig. 15; Pl. 108, fig. 15. For description of topotype material see Price 1974, p. 842, pl. 112, figs. 1–8, ?9. Rostral plate since recognized and figured here together with free cheek not previously figured

Panderia edita Bruton?*

Harpidella (*Harpidella*) *lacrymosa* sp. nov.*

Proetus (s.l.) cf. *berwynensis* (Whittington)*

Phillipsinella parabola (Barrande) *aquilonia* Ingham. Pl. 108, fig. 16

Harpetid gen et sp. indet. Not figured. See Reed 1905*a*, p. 97, pl. 4, fig. 1, and Whittington 1950*b*, p. 32

Nankinolithus cf. *granulatus* (Wahlenberg)*

Tretaspis moeldenensis moeldenensis Cave†
T. cf. *radialis* Lamont
T. aff. *radialis* Lamont
T. hadelandica Størmer *brachystichus* Ingham
} See Price 1977

Dionide sp. indet.*

Raphiophorus cf. *tenellus* (Barrande)*

Lonchodomas aff. *pennatus* (La Touche)*

L. cf. *drummuckensis* (Reed)*
Ceraurinella intermedia (Kielan). Pl. 110, figs. 7, 8.
Hadromeros cf. *keisleyensis* (Reed). Not figured. See Lane 1971, p. 20, pl. 3, figs. 8–11, pl. 4, figs. 1–4.
Lehua princeps (Reed)†. Not figured. Now that both cranidium (Lane 1971, p. 36, pl. 7, figs. 17*a*, *b*) and pygidium (Price 1974, p. 848, pl. 113, fig. 12) have been described, the species is placed firmly in genus *Lehua*
Pseudosphaerexochus tectus Ingham. Pl. 110, figs. 9–11. Previously listed in Sholeshook faunal lists as *P. octolobatus* (McCoy)
P. juvenis (Salter)†*
Sphaerocoryphe aff. *thomsoni* Reed*
Encrinuroides sexcostatus (Salter)†. Not figured. See Whittington 1950*a*, p. 535, pl. 68, figs. 7–16, text-fig. 2 and Price 1974, p. 856, pl. 115, figs. 1–8
Atractopyge scabra Dean? Pl. 110, fig. 17. See discussion of *A.* aff. *scabra*
Atractopyge aff. *scabra* Dean*
Cybeloides (*Paracybeloides*) *girvanensis* (Reed). Pl. 110, fig. 16; Pl. 111, fig. 5
Dindymene longicaudata Kielan*
Staurocephalus cf. *clavifrons* Angelin*
Calymene (s.l.) cf. *prolata* Ingham*
Flexicalymene cavei Price†*
Prionocheilus cf. *obtusus* (McCoy)*
Brongniartella cf. *marocana* Destombes*
Duftonia geniculata Ingham?*
Kloucekia (*Kloucekia*) *robertsi* (Reed)† } Not figured. See Price 1974, p. 857, pl. 115, figs. 9–14; pl. 116, figs.
K. (*Kloucekia*) *extensa* Price† } 1, 2 and p. 862; text-fig. 2*a*–*k*
Liocnemis recurvus (Linnarsson)*
Calyptaulax planiformis Dean*
Toxochasmops marri (Reed). Pl. 112, figs. 16, 17. See also Reed 1904, pl. 12, fig. 3 and Cocks and Price 1975, pl. 81, fig. 4
Platylichas noctua sp. nov.†*
P. angulatus Warburg?*
Trochurus sp. indet.*
Whittingtonia whittingtoni Kielan*
Proceratocephala cf. *terribilis* (Reed)*
Primaspis llandowrorensis sp. nov.†*
P. sp. indet.*
Diacanthaspis? *turnbulli* (Reed)†. Not figured. See Price 1974, p. 864, pl. 116, figs. 3–5
Glaphurella cf. *harknessi* (Reed)*

SYSTEMATIC DESCRIPTIONS

Family REMOPLEURIDAE Hawle and Corda, 1847

Genus REMOPLEURIDES Portlock, 1843

Type species. Remopleurides colbii Portlock, 1843.

Remopleurides cf. *colbii* Portlock, 1843

Plate 107, figs. 4–8

1885 *Remopleurides longicostatus*, Portl.; Marr and Roberts, faunal list p. 481.
1885 *Remopleurides dorso-spinifer*, Portl.; Marr and Roberts, faunal list p. 481.
1905*a* *Remopleurides Salteri*, Reed, var. *girvanensis*; Reed, p. 98, pl. 4, fig. 3.
1914 *Remopleurides longicostatus* Portl.; Strahan, Cantrill, Dixon, Thomas, and Jones, table p. 64.
1914 *Remopleurides colbii* Portl.; Strahan *et al.* (*pars*), list p. 71.
1914 *Remopleurides salteri* Reed; Strahan *et al.*, p. 75.
1966 *Remopleurides* cf. *colbii* Portlock; Whittington (*pars*), p. 75, pl. 22, figs. 5, 6, 9.
?1966 *Remopleurides* cf. *colbii* Portlock; Whittington (*pars*), p. 75, pl. 22, fig. 7; pl. 23, figs. 1–6.
1973*a* *Remopleurides* aff. *colbii* Portlock; Price, tables 1–3.
1975 *Remopleurides* sp.; Cocks and Price, p. 705, pl. 81, fig. 5.

Horizons and localities. Apart from the occurrences shown in Table 1, ranges through the Slade and Redhill Mudstone Formation around Haverfordwest (to locality I of Cocks and Price 1975) and is known also from the high Slade and Redhill Mudstones just south of Little Clerkenhill, 9 km further east (Grid ref. SN 045 150).

Description. Cranidium about as wide (tr.) as long (sag.) and moderately convex transversely. In lateral profile (Pl. 107, fig. 4) just less than posterior three-fifths of length straight, rest curved evenly through about 90°. Glabellar width (tr.) immediately in front of occipital furrow slightly over half maximum width achieved just behind mid-length. Anterior tongue of similar width (tr.) posteriorly, tapers very slightly forwards. Lateral glabellar furrows (Pl. 107, fig. 7) faint, evenly spaced (exsag.). 1p and 2p sub-parallel, gently convex anteriorly; separated longitudinally by about 15% of sagittal cranidial length and mesially by about 30% of maximum glabellar width; not reaching axial furrows. 3p furrows short (tr.), their adaxial ends slightly further apart than those of the 1p and 2p. Occipital furrow straight, deep, and narrow. Occipital ring strongly arched transversely, broad (sag. and exsag.) mesially; convex posterior margin bears row of (?eighteen) prominent, backwardly directed tubercles. Palpebral lobes narrow (tr.) anteriorly, broaden posteriorly, and indent pre-occipital part of glabella. Librigenae (see Whittington 1966, pl. 22, figs. 5, 9) narrow (tr.) anteriorly, widening posteriorly and produced into long, gently curved, stout genal spines; no sub-genal notch. Visual surface of eye surrounded by broad furrow and prominent external rim. Ventral surface of doublure with strong, sub-parallel ridges separated by broad grooves which are themselves striated. Hypostoma not known. Thorax incompletely known; axis strongly convex, rings broad (sag. and exsag.), dorsally flat, slightly expanded abaxially, separated by broad articulating furrows. Pleurae narrow (tr.), strongly bent-down, antero-laterally rounded, postero-laterally drawn into short spines; inner anterior corners bear large articulating bosses fitting sockets in previous segments. Pleural doublure bears strong longitudinal grooves. One partial thorax, SM A30963, from the high Slade and Redhill Mudstones, bears a long median spine but the specimen does not show clearly which ring this is on.

Pygidium (Pl. 107, fig. 8 and Cocks and Price 1975, pl. 81, fig. 5) sub-triangular. First axial ring narrow (sag. and exsag.) mesially but much expanded at tips; second ring represented by pair of elongated, postero-laterally directed lobes separated by longitudinal furrow. Faint, narrow (tr.) posteriorly tapering post-axial ridge. Margin with two pairs of spines, anterior pair slender, thorn-like, gently curved adaxially, posterior pair broad-based and much larger. Doublure broad with fine transverse terrace-lines arranged in posteriorly convex arc.

Discussion. The Sholeshook specimens are similar to the holotype of *R. colbii* as redescribed by Whittington (1950*a*, p. 540, pl. 70, figs. 1, 4, 5) though that specimen is too incomplete to show either the form of the posterior pygidial spines or whether a short 3p lateral glabellar furrow is present. Similar also to *R. colbii* and the South Welsh specimens is the species described by Whittington (1966, p. 75, pl. 22, fig. 7; pl. 23, figs. 1–6) from the Rhiwlas Limestone—though it is not well enough known for detailed comparison. A pygidium with similarly large posterior spines to those of the South Welsh form is seen in the species described by Ingham (1970, p. 13, pl. 1, figs. 22–25, ?17–21) from the Cautley Mudstones as *Remopleurides* sp. B. That form, however, has a large sub-genal notch and appears to bear a surface Bertillon pattern of fine ridges.

Family SCUTELLUIDAE Richter and Richter, 1925

Genus STYGINA Salter, 1853

Type species. Asaphus latifrons Portlock, 1843.

Stygina sp. indet.

Plate 107, fig. 12

1885 *Stygina*; Marr and Roberts, list p. 480 (*pars*).
1973*a* *Stygina*? sp. indet.; Price, table 2.

Material. SM A31595, internal mould of incomplete pygidium and posterior-most part of thorax (enrolled), from the high Sholeshook Limestone Formation of Prendergast Place, Haverfordwest (locality 8b, 8c, or 8d).

Discussion. In features such as the broad, concave border, the fine sub-parallel terrace-lines on the ventral mould of the doublure, the long, gradually tapering axis only weakly defined posteriorly, and the post-axial ridge, the specimen shows much similarity with the pygidia of the lectotype and other topotype specimens of *S. latifrons* figured by Whittington (1950, pl. 72, figs. 2, 3, 6, 9). The axial furrows are shallow and the pygidium thus differs from that of the form figured by Whittington (1966, pl. 21, figs. 13–15) from the Rhiwlas Limestone of North Wales where they are deeply incised. In addition the axis of the Rhiwlas form appears to be narrower (tr.) anteriorly and to taper less rapidly back than in either *S. latifrons* or the Sholeshook form.

Family ASAPHIDAE Burmeister, 1843
Subfamily ASAPHINAE Burmeister, 1843
Genus OPSIMASAPHUS Kielan, 1960

Type species. Opsimasaphus jaanussoni Kielan, 1960.

Opsimasaphus sp. indet.

Plate 107, figs. 10–11

1914 *Asaphus*?; Strahan *et al.*, p. 76.
1973*a* *Opsimasaphus*? sp. indet.; Price, tables 1, 2, 7.

Material. BM It9257, internal mould of incomplete hypostoma from near middle of Sholeshook Limestone Formation, locality 9e, Sholeshook. A poorly preserved pygidium, GSM H.T. 480, from the basal Slade and Redhill Mudstones near Clarbeston Road Station (locality 6a) probably also belongs here.

Description. Hypostoma with convex, sub-ovoid central body. Lateral border broadest (tr.) opposite posterior margin of central body, extended back, ornamented with faint, gently sinuous terrace-lines, and bifurcate posteriorly where it is excavated by a deep, anteriorly expanded notch. Lateral border furrow deepest and broadest posteriorly; transverse furrow wide (sag. and exsag.) and shallow. A small, faint median tubercle is present at the posterior margin of the central body and maculae are developed behind the abaxial ends of the transverse furrow.

EXPLANATION OF PLATE 107

Figs. 1–3. *Trinodus tardus* (Barrande). 1, SM A31383, internal mould of pygidium from basal Slade and Redhill Mudstones of Pelcomb Cross (locality 2), dorsal view. 2, SM A77583a, internal mould of cephalon from basal Sholeshook Limestone of Pentre-howell road section (locality 17), left lateral view. 3, SM A31378, internal mould of cephalon from Sholeshook Limestone of Sholeshook railway cutting, dorsal view. All ×8.

Figs. 4–8. *Remopleurides* cf. *colbii* Portlock. 4–6, SM A77953, internal mould of cranidium from high Sholeshook Limestone of Prendergast (locality 8c), left lateral, dorsal, and anterior views, ×4. 7, SM A30721, internal mould of cranidium showing lateral glabellar furrows, Slade and Redhill Mudstones of Upper Slade, Haverfordwest, dorsal view, ×4. 8, SM A98065, internal mould of pygidium from high Sholeshook Limestone (topmost locality 8d), Prendergast, dorsal view, ×6.

Fig. 9. *Amphitryon radians* (Barrande)? BM In54167a, internal mould of incomplete cranidium from basal Slade and Redhill Mudstones of Rudbaxton (locality 4), dorsal view, ×6.

Figs. 10, 11. *Opsimasaphus* sp. indet. 10, BM It9257, internal mould of incomplete hypostoma, middle Sholeshook Limestone, locality 9e, Sholeshook, ventral view. 11, GSM H.T. 480, flattened and sheared internal mould of pygidium from basal Slade and Redhill Mudstones of Clarbeston Road Station (locality 6a), dorsal view. Both ×1½.

Fig. 12. *Stygina* sp. indet. SM A31595, internal mould of pygidium and posterior part of thorax (enrolled) from the high Sholeshook Limestone of Prendergast (locality 8b, c, or d), pygidium in dorsal view, ×3.

Figs. 13, 14. *Illaenus* (*Parillaenus*) cf. *fallax* Holm. 13, BM In54706, internal mould of pygidium from Craig-y-deilo quarry, Llandowror, dorsal view, ×1. 14, BM In54464, internal mould of cranidium from high Sholeshook Limestone (locality 8b), Prendergast, dorsal view, ×1½.

Fig. 15. *Stenopareia bowmanni* (Salter). SM A99092b, cast from external mould of rostral plate, high Sholeshook Limestone (locality 8d) of Prendergast, ventral view, ×2½.

Figs. 16, 17. *Proetus* (s.l.) cf. *berwynensis* (Whittington). 16, SM A77821, cast from external mould of incomplete cranidium, Sholeshook Limestone horizon, Robeston Wathen (locality 10a), dorsal view, ×8. 17, SM A99093, internal mould of pygidium, same horizon and locality, dorsal view, ×6.


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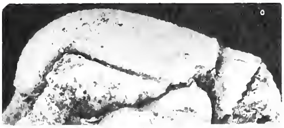
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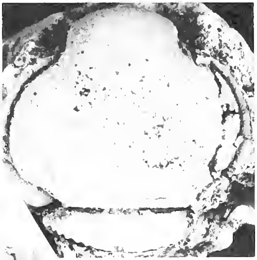
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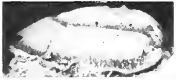
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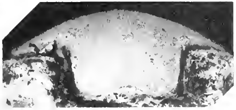
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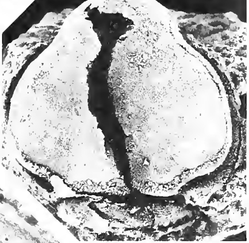
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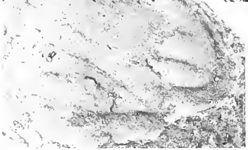
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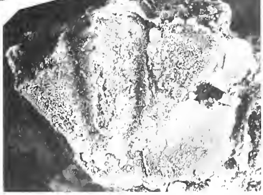
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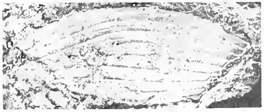
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PRICE, Sholeshook trilobites

Pygidium with long (sag.), narrow, gradually tapering axis and abaxially expanding, unfurrowed pleural ribs separated by strong furrows. At least seven axial rings are present and there is room for several more on the anteriorly damaged portion of the axis; there appear to be eight inter-pleural furrows. Although the ventral mould of the doublure is not completely exposed, a broad band of concentric terrace-lines is visible postero-laterally.

Discussion. The hypostoma is very similar to that of *O. jaanussoni* originally figured by Barrande (1852, pl. 31, fig. 6; pl. 32, fig. 6) from the Králův Dvůr Formation of Bohemia. That of *O. radiatus* Salter figured by Whittington (1966, pl. 24, fig. 6) from the Crugan Mudstone Formation of north Wales is similar in over-all form but differs in that the posterior notch is sub-angular anteriorly and not with a rounded anterior expansion as in the south Welsh and Bohemian forms.

Family ILLAENIDAE Hawle and Corda, 1847
Subfamily ILLAENINAE Hawle and Corda, 1847
Genus ILLAENUS Dalman, 1827
Subgenus PARILLAENUS Jaanusson, 1954

Type species. Illaenus fallax Holm, 1882.

Illaenus (*Parillaenus*) cf. *fallax* Holm, 1882

Plate 107, figs. 13–14; Plate 108, figs. 1–2

1885 *Illaenus Bowmanni*, Salt.; Marr & Roberts (*pars*), pp. 480–481.
1914 *Illaenus davisi* Salter; Strahan *et al.*, table p. 63.
1933 *Illaenus bowmanni* Salter; Reed (*pars*), pp. 124–125.
1973*a* *Illaenus* (*Parillaenus*) cf. *fallax* Holm; Price, tables 1–4.
1974 *Illaenus* (*Parillaenus*) cf. *fallax* Holm; Price, p. 844 (top).

Horizons and localities as in Table 1. Not known from Slade and Redhill Mudstone Formation.

Description. Entire exoskeleton sub-oval in outline (Pl. 108, fig. 1), almost $1\frac{3}{4}$ times as long (sag.) as wide (tr.); isopygous. Cephalon sub-semicircular in outline, moderately and evenly convex (sag., tr.). Axial furrows broad and shallow, extending forwards to about half cephalic length from posterior margin; rear sections sub-parallel with very slight abaxially convex curvatures, then, from about mid-level of palpebral lobes, furrows curve sigmoidally first adaxially and then outwards before dying out opposite anterior ends of palpebral lobes. Maximum width (tr.) between axial furrows about three-fifths of maximum width of cranidium; latter achieved on mid-level of palpebral lobes. Palpebral lobes long (exsag.) and crescentic, occupying about one-quarter of total cephalic length (sag.) and situated at about two-thirds of their own length (exsag.) from posterior margin. Posterior branches of facial sutures directed straight back from palpebral lobes; anterior branches curve at first gently outwards but then converge as they approach the anterior margin and become confluent on the ventral surface. Free cheeks thus sub-triangular in form, declined very steeply outwards, with rounded genal angles.

Thorax of ten segments, with shallow but broad and distinct axial furrows. Convex axis occupies over half total thoracic width anteriorly, remains sub-parallel over anterior-most five or six segments then tapers gradually back. Axial rings flat in lateral view. Pleurae simple; flat and horizontal adaxially, deflected postero-ventrally at fulcrum in gentle, posteriorly convex curves; abaxial extremities truncated antero-laterally; indistinctly separated articulating facets developed. Horizontal adaxial sections of pleurae become broader (tr.) posteriorly along the thorax (Pl. 108, fig. 1).

Pygidium about $1\frac{1}{4}$ times as broad (tr.) as long (sag.), convex transversely and in lateral profile rather flat over most of length but dropping steeply posteriorly. Axis anteriorly occupies about two-fifths of total width (tr.), is moderately convex, and bounded by shallow, ill-defined furrows which converge rapidly back. Anterior margins of pleural lobes transverse adaxially for length equivalent to about one-third of axial width then deflected gently back. Behind, shallow but broad and distinct furrows run obliquely back from anterior ends of axial furrows diverging at about 130°. Doublure of even width around margin and posteriorly occupying about one-quarter of total pygidial length (sag.); bearing rather widely spaced concentric terrace-lines.

Discussion. Holm's material of *I. fallax* awaits modern redescription, but to judge from his original figures the axial furrows appear to extend less far forward on the cranidium than in the south Welsh material. This difference also applies to cranidia figured by Ingham (1970, p. 19, pl. 2, figs. 10–20) from the high Caradoc and the Pusgillian and Cautleyan Stages at Cautley, and here there appear to be slight differences in cephalic proportions also—though much of the material from both south Wales and Cautley is distorted. In those pygidia figured by Holm which are most like the Sholeshook specimens (e.g. 1882, pl. 2, figs. 15, 18) the doublure appears to be narrower antero-laterally. *I.* (*P.*) *davisi* Salter, from the Rhiwlas Limestone of north Wales (see Whittington 1966, p. 67, pl. 20, figs. 16–23; pl. 21, figs. 1–4, 6–9) differs in having a pygidium which is strongly humped medially and has a much broader doublure.

Subfamily PANDERIINAE Bruton, 1968
Genus PANDERIA Volborth, 1863

Type species. Panderia triquetra Volborth, 1863.

Panderia edita Bruton, 1968?

Plate 108, figs. 3–8

1973*a* *Panderia* aff. *edita* Bruton; Price, pp. 233, 243, tables 1–4.

Horizons and localities. Apart from the Sholeshook Limestone occurrences shown in Table 1, the species ranges into the basal Slade and Redhill Mudstones at Prendergast (locality 8a) and is known also from the 'Bala Limestone' outcrop near Trefanty, 4 km south-east of St. Clears (Strahan, Cantrill, Dixon, and Thomas 1909, p. 56; Price 1973*a*, p. 243).

Description. Cephalon strongly convex (tr. and sag.); sub-semicircular in lateral profile (Pl. 108, fig. 5). Glabella about $1\frac{1}{4}$ times as long (sag.) as wide (tr.) with maximum width on mid-level of palpebral lobes. At this level also is a small median tubercle. Broad, shallow occipital furrow present only faintly mesially but deep occipital pits are developed where it meets the axial furrows. Latter deep and broad posteriorly where they outline small but distinct postero-lateral swellings of glabella (Pl. 108, fig. 4) then run forwards shallowing, at first straight and slightly divergent as viewed normally to the occipital region ('dorsally' *sensu* Bruton 1968) but opposite palpebral lobes are bowed outwards in distinctive geniculations and then deflected again abaxially to meet facial sutures just in front of palpebral lobes. Latter broad (tr.) and crescentic, occupying almost two-fifths of total glabellar length and situated at about two-thirds their own length from posterior margin. Short posterior branches of facial suture postero-mesially convex. Anterior branches converge for short distance and then gradually diverge and again converge in gentle curves to define an anterior glabellar area which is sub-rectangular with broadly rounded antero-lateral margins and attains a maximum width (tr.) of about nine-tenths the maximum glabellar width. Free cheeks in lateral view with broad concave embayments along antero-lateral margins—probably to accommodate edge of pygidium during enrolment (cf. Bruton 1968, p. 26, pl. 9, fig. 5). Eye lobes surrounded by prominent broad furrows.

Pygidium sub-semicircular in outline. Moderately convex, well-defined axis occupies one-third of total width anteriorly and tapers only gradually back reaching to two-thirds pygidial length, its posterior end rounded. Axial furrows broad and shallow. Anterior margins of pleural lobes transverse adaxially but about half-way out from axial furrows deflected gently posteriorly (Pl. 108, fig. 8). Broad, gently down-turned triangular facets are developed antero-laterally. Doublure narrow, occupying only 10–15% total pygidial length at posterior margin and narrowing antero-laterally.

Discussion. The south Welsh cranidia show much similarity with those of *P. edita* Bruton (1968, p. 25, pl. 9, figs. 3–8; pl. 10, figs. 1–3, 8) from the Boda Limestone (Harju Series) of the Siljan district, Sweden. While the anterior part of the glabella in the Welsh specimens is by no means as long (sag. and exsag.) as in one of the specimens figured by Bruton (pl. 10, fig. 2) it is of similar length to that of the holotype (Bruton 1968, pl. 9, fig. 7). The geniculation in the course of the axial furrows in the Welsh form, however, appears to be more prominent than in the Swedish material. No pygidium is known for *P. edita*. The form described by Dean (1977, p. 108, pl. 51, figs. 7, 8; pl. 52, figs. 1–14, 16, 17) from the Chair of Kildare Limestone as *P.* cf. *edita* differs from the south Welsh species in having anterior branches to the facial suture which converge in even curves and define a relatively shorter (sag.), frontally narrower (tr.) anterior glabellar area, in having free cheeks which are broadest further anteriorly and in having a pygidium with a relatively broader axis and much wider doublure. *P. megalophthalma* Linnarsson (Bruton 1968, p. 26, pl. 10, figs. 5, 6, 9; pl. 11, figs. 1, 5–10) differs in having a relatively shorter (sag.) and broader glabella lacking the postero-lateral swellings, in having broader (tr.) free cheeks, straighter posterior branches to the facial sutures and a much wider pygidial doublure. The north Welsh form *P. lewisi* (Salter), known only from the holotype (Bruton 1968, p. 28, pl. 10, fig. 7; pl. 11, figs. 2–4), also has proportionally broader (tr.) free cheeks than the south Welsh species. Examination of the holotype shows that in frontal view the anterior branches of the facial sutures converge evenly forwards and are not sinuous.

Family AULACOPLEURIDAE Angelin, 1854
Subfamily AULACOPLEURINAE Angelin, 1854
Genus HARPIDELLA McCoy, 1849
Subgenus HARPIDELLA McCoy, 1849

Type species. *Harpes*? *megalops* McCoy, 1846.

Remarks. For diagnosis of genus and subgenus, discussion, and renewed separation of *Harpidella* from genus *Otarion* see Thomas and Owens 1978, p. 71.

Harpidella (*Harpidella*) *lacrymosa* sp. nov.

Plate 108, figs. 10–14

1885 *Cyphaspis megalops*, M'Coy; Marr and Roberts, list p. 481.
1914 *Cyphaspis megalops* (McCoy); Strahan *et al*., table p. 63.
1973*a* *Otarion* aff. *tenuis* Kielan; Price, tables 1–4.

Holotype. SM A31471 (Pl. 108, fig. 10), incomplete internal mould of exoskeleton from Sholeshook Limestone of Sholeshook railway cutting.

Horizons and localities. See Table 1.

Diagnosis. Species of *Harpidella* (*Harpidella*) with elongate, pear-shaped medio-frontal glabellar lobe, drop-shaped basal lateral lobes, very small 2p lobes; large eye-lobes reaching almost to posterior border furrow; free cheeks with shallow lateral border furrows, broad convex borders, and concave lateral margins near bases of

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EXPLANATION OF PLATE 108

Figs. 1, 2. *Illaenus* (*Parillaenus*) cf. *fallax* Holm. SM A31500, internal mould of entire articulated specimen from the Sholeshook Limestone of Sholeshook, dorsal and right lateral views, × 1½.

Figs. 3–8. *Panderia edita* Bruton? 3, 4, HM A9572a, internal mould of incomplete cephalon from the 'Bala Limestone' of Trefanty, 4 km south-east of St. Clears, dorsal view as used herein and 'dorsal' view sensu Bruton 1968 (normal to occipital region), × 8. 5, 6, SM A31503, internal mould of cephalon from Sholeshook Limestone of Sholeshook railway cutting, left lateral and anterior views, × 6. 7, BM It9290, internal mould of pygidium from Sholeshook Limestone horizon at Robeston Wathen (locality 10a), dorsal view, × 4. 8, SM A99096, internal mould of pygidium from high Sholeshook Limestone (locality 8c) of Prendergast, dorsal view, × 6.

Fig. 9. *Amphitryon radians* (Barrande)? SM A77947, internal mould of small, incomplete cranidium from high Sholeshook Limestone of Prendergast (locality 8b or 8c), dorsal view, × 8.

Figs. 10–14. *Harpidella* (*Harpidella*) *lacrymosa* sp. nov. 10, SM A31471, HOLOTYPE, internal mould of incomplete articulated cephalon and thorax from Sholeshook Limestone of Sholeshook railway cutting, dorsal view, × 8. 11, 12, SM A77536, internal mould of incomplete cranidium, middle Sholeshook Limestone, locality 9e, Sholeshook, dorsal and left lateral views, × 8. 13, SM A77592b, cast from external mould of left free cheek, horizon and locality as for figs. 11, 12, dorsal view, × 8. 14, SM A31470, internal mould of incomplete articulated exoskeleton and SM A104833, external mould of incomplete cephalon, Sholeshook Limestone of Sholeshook railway cutting, A31470 in dorsal view, × 8.

Fig. 15. *Stenopareia bowmanni* (Salter). HM A10397, internal mould of right free cheek, middle Sholeshook Limestone, Lan-y-gaer (locality 16b), Llandowror, dorsal view, × 2.


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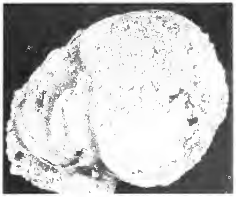
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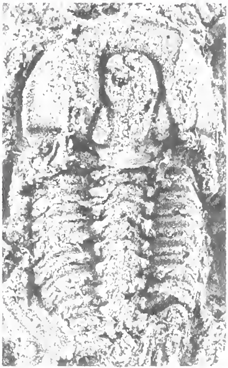
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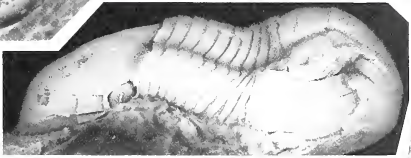
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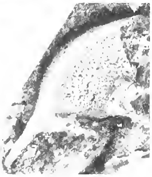
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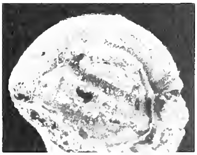
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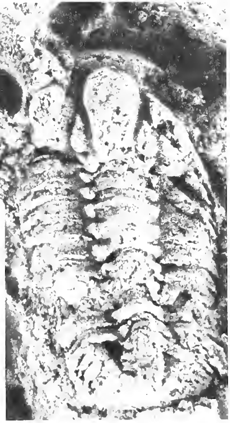
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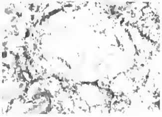
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PRICE, Sholeshook trilobites

short, slender genal spines; subdued cephalic ornament of fine granules, free cheeks in addition pitted, borders and genal spines smooth.

Description. Cephalon semicircular in outline and moderately convex (tr.). Glabella sub-parabolic, broadest (tr.) posteriorly where occupies about one-third of total cephalic width. Median and frontal lobes together form distinctive pear-shaped unit, strongly convex (tr.) and narrowest posteriorly. Anterior part of this unit defined by deep, broad axial furrows which anteriorly contain shallow antero-lateral pits and by the broad but shallower pre-glabellar furrow. Rear portion defined by posteriorly convergent 1p lateral glabellar furrows which are broad and deep and form continuations of the anterior parts of the axial furrows; they run back to the occipital furrow and isolate the basal lateral lobes from the median lobe of the glabella. Basal lateral lobes drop-shaped, strongly convex (tr.), occupying about one-third total glabellar length. Basal lobes defined abaxially by rear portions of axial furrows; these posteriorly divergent, narrower, and shallower than either anterior portions or 1p lateral furrows. 2p furrows never clearly seen but appear to be developed faintly on at least two specimens (SM A77950, not figured, and the holotype) just in front of anterior ends of 1p furrows and thus delimiting very small 2p lateral lobes. Occipital furrow broad and shallow; ring rather narrow (sag. and exsag.), mesially transverse and sub-parallel sided but abaxially narrowing and curving forwards towards axial furrows. Pre-glabellar field drops in steep, convex slope to broad, shallow anterior border furrow. Anterior border of about same width as furrow, moderately convex and sloping forward less steeply than pre-glabellar field (Pl. 108, fig. 12). Eye-lobes large, occupying almost one-third cephalic length; their mid-lengths occur slightly in front of the basal lateral lobes and they reach posteriorly almost to the posterior border furrow. Palpebral lobes also large but form not clearly seen. Anterior branches of facial sutures diverge at 40–50° until reaching anterior border where they are deflected adaxially and run obliquely across border leaving narrow, triangular anterior tongues to free cheeks (Pl. 108, fig. 13). Posterior branches curve out and gently back. Free cheeks drop steeply to shallow lateral border furrows and broad, convex borders and are extended postero-laterally as relatively short, slender genal spines which carry a faint median furrow. Outer margins of genal spines and lateral borders merge in abaxially concave curves. Transverse posterior border furrows broad and deep; borders narrow and strongly convex adaxially but much broader and more gently convex towards genal angles. Cephalic surface bears fine, rather subdued granulation; free cheeks in addition irregularly pitted; borders and genal spines smooth.

Thorax poorly preserved and number of segments uncertain, though at least ten. Strongly convex axis occupies just over one-third total width (tr.) anteriorly. Axial rings convex, separated by strong articulating furrows which abaxially deepen to apodemal slots separating prominent rounded axial lobes. Axial furrows broad but shallow. Inner portions of pleurae transverse and horizontal, then bent down and deflected posteriorly at fulcrum; divided roughly along median line by broad, shallow pleural furrows which gradually narrow outwards; distal extremities bluntly terminated. Pygidium only very poorly preserved; much broader (tr.) than long (sag.), posterior margin rounded and axis well defined anteriorly.

Discussion. H. (*H.*) *lacrymosa* sp. nov. is most similar to '*Otarion*' *tenue* Kielan (1960, p. 63, pl. 2, figs. 1–2; text-fig. 15) from the '*Staurocephalus clavifrons* Zone' of Poland but differs as follows: eye-lobes larger and set closer to posterior border furrows; genal spines slenderer, narrower-based, and not carrying continuations of lateral and posterior border furrows; lateral border wide and prominent, border furrow weak; anterior border furrow not wider than anterior border; cephalic ornament more subdued, comprising smaller and more closely spaced granules, borders and genal spines not ornamented; anterior thoracic pleurae not sharply pointed. Cranidia from the Irish Chair of Kildare Limestone figured by Dean (1974, p. 68, pl. 28, figs. 5, 8, 10, 12, 13; pl. 29, figs. 3, 5) as '*O*', cf. *tenue* differ from both Polish and Welsh specimens in having more divergent anterior branches to the facial sutures and in possessing broader (sag. and exsag.) anterior borders which are more strongly arched anteriorly. The Irish specimens are more coarsely ornamented than those from Wales.

Family PROETIDAE Salter, 1864
Genus PROETUS Steininger, 1831
Proetus (s.l.) cf. *berwynensis* (Whittington, 1966)

Plate 107, figs. 16–17

1909 *Proetus* cf. *brachypygus* Marr and Nicholson; Strahan *et al.*, table p. 58.
1973*a* *Astroproetus* aff. *berwynensis* Whittington; Price, pp. 233, 243.
1973 *Proetus* (s.l.) cf. *berwynensis* Whittington; Owens, p. 20, pl. 1, figs. 2–7.

Horizons and localities. Relatively abundant in the Sholeshook Limestone horizon at Robeston Wathen (locality 10a). Also occurs in the 'Bala Limestones' of Trewern Quarry 3 km north-west of Whitland (Strahan *et al.* 1914, p. 56) and Bron-haul about 2·5 km east-south-east of Llandowror (Strahan *et al.* 1909, p. 56).

Discussion. Owens (1973, see synonomy), who illustrated several specimens of this form, pointed out the close similarity to *P. berwynensis* (Whittington), a species known only from a single specimen (Whittington 1966, pl. 25, figs. 14–16; Owens 1973, pl. 1, fig. 1) from the Ashgill Dolhir Beds of Cynwyd, 3 km south-west of Corwen, Clwyd. This holotype of *P. berwynensis* has the genal angles poorly preserved and it is uncertain whether or not genal spines are developed as in the South Welsh specimens (Owens 1973, pl. 1, figs. 2, 5).

One of the specimens figured here, a cast from an incomplete external mould of the cranidium (Pl. 107, fig. 16) shows the short (sag. and exsag.) pre-glabellar field, a glabellar surface ornamentation of scattered granules of 0·075–0·1 mm and a prominent occipital tubercle. The other specimen is the internal mould of a pygidium (Pl. 107, fig. 17). The axis comprises, in addition to the half-ring, four axial rings and a short terminal piece; the doublure extends mesially almost to the tip of the axis.

Family TRINUCLEIDAE Hawle and Corda, 1847
Subfamily TRINUCLEINAE Hawle and Corda, 1847
Genus NANKINOLITHUS Lu, 1954

Type species. Nankinolithus nankinensis Lu, 1954.

Remarks. Ingham (1970, p. 44) in his discussion of genus *Tretaspis* McCoy referred to and briefly characterized a species-group typified by *T. granulata* (Wahlenberg) and *T. portrainensis* Lamont. Such forms have subsequently been removed from *Tretaspis* and placed in genus *Nankinolithus* Lu (Hughes *et al.*, 1975, pp. 558–559, see p. 558 for diagnosis).

Nankinolithus cf. *granulatus* (Wahlenberg, 1818)

Plate 109, figs. 1–10

1885 *Trinucleus seticornis*, var. *Bucklandi*, Barr.; Marr and Roberts, pp. 480, 481.
1914 *Trinucleus seticornis* (His.); Strahan *et al.* (*pars*), table p. 64, faunal lists p. 76.
1914 *Trinucleus seticornis* (His.), var. *bucklandi* Barr.; Strahan *et al.*, table p. 64.
1916 *Trinucleus seticornis* (His.). var. *bucklandi* Barr.; Cantrill *et al.*, faunal list p. 50.
1973*a* *Tretaspis* cf. *granulata* (Wahlenberg); Price, pp. 229, 234, 241, tables 1–3, 7.

Horizons and localities. Abundant in basal 2 or 3 m of Sholeshook Limestone at Sholeshook but rarer in low Sholeshook Limestone around Llandowror (locality 19); also abundant in basal Slade and Redhill Mudstones between Pelcomb and Clarbeston Road Station (localities 1–6).

Description. Cephalon almost as broad (tr.) as long. Occipital ring moderately arched transversely, longitudinally narrow, and not strongly convex, almost straight in dorsal view; furrow abaxially containing deep, ovoid apodemal slots. 1p apodemal slots converge anteriorly at about 110°. 2p furrows in form of large ovoid pits diverging anteriorly at 110–120°. 3p lateral furrows usually visible, even in internal moulds, as shallow ovoid pits near mid-length of pseudofrontal lobe. Anterior fossulae only developed as very shallow depressions, not always visible. Genal lobes moderately convex (tr. and exsag.), steeply declined antero-laterally but not overhanging fringe; not bearing lateral tubercles or eye-ridges. Both pseudofrontal glabellar lobe and genal lobes smooth. Posterior border furrows shallow, abaxially containing large posterior fossulae. Posterior border narrow and only weakly convex. Upper lamella of fringe anteriorly comprises steep, slightly concave genal roll merging into narrow horizontal brim; laterally drops outwards in smooth, gently concave curve. Genal prolongations reach almost as far back as posterior margin of pygidium (Pl. 109, fig. 2). Long slender genal spines produced beyond these (Pl. 109, fig. 10) have strong ventral ridges continuous with girder. Pits of E_2, E_1, and I_1 arcs radially in line. Frontally and antero-laterally on upper lamella exist as clearly separate pits (Pl. 109, fig. 8), but on genal prolongations E_1 and I_1 tend to be contained in short radial sulci (Pl. 109, fig. 10) and occasionally these may contain of E_2 also; E_1 and E_2 gradually merge posteriorly but usually remain present as separable pits in all but posterior-most two or three radii. On a few specimens the E arcs are most closely merged antero-laterally and become slightly more separated posteriorly (Pl. 109, fig. 10). Lower lamella has more distinct change of slope between genal roll and brim and a broad girder is present (Pl. 109, figs. 2, 6); E_1 and E_2 pits gradually merge posteriorly and are present beyond R12 or R13 as conjunct pit-pairs (Pl. 109, figs. 2, 5–6), though merging completely only in posterior-most two or three radii. Number of pits in E_1 (half-fringe) ranges from 28 (2 specimens), through 29 to 32 (1 specimen in each case). On all specimens the pits of the innermost two I arcs (I_n and that adjacent) are radially in line (Pl. 109, figs. 3, 4, 8) but pits of the arcs between these and I_1 are arranged very irregularly and difficult to count (see Pl. 109, fig. 6). Usually there are 4 I arcs frontally (I_{1-3}, I_n) and antero-laterally 5 or 6 (i.e. I_4 or I_4 and I_5 also present); at least 1 specimen (SM A77527 from Sholeshook) appears to have 7 I arcs (I_{1-6}, I_n) antero-laterally. The number of I arcs increases by intercalation on the genal prolongations until there are 13 (4 specimens), 14 (2 specimens), 15 (1 specimen), 16 (4 specimens), or 17 (3 specimens) pits in the posterior row. Two specimens differ from description so far given. One, a fringe fragment shown in Pl. 109, fig. 7 is unique in showing well-developed sulci containing pits of the E_2, E_1, and I_1 arcs. The other, the cephalon seen in Pl. 109, figs. 3, 4, is unique in that while two E arcs are developed frontally on the upper lamella only one E arc is present laterally from about R16.

Axis of thorax strongly convex, occupying one-fifth of total width anteriorly; rings broadest (sag. and exsag.) mesially where gently arched forward, narrow and curved forwards abaxially; dorsal surfaces flat in lateral profile. Axial furrows broad and prominent. Pleural lobes flat. Pleurae transverse and horizontal for most of length but deflected ventrally and slightly posteriorly at distal ends. Pleural furrows adaxially narrow, commence near inner anterior corners of pleurae and run slightly obliquely, broadening outwards and separating narrow anterior and broad, strongly convex posterior pleural bands.

Pygidium about 2½ times as wide as long, with convex postero-lateral margins. Gently convex axis, anterior occupies one-quarter of total width and tapers back at 35°. Mesially broad articulating furrows become elongated apodemal pits abaxially; eight such pairs of pits developed. Flat pleural regions crossed by five broad (exsag.), abaxially expanding pleural bands increasingly faintly defined posteriorly. Anterior-most bands carry narrow, faint pleural furrows and are separated by broad interpleural furrows. Strong sub-marginal rim. Slightly bevelled posterior margin carries faint, irregular terrace-lines.

Discussion. Material, including the holotype, of '*Tretaspis*' *granulata* described by Kielan (1960, p. 171, pl. 32, figs. 1–3; pl. 34, figs. 1, 2; pl. 35, figs. 1, 2; pl. 36, fig. 6; text-fig. 49) from the upper Ordovician of Poland, Sweden, and Bohemia differs mainly in the presence (both frontally and laterally on the fringe upper lamella) of well-developed sulci containing the E_2, E_1, and I_1 pits.

EXPLANATION OF PLATE 109

Figs. 1–10. *Nankinolithus* cf. *granulatus* (Wahlenberg). 1, 2, SM A31606b, a, cast from external mould and internal mould of articulated exoskeleton from low horizon in Slade and Redhill Mudstones near Pelcomb Cross (locality 2), dorsal views, × 3. 3, 4, GSM TCC. 1736, internal mould of large, well-preserved cephalon from low(?) horizon in Slade and Redhill Mudstones, quarry south of Marlsborough, 7 km west-north-west of Haverfordwest, left-lateral and dorsal views, × 3. 5, 6, SM A77526, internal mould of incomplete cephalon from basal Sholeshook Limestone, south end of Sholeshook railway cutting, dorsal and anterior views, × 3. 7, SM A77675a, fragment of upper lamella of fringe with E_2, E_1, and I_1 pits in well-developed sulci, basal Slade and Redhill Mudstones south-west of Knock (locality 3), oblique view, × 4. 8, SM A31616, slightly distorted internal mould of cephalon, horizon, and locality as for figs. 5, 6, anterior view, × 4. 9, GSM TCC. 1178, cast from external mould of pygidium, horizon, and locality as figs. 5, 6, dorsal view, × 3. 10, SM A77700, left genal area and prolongation of fringe upper lamella and genal spine, basal Slade and Redhill Mudstones of Withy Hedge (locality 5), oblique view, × 3.

Figs. 11, 12. *Dionide* sp. indet. 11, SM A31619, internal mould of partial cephalon, horizon, and locality as for figs. 1, 2, dorsal view, × 6. 12, SM A77534, internal mould of incomplete cephalon from middle Sholeshook Limestone, locality 9e, Sholeshook.

Fig. 13. *Lonchodomas* aff. *pennatus* (La Touche). SM A77629, cast from incomplete external mould of cranidium, horizon, and locality as for fig. 7, dorsal view, × 10.

Figs. 14–16. *Raphiophorus* cf. *tenellus* (Barrande). 14, 15, BM It8101b, a, external mould showing base of frontal spine and internal mould of cranidium, horizon, and locality as for fig. 12, dorsal views, × 10. BM It8091a, internal mould of small incomplete articulated exoskeleton, same horizon and locality, dorsal view, × 10.


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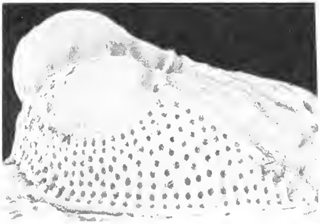
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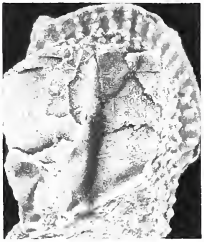
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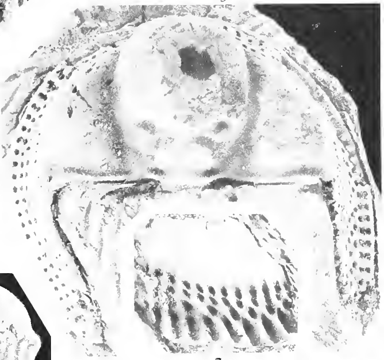
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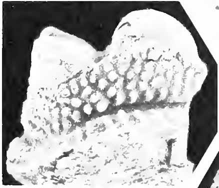
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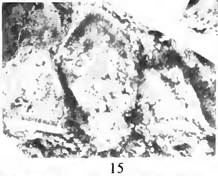
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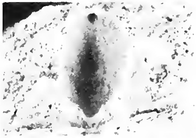
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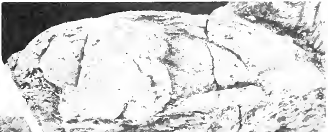
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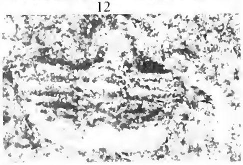
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PRICE, Sholeshook trilobites

Although the species is described as having two E arcs present anteriorly and only one developed laterally (Kielan 1960, p. 172), several of the illustrated specimens show separate E_1 and E_2 arcs present in all but the posterior-most two or three radii of the fringe as in the south Welsh material. The south Welsh specimens appear to have similar numbers of pit arcs frontally on the fringe but rather more in the posterior row (cf. Kielan's fig. 49). Kielan does not give figures for the number of E_1 pits in the half-fringe but, to judge from the illustrations and a few Polish specimens in the collections of the British Museum (Natural History), the number ranges from around twenty-seven to around thirty-one.

Family DIONIDIDAE Gürich, 1907
Genus DIONIDE Barrande, 1847

Type species. Dionide formosa Barrande, 1846.

Dionide sp. indet.

Plate 109, figs. 11, 12

1885 *Illaenus* (young); Marr and Roberts, faunal list p. 481.
1973*a* *Dionide* sp. indet.; Price, tables 1, 2.

Material. Two internal moulds of incomplete cephala; SM A31619 from basal Slade and Redhill Mudstones near Pelcomb Cross (locality 2) and SM A77534 from middle Sholeshook Limestone, locality 9e, Sholeshook.

Description. Cephalon much wider (tr.) than long (sag.). Glabella sub-quadrate, narrowest (tr.) across occipital ring and narrowing again just in front of mid-length; moderately convex (tr.). Occipital ring narrow and convex (sag. and exsag.), occipital furrow narrow; both gently arched forward. Deep 1p lateral glabellar furrows run forward from occipital furrow diverging slightly and reaching to about one-quarter of total glabellar length. Genal lobes sub-quadrant shaped, apparently pitted (Pl. 109, fig. 11), and one specimen (Pl. 109, fig. 12) shows traces of what appear to be genal caecae. This same specimen also clearly shows the inner margin of the fringe and a ventral mould of the lower lamella with tuberculation reflecting the fringe pitting. Posterior border broad and strongly convex (sag. and exsag.).

Discussion. The incompleteness of these specimens does not permit very useful comparison with other dionidid species. It may be noted, however, that the narrowing (tr.) of the glabellar around its mid-length is an unusual feature though it may be seen also in specimens of *D. richardsoni* Reed from the upper Whitehouse Beds of Girvan (Reed 1903, pl. 4, fig. 3). Ingham (1974, p. 64) has noted that specimens of Reed's species from the upper Whitehouse Beds and those from the upper Drummuck Group represent distinct forms.

Family RAPHIOPHORIDAE Angelin, 1854
Genus RAPHIOPHORUS Angelin, 1854

Type species. Raphiophorus setirostris Angelin, 1854.

Raphiophorus cf. *tenellus* (Barrande, 1872)

Plate 109, figs. 14–16

1885 *Ampyx tumidus* Forbes; Marr and Roberts (*pars*), lower list p. 481.
1973*a* *Raphiophorus* sp. indet.; Price, tables 1, 2.

Material. Internal and external moulds of small articulated exoskeleton (Pl. 109, fig. 16) and of cranidium (Pl. 109, figs. 14, 15) both from locality 9e, Sholeshook, and two internal moulds of cranidia (SM A31384–5) from the basal Slade and Redhill Mudstones of Pelcomb Cross (locality 2). A partial cranidial external mould (SM A99477) from the basal Slade and Redhill Mudstones south-west of Knock (locality 3) probably also belongs here.

Description. Ovoid glabella strongly convex transversely, moderately so longitudinally; anteriorly bluntly pointed and projecting well beyond fixed cheeks, posteriorly contracts (tr.) rapidly between broad triangular depressions confluent with axial and occipital furrows. Latter furrow narrow, shallow mesially. Sub-triangular fixed cheeks strongly declined antero-laterally. Posterior border furrows strong, set slightly oblique, deepening abaxially; borders broad and prominent. Occipital ring narrow (sag. and exsag.), gently arched dorsally. Cranidial external moulds show position of circular-sectioned frontal spine, also apparent lack of surface ornamentation. The articulated Sholeshook specimen appears foreshortened due to folding between the thoracic segments and the absence of the anterior part of the glabella but shows the course of the genal spine and the relatively large pygidium with its broad border.

Discussion. The South Welsh specimens are most like *R. tenellus* from the Ashgill of Sweden, Poland, and Bohemia (Kielan 1960, p. 165, pl. 35, fig. 6; Whittington 1968, p. 94, text-fig. 6). *R. tenellus* is like *R. setirostris* in general form but the type species appears to have a relatively shorter (sag.) and wider glabella projecting less far beyond the fixed cheeks and with a shorter constricted posterior section. *R. acus* (Troedsson) from the Ashgill of Poland (Kielan 1960, p. 168, pl. 32, fig. 4; pl. 35, fig. 7) and the high Rawtheyan of the southern Lake District (McNamara 1979*b*, table 2) has a glabella which projects less far forward than in either *R. tenellus* or *R. setirostris* and which is broadly rounded anteriorly; it also has relatively longer (exsag.) and narrower fixed cheeks which are strongly convex antero-laterally and a smaller pygidium.

Genus LONCHODOMAS Angelin, 1854

Type species. Ampyx rostratus Sars, 1835.

Lonchodomas aff. *pennatus* (La Touche, 1884)

Plate 109, fig. 13; Plate 110, figs. 1–3

1885 *Ampyx tumidus* Forbes; Marr and Roberts (*pars*), higher list p. 481.
1914 *Ampyx tumidus* Forbes; Strahan *et al.*, table p. 63.
1973*a* *Lonchodomas tumidus* (Forbes); Price (*pars*), tables 1–3, 7.

Horizons and localities. Apart from occurrences shown in Table 1, also abundant in basal Slade and Redhill Mudstones to north and west of Haverfordwest (localities 2, 3, 5).

Description. Cranidium broadly triangular with sagittal length (excluding frontal spine) about four-fifths the maximum width. Glabella about twice as long (sag.) as wide (tr.) with maximum width just in front of mid-length; strongly convex (tr.), standing high above fixigenae, frequently carinated; produced anteriorly into long, slender frontal spine (Pl. 110, fig. 1) which is sub-square in cross-section. Broad, shallow axial furrows separated by one-fifth of cranidial width posteriorly, diverging forwards at about 40°, containing deep, slot-like fossulae anteriorly. Fixigenae about as long (exsag.) as posteriorly wide (tr.); only gently convex. Occipital furrow continuous with posterior border furrows, both broad and shallow, latter contain small, deep, round pits abaxially. Occipital ring very narrow (sag. and exsag.), gently arched posteriorly, continuous laterally with very narrow but convex posterior borders. External moulds show cranidial surface covered with small pits of about 0·03 mm diameter (Pl. 109, fig. 13).

Pygidium more than twice as wide (tr.) as long (sag.) and broadly rounded posteriorly. Axis moderately convex (tr.) and raised above pleural lobes, occupies one-third total width anteriorly and tapers back at 30°. On internal moulds only articulating furrow on axis are clearly visible but there are faint indications behind of several paired pits. A pydium with some of the exoskeleton preserved (SM A77766) shows eight pairs of raised muscle scars on the axis. Axial furrows shallow and indistinct. Pleural lobes only gently convex, with steeply declined wide borders; only one pair of pleural furrows is clearly visible though there appear to be faint traces of two or three pairs of ribs behind.

Discussion. The South Welsh cranidia are similar in outline and proportions to cranidia of the high Caradoc–low Ashgill form *L. pennatus* (see Dean 1960, pl. 11, figs. 2, 5, 8–12; 1962, pl. 6, figs. 1, 3–5, 9, 12) but differ in the pitting of the cranidial surface and the much shallower posterior border furrows. In these features they are like cranidia of the form described by Ingham (1974, p. 65, pl. 11, figs. 6–14) as *L.* aff. *pennatus* from Zones 1 and 2 (and possibly 4) of the Cautley Mudstones. None of the south

Welsh pygidia, however, show clearly the development of the two or more pleural furrows seen in the Cautley form. Ingham noted the similarity between the Cautley form he described and a specimen, probably from the Dolhir Beds near Corwen, referred by Whittington (1968, pl. 30, figs. 13, 15, 18–20) to *L. tumidus* (Forbes). As in the south Welsh specimens, the pygidium of this form shows only one clear pair of pleural furrows.

Lonchodomas cf. *drummuckensis* (Reed, 1903)

Plate 110, figs. 4–6

1914 *Ampyx drummuckensis* Reed; Strahan *et al.*, table p. 63.
1973*a* *Lonchodomas tumidus* (Forbes); Price (*pars*), tables 1–3.
?1974 *Lonchodomas* aff. *portlocki* (Barrande); Ingham, pp. 65–66, pl. 12, figs. 1–13.

Material. Articulated pygidium and incomplete thorax, three pygidia and one small, incomplete cranidium, all from either the top 4 m of the Sholeshook Limestone or the base of the overlying Slade and Redhill Mudstones (localities topmost 8d to basal 8a) at Prendergast Place. A few distorted or incomplete larger cranidia from the same localities probably belong here too (e.g. SM A31158), and an incomplete cranidium (HM A9656) from the basal Slade and Redhill Mudstones of Clog-y-fran (locality 15) near Llandowror.

Description. Most complete and undistorted cranidium very small (Pl. 110, fig. 6); broadly triangular with sagittal length just over four-fifths maximum width. Glabella, excluding frontal spine, over twice as long (sag.) as wide (tr.) with maximum width at about two-fifths its length from posterior margin; only moderately convex (tr.), slightly carinate anteriorly. Axial furrows shallow and indistinct, diverging forwards at about 50°, with

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EXPLANATION OF PLATE 110

Figs. 1–3. *Lonchodomas* aff. *pennatus* (La Touche). 1, SM A77701, internal mould of partial cranidium showing form of frontal spine, basal Slade and Redhill Mudstones of Withy Hedge (locality 5), dorsal view, × 2. 2, SM A77632, poorly preserved internal mould of pygidium from same locality, dorsal view, × 6. 3, SM A77684a, internal mould of incomplete cranidium from basal Slade and Redhill Mudstones south-west of Knock (locality 3), dorsal view, × 8.

Figs. 4–6. *Lonchodomas* cf. *drummuckensis* (Reed). 4, SM A104835a, internal mould of pygidium and incomplete thorax from basal Slade and Redhill Mudstones of Prendergast (locality 8a), dorsal view, × 2. 5, BM It9249, distorted internal mould of pygidium from highest Sholeshook Limestone of Prendergast (locality 8b), dorsal view, × 3. 6, BM It9247, internal mould of small partial cranidium from the high Sholeshook Limestone (topmost locality 8d) of Prendergast, dorsal view, × 10.

Figs. 7, 8. *Ceraurinella intermedia* (Kielan). 7, SM A31585, internal mould of incomplete pygidium from the Sholeshook Limestone of Sholeshook railway cutting, dorsal view, × 3. 8, BM It9216, internal mould of slightly distorted incomplete cranidium, horizon, and locality as for fig. 4, dorsal view, × 3.

Figs. 9–11. *Pseudosphaerexochus tectus* Ingham. 9, SM A77875, cast from external mould of pygidium from the high Sholeshook Limestone, locality 9g, Sholeshook, dorsal view, × 5. 10, 11, SM A31586, internal mould of cranidium from Sholeshook Limestone of Sholeshook, right lateral view, × 3, and dorsal view, × 2.

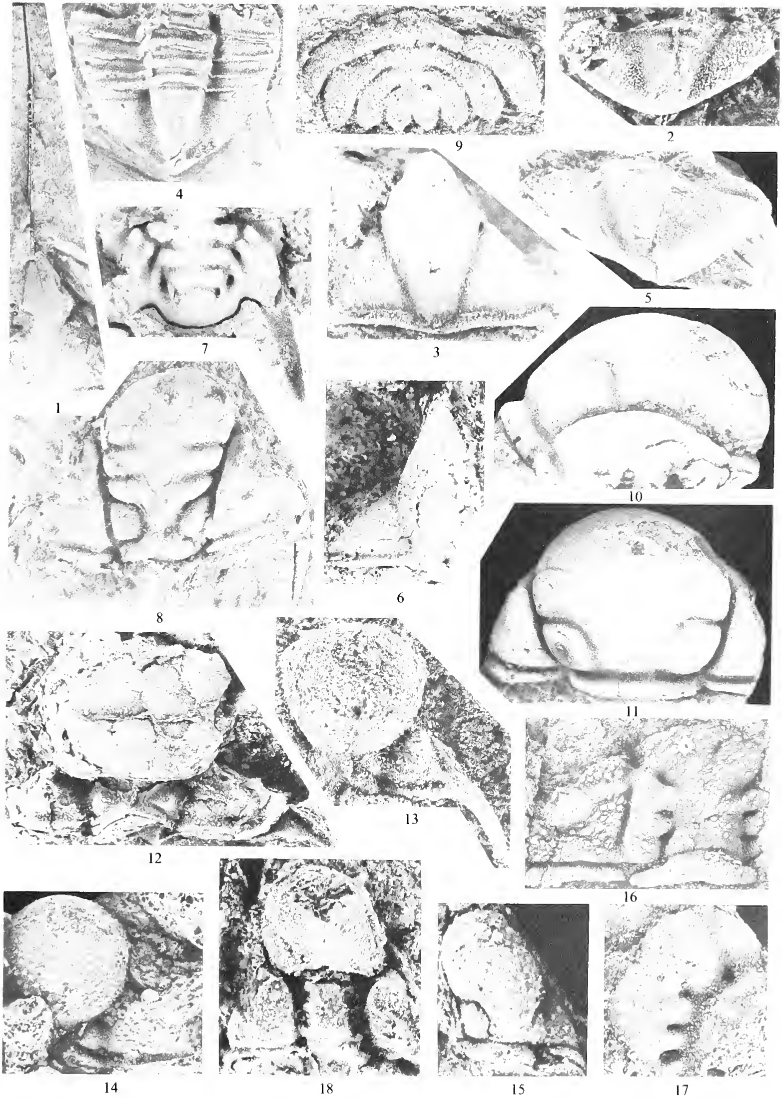
Figs. 12–14. *Sphaerocoryphe* aff. *thomsoni* Reed. 12, HM A9733, internal mould of flattened, incomplete cranidium from the low Sholeshook Limestone, track south of Craig-y-deilo quarry, Llandowror (locality 18d), dorsal view, × 4. 13, BM In54702, cast from external mould of partial cranidium from Sholeshook Limestone of Craig-y-deilo quarry, Llandowror, dorsal view, × 4. 14, BM It9245, cast from external mould of partial cranidium from middle Sholeshook Limestone, locality 9e, Sholeshook, dorsal view, × 4.

Fig. 15. *Pseudosphaerexochus juvenis* (Salter). SM A77887b, cast from external mould of small cranidium from middle Sholeshook Limestone, locality 9e, Sholeshook, dorsal view, × 10.

Fig. 16. *Cybeloides* (*Paracybeloides*) *girvanensis* (Reed). SM A77531, cast from external mould of incomplete cranidium from the Sholeshook Limestone of Sholeshook railway cutting, dorsal view, × 4.

Fig. 17. *Atractopyge scabra* Dean? SM A77971, partial internal mould of cranidium from $9\frac{1}{2}$–10 m above base of Sholeshook Limestone in Mylet road section (locality 24a), Llandowror, dorsal view, × 3.

Fig. 18. *Staurocephalus* cf. *clavifrons* Angelin. HM A9751, internal mould of cranidium, horizon, and locality as for fig. 12, dorsal view, × 6.



PRICE, Sholeshook trilobites

small, slot-like fossulae anteriorly. Fixed cheeks about three-quarters as long (exsag.) as wide (tr.) and gently convex dorsally, though dropping steeply antero-laterally. Posterior border furrows shallow and indistinct adaxially but on internal moulds deepen and widen outwards into broad slots. Occipital furrow shallow and indistinct; ring continuous with posterior borders, gently arched posteriorly. Posterior borders convex (exsag.) and distinct, about as broad as posterior border furrows.

Other much larger cranidia fragmentary or distorted but agree in showing shallow axial furrows, strongly developed posterior borders, and border furrows which are indistinct adaxially but well developed laterally; some show the free anterior part of the glabella to be sub-circular in section.

Thorax known from posterior four segments (Pl. 110, fig. 4). Axis occupies about one-third total width; rings flat (sag. and exsag.) dorsally, ring furrows shallow mesially and laterally but deepened between into paired slots. Axial furrows broad and deep. Pleural furrow on anterior-most segment (second) continuous and transverse but on those behind runs obliquely out and forwards from position about one-third pleural width from axial furrow. Pygidium just less than twice as wide (tr.) as long (sag.) and bluntly pointed posteriorly. Axis occupying just less than one-third total width anteriorly and tapering back at 30°; behind the articulating furrow internal moulds show a series of six (Pl. 110, fig. 4) or seven (Pl. 110, fig. 5) pairs of elongated (tr.) pits. Axial furrows broad and distinct. Pleural lobes with gently convex and steeply declined postero-lateral margins. Single pair of pleural furrows, shallow adaxially but distinct for outer two-thirds of length and curving forwards towards antero-lateral corners of pleural lobes.

Discussion. The South Welsh pygidia closely resemble those of the Rawtheyan form from Cautley described by Ingham (1974) as *L.* aff. *portlocki* (Barrande) and also those of *L. drummuckensis* (Reed 1903, p. 18, pl. 3, figs. 1-5) from the late Rawtheyan upper Drummuck Group of Girvan. The Polish and Bohemian Ashgill species *L. portlocki* (see Kielan 1960, pl. 33, fig. 8; pl. 35, fig. 4) has a pygidium which is relatively much shorter (sag.). The specimens figured by Kielan are small but even on a much larger Polish specimen in the Sedgwick Museum (A44183) the pygidium is three times as wide as long and posteriorly broadly rounded. The small Sholeshook cranidium strikingly resembles a small one figured by Ingham (1974, pl. 12, fig. 5) as *L.* aff. *portlocki* but differs from his larger cranidia. These are said to differ from cranidia of *L. drummuckensis* in having a relatively shorter, less inflated, and less well-defined glabella. The lack of large south Welsh cranidia makes similar comparisons difficult. From the small Sholeshook cranidium alone the glabella does appear to be similar to that of *L. drummuckensis* to judge from specimens of the latter in the Sedgwick Museum (e.g. A10918, A11103, A52598), though these differ slightly from the South Welsh form in possessing narrower (exsag.) posterior borders.

Family CHEIRURIDAE Hawle and Corda, 1847
Subfamily ECCOPTOCHILINAE Lane, 1971
Genus PSEUDOSPHAEREXOCHUS Schmidt, 1881

Type species. *Sphaerexochus hemicranium* Kutorga, 1854.

Pseudosphaerexochus juvenis (Salter, 1848)

Plate 110, fig. 15; Plate 111, figs. 8-11

1974 *Pseudosphaerexochus* (*Pseudosphaerexochus*) *juvenis* (Salter); Price, pp. 849-850, pl. 113, figs. 5-9. Includes full synonomy.
?1974 *Pseudosphaerexochus conformis* (Angelin); Ingham, pp. 70-71, pl. 14, figs. 6-12.

Lectotype. Subsequently designated Whittington 1965, p. 40; GSM 24534, internal mould of cranidium from Sholeshook Limestone of Sholeshook; figured Whittington 1965, pl. 12, figs. 2, 4, 8.

Horizons and localities. See Table 1.

Description. The lectotype and other GSM specimens used by Whittington (1965, see synonomy) in his redescription of *P. juvenis* are all indifferently preserved and most are distorted. Better-preserved topotype cranidia described here, give a much improved idea of the characters of this form. Cranidium about $1\frac{1}{4}$

times as wide (tr.) as long (sag.). Glabella occupies three-fifths total cranidial width; ovoid in outline with parabolic anterior margin; pre-occipital length about four-fifths maximum width, latter on level of 2p lateral lobes; strongly convex (tr. and sag.), in lateral profile greatest convexity is over anterior half, frontal lobe dropping steeply forward (Pl. 111, fig. 10). Basal lateral lobes in dorsal view are obliquely elongated ovoids, each occupying one-fifth of maximum glabellar width (tr.) and separated posteriorly by about $1\frac{1}{2}$ times this width. Basal lateral furrows broad and deep abaxially, gently curved, dying out before reaching occipital furrow. Exsaggital length of 2p lateral lobes about two-thirds that of basal lobes, 3p lobes slightly shorter. 2p and 3p furrows shallower and narrower than 1p and short (tr.) in dorsal view. Occipital furrow broad and deep, ring broad and convex (sag. and exsag.), both arched posteriorly in dorsal view. Axial furrows deep and slot-like, confluent with broad anterior border furrow, containing small round pits just in front of 3p furrows. Convex (tr.) fixed cheeks with concave antero-lateral margins in dorsal view, genal angles broadly rounded, no genal spine seen. Posterior border furrows broad and deep adaxially, shallowing outwards, borders narrow and convex adaxially, broadening and flattening outwards. Palpebral lobes of similar length (exsag.) to 2p lateral glabellar lobes, situated slightly behind them, running obliquely out and back, gently convex antero-laterally; palpebral furrows broad and distinct. Posterior branches of facial sutures meet lateral borders in rounded curves. External surface of glabella covered with scattered large granules or small tubercles (Pl. 111, fig. 11) which are more prominent in small specimens (Pl. 110, fig. 15). On internal moulds the glabella is sometimes finely granulated. Fixigenal surface strongly pitted, pits usually visible on internal moulds.

Librigenae, thorax, and hypostoma unknown. Pygidium known only from incomplete specimens of which the best have been figured previously (Whittington 1968, pl. 31, fig. 17; Price 1974, pl. 113, fig. 9).

Discussion. The ovoid glabella with its frontally parabolic outline, its more gently curved basal furrows and relatively narrower basal lobes, and its ornament of scattered large granules clearly differs from that of *P. tectus* Ingham also common in the Sholeshook Limestone (see Pl. 110, figs. 10, 11). In cranidial characters. *P. juvenis* is more like *P. octolobatus* (McCoy) (see Lane 1971, pl. 8) but that form has a glabella which is relatively broader posteriorly, with a shorter (sag. and exsag.), more broadly rounded frontal lobe and less strongly convex anteriorly in lateral profile; also the palpebral lobes are shorter and placed further forward and the ornament includes fine as well as scattered coarse granules.

Cranidia from the Chair of Kildare and Kiesley Limestones figured by Dean (1971, pl. 9, figs. 3, 4, 8; pl. 10, figs. 1–3, 6, 8, 10–12; pl. 11, figs. 4–8, 11, 12) as *P. conformis* Angelin bear prominent genal spines. The glabella of these forms is more broadly rounded frontally than that of *P. juvenis* and more evenly convex in lateral profile with a shorter and less steeply inclined frontal lobe and more prominent surface tubercles. In cranidia from the Chair of Kildare Limestone (e.g. pl. 9, fig. 4) the 3p lateral glabellar lobes are longer than the 2p. Pygidia figured by Ingham (1974, pl. 14, figs. 8–10) as *P. conformis* from Zones 2 and 3 of the Cautley Mudstones are strikingly similar to those from the Sholeshook Limestone here referred to *P. juvenis* (cf. Price 1974, pl. 113, fig. 9), even to the surface perforations. They are not, even the smallest of them, like the small pygidium figured by Dean (1971, pl. 10, figs. 4, 5) from the Chair of Kildare Limestone in which the pleural regions are extremely narrow and the spines longer, slenderer, and directed more strongly posteriorly. The fragmentary and distorted cranidia from Cautley (Ingham 1974, pl. 14, figs. 6, 7, 11, 12) do not allow close comparison with other forms.

Subfamily DEIPHONINAE Raymond, 1913

Genus SPHAEROCORYPHE Angelin, 1854

Type species. Sphaerocoryphe dentata Angelin, 1854.

Sphaerocoryphe aff. *thomsoni* Reed, 1906

Plate 110, figs. 12–14

1973*a* *Sphaerocoryphe* cf. *thompsoni* Reed; Price, tables 1–3.

Material, horizons, and localities. HM A9733, internal mould of flattened, incomplete cranidium, low Sholeshook Limestone, track south of Craig-y-deilo quarry, Llandowror (locality 18d); BM In54702, external mould of partial cranidium, Sholeshook Limestone, Craig-y-deilo quarry; SM A31590, internal mould of partial cranidium, Sholeshook railway cutting; BM It9245, external mould of partial cranidium, locality 9e, Sholeshook.

Description. Anterior part of glabella sub-spherical, twice as wide (tr.) as central lobe behind and separated by broad, mesially shallow furrow deepening laterally to pair of apodemal pits. Low posterior part of glabella short (sag. and exsag.), broader (tr.) than long (sag.), only moderately convex (tr.). Basal lateral glabellar lobes sub-triangular, small but distinct, strongly convex (exsag.). Occipital furrow shallow and gently arched forward mesially, abaxially deepens to pair of apodemal pits. Occipital ring moderately broad (sag. and exsag.), arched forward mesially and abaxially curving forwards around apodemal pits. Axial furrows broad, posteriorly sub-parallel, containing occipital and 1p apodemal pits but shallow opposite 1p lateral lobes. Sub-triangular fixed cheeks strongly convex, apically bearing pedunculate palpebral lobes; dropping steeply to broad, deep posterior border furrows; posterior borders broad (exsag.) and convex. Broad, convex lateral borders separated from inner parts of cheeks by prominent furrows; bear two short, broad-based pro-fixigenal spines (pl. 110, fig. 12) of which posterior is larger. Lateral and posterior borders produced into long, stout, gradually tapering fixigenal spines. Inflated part of glabella with ornamentation of prominent tubercles and much smaller granules densely scattered between (Pl. 110, fig. 14); tubercles large (0·2–0·25 mm) and widely spaced apically, smaller and more densely packed marginally. Convex surface of cheeks pitted, though not strongly.

Discussion. Lane (1971, p. 64, pl. 13, figs. 1–4, 6–8, 10–18; pl. 15, fig. 9) selected a lectotype from amongst Reed's material and redescribed this and other specimens of *S. thomsoni* from the Starfish Bed of Girvan. The cranidia of that species are similar in over-all form and proportions to those described above and the only major difference appears to be the much coarser glabellar tuberculation in the south Welsh specimens. *S. kingi* Ingham (1974, pp. 71–74, pl. 14, figs. 13–17; text-fig. 22) from the Rawtheyan Stage of the Cautley Mudstones also has a more subdued glabellar ornamentation than the Sholeshook specimens and the fixed cheeks are relatively much broader (tr.). *S. punctata* (Angelin 1854, p. 77, pl. 39, fig. 6; Warburg 1925, pp. 390, 421; pl. 10, figs. 43–49) from the Boda Limestone of Sweden is in need of redescription. A cranidium from the Chair of Kildare Limestone of eastern Ireland referred to this species by Dean (1971, p. 33, pl. 16, figs. 1, 4, 7, 10) has a coarse glabellar tuberculation like the south Welsh form but the inflated anterior glabellar region appears to be proportionally smaller and the fixed cheeks are much more strongly pitted.

Family ENCRINURIDAE Angelin, 1854
Subfamily CYBELINAE Holliday, 1942
Genus ATRACTOPYGE Hawle and Corda, 1847

Type species. Calymene ?verrucosa Dalman, 1827.

Atractopyge aff. *scabra* Dean, 1962

Plate 111, figs. 1–4

1848 *Cybele sexcostata*, Salter, p. 343, pl. 8, figs. 9, 9*a*, 9*b*, *non* 10.
1853 *C.* (*Calym.*) *verrucosa*, Dalman; Salter, Articla 4, p. 4.
1866 *Cybele verrucosa*, Dalm.; Salter, p. 324, pl. 19, fig. 7.
1885 *Cybele verrucosa*, Dalm.; Marr and Roberts, pp. 480, 481.
1909 *Cybele verrucosa* (Dalm.); Strahan *et al.*, table p. 58.
1914 *Cybele verrucosa* (Dalm.); Strahan *et al.*, table p. 63.
1973 *Atractopyge scabra* Dean; Price (*pars*), tables 1–3, list p. 233.
?1974 *Atractopyge* sp.; Ingham, p. 82, pl. 17, figs. 1–6.

Horizons and localities. As in Table 1; not known from Slade and Redhill Mudstones other than at Prendergast (locality 8a).

Description. Clavate glabella strongly convex (tr.); maximum width across frontal lobe less than pre-occipital length. Occipital ring broad and strongly convex (sag. and exsag.), mesially arched forward; abaxially broadened to form forward-curving occipital lobes. Occipital furrow broad and shallow mesially, abaxially dropping to deep, circular pits. Basal lateral lobes sub-triangular, anterior margins set strongly oblique. 1p furrows are deep apodemal slots with triangular outlines and tendency to bifurcate adaxially. 2p and 3p lobes of approximately equal length (exsag.) adaxially, set slightly oblique; 2p lobe narrows outwards, 3p sub-parallel sided. 2p furrows deep, ovoid apodemal pits oblique in same manner as 2p and 3p lobes. 3p slots oblique, posteriorly divergent, broadening (exsag.) inwards and continued adaxially as short, shallow bifurcating branches. Median lobe narrowest on level of 1p lateral furrows, widening only very gently forwards. Glabella expands rapidly in front of 3p lobes to maximum width three times that at 1p furrows. Frontal lobe drops anteriorly in steep, convex slope. Anterior border furrow narrow but distinct, transverse mesially; distally is deflected postero-laterally and broadens; thus has form of three shortest sides of trapezium. Frontal glabellar lobe and anterior border can also have similar outline (Pl. 111, fig. 4) but usually appear more rounded. Axial furrows deep and broad; containing deep circular pits near ends of anterior border furrow. Fixed cheeks much wider (tr.) than long (exsag.), strongly convex (exsag.), dropping steeply to axial furrows; surmounted by palpebral lobes which form parts of long, slender eye-stalks. These opposite 2p furrows and posterior halves of 3p lobes, separated from axial furrows by distance equal to width of median lobe at that level. Eye-ridges run inwards and forwards to positions opposite 3p furrows. Behind these ridges are furrows which are narrow adaxially but expand outwards to form, around the bases of the palpebral lobes, prominent depressed areas granulated and pitted but devoid of the coarse tubercles seen on the rest of the cheek surface. Posterior border furrows broad, deep slots adaxially, borders strongly convex over transverse inner halves then broaden as curve out and back. Free cheeks quadrant-shaped; convex inner portions surmounted by narrow eye-stalks and separated from broad, convex borders by strong furrows; borders produced into narrow anterior 'tongues' whose ends are deflected ventrally. Cranidial surface ornamented with small, closely spaced granules (0·04–0·07 mm); in addition there are numerous much larger (up to 0·75 mm), scattered, apically perforated tubercles, themselves granulated and absent only from the major furrows. On mesial section of anterior border large tubercles form two alternating rows. Many of tubercles on glabella developed in relatively constant symmetrical pattern. Surfaces of fixed cheeks irregularly pitted.

Hypostoma and rostral plate unknown; rostral suture runs along straight margin of mesial section of anterior border, connective sutures along adaxial margins of extreme inner ends of anterior 'tongues' of free cheeks.

Pygidium slightly longer (sag.) than broad (tr.). Axis moderately convex (tr.), tapers posteriorly at 20°; up to twenty rings in well-preserved material. Only first four rings continuous across axis, fifth and subsequent ring furrows fail to reach axial furrows. Posteriorly ring furrows also become increasingly shallower mesially though usually continuous as far back as eighth or ninth after which axis smooth mesially, ring furrows existing as paired apodemal slots. Sharply pointed, convex (tr.) terminal piece merges anteriorly with smooth lateral borders of axis. Four pleural ribs continuous with first four axial rings. First pair curve abaxially to mid-length of pygidium, then gently adaxially, those behind increasingly curved until fourth pair lie sub-parallel to axial furrows. Ribs separated by narrow, depressed anterior pleural bands, terminate in short, free, blunt points arranged *en echelon* with tips of second pair lying level with axial tip.

Discussion. The form described here is closely similar in over-all form to specimens of *A. scabra* Dean recently described by Ingham (1974, p. 79, pl. 16, figs. 2–14; text-fig. 24) from the Pusgillian and low Cautleyan Stages of the Cautley Mudstones but differs in a few features. In *A. scabra* the 2p lateral glabellar lobes are noticeably shorter (exsag.) than the 3p. In Sholeshook material this does appear to be the case in a few cranidia from the basal 14 or 15 m of the formation around Llandowror and the basal 2 or 3 m of Sholeshook railway cutting, and these forms have been herein tentatively referred to *A. scabra* (see Pl. 110, fig. 17). In all other specimens the 2p and 3p lobes are of sub-equal length, the 2p in some cases being slightly longer. The glabellar tuberculation in the south Welsh form differs from that of *A. scabra* in that the paired tubercles are relatively less prominent, the others larger and more numerous. On the pygidium the axial ring furrows appear to be mesially continuous further posteriorly than in *A. scabra* and the pointed ends of the pleurae do not reach so far posteriorly; only the third and fourth spines project beyond the axial tip, the first pair terminate well in front.

The Sholeshook cranidia are more like those referred by Ingham (1974) to *Atractopyge* sp. from Cautleyan Zone 4, though here the 3p lateral glabellar lobes are implied to be consistently shorter than the 2p. The second and third lateral glabellar lobes are approximately the same length in the holotype cranidium of *A. verrucosa* (see Dean 1974, text-fig. 4) but the specimen is much larger than the Sholeshook specimens and the glabella appears to have a relatively much wider (tr.) median lobe and consequently a less clavate outline. *A. verrucosa* is known only from the holotype and topotype specimens are needed before the species can be closely compared with other forms. The form from the

Birdshill Limestone termed *A.* cf. *verrucosa* by Dean (1974, p. 97; 1971, pls. 14, 15) has a less clavate, less convex (tr.) glabella than the Sholeshook form and on the pygidium the pleural spines appear to extend much further posteriorly (Dean 1971, pl. 14, figs. 8, 9).

Subfamily DINDYMENINAE Přibyl, 1953
Genus DINDYMENE Hawle and Corda, 1847

Type species. Dindymene fidericiaugusti Hawle and Corda, 1847.

Dindymene longicaudata Kielan, 1960

Plate 112, figs. 2–5

1973*a* *Dindymene longicaudata* Kielan; Price, tables 1, 2, 7.
1973*b* *Dindymene longicaudata* Kielan; Price, p. 538.

Holotype. Figured Kielan 1960, pl. 30, fig. 2; IG No. 2. II. 108, almost complete exoskeleton from *Staurocephalus clavifrons* Zone of Brzezinki, Poland.

Material. BM In54166a, b, internal and external moulds of distorted cranidium; In54161, 54164, GSM H.T. 913, internal moulds of incomplete pygidia, all from the basal Slade and Redhill Mudstones of Rudbaxton (locality 4); SM A77566a, b, internal and external moulds of pygidium from Sholeshook Limestone, locality 9e, Sholeshook.

Description. Cranidium in dorsal view broader (tr.) than long (sag.); strongly convex (tr. and sag.). Occipital ring broad and convex (sag. and exsag.), abaxially curving forwards around deep pits at ends of broad, shallow occipital furrow. Posterior borders adaxially strongly convex (exsag.), outwards gradually narrowing to genal angles but there broaden considerably and curve forwards; border furrows deep and slot-like adaxially. Axial furrows deep and broad posteriorly where converge forwards slightly. Within them a second apodemal pit, forward of the occipital pit, represents 1p lateral furrow. Short 1p lobe developed on median lobe between two

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EXPLANATION OF PLATE 111

Figs. 1–4. *Atractopyge* aff. *scabra* Dean. 1, GSM 24546, internal mould of incomplete cranidium from Sholeshook Limestone of Sholeshook, dorsal view, ×2. 2, SM A31458, cast from external mould of incomplete pygidium, Sholeshook Limestone of Sholeshook, dorsal view, ×3. 3, SM A53005b, cast from external mould of cranidium from the high Sholeshook Limestone, locality 9h, Sholeshook, dorsal view, ×3. 4, GSM 24543, cast from external mould of cranidium from Sholeshook Limestone of Sholeshook, dorsal view, ×3; together with counterpart internal mould GSM 24545, original of Salter 1848, pl. 8, fig. 9, 9*b*.

Fig. 5. *Cybeloides* (*Paracybeloides*) *girvanensis* (Reed). BM It9251, cast from external mould of incomplete pygidium from high Sholeshook Limestone of Prendergast (locality 8c), dorsal view, ×6.

Figs. 6, 7. *Prionocheilus* cf. *obtusus* (McCoy). 6, SM A104837, distorted internal mould of cranidium from basal Sholeshook Limestone of Moldin (locality 25), near Llandowror, dorsal view, ×4. 7, SM A77943, internal mould of incomplete cranidium from high Sholeshook Limestone, locality 9h, Sholeshook, right lateral view, ×4; see also Pl. 110, fig. 1.

Figs. 8–11. *Pseudosphaerexochus juvenis* (Salter). 8, SM A31417, internal mould of cranidium from Sholeshook Limestone of Sholeshook railway cutting, dorsal view, ×2. 9, 10, SM A31432, internal mould of incomplete cranidium from the high Sholeshook Limestone of Prendergast, dorsal and right lateral views, ×2. 11, SM A77570, part of cast from external mould of partial cranidium from the high Sholeshook Limestone, locality 9b, Sholeshook, oblique view to show surface ornament, ×5.

Figs. 12–14. *Calymene* (s.l.) cf. *prolata* Ingham. 12, HM A9767, internal mould of incomplete cranidium from the low Sholeshook Limestone (locality 18b) of Craig-y-deilo quarry, Llandowror, dorsal view, ×2. 13, 14, GSM TJ. 843, internal mould of incomplete cranidium from about 24 m above the base of the Slade and Redhill Mudstones at Robeston Wathen (locality 10c), dorsal and left lateral views, ×3.


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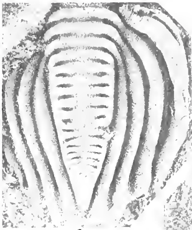
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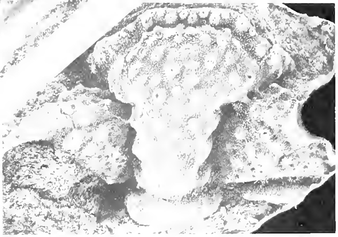
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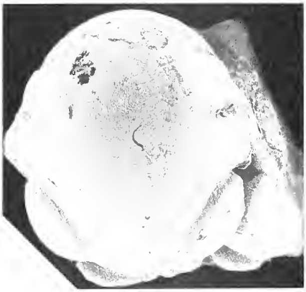
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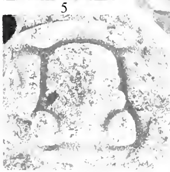
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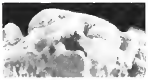
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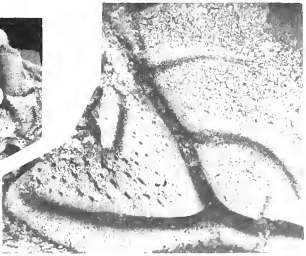
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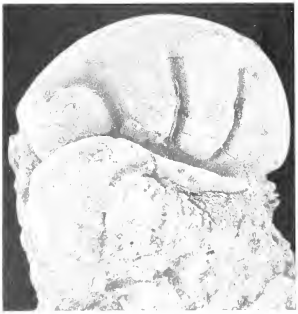
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PRICE, Sholeshook trilobites

pits. Axial furrows narrow anteriorly as diverge round strongly convex (tr.) frontal lobe. Quadrant-shaped fixed cheeks strongly convex, dropping steeply to posterior parts of axial furrows and posterior border furrows and more gently anteriorly and laterally to broad, shallow border furrow. Base of right genal spine just visible on available cranidium curving gently anteriorly. Cast from external mould (Pl. 6, fig. 4) shows genal surfaces closely pitted and bearing scattered granules, glabella with even pattern of well-spaced small granules and scattered larger ones. Apically glabella bears prominent stout spine.

Triangular pygidial axis comprises eleven rings, first strongly convex (sag. and exsag.), those behind gradually less so. Ring furrows deepest towards abaxial ends, leaving, behind second ring, shallow mesial portions of about one-third axial width and narrow lateral borders; becoming fainter posteriorly so that rings behind fourth not clearly separated in mesial region. Three pairs of pleural ribs. First two continuous with first two axial rings then deflected posteriorly in smooth curves, separated from each other and from axis by strong furrows. Third segments pressed close to sides of axis, separated from it posteriorly by two short, shallow furrows meeting in acute-angled 'v'. Pleurae terminate as stout, free spines; tips of inner two form straight line transverse to axis, first terminate in front of this.

Discussion. The over-all similarity of the cranidium and the very close similarity of the pygidium to those of *D. longicaudata* described by Kielan (1960, p. 153, pl. 26, fig. 5; pl. 28, fig. 5; pl. 29, fig. 4; pl. 30, figs. 1–3; text-fig. 43) from the Ashgill Series of Poland, Bornholm, Scania, and Västergötland, leave little doubt as to the specific identity. As Kielan shows in her table 6 (opposite p. 148), the pygidia of known species of *Dindymene* are quite distinctive. Also distinctive of *D. longicaudata* are the stout glabellar spine and the forwardly directed genal spines.

EXPLANATION OF PLATE 112

Fig. 1. *Prionocheilus* cf. *obtusus* (McCoy), SM A77943, internal mould of incomplete cranidium from high Sholeshook Limestone, locality 9h, Sholeshook, dorsal view, × 4; see also Pl. 109, fig. 7.

Figs. 2–5. *Dindymene longicaudata* Kielan. 2–4, BM In54166a, b, internal mould of distorted cranidium from basal Slade and Redhill Mudstones of Rudbaxton quarry (locality 4) in left lateral and dorsal views and cast from partial external mould in left lateral view, all × 6. 5, SM A77566b, cast from external mould of pygidium from middle Sholeshook Limestone, locality 9e, Sholeshook, dorsal view, × 6.

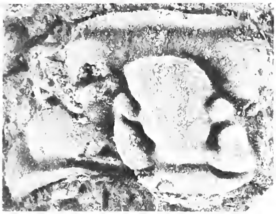
Figs. 6–8. *Brongniartella* cf. *marocana* Destombes. 6, SM A31174, internal mould of distorted, incomplete cephalon from Slade and Redhill Mudstones of Redhill quarry (locality 7), dorsal view, $\times \frac{3}{4}$. 7, SM A104836, internal mould of cranidium showing traces of lateral glabellar furrows, same horizon and locality, dorsal view, × 1. 8, SM A31172, internal mould of pygidium and partial thorax, same horizon and locality, dorsal view, × 1.

Figs. 9–11. *Duftonia geniculata* Ingham? 9, GSM Pg. 134, cast from external mould of articulated thorax and pygidium from the high Sholeshook Limestone of Prendergast (locality 8b or 8c), dorsal view, × 3. 10, BM In54163b, cast from external mould of small, incomplete cranidium from basal Slade and Redhill Mudstones south-west of Knock (locality 3), dorsal view, × 8. 11, BM In54162b, cast from external mould of small, almost complete cranidium, same horizon and locality, dorsal view, × 8.

Figs. 12, 13. *Liocnemis recurvus* (Linnarsson). 12, SM A77634, internal mould of incomplete cranidium from basal Slade and Redhill Mudstones south-west of Knock (locality 3), dorsal view, × 8. 13, BM In54224a, internal mould of distorted incomplete cranidium from same horizon and locality, dorsal view, × 6.

Figs. 14, 15. *Calyptaulax planiformis* Dean. 14, SM A77518, internal mould of incomplete cranidium from the middle Sholeshook Limestone, locality 9e, Sholeshook, dorsal view, × 3. 15, GSM JM. 454, internal mould of incomplete pygidium from about 30 m above base of Slade and Redhill Mudstones at Cilrath Fawr, 3 km east-north-east of Robeston Wathen, dorsal view, × 4.

Figs. 16, 17. *Toxochasmops marri* (Reed), NMW.21.306.G.20a, internal mould of incomplete cranidium from the Sholeshook Limestone of Craig-y-deilo quarry, Llandowror, antero-dorsal oblique view and dorsal view, $\times 1\frac{1}{2}$.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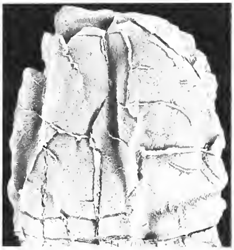
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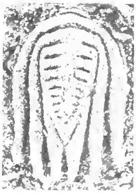
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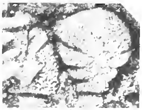
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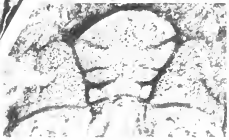
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13

PRICE, Sholeshook trilobites

Family STAUROCEPHALIDAE Prantl and Přibyl, 1948
Genus STAUROCEPHALUS Barrande, 1846

Type species. Staurocephalus murchisoni Barrande, 1846.

Staurocephalus cf. *clavifrons* Angelin, 1854

Plate 110, fig. 18

1885 *Staurocephalus globiceps*, Portl.; Marr and Roberts, p. 481.
1973*a* *Staurocephalus clavifrons* Angelin; Price, tables 1–3, 7, p. 245.

Material, horizons, and localities. Not common but appears to range through Sholeshook Limestone Formation (see Table 1). Known also from basal Slade and Redhill Mudstones near Pelcomb Cross (locality 2) but not from elsewhere in that formation. Total of fifteen cranidia; thorax, pygidium, free-cheek, hypostoma, and rostral plate not yet known.

Description. Median lobe of glabella tapers slightly forwards bounded by very broad, deep axial furrows and indented laterally by large, shallow pits representing 1p and 2p lateral furrows of which 2p are distinctly larger. Pits representing 3p furrows small, shallow, and indistinct, situated near ends of broad, smooth furrow separating hemispherical frontal glabellar lobe from median lobe. Lateral glabellar lobes of sub-equal exsagittal length adaxially; basal lobes longer transversely, expanding (exsag.) slightly abaxially. Behind are small, deep, round apodemal pits at ends of occipital furrow; furrow straight and shallow mesially. Occipital ring mesially broad (sag. and exsag.), narrowing and curving forwards distally. Fixed cheeks strongly convex, standing higher than median lobe and dropping to axial furrows in steep, convex slopes; apically bearing prominent palpebral lobes surrounded by shallow furrows, their mid-lengths on the level of the 2p lateral lobes. Posterior border furrows narrow. Posterior borders narrow and strongly convex adaxially but broadening considerably towards genal angle. Cranidial surface tuberculated but no external moulds are available to show form of ornamentation in detail.

Discussion. On the basis of the cranidium alone the South Welsh form cannot be distinguished either from the holotype cranidium of *S. clavifrons* (Angelin 1854, pl. 24, fig. 8; Kielan 1957, pl. 4, fig. 1) or from other material referred to the species by Kielan (1957, p. 163) or subsequently by Whittington (1965, p. 53) or Dean (1971, p. 40). Following Ingham's remarks (1977, p. 89) on differences between the Polish specimens included in the species by Kielan and specimens from the Cystoid Limestone of the Cautley area and on the occurrence of a further potentially distinguishable form from the Swindale Limestone of Cross Fell (Ingham's pl. 19, figs. 8–10), it appears that *S. clavifrons* as previously recognized may be capable of further subdivision. The south Welsh form is therefore only compared with Angelin's species.

Family CALYMENIDAE Milne Edwards, 1840
Subfamily CALYMENINAE Milne Edwards, 1840
Genus CALYMENE Brongniart, 1822

Type species. Calymene blumenbachii Brongniart, 1822.

Calymene (s.l.) cf. *prolata* Ingham, 1977

Plate 111, figs. 12–14

1914 *Calymene blumenbachi* Brongn., var. *caractaci* Salter; Strahan *et al.* (*pars*), list p. 67.
1914 *Calymene* sp.; Strahan *et al.* (*pars*), table p. 70.
1973*a* *Diacalymene* cf. *marginata* Shirley; Price, p. 234.

Material, horizons, and localities. Three internal moulds of incomplete cranidia, GSM J.M. 396, GSM T.J. 483, and HM A9767, respectively from about 18 m above the base of the Slade and Redhill Mudstones at Cilrath-fawr, 2·25 km north-north-east of Narberth, about 24 m above the base of the same formation at Robeston Wathen (locality 10c), and from a low horizon in the Sholeshook Limestone of Craig-y-deilo quarry, Llandowror (locality 18b).

Discussion. The available cranidia show a bell-shaped glabella with very prominent, convex (tr. and exsag.) 1p lateral lobes, relatively large, rounded and convex 2p lobes with genal buttresses opposite and small 3p lobes. The frontal lobe occupies just less than one-third the pre-occipital glabellar length, is twice to 2½ times as wide as long, broadly rounded frontally, and extends well beyond the fixed cheeks which are angulated antero-mesially. The pre-glabellar area is strongly upturned, unridged and roll-like in cross-section, longer (exsag.) opposite the axial furrows, and separated from the frontal lobe by a deep, slot-like furrow. These characteristics are shared with *C. prolata* Ingham (1977, pp. 102–103, pl. 22, figs. 11–17) from Zone 3 of the Cautley Mudstones of northern England but the south Welsh specimens appear to differ slightly from the illustrated cranidia of *C. prolata* in possessing basal lateral lobes which are more quadrate in outline and in having rather less obviously bifurcating 1p lateral furrows.

Subfamily FLEXICALYMENINAE Siveter, 1977

Genus FLEXICALYMENE Shirley, 1936

Type species. *Calymene blumenbachii* var. *caractaci* Salter, 1865.

Flexicalymene cavei Price, 1974

1973*a* *Flexicalymene* sp. nov.; Price, tables 1–4.
1974 *Flexicalymene cavei* Price, pp. 852–856, pl. 114, figs. 1–15.

Holotype. Figured Price 1974, pl. 114, figs. 1, 2; SM A57050, internal mould of cranidium from the basal Sholeshook Limestone of Moldin (locality 25), near Llandowror.

Horizons and localities as in Table 1. Not known from Slade and Redhill Mudstones other than where ranges up from underlying Sholeshook Limestone at localities 8a and 15.

Discussion. The form has been fully described elsewhere (Price 1974). Siveter (1977, p. 355) has referred to the similarity between *F. cavei* and *F. declinata* (Hawle and Corda 1847) from the Králův Dvůr Formation of Bohemia. This similarity is not apparent from Barrande's figures (1852, pl. 43, figs. 53–58) but Dr. Siveter has kindly supplied the author with photographs of Bohemian specimens of *F. declinata*, including the lectotype (selected Marek *in* Horný and Bastl 1970, p. 114). Though these show that the two forms are closely related, there do appear to be differences. The glabella of the Bohemian form is relatively rather broader (tr.) and shorter (sag.), with the frontal lobe, in particular, shorter (sag. and exsag.) and less broadly rounded anteriorly. The 3p lateral glabellar lobes appear longer (tr.) and separated from the frontal lobe by more strongly developed 3p furrows, and the 1p lateral furrows curve adaxially at their inner ends to give the median lobe a distinctive, postero-laterally convex outline not seen in South Welsh specimens. In addition, to judge from Barrande's figures (1852, pl. 43, figs. 57, 58), the hypostoma may lack the prominent maculae seen on that of *F. cavei* (Price 1974, pl. 114, fig. 8).

Subfamily PHAROSTOMATINAE Hupé, 1953

Genus PRIONOCHEILUS Rouault, 1847

Type species. *Prionocheilus verneuili* Rouault, 1847.

Remarks. Both Siveter (1977, pp. 339, 393) and Ingham (1977, p. 103) have recently reviewed the difficulties surrounding the choice between *Pharostoma* Hawle and Corda and its senior synonym *Prionocheilus*. The balance of recent usage appears to be in favour of *Prionocheilus*.

Prionocheilus cf. *obtusus* (McCoy, 1846)

Plate 111, figs. 6–7; Plate 112, fig. 1

1973*a* *Pharostoma* cf. *obtusum* (M'Coy); Price, tables 1–4.

Material, horizons, and localities. Ten partial or incomplete cranidia from the following horizons and localities: the basal Sholeshook Limestone at Moldin (locality 25) and in the Mylet road section (24a); the low Sholeshook Limestone of Craig-y-deilo quarry (18c); the railway cutting, locality 9e and locality 9h at Sholeshook; the Sholeshook Limestone at Lan-y-gaer (16b); and the highest Sholeshook Limestone at Prendergast (locality 8b).

Discussion. Cranidia from the Sholeshook Limestone are similar in over-all form and proportions and in most details of morphology to the holotype of *P. obtusus* (McCoy) redescribed by Whittington (1965, pp. 55–56, pl. 16, figs. 1–3, 6) from the Chair of Kildare Limestone and refigured, together with topotype cranidia by Dean (1971, pl. 18, figs. 6, 8, 10, 12, 13, 15). They appear to differ, however, in that the basal lateral glabellar lobes in several Sholeshook specimens are distinctly sub-quadrate in outline (e.g. Pl. 112, fig. 1) and in that small 3p lateral glabellar lobes are clearly visible in most Sholeshook specimens. In the outline of the 1p lateral glabellar lobes the South Welsh specimens resemble *P. cautleyensis* Ingham (1977, pp. 104–105, pl. 22, figs. 19–23) from the Cautleyan Stage of the Cautley Mudstones, but that form has relatively much wider (tr.) 1p lateral lobes, a narrower (tr.) frontal glabellar lobe, more strongly developed subsidiary lobes between the 1p and 2p lateral lobes, and a mesially very short (sag. and exsag.) pre-glabellar field. The pre-glabellar field in the Sholeshook specimens appears to be of similar length and convexity to that of *P. obtusus.*

Family HOMALONOTIDAE Chapman, 1890
Genus BRONGNIARTELLA Reed, 1918

Type species. Homalonotus bisulcatus McCoy, 1851.

Brongniartella cf. *marocana* Destombes, 1966

Plate 112, figs. 6–8

1885 *Homalonotus*?; Marr and Roberts, p. 480.
1885 *Homalonotus bisulcatus*, Salt.; Marr and Roberts, p. 482.
1914 *Homalonotus rudis*? Salt.; Strahan *et al.*, table p. 74.
1973*a* *Brongniartella* sp.; Price, pp. 229–230, 242, tables 1, 2.

Material, horizons, and localities. One partial pygidium from the highest Sholeshook Limestone of Prendergast (locality 8b); 1 pygidium from the basal Slade and Redhill Mudstones of Prendergast (8a); 1 partial pygidium, 2 pygidia with partial thoraxes, 2 incomplete cranidia, and 1 incomplete cephalon all from the Slade and Redhill Mudstones of Redhill quarry (locality 7); all internal moulds. ?Other fragmental material from localities 7, 8a, b, c, and 9d.

Description. Cephalon sub-semicircular. Weakly convex glabella trapezoid in outline, its lateral margins gently convex posteriorly and concave near the mid-length; width (tr.) just in front of occipital furrow slightly less than pre-occipital length and twice width at anterior margin. One specimen (Pl. 112, fig. 7) faintly shows lateral glabellar furrows; 1p furrows commence abaxially at one-third pre-occipital glabellar length and curve inwards for about one-quarter of glabellar width at that level, 2p furrows commence abaxially at half pre-occipital length and curve sigmoidally inwards and back, 3p furrows very faint. Occipital furrow narrow but distinct, sinuous, curved forward mesially and abaxially. Occipital ring occupies one-seventh glabellar length (sag.). Axial furrows shallow, very broad posteriorly but narrow forwards. Anterior border furrow broad and shallow, anterior border only weakly convex (sag. and exsag.). Gently convex (tr.) anterior portions of fixed cheeks each about half anterior width of glabella. Short (exsag.) palpebral lobes on level of cranidial mid-length. Posterior border furrows broad and shallow, borders flat (exsag.), broader (exsag.) than occipital ring. Free cheeks with indistinct borders and border furrows.

Thoracic axis occupies over one-third total width, defined by shallow axial furrows; rings separated from half-rings by broad, strong, articulating furrows. Pleurae bear deeply incised, curved pleural furrows. Pygidium sub-parabolic, moderately convex (tr.). Axis anteriorly occupying less than one-third total width, defined by broad, deep axial furrows and tapering gradually to a well-defined, bluntly rounded distal end which almost(?) reaches posterior margin. Axis composed of nine broad, flat axial rings and narrow articulating half-ring. Pleurae show seven abaxially broadening ribs and outwardly and backwardly curving inter-rib furrows which do not reach lateral margins.

Discussion. B. marocana Destombes (1966, p. 34, pl. 1, figs. 1–8) from the Upper Ktaoua Formation of the Moroccan Anti-Atlas is closely similar to the south Welsh form in glabellar shape and agrees in showing faint lateral glabellar furrows and in the posteriorly broad axial furrows and the position of the palpebral lobes. The pygidium is similar in over-all form but the axial furrows, ring furrows, and pleural furrows are weaker than in the south Welsh material and the axis is less well developed posteriorly. In this latter respect the South Welsh pygidia are closer to those of the form from Zone 5 of the Rawtheyan Stage of the Cautley Mudstones referred with question by Ingham (1977, p. 109, pl. 24, figs. 1–4) to *B. robusta* (Lesperance) in which the axial tip is slightly swollen. Neither that species, however, nor the type material of *B. robusta* (Lesperance 1968, p. 822, pl. 106, figs. 8–13) from the 'Upper Ashgill' part of the Whitehead Formation of Percé, Quebec, show any sign of glabellar furrows and both forms are said to have only eight rings on the pygidial axis. In *B. platynotus* (Dalman) from the late Ashgill of Poland, Sweden, and Czechoslovakia (Kielan 1960, p. 116, pl. 19, figs. 1–3) the glabella narrows more sharply anteriorly than in the south Welsh form and the eyes are much further forward. As Ingham has noted (1977, p. 110), *B. marocana* is more closely related to forms such as *B. sedgwicki* (Salter) and *B. robusta* than it is to *B. platynotus*.

Family DALMANITIDAE Vogdes, 1890
Subfamily DALMANITINAE Destombes, 1972
Genus DUFTONIA Dean, 1959

Type species. Duftonia lacunosa Dean, 1959.

Duftonia geniculata Ingham, 1977?

Plate 112, figs. 9–11

1973*a* *Duftonia* cf. *lacunosa* Dean; Price, tables 2, 7.
?1977 *Duftonia geniculata* Ingham, p. 114, pl. 26, figs. 12–19; text-fig. 28*b*.

Holotype. Figured Ingham 1977, pl. 26, figs. 12, 13; HM A5540a, b, internal and external moulds of damaged cranidium from the mid-Rawtheyan Swindale Limestone of Cross Fell.

Material, horizons, and localities. BM In54162a, b, 54163a, b, internal and external moulds of incomplete cranidia, In54164, internal mould of pygidium, all from basal Slade and Redhill Mudstones near Pelcomb, 4 km north-west of Haverfordwest (locality 3); GSM Pg. 133, 134, internal and external moulds of articulated thorax and pygidium and Pg. 123, internal mould of pygidium, from the high Sholeshook Limestone of Prendergast (locality 8b or 8c).

Description. Two available cranidia small and poorly preserved. Both show a rather weakly developed geniculation in the course of the 3p lateral glabellar furrows. Outer margins of 3p lateral lobes not independently convex and postero-laterally do not project further into axial furrows than antero-lateral corners of 2p lobes. Palpebral lobes relatively short (exsag.), extend back to level opposite anterior parts of 2p lateral lobes. Preservation too poor to show glabellar ornamentation. Thorax of eleven segments, tapering gradually posteriorly. Axis strongly convex, occupies over one-third total width (tr.) anteriorly. On cast of external mould (Pl. 112, fig. 9) axial rings sub-rectangular in dorsal outline, arched forward mesially and again curving gently forwards and slightly broadening (exsag.) abaxially. Articulating furrows broad and shallow mesially but drop abaxially into deep apodemal slots. On internal moulds these slots separate prominent, rounded axial lobes. Axial furrows narrow and rather weak. Pleurae flat-lying over inner portions but strongly deflected ventrally at fulcrum; divided by strong pleural furrows into broad posterior and narrow anterior convex pleural bands; becoming much flatter towards broad, rounded abaxial extremities. Thoracic surface appears to be finely granulated. Pygidial axis with four well-defined rings anteriorly and indications of two more behind. Axial furrows die out at less than two-thirds pygidial length from anterior margin. Pleurae crossed by three broad pleural ribs divided by strong pleural furrows and defined by broad interpleural furrows which extend further laterally, though neither set reaches the lateral margins.

Discussion. The small size and poor preservation of the south Welsh cranidia preclude complete comparison, but in all their visible features they appear close to those of *D. geniculata* as described by

Ingham (1977) from the mid-Rawtheyan Swindale Limestone of Cross Fell and from Zones 5 and 6 of the Cautley Mudstones, as do the south Welsh pygidia. No thorax is known for *D. geniculata*.

Family PTERYGOMETOPIDAE Reed, 1905*b*
Subfamily PTERYGOMETOPINAE Reed, 1905*b*
Genus LIOCNEMIS Kielan, 1960

Type species. Phacops recurvus Linnarsson, 1869.

Liocnemis recurvus (Linnarsson, 1869)

Plate 112, figs. 12, 13; Plate 113, fig. 16

1869 *Phacops recurvus* Linnarsson; p. 59, pl. 1, figs. 1, 2.
1885 *Phacops Brongniarti*, Portl.; Marr and Roberts (*pars*), p. 481 (lowest two faunal lists).
1960 *Liocnemis recurvus* (Linnarsson); Kielan, pp. 121–123, pl. 9, figs. 11, 12; pl. 21, figs. 8–11; pl. 22, figs. 1, 2; text-fig. 32.
1973*a* *Liocnemis* cf. *recurvus* (Linnarsson); Price, table 7.

Type specimens. The original specimens figured by Linnarsson (1869) have not been located (see Kielan 1960, p. 123).

Material, horizons, and localities. BM In54220a, b, 54224a, b, internal and external moulds of distorted, incomplete cranidia; SM A31543, 31544, 31546, 77634, 77935, internal moulds of incomplete cranidia, mostly distorted, and SM A77627, internal mould of pygidium; all from the basal Slade and Redhill Mudstones near Pelcomb (localities 2, 3) 4 km north-west of Haverfordwest. SM A31545, the fragmentary external mould of a cranidium from the same horizon at Clarbeston Road Station (locality 6b) may also belong here.

Discussion. Kielan (1960) has provided a full description of this species which does not require repetition. Distortion of the south Welsh cranidia makes it difficult to establish the exact proportional length of the frontal glabellar lobe which on most specimens is strongly bent-down; it does appear, however, to be slightly longer than the rest of the glabella as in the Swedish and Polish material of *L. recurvus* figured by Kielan (1960).

Genus CALYPTAULAX Cooper, 1930

Type species. Calyptaulax glabella Cooper, 1930.

Calyptaulax planiformis Dean, 1962

Plate 112, figs. 14, 15

1885 *Phacops Brongniarti*, Portl.; Marr and Roberts (*pars*), pp. 480, 482.
1962 *Calyptaulax* planiformis Dean, p. 98, pl. 13, figs. 1–5.
1973*a* *Calyptaulax planiformis* Dean; Price, p. 233, tables 1–4.
1975 *Calyptaulax* sp.; Cocks and Price, list p. 705, pl. 81, fig. 6.

Holotype. Figured Dean 1962, pl. 13, fig. 4, BM In50138, internal mould of cranidium from the Pusgillian Stage, Swindale Beck, Cross Fell.

Horizons and localities. As in Table 1. Appears also to range through the Slade and Redhill Mudstone Formation.

Discussion. C. norvegicus Størmer (1945, p. 417, pl. 4, figs. 2, 3) from the Gagnum Shale of Hadeland is closely similar to *C. planiformis*. Dr. A. Owen informs me that in Størmer's illustration the holotype cranidium was tilted forward slightly thus foreshortening the frontal lobe. There thus appear to be no important differences in cranidial proportions between the two forms and the main distinction rests on the pygidial differences referred to by Dean (1962, p. 99). In this respect south Welsh pygidia are like the holotype and paratype pygidia of *C. planiformis*, with a relatively long axis and at least the first three interpleural furrows reaching the pygidial margin (Pl. 6, fig. 15). The form described by Whittington (1962, p. 12, pl. 2, figs. 17, 18; pl. 3, figs. 15, 16) as *C.* aff. *norvegicus* from the Rhiwlas Limestone of North Wales differs from the south Welsh form in that the 3p lateral glabellar lobes are narrower (tr.) anteriorly and the 3p furrows strongly geniculated and here also, as in the pygidium of *C. norvegicus* figured by Størmer, the pygidial border appears to be smooth. It may be of significance that both Whittington and Størmer refer in their descriptions to circular or sub-circular 1p lateral glabellar lobes whereas in the south Welsh specimens, and apparently in those figured by Dean (1962, pl. 13, figs. 1–3), the outline is distinctly sub-quadrilateral and angular. The validity of the differences referred to here between *C. planiformis* and *C. norvegicus* must remain uncertain until more material of the latter is illustrated. For the present the South Welsh specimens are best referred to *C. planiformis*.

Family LICHIDAE Hawle and Corda, 1847
Subfamily HOMOLICHINAE Phleger, 1936
Genus PLATYLICHAS Gürich, 1901

Type species. Lichas margaritifera Nieszkowski, 1857.

Platylichas noctua sp. nov.

Plate 113, figs. 1–9; Plate 114, fig. 7.

1848 *Lichas laxatus*, McCoy; Salter (*pars*), p. 340, pl. 8, figs. 4, 4*a* (*non* 5, 6).
1866 *Lichas laxatus*, M'Coy; Salter (*pars*), p. 324, pl. 19, fig. 1 (*non* 2, 3).
1885 *Lichas laxatus*, M'Coy; Marr and Roberts, lists pp. 480, 481.
1909 *Lichas laxatus* McCoy; Strahan *et al.*, table p. 58.
1914 *Lichas laxatus* McCoy; Strahan *et al.*, table p. 63.
1973*a* *Platylichas* cf. *laxatus* M'Coy; Price, tables 1–4, 7, list p. 242.

Holotype. (Pl. 113, figs. 4–6), GSM 19475, internal mould of incomplete cranidium (?together with GSM 19479, original of Salter 1848, pl. 8, fig. 4), Sholeshook Limestone of Sholeshook.

Diagnosis. Species of *Platylichas* with very wide (tr.), D-shaped composite glabellar lobes, narrow median lobe between and relatively wide (tr.) and short frontal lobe; palpebral lobes occupy up to four-fifths length (exsag.) of composite lobes; hypostoma with anterior lobe of median body coarsely granulated and lateral borders bearing a few raised ridges; pygidial border spines long, only gradually tapering, first two with convex outer margins.

Horizons and localities. In addition to occurrences shown in Table 1, known also from Slade and Redhill Mudstones of Redhill Quarry (locality 7) and basal Slade and Redhill Mudstones near Pelcomb (locality 3) and Rudbaxton (4).

Description. Width (tr.) of cranidium greatest posteriorly where about twice sagittal length. Glabella also widest posteriorly, width across frontal lobe being only three-quarters that at occipital ring. Latter broadest (sag. and exsag.) mesially, narrowing and curving forwards behind ovoid occipital lobes. Median lobe narrowest just behind mid-length of composite lobes, occupying one-sixth glabellar width at that level. Composite lobes occupy just over two-fifths cranidial length, very wide (tr.) and prominent, separated from rest of glabellar by deep, strongly curved longitudinal furrows; stand slightly above median lobe (Pl. 113, fig. 5), most of their surface horizontal but dropping steeply antero-laterally in front of anterior ends of palpebral furrows. Frontal lobe $2\frac{1}{2}$–3 times as wide (tr.) as long (sag.), broadly rounded frontally, occupying about one-quarter of cranidial length (sag.) and dropping steeply anteriorly (Pl. 113, fig. 6) to strong pre-glabellar furrow and broad, flat anterior border. Border narrows laterally where crossed at low angle by anterior branches of facial sutures (Pl. 113, fig. 4). Shallow axial furrows diverge forwards at about 55°. Palpebral lobes broad, prominent, and strongly curved, three-quarters to four-fifths length of composite glabellar lobes and standing on same level. Separated from rest of fixed cheeks by poorly defined palpebral furrows which at their mid-lengths are exsagittally in line with abaxial ends of occipital ring. Fixed cheeks moderately convex (exsag.) behind palpebral lobes, separated by deep furrows from occipital lobes. Anterior branches of facial sutures at first diverge and then converge forwards sub-linearly; posterior branches curve sigmoidally out and back to cross posterior border at angle of about 50°. Cranidial surface ornamented with granules of two sizes (Pl. 113, fig. 8), the larger about 0·15 mm and evenly distributed, the space between filled by the smaller. Occipital ring bears prominent median tubercle near posterior margin.

Hypostoma (Pl. 113, figs. 2, 3; Pl. 114, fig. 7) sub-quadrate, broadest on level of posterior border furrow. Median body moderately convex (tr.), divided by short but strong median furrows. Anterior lobe large, rounded. Posterior lobe short (sag. and exsag.), about two-thirds width (tr.) of anterior lobe. Anterior border narrow. Small anterior wings sub-triangular, directed dorsally. Lateral notches broad (exsag.), shallow in side view. Lateral and posterior border furrows deep, posterior border broad and moderately convex (sag. and exsag.); posterior margin bifurcate with broad (tr.), shallow median notch. Anterior lobe of median body evenly covered with large (0·03 mm) granules and lateral borders bear a few raised, anastomosing lines running sub-parallel to lateral margins.

Thorax (Pl. 113, fig. 9) incompletely known. Axis broad (tr.), tapering back only gradually, with broad (sag. and exsag.), sub-rectangular axial rings. Axial furrows narrow but deep. Pleurae become narrower (exsag.) abaxially and are deflected posteriorly at fulcrum as long, backwardly directed pleural spines. Pleural furrows commence at axial furrows near anterior margin of each segment then curve gently outwards and towards mid-line.

Axis of pygidium moderately convex (tr.), tapering only gradually back. Four narrow and convex (sag. and exsag.) axial rings are separated by ring furrows which gradually shallow posteriorly until fourth is only developed laterally and does not reach axial furrows. Behind it posterior portion of axis is more convex (tr.) and drops steeply in line with anterior ends of third interpleural furrows. Post-axial ridge at first narrows posteriorly more rapidly than axis but then expands again towards posterior border furrow. Axial furrows broad and deep. Pleural lobes crossed by pleural and interpleural furrows of equal prominence; three pleural ribs. First two developed into border spines which are long, taper only gradually, and curve backwards and inwards with evenly convex lateral margins. Gently convex border and shallow border furrow only clearly developed behind posterior band of second pleural rib (Pl. 113, fig. 7). Third pair of backwardly directed, broad-based border spines set close together behind axis. Doublure of thorax and pygidium broad, with widely spaced terrace-lines. External surface of both granulated in same manner as cranidium though on smaller specimens the granulation is relatively coarser.

Discussion. In common with many other upper Ordovician species of *Platylichas*, the Sholeshook form was long identified with *P. laxatus* (McCoy 1846, p. 51, pl. 4, fig. 9), a species erected on the basis of a partial cranidium from strata at Ballygarvan Bridge, New Ross, Eire, the exact age of which is uncertain. Dean (1963, pl. 43, fig. 10) refigured this holotype and a more complete topotype

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EXPLANATION OF PLATE 113

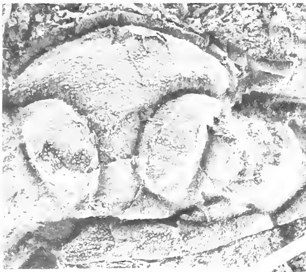
Figs. 1–9. *Platylichas noctua* sp. nov. 1, SM A31531, testate, incomplete cranidium from the Sholeshook Limestone of Sholeshook railway cutting, dorsal view, × 4. 2, 3, SM A104839, internal mould of hypostoma from the basal Sholeshook Limestone of Moldin (locality 25) near Llandowror, ventral and right lateral views, × 4. 4–6, GSM 19475, internal mould of incomplete cranidium, HOLOTYPE (?together with GSM 19479, original of Salter 1848, pl. 8, fig. 4), Sholeshook Limestone of Sholeshook, dorsal, anterior, and antero-lateral oblique views, × 4. 7, SM A31513, cast from external mould of incomplete pygidium from high Sholeshook Limestone of Prendergast, dorsal view, × 6. 8, GSM 19479, cast from external mould of incomplete cranidium (?together with GSM 19475, original of Salter 1848, pl. 8, fig. 4), Sholeshook Limestone of Sholeshook, oblique view, × 4. 9, SM A31530, testate internal mould of incomplete articulated thorax and pygidium from Sholeshook Limestone of Sholeshook railway cutting, dorsal view, × $1\frac{1}{2}$.

Figs. 10, 11. *Platylichas angulatus* Warburg? 10, BM It9261, cast from external mould of incomplete cranidium from the Sholeshook Limestone horizon at Robeston Wathen, flattened, dorsal view, × 5. 11, BM It9263, internal mould of incomplete hypostoma, same horizon and locality, ventral view, × 4.

Figs. 12–14. *Trochurus* sp. indet., GSM Pg. 291, internal mould of poorly preserved, incomplete cranidium from the Sholeshook Limestone, 'middle section' of Sholeshook railway cutting, dorsal, right lateral, and anterior views, × 5.

Fig. 15. *Glaphurella* cf. *harknessi* (Reed), GSM Pg. 299, internal mould of cranidium from same horizon and locality as original of figs. 12–14, left lateral view, × 4. See also Pl. 114, figs. 17, 18.

Fig. 16. *Liocnemis recurvus* (Linnarsson), SM A77627, internal mould of pygidium from the basal Slade and Redhill Mudstones south-west of Knock (locality 3), dorsal view, × 8.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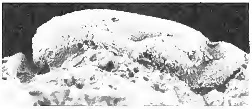
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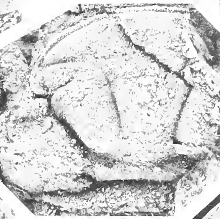
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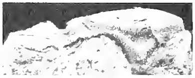
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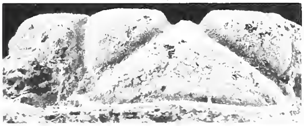
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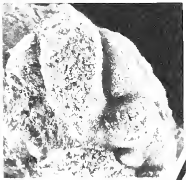
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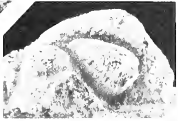
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PRICE, Sholeshook trilobites

cranidium was figured by Tripp (1958, pl. 84, fig. 4). *P. laxatus* differs from *P. noctua* in having narrower (tr.) composite glabellar lobes with a relatively wider median lobe between; the median lobe is narrowest further posteriorly and expands much more gradually anteriorly into a relatively longer (sag. and exsag.) and narrower (tr.) frontal lobe. Dean (1963, pp. 235–237, pl. 43, figs. 1, 2, 5, 8, 11, 12) also assigned to *P. laxatus* material from the Actonian Stage of south Shropshire. The cranidia appear to be similar to the Irish specimens; the hypostoma differs from that of *P. noctua* in that the maximum width is attained further anteriorly, across the shoulders, and is comparable to that on the level of the anterior wings, also the posterior lobe of the central body is smaller.

P. nodulosus (McCoy) from the Longvillian Stage of the Bala area (Whittington 1962, pp. 25–28, pl. 6, figs. 12, 13; pl. 7, figs. 1–14, 19; 1968, pp. 100–101, pl. 31, figs. 5, 6, 8–11, 14) differs in having a broader median glabellar lobe with the posterior part inflated as a distinct ring, in having shorter palpebral lobes and in having a much wider (sag. and exsag.) anterior border. In *P. glenos* Whittington (1962, pp. 28–31, pl. 7, figs. 15, 16; pl. 8) from the Rhiwlas Limestone of north Wales and the Chair of Kildare Limestone of eastern Ireland (Dean 1974, pp. 81–83, pl. 33, fig. 12; pl. 36, figs. 3–5, 7, 9–11; pl. 37, figs. 1–3, 5, 7, 10; pl. 38, figs. 3, 4, 7, 11, 12) the palpebral lobes are long as in *P. noctua* but the composite lobes are less wide and tend to be posteriorly pointed in outline, the frontal lobe is relatively longer (sag. and exsag.), less broad, and with a more strongly convex anterior margin and the median lobe does not expand so rapidly near its posterior margin. The hypostoma is much more finely granulated and carries many more anastomosing ridges on the lateral borders (Whittington 1962, pl. 8, fig. 10), the posterior lobe of the central body is narrower (tr.) and the posterior border more strongly convex (sag. and exsag.). The pygidial border spines are shorter, much more slender, and have concave lateral margins. The hypostoma of *P. crescenticus* (Reed, 1935, pp. 29–31, pl. 3, figs. 13–16) from the upper Drummuck Group of Girvan is similar to that of *P. glenos* in having a finer granulation and more anastomosing ridges than that of *P. noctua*; in addition the posterior lobe of the median body is relatively smaller and separated by less prominent median furrows and the posterior margin has a far narrower (tr.) median notch. The glabella has a broader median lobe which expands more gradually posteriorly and relatively narrower composite and frontal lobes. If Tripp (1958, p. 579) is correct in considering *P. vicinus* (Reed, 1935, p. 33, pl. 3, fig. 12) to be a synonym of *P. crescenticus* then the pygidium of the latter form differs from that of *P. noctua* in having shorter border spines with less strongly curved outer margins.

Platylichas angulatus Warburg, 1925?

Plate 113, figs. 10–11; Plate 114, fig. 6

1973*a* *Platylichas* sp. ?nov.; Price, list p. 233.

Material. BM It9261, 9262, 9263, SM A77810, respectively external mould of incomplete, flattened cranidium and internal moulds of three incomplete hypostomata from the Sholeshook Limestone horizon at Robeston Wathen.

Description. Glabella equally wide (tr.) across frontal lobe and occipital ring. Latter broadest (sag. and exsag.) mesially, behind ovoid occipital lobes narrows and curves forwards. Median lobe broad (tr.), narrowest just behind mid-length of palpebral lobes, expanding forwards at about 40°; moderately convex (tr.), standing slightly higher than composite lobes; posterior portion developed as distinct convex (sag. and exsag.) ring almost twice as wide as narrowest part of median lobe and separated by broad shallow furrow. Composite lobes large, sub-triangular, moderately convex (tr.). Strongly curved longitudinal furrows become shallow and indistinct antero-mesially and postero-mesially. Frontal lobe short and wide, sharply angulate laterally, with only moderately convex anterior margin; separated by narrow, distinct furrow from narrow, convex (sag. and exsag.) anterior border. Axial furrows deep and broad posteriorly. Palpebral lobes broad (tr.), strongly curved, about half-length (exsag.) of composite glabellar lobes and situated opposite posterior halves of these. Surface of cranidium with exception of anterior border ornamented with variably sized, irregularly spaced granules, the largest, on the median lobe and posterior two-thirds of composite lobes, very prominent, attaining *c.* 0·03 mm; granulation markedly finer anteriorly and antero-laterally. Occipital ring bears small, posteriorly placed median tubercle.

Hypostoma broader (tr.) than long (sag.); maximum width attained at about level of posterior border furrow;

anterior margin bluntly pointed. Median body sub-pentagonal in outline, only gently convex, divided by short (tr.) but broad and deep middle furrows. Anterior lobe about twice as broad (tr.) as long (sag.), broadest at about mid-length, anterior margin bluntly pointed, lateral margins straight and posteriorly convergent. Posterior lobe short (sag. and exsag.). Anterior border absent. Anterior wings small. Lateral notch shallow (tr.). Lateral borders broaden posteriorly until about level of posterior border furrow. Lateral border furrows deep, sublinear, posteriorly convergent; posterior border furrow shallower, transverse. Posterior border bifurcate with broad median notch.

Discussion. P. angulatus was described by Warburg (1925, p. 286, pl. 7, figs. 28–30) on the basis of two cranidia from the Boda Limestone of Kallholn, Dalarne, Sweden. Her original figures are too small to permit close comparison with other forms. More recently Dean (1974, p. 83, pl. 37, figs. 4, 6, 8, 9; pl. 38, figs. 1, 6) referred two cranidia from the Chair of Kildare Limestone to Warburg's species. Although very similar in over-all form, these two cranidia show some differences from the south Welsh specimen. The median glabellar lobe does not narrow so markedly, the transverse posterior portion is relatively longer (sag. and exsag.) and less wide (tr.) and apparently less well separated from the anterior part and the granulation on the median and composite lobes is less coarse than on the south Welsh specimen. Hypostomata have not been described for either the Boda Limestone or the Chair of Kildare Limestone form. More certain identification of the south Welsh form must await redescription of *P. angulatus* from Boda Limestone material.

Subfamily CERATARGINAE Tripp, 1957
Genus TROCHURUS Beyrich, 1845

Type species. Trochurus speciosus Beyrich, 1845.

Trochurus sp. indet.

Plate 113, figs. 12–14

1914 *Lichas bulbiceps* Reed ?Phillips MS.; Strahan *et al.*, table p. 63.
1973*a* *Trochurus* sp. indet.; Price, table 2.

Material. GSM Pg. 291, internal mould of incomplete cranidium from the middle section of Sholeshook railway cutting.

Discussion. The poorly preserved, incomplete cranidium is similar in over-all form to the holotype cranidium of *T. toernquisti* (Gürich) figured by Warburg (1925, pl. 7, figs. 1, 2) from the Boda Limestone of Boda, Dalarne, Sweden, but differs in that the 1p glabellar lobes appear to be relatively longer (exsag.) and the bullar lobes narrower (tr.) and more triangular in dorsal view. Both Warburg (1925, p. 259) and Dean (1974, pp. 87–88, pl. 35, figs. 2, 3, 5, 8, 11) referred specimens from the Chair of Kildare Limestone of eastern Ireland to *T. toernquisti*. To judge from the Irish specimens figured by Dean, the Sholeshook form has both the median glabellar lobe and the bullar lobes relatively longer (sag. and exsag.) and narrower (tr.).

Family ODONTOPLEURIDAE Burmeister, 1843
Subfamily MIRASPIDINAE R. & E. Richter, 1917
Genus WHITTINGTONIA Prantl and Přibyl, 1949

Type species. Acidaspis bispinosa McCoy, 1846.

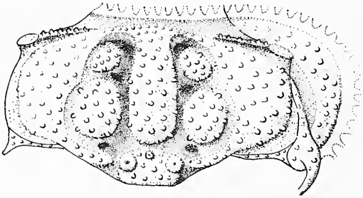
Whittingtonia whittingtoni Kielan, 1960

Plate 114, figs. 1–3

1960 *Whittingtonia whittingtoni* Kielan, pp. 109–111, pl. 16, fig. 5; pl. 18, figs. 1–4; text-fig. 28.
1965 *Whittingtonia* cf. *whittingtoni* Kielan; Whittington, pp. 34–35, pl. 9, figs. 11–17.
1968 *Whittingtonia whittingtoni* Kielan; Whittington, p. 100, pl. 31, figs. 1–3.
1973*a* *Whittingtonia whittingtoni* Kielan; Price, p. 245, table 7.
1973*b* *Whittingtonia whittingtoni* Kielan; Price, p. 538.

Material. In54227, internal mould of almost complete, slightly distorted cephalon, basal Slade and Redhill Mudstones, road-section at crossways south-west of Knock (locality 3), 4 km north-west of Haverfordwest; SM A31364, internal mould of incomplete cephalon, same horizon near Pelcomb Cross (locality 2), 4 km west-north-west of Haverfordwest.

Discussion. The prominent, strongly convex (tr. and sag.) fronto-median glabellar lobe is similar in both dorsal and anterior views to those of specimens figured by Kielan (see synonomy) from the upper Ordovician of Poland and by Whittington from the Rhiwlas Limestone of north Wales, particularly to the latter. In lateral profile this lobe on one specimen (Pl. 114, fig. 3) appears to be rather more convex and to overhang the anterior border less, but these differences may well be due to distortion. Abaxially the median lobe drops steeply to broad, deep axial furrows which contain only weakly developed 1p and 2p lateral lobes; in this respect the cephala are more like those described by Whittington (1965, p. 34). In all other features, the short, stout occipital spines, the elongated (tr.) occipital node, the large eyes, the broad, deep palpebral furrows and prominent eye-ridges, the form



TEXT-FIG. 1. *Proceratocephala* cf. *terribilis* (Reed, 1914); reconstruction of cephalon approximately × 6·5, based largely on original of Plate 114, fig. 4. Details of spinose margin to anterior and lateral border (dotted) hypothetical.

EXPLANATION OF PLATE 114

Figs. 1–3. *Whittingtonia whittingtoni* Kielan, BM In54227, internal mould of almost complete, slightly distorted cephalon from the basal Slade and Redhill Mudstones south-west of Knock (locality 3), dorsal, anterior, and right lateral views, × 10.

Figs. 4, 5. *Proceratocephala* cf. *terribilis* (Reed). 4, GSM Pg. 487, internal mould of almost complete cephalon from the high Sholeshook Limestone of locality 9h, Sholeshook, dorsal view, × 6. 5, SM A77582a, testate, incomplete cranidium from the basal Sholeshook Limestone of the Pentre-howell road section (locality 17), Llandowror, dorsal view, × 6.

Fig. 6. *Platylichas angulatus* Warburg?, BM It9262, internal mould of incomplete hypostoma from the Sholeshook Limestone horizon at Robeston Wathen, ventral view, × 4.

Fig. 7. *Platylichas noctua* sp. nov., SM A31537b, cast from external mould of hypostoma, Sholeshook Limestone of Sholeshook railway cutting, ventral view, × 4.

Figs. 8–15. *Primaspis llandowrorensis* sp. nov. 8, 9, HM A9633, internal mould of incomplete cranidium from the high Sholeshook Limestone of Lan-y-gaer (locality 16a), near Llandowror, anterior and dorsal views, × 4. 10, NMW.21.306.G.17, external mould of pygidium from the Slade and Redhill Mudstones of Old Pale, near Llandowror, dorsal view, × 5. 11–14. GSM 21053/5213, HOLOTYPE, cast from internal mould of posterior part of thorax and pygidium with ventral mould of pygidial doublure, cast from partial external mould of cephalon and thorax and internal mould (including counterpart to above) of incomplete articulated exoskeleton (enrolled) from Sholeshook Limestone of Craig-y-deilo quarry, Llandowror, figs. 11–13 dorsal views, fig. 14 antero-lateral oblique, all × 4. 15, BM It9266b, cast from external mould of left free cheek from the Sholeshook Limestone horizon at Robeston Wathen, dorsal view, × 8.

Fig. 16. *Primaspis* sp. indet., SM A77514b, cast from external mould of incomplete pygidium from the highest Sholeshook Limestone of Prendergast (locality 8b), dorsal view, × 5.

Figs. 17, 18. *Glaphurella* cf. *harknessi* (Reed), GSM Pg. 296/299, cast from partial external mould of cranidium in dorsal view and counterpart internal mould of cranidium in dorsal view, Sholeshook Limestone, 'middle section' of Sholeshook railway cutting, both × 4; see also Pl. 113, fig. 15.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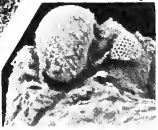
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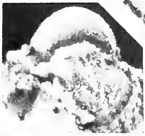
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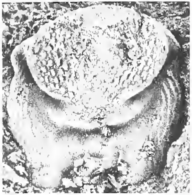
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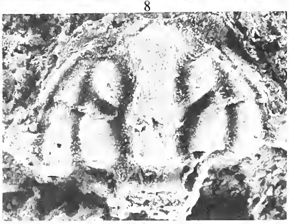
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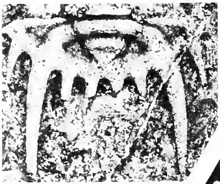
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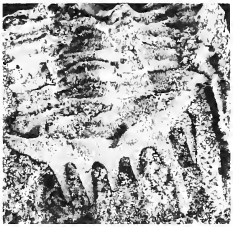
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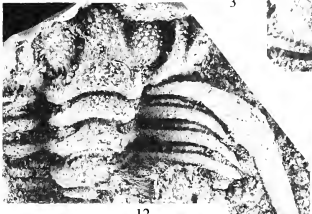
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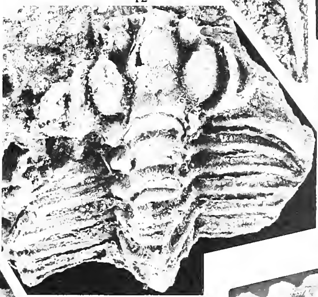
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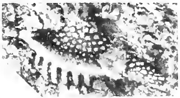
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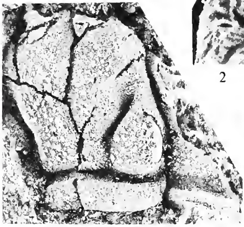
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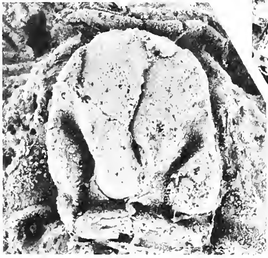
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PRICE, Sholeshook trilobites

of the cheeks and surface ornamentation, the specimens resemble closely the material described by both Kielan and Whittington. Kielan (1960, p. 111), Bruton (1966, p. 28), and Dean (1974, p. 94) have discussed the differences between *W. whittingtoni* and the type species, *W. bispinosa*, from the Chair of Kildare Limestone.

Genus PROCERATOCEPHALA Prantl and Přibyl, 1949

Type species. Acidaspis terribilis Reed, 1914.

Proceratocephala cf. *terribilis* (Reed, 1914)

Plate 114, figs. 4, 5; text-fig. 1

1914 *Acidaspis* sp.; Strahan *et al.*, table p. 63.
1973*a* *Proceratocephala* cf. *terribilis* (Reed); Price, tables 1–4.

Material, horizons, and localities. GSM Pg. 487, internal mould of almost complete cephalon, high Sholeshook Limestone, Sholeshook (9h); HM A9702, A9704, internal moulds of cranidia, low Sholeshook Limestone, track south of Craig-y-deilo quarry, Llandowror (18d); SM A77582a, b, A77754a, b, counterpart moulds of cranidia, basal Sholeshook Limestone, Pentre-howell road section (17); SM A77989, internal mould of incomplete cranidium 9½–10 m above base of Sholeshook Limestone in Mylet road section (24a).

Description. Cranidium elliptical in outline, twice as broad (tr.) as long (sag.). Axial furrows deepest posteriorly where strongly divergent, broad and distinct over most of length but only faintly developed forward of 2p lateral lobes. Glabella broadest (tr.) at mid-level of 1p lateral lobes. Median lobe roughly semi-cylindrical, narrowing slightly anteriorly; strongly convex (tr.), bounded by deep, broad longitudinal furrows. Large 1p lateral lobes ovoid, strongly convex. 2p lobes of similar form but only half length (exsag.) of basal lobes; separated from them by broad, adaxially deepening 1p lateral furrows. Small 3p lateral lobes fused to median lobe to form narrow (sag. and exsag.), transverse anterior section. Occipital furrow broad, mesially shallow; ring very broad, bearing large, paired occipital spines, small median tubercle near anterior margin. Longitudinal furrows contain shallow apodemal pits where they merge with the 1p and 2p lateral furrows and with the longitudinal furrows. Fixed cheeks strongly convex and steeply declined postero-laterally; antero-mesially not distinctly separated from transverse anterior section of antero-median lobe, posteriorly only weakly separated from occipital ring. Posterior border furrow broad, curving strongly forwards abaxially; border narrow adaxially, broadening and curving gently forwards distally. Anterior border furrow broad; border narrow (sag. and exsag.) but form not clearly seen. Antero-laterally on cranidium narrow (exsag.) eye-ridges run out and slightly back to small palpebral lobes situated opposite 2p lateral furrows. Posterior branches of facial sutures run back in gently sigmoidal curves, the anterior sections concave adaxially. Anterior branches abaxially run close to eye-ridges before curving forwards to cross anterior border at low angle. Free cheeks crescentic. Strongly convex sutural ridges broaden posteriorly and give rise to broad-based librigenal spines. Broad furrows, anteriorly convergent with anterior border furrow, separate sutural ridges from remaining convex portions of cheeks. Lateral borders broad (tr.) and spinose but number and size of spines not clear. Cranidial surface ornamented with prominent, closely spaced tubercles of *c.* 0·15–0·2 mm.

Discussion. Whittington (1956, p. 515, pl. 59, fig. 13; pl. 60, figs. 2, 3, 5, 6, 10) selected a lectotype for *P. terribilis* from among Reed's syntypes and redescribed this and other material from the Rawtheyan Starfish Bed of Girvan. In cranidial characters the south Welsh specimens do not significantly differ from this material though the poor preservation of the free cheeks and the present lack of other parts of the exoskeleton preclude a full comparison. The subspecies *P. terribilis bituberculata* Kielan (1960, p. 107, pl. 3, fig. 3; pl. 16, fig. 1) from the upper Ordovician of Poland differs from both the Scottish and south Welsh specimens in showing in addition to the general surface tuberculation several much larger, regularly positioned tubercles on the cranidium.

Subfamily ODONTOPLEURINAE Burmeister, 1843

Genus PRIMASPIS R. and E. Richter, 1917

Type species. Odontopleura primordialis Barrande, 1846.

Primaspis llandowrorensis sp. nov.

Plate 114, figs. 8–15

1973*a* *Primaspis* aff. *semievoluta* (Reed); Price, list p. 233, table 2.

Holotype. GSM 5213, 21053 (Pl. 8, figs. 11–13), internal and external moulds of incomplete articulated exoskeleton from Craig-y-deilo quarry, Llandowror.

Paratypes. NMW 21.306.G17, external mould of pygidium and NMW 21.306.G18, internal mould of free cheek, both from Slade and Redhill Mudstones of Coed Old Pale, near Llandowror; HM A9633, internal mould of cranidium, high Sholeshook Limestone, Lan-y-gaer (locality 16a); BM It9264, 9265, 9266a, b, internal mould of partial cranidium, external mould of incomplete pygidium, and counterpart moulds of free-cheek, from Sholeshook Limestone of Robeston Wathen; SM A77994, poor internal mould of free cheek from 9½–10 m above base of Sholeshook Limestone in Mylet Road section (locality 24a), Llandowror. This comprises all available material.

Diagnosis. *Primaspis* with relatively narrow (tr.) median glabellar lobe, small, poorly differentiated 3p lateral lobes, centrally (not posteriorly) positioned occipital tubercle and stout genal spines, particularly broad where they join the posterior borders; pygidium with only one pair of anterior secondary border spines and outermost posterior pair of secondary spines not fused with bases of major spines; sculpture of small, well-spaced granules.

Description. Cranidium broadest posteriorly where width about 2½ times sagittal length. Glabella broadest at mid-level of 1p lateral lobes; width here about equal to pre-occipital length. Occipital ring strongly convex (tr.), broad and sub-parallel sided mesially with prominent centrally positioned median tubercle, narrows sharply behind posterior ends of 1p lateral furrows and then curves forward to form prominent occipital lobes. Occipital furrow broad and prominent. Large 1p lateral lobes ovoid, 1½ times as long (exsag.) as wide (tr.), strongly convex; long axes diverge forward at *c*. 25°. 2p lobes about two-thirds length of 1p, of similar form and orientation. 1p and 2p lateral furrows prominent, curving in and strongly back completely separating 1p and 2p lobes from median lobe; 1p furrow deeper than 2p. 3p lateral lobes very small, with only slight independent convexity; oriented antero-laterally and defined anteriorly by broad but short and shallow 3p furrows. Median lobe strongly convex (tr.), narrowest (tr.) at mid-level of 2p lateral lobes, widest at about three-quarters length of 1p lobes. Frontal lobe about as wide (tr.) as posterior part of median lobe, roughly semicircular, dropping steeply to broad anterior border furrow. Anterior border narrow (sag. and exsag.) and upturned (Pl. 114, fig. 9). Axial furrows broad and deep posteriorly. Elongated triangular strips of fixed cheeks lie outside axial furrows, broadening and becoming more strongly convex posteriorly. Antero-laterally to these strips, separated by strong furrows, narrow convex eye-ridges run back to palpebral lobes situated opposite posterior halves of 1p lateral lobes. Anterior branches of facial sutures curve forwards and adaxially, gradually diverging from eye-ridges; posterior branches curve out and gradually back. Convex posterior borders narrow adaxially, broadening rapidly outwards. Free cheeks crescentic; at inner posterior corners bear eyes on stout, elongated stalks (Pl. 114, fig. 14); extended postero-laterally as long, stout, broad-based librigenal spines. Lateral border furrow broad; narrow, convex border appears to bear about thirteen slender border spines, longest posteriorly. Cephalic surface ornamented with prominent, well-spaced granules of up to 0·175 mm.

Hypostoma unknown. Thorax of ten segments. Axis strongly convex, occupying less than one-third total width anteriorly. Axial rings convex (sag. and exsag.), broadest mesially, abaxially narrowing then curving forwards to form axial lobes. Articulating furrows broad and shallow mesially, outwards forming deep apodemal slots. Axial furrows shallow. Pleurae comprise broad, strongly convex posterior bands separated by narrow, distinct pleural furrows from lower, narrow, convex anterior bands which bear a row of about six regularly spaced, small tubercles. Inner portions of pleurae horizontal but at fulcrum deflected ventrally and posteriorly; posterior bands have prominent fulcral expansions (Pl. 114, fig. 13). Axial rings and posterior pleural bands with similar ornament to that of cephalon.

Pygidium, discounting border spines, sub-triangular, about three times as wide (tr.) as long (sag.). Axis occupies one-third total width anteriorly, tapers back rapidly. First axial ring strongly convex longitudinally, moderately so transversely, clearly defined; second ring about two-thirds as wide (tr.), lower, less convex (sag. and exsag.), followed by low triangular terminal portion fused to convex posterior border. Convex pleural ridge curves out and strongly back and swells slightly as it approaches posterior border; pleural areas between it the axis and the borders depressed. Border spines long, gradually tapering. Between the major spines are four secondary posterior spines of which the outermost are not fused with the bases of the major spines; only one pair of anterior secondary spines is present. Ornament of well-spaced granules poorly preserved.

Discussion. In cephalic features *P. llandowrorensis* sp. nov. shows much over-all similarity to *P. bucculenta* McNamara (1979*a*, p. 86, pl. 12, figs. 10–19) from Cautleyan Zone 3 in the southern Lake District. In that form, however, the fixigenae are much broader (tr.) posteriorly, the librigenal spines appear shorter and more rapidly tapering and the librigenal denticles are shorter. Like *P. bucculenta* the south Welsh form differs from *P. evoluta* (Tornquist) from the upper Ordovician of Sweden (see Bruton 1966, p. 4, pl. 1, figs. 1–9; pl. 4, fig. 9; text-fig. 2*a*) and north Wales (Whittington 1968, p. 98, pl. 30, figs. 25–30) in having a relatively narrower median glabellar lobe, larger 2p lateral lobes, smaller, less prominent and less anteriorly divergent 3p lobes, a greater number of librigenal border spines, and a central occipital tubercle.

In pygidial characters *P. llandowrorensis* differs from both these forms in lacking the fusion between an outermost (third) pair of posterior secondary border spines and the bases of the macrospines. It lacks the second anterior secondary border spines of *P. evoluta* and in over-all form is relatively longer (sag.) and less broad (tr.). *P. bucculenta*, like *P. llandowrorensis*, has only one anterior secondary spine but the macrospines in *P. llandowrorensis* are much longer, narrower-based, and less strongly curved. The anterior secondary spines appear longer also and the pygidial tuberculation is much finer. The lack of the fused border spines together with the presence of only one pair of anterior secondary spines appear to distinguish the pygidium of *P. llandowrorensis* from that of any other known species of the genus.

Primaspis sp. indet.

Plate 114, fig. 16

1973*a* *Primaspis* cf. *evoluta* (Tornquist); Price, tables 1, 2.

Material. Single specimen, SM A77514a, b, internal and external moulds of incomplete pygidium from the highest Sholeshook Limestone of Prendergast Place (locality 8b), Haverfordwest.

Description. Axis strongly convex; anteriorly with well-developed articulating ring separated by broad furrow. First axial ring strongly convex (sag. and exsag.); second lower and less wide (tr.), bearing pair of large but ill-defined tubercles and followed by a low, rapidly tapering (tr.) terminal portion fused with the convex posterior border. Strongly convex pleural ridge curved outwards and posteriorly. Between ridge, axis, and posterior border pleural areas depressed. Posteriorly there are six secondary spines of which the outermost are small and fused with the swollen bases of the major spines. All the spines but particularly the major spines, the posterior border, the pleural ridge, and the first axial ring are ornamented with prominent granules.

Discussion. In over-all form and proportions and in the character of the ornamentation the incomplete Prendergast pygidium resembles the corresponding portions of the pygidia of both *P. evoluta* (cf. Bruton 1966, pl. 1, figs. 6–7; pl. 4, fig. 9; text-fig. 2*a*) and *P. bucculenta* (cf. McNamara 1979*a*, pl. 12, figs. 16, 18, 19). The border spines are relatively shorter and stouter than those of *P. bestorpensis* Bruton (1966, pp. 7–9, pl. 2, figs. 1, 2, 5–6; text-fig. 2*b*) from the Bestorp Limestone (basal Harju Series) of Västergötland, and the depressed pleural areas lack the coarse granulation seen in that form. In the absence of the antero-lateral parts of the pygidium further comparisons are not possible.

?Family GLAPHURIDAE Hupé, 1953
Genus GLAPHURELLA Dean, 1971

Type species. Cyphaspis ? *Harknessi* Reed, 1896.

Glaphurella cf. *harknessi* (Reed, 1896)

Plate 114, figs. 17, 18

1905*a* *Cyphaspis* cf. *Harknessi*, Reed; Reed, p. 98.
1914 *Proetus harknessi* Reed; Strahan *et al.*, table p. 64.
1973*a* *Glaphurella* cf. *harknessi* (Reed); Price, tables 1, 2.

Material, horizons, and localities. SM A104833, internal mould of partial cranidium, Sholeshook Limestone, Sholeshook; GSM Pg. 296, 299, internal and external moulds of cranidium, middle section of Sholeshook railway cutting; GSM Pg. 280, internal mould of flattened partial cranidium, same horizon and locality; SM A77948, internal mould of partial cranidium, locality 9e, Sholeshook; SM A30940, internal mould of incomplete cranidium, basal Slade and Redhill Mudstones south-west of Knock (locality 3).

Discussion. Dean (1971, p. 44, pl. 22, figs. 3–10, 12, 13; pl. 23, fig. 1) redescribed the holotype cranidium of *G. harknessi* from the Keisley Limestone of Cross Fell together with better-preserved specimens from the Chair of Kildare Limestone of eastern Ireland. The south Welsh specimens are similar in general form and in details of ornamentation but appear to have glabellae which are consistently relatively longer (sag.) and less wide (tr.) than in the cranidia figured by Dean and which do not drop so steeply anteriorly. Also, although the 2p lateral glabellar furrows are just visible on internal moulds of some of the south Welsh cranidia, none of them show any signs of glabellar lobation anterior to these. Such differences may simply be the effects of distortion and poor preservation but until better specimens are available the south Welsh form is probably best only compared with *G. harknessi*.

RANGES, ABUNDANCES, AND FAUNAL COMPARISONS

The known ranges or restricted occurrences of trilobite species within the three developments of the Sholeshook Limestone Formation, together with indications of their relative abundance, are given in Table 1. The five categories in the list of abundances are based primarily on the relative numbers of specimens in the author's collections and in other recent collections from the formation where an attempt has been made to retain all potentially identifiable material (e.g. S. F. Morris collection BM, J. K. Ingham collection HM)—though some of the forms listed as rare are known only from old collections. Each of these categories is a generalization for the formation as a whole or for those parts of it in which the particular taxon occurs; it has not been possible to sample in a sufficiently controlled way throughout all developments of the Sholeshook Limestone to give a more rigorous quantitative assessment of the abundance of each form or to chart variations in abundance at different horizons. In comparing the Sholeshook trilobites with other Ashgill trilobite faunas it is most useful to deal with comparisons at specific level separately from those at generic level. This is because the specific composition of the fauna is the basis for assessing the precise age and correlation of the formation while differences from other Ashgill faunas in generic composition probably relate to factors other than age relationships.

The age and correlation of the Sholeshook Limestone have been extensively discussed elsewhere (Price 1973*a*, *b*, 1980) and it is now considered that the formation ranges from high Cautleyan Zone 1 to Rawtheyan Zone 5. This conclusion is based on comparisons of the vertical distribution of trilobite species in the formation with the stratigraphical ranges of identical or closely allied species in the type Ashgill succession at Cautley (Ingham 1966, 1972–7). A precise correlation between the two successions is possible because they have large numbers of species in common. Several species of *Tretaspis* from Sholeshook and species of *Illaenus*, *Stenopareia*, *Pseudosphaerexochus*, *Calymene* (s.l.), *Flexicalymene*, *Kloucekia*, *Duftonia*, and *Toxochasmops* are all considered to be conspecific and species of *Atractopyge*, *Lonchodomas*, and *Hadromeros* very probably conspecific with forms of Cautleyan or lowest Rawtheyan age at Cautley.

Accepting this correlation, the occurrence in low to middle horizons of the Sholeshook Limestone of a few species occurring elsewhere in Rawtheyan horizons extends their stratigraphical ranges (Price 1973*a*, *b*). This argument was initially made with reference to elements of the '*Phillipsinella parabola—Staurocephalus clavifrons* fauna' where there is some confirmatory evidence for pre-Rawtheyan occurrences from other sections (Price 1973*b*) but it has been recently extended to apply also to other forms such as *Prionocheilus* cf. *obtusus* and *Glaphurella* cf. *harknessi* (Price 1980). Thus certain species in the Sholeshook trilobite fauna appear to be long-ranging and are common to younger faunas such as those of the Rhiwlas Limestone of north Wales (Whittington 1962–1968) and the Chair of Kildare Limestone of eastern Ireland (Dean 1971–1978). They are, however, relatively few in number and when such faunas are fully compared with the Sholeshook fauna the difference in age is reflected in the presence of different species of, for example, *Illaenus*, *Tretaspis*, *Lonchodomas*, *Pseudosphaerexochus*, and *Platylichas*; over-all the number of species in common is much smaller than in the case of the Cautleyan fauna of the Cautley Mudstones referred to earlier.

Nearly all the genera present in the faunas so far discussed and in other Ashgill trilobite faunas are known to range through the Cautleyan and Rawtheyan Stages. Most of them are known to be geographically wide ranging. It can reasonably be argued therefore that where these faunas differ in generic composition it is largely as a result of differences in palaeoenvironmental factors. Although the environmental significance of Ashgill trilobite faunas is as yet only poorly understood, there do appear to be at least two reasonably clear associations between facies and fauna which can be referred to here and used as a basis for comparison with the Sholeshook fauna.

The first of these associations relates to the faunas of light-coloured, relatively pure, biosparite limestone developments often considered to be, at least in part, of 'reef' facies. These are here taken to be relatively shallow-water accumulations probably representing shelf-edge or near shelf-edge environments. Examples are the Boda Limestone of Sweden, the Chair of Kildare Limestone of eastern Ireland, and the Keisley Limestone of northern England all usually considered to be Rawtheyan in age, at least partially. These formations have trilobite faunas represented almost entirely by disarticulated remains. Broadly their faunas appear to be characterized by the importance in them of illaenids, cheirurids, and lichids (illaenid-cheirurid community type of Fortey, 1975). To a much greater extent than in the Sholeshook fauna these groups are both numerically predominant and generically diverse. When an over-all comparison is made the Sholeshook fauna does have a number of genera in common (cf. Dean 1978, table p. 111) such as *Atractopyge*, *Hadromeros*, *Pseudosphaerexochus*, *Platylichas*, *Illaenus*, *Stenopareia*, *Panderia*, *Prionocheilus*, and the rarer forms *Trochurus*, *Sphaerocoryphe*, and *Glaphurella*. This is as far as the similarity can be taken, however, for many other forms apparently characteristic of the pure limestone association are not represented at Sholeshook—*Sphaerexochus*, *Holotrachelus*, *Stenoblepharum*, *Decoroproetus*, *Dicranopeltis*, *Toernquistia*, and isocolids are notable examples. Similarly the pure limestone faunas themselves completely lack the following Sholeshook genera: *Calyptaulax*, *Kloucekia*, *Duftonia*, *Liocnemis*, *Lonchodomas*, *Raphiophorus*, *Flexicalymene*, *Brongniartella*, *Opsimasaphus*, *Encrinuroides*, *Dindymene*, *Amphitryon*, *Dionide*, and *Nankinolithus*. Chasmopines are also completely absent from them and though *Tretaspis* may be present it is usually very rare.

Many of the Sholeshook genera listed above as being absent from the pure limestone association appear to be more characteristic of a second distinct association. This relates to certain mudstone sequences here taken to represent deeper-water, low-energy environments probably considerably down-slope from the platform edge. Good examples are the mudstones of the '*Staurocephalus clavifrons* Zone' of Poland and the Králův Dvůr Formation of Bohemia (Kielan 1960; Havlicek and Vaněk 1966); in Wales the Ashgill mudstones of Grugan and Llanystwmdwy in the Lleyn Peninsula (Matley 1938; Harper 1956) appear to be of similar type. Their faunas usually contain a significant proportion of complete or almost complete articulated exoskeletons. Among trilobites which appear to be important and characteristic elements of such faunas are several genera which occur at Sholeshook: *Liocnemis*, *Lonchodomas*, *Raphiophorus*, *Opsimasaphus*, *Dindymene*, *Amphitryon*, *Dionide*, and *Nankinolithus*. With the exception of *Nankinolithus* these genera are among the rarer elements of the Sholeshook fauna and even *Nankinolithus* is only abundant at Sholeshook within a very restricted vertical range. At Crugan *Duftonia* occurs in association with the genera listed above. *Kloucekia*, *Flexicalymene*, and *Brongniartella* may also be less ubiquitous members of this mudstone association. The Polish and Bohemian mudstone faunas also contain many elements, possibly representing genera preferring even deeper water conditions—perhaps in foot-of-slope and basinal environments, not known from Sholeshook (though present elsewhere in Wales in the mudstones of the Abercwmeiddaw Group of the Corris–Ddinas Mawddwy area; P. M. Magor and J. K. Ingham coll.). These include *Novaspis*, several cyclopygid genera and telephinids.

On general sedimentological and stratigraphical evidence the Sholeshook Limestone probably represents an environment in the middle to upper part of the slope between platform edge and basin where deposition took place under relatively high energy conditions (skeletal material largely disarticulated, often broken) and was dominantly clastic but with some carbonate content. In this sense it would represent an environment intermediate between that represented by low-energy, deeper-water mudstones on the one hand and by shallow-water carbonate accumulations on the other. It is suggested that this 'intermediate' nature of the environment may be reflected in the variety of genera in the trilobite fauna which embraces both forms more common in deeper-water mudstones and forms occurring in pure limestones.

A few Sholeshook forms—*Calyptaulax*, *Encrinuroides*, and *Toxochasmops* (in fact chasmopines in general)—do not appear to be usual members of either the pure limestone or the mudstone associations and may be restricted to faunas of an 'intermediate' nature related to shallower-clastic and impure carbonate sequences. Another characteristic of such faunas is an abundance of *Tretaspis*; the genus becomes rare, as mentioned earlier, in pure limestone faunas and appears to be progressively replaced in deeper environments by first *Nankinolithus* and then *Novaspis*. Ultimately it may prove possible to characterize 'intermediate' faunas more fully as a separate third association though clearly this would overlap with both the carbonate and mudstone associations.

Overlap of this kind might prove useful, however, in permitting within a broad 'intermediate' association some distinction between faunas of deeper and shallower water affinities. For instance, when the Sholeshook trilobites are compared with those from the Cautleyan Stage of the Cautley area (Ingham 1966, 1970–1977) one major difference is the absence of those Sholeshook genera listed as being characteristic of the deeper-water mudstone association—*Liocnemis*, *Raphiophorus*, *Opsimasaphus*, *Dindymene*, *Amphitryon*, *Dionide*, and *Nankinolithus* (*Lonchodomas* is an exception). *Duftonia*, *Kloucekia*, *Brongniartella* and *Flexicalymene* are also absent. In view of what has been said in earlier sections these differences would suggest that the Cautleyan rocks at Cautley were deposited under shallower water conditions than was the Sholeshook Limestone. This suggested difference in environment might also relate to other faunal differences. For example, the Sholeshook genus *Flexicalymene* is replaced at Cautley by species of *Calymene* (s.l.) ('*Diacalymene*') and *Gravicalymene*, and *Harpidella* is replaced by *Otarion*. The odontopleurids at Cautley are represented by *Acidaspis* in addition to *Primaspis*, and *Decoroproetus* is common.

Similar differences are seen when the Sholeshook fauna is compared with that of the Birdshill Limestone, probably of Pusgillian–low Cautleyan age, of the Llandeilo area. Here again the *Harpidella* of the Sholeshook fauna is replaced by *Otarion*, the *Flexicalymene* is replaced by *Gravicalymene*, and both *Acidaspis* and *Decoroproetus* are present. The Birdshill Limestone is a light-coloured, relatively pure limestone, coarse grained, sparry, and largely bioclastic; all of these characters suggest a relatively shallow-water origin. The fauna, however, differs from that of the Cautleyan Stage at Cautley, probably as a reflection of its closer affinity with the pure carbonate association outlined earlier, in that species of *Platylichas* are important elements, *Holotrachelus* may also be present and *Tretaspis* is very rare (information based on collections from Birdshill Limestone in BM). The Rhiwlas Limestone of north Wales is faunally more like the Sholeshook Limestone in containing a number of genera like *Amphitryon*, *Dindymene*, *Opsimasaphus*, *Lonchodomas*, *Raphiophorus*, and *Cyclopyge* associated with deeper mudstone environments as well as forms like *Encrinuroides*, *Platylichas*, *Prionocheilus*, *Sphaerocoryphe*, and *Ulugtella* (last named noted by Dean 1978, p. 113). Like the Sholeshook Limestone it may represent an environment towards the deeper part of the 'intermediate' (broadly mid-slope) range.

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PALAEOBIOLOGY OF UPPER CRETACEOUS BELEMNITES FROM THE PHOSPHATIC CHALK OF THE ANGLO-PARIS BASIN

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ABSTRACT. The phosphatic chalks of northern France exhibit a tripartite belemnite biostratigraphy, with *Actinocamax verus* Miller at their base, *Gonioteuthis* ex gr. *quadrata* in their upper portions, and *G. quadrata quadrata* and *Belemnitella praecursor* Stolley at their summit. *G. granulata* (Blainville) is identified from isolated specimens collected from the base of the sequences; *G. granulataquadrata* (Stolley) is recognized within 'populations' from the summit of phosphatic chalks. Principal component factor analysis suggests that variation in guard morphology may be attributed to differences in guard size and to the evolutionary stage reached by individuals within the gradualistic series formed by the genus *Gonioteuthis*. Heterogeneity in one sample is the result of mixing of juvenile and mature populations caused by a catastrophic event, probably a storm. The presence of juveniles in all samples indicates a near-shore environment which was the normal habitat of belemnites. Hardgrounds show associated concentrations of belemnites because of greater food availability and their suitability as breeding sites.

BELEMNITES occur throughout the Santonian to early Campanian sequences of the Anglo-Paris Basin, but their rarity may be measured by the observations of Rowe (1908, p. 311) who obtained only ten specimens of *Gonioteuthis* from the entire Campanian section on the Isle of Wight during more than two months' intensive collecting. Similarly, Brydone (1914) stated that only thirteen accurately located and identifiable specimens of *Gonioteuthis* had previously been recorded from the Chalk of Hampshire and Sussex. The infrequency of belemnites in soft white chalks of this age has been noted by other authors in sequences outside the Anglo-Paris Basin (e.g. Ernst 1964; Christensen 1976*b*). Belemnites, in particular *Gonioteuthis* and *Actinocamax verus* Miller are, however, common and at some levels extremely abundant in the phosphatic chalk lithofacies. Consequently, while the sporadic occurrence of belemnites in soft white chalks has led to the inapplicability of population analyses, material from phosphatic chalks provides a unique opportunity to examine accurately located 'populations', rather than isolated specimens.

PHOSPHATIC CHALK STRATIGRAPHY

Lithostratigraphy. The phosphatic chalks of Picardy in northern France are pelletal chalks rich in light-brown granules of phosphatized carbonate, many of which are of faecal origin (Cayeux 1939; Willcox 1953; Tabatabaï 1977), and contain in excess of 5% P_2O_5. They occur in small groups of, or isolated troughs up to 1 km in length, 250 m wide and 30 m deep in the soft white chalks of the Santonian–early Campanian of northern France and southern England. These troughs, termed cuvettes (e.g. de Grossouvre 1901), have an erosional origin and are floored by a well-developed hardground, termed the basal hardground.

On top of the basal hardground there rests up to 15 m of phosphatic chalk which contains a prolific and distinctive fauna at its base, including '*Terebella*' *phosphatica* Leriche (an agglutinated worm tube) and *Diblasus arborescens* Parent (a compound coral) (Jarvis 1980). The final phosphatic chalk development is no younger than early Campanian in age and usually contains distinctive bands of *Offaster pilula* Lamarck and *G. quadrata quadrata* (Blainville). The genesis of these deposits is discussed elsewhere (Jarvis 1980). Despite the relative abundance of fauna at certain levels within phosphatic chalks, little information has been published on their macrofauna, although short faunal

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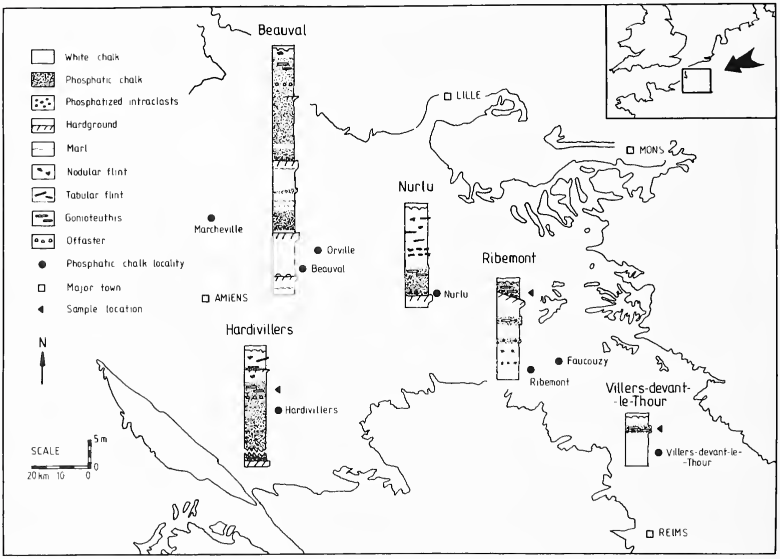
lists and descriptions are provided by Leriche (1908, 1911). The common occurrence of *G.* ex gr. *quadrata* in the upper portion of phosphatic chalks has been noted previously by several authors (Lasne 1902; Gosselet 1901; de Grossouvre 1894, 1899, 1901, 1907; Leriche 1908, 1911; Jarvis 1980).

A large 'population' of over 200 guards was collected by the author in 1977–1978 from the abandoned phosphorite quarry near Hardivillers (Oise). A further 100 guards were collected from Ribemont (Aisne) and Villers-devant-le-Thour (Ardennes) quarries, together with additional comparative material from several other phosphatic chalk localities. All of the material utilized in the present study (deposited in the Oxford University Museum—OUM) was collected, where possible, *in situ* and carefully localized by reference to the lithostratigraphy. The location [Lambert coordinates provide an east-west (x) and north-south (y) position (± 50 m) on a standard map-grid, plus the height (z) above sea-level (± 5 m)] and lithostratigraphy (text-fig. 1) of the three quarries is described briefly, and in addition details are provided for Beauval quarry (Somme), since this provides the most complete extant example of the phosphatic chalk lithofacies, and is the source of much of the comparative material.

Hardivillers quarry (Oise) x 593,22 y 213,74 z 120. A large complex of abandoned quarries lying 1·5 km north-east of the village of Hardivillers, north of the N30 between Hardivillers and Breteuil. Although mentioned by a number of authors (Buteux 1849; Lasne 1890, 1892; de Mercey 1887; Meunier 1891; de Grossouvre 1901, 1907; Tabatabaï 1977), little has been published on the succession. The quarries expose a 4–12-m-thick bed of phosphatic chalk resting on top of a strongly indurated and mineralized basal hardground. The succession may be divided conveniently into three units: a lower white chalk, a phosphatic chalk, and an upper white chalk. Two



TEXT-FIG. 1. Location and lithostratigraphy of phosphatic chalk localities referred to in the text. The solid lines are the limit of the Upper Cretaceous outcrop.

major biostratigraphical marker horizons are present within the phosphatic chalk: a lower 30-cm bed of abundant *O. pilula*, termed the Hardivillers Offaster Bed, and an upper 1-m-thick bed with abundant *G. q. quadrata*, termed the Hardivillers Gonioteuthis Bed. The bulk of material considered in this paper originates from the latter bed which yielded 270 specimens (OUM KZ6001–KZ6270), of which 136 were complete guards.

Ribemont quarry (Aisne) *x* 193,47 *y* 340,63 *z* 90, A small, intermittently worked quarry, 2 km south-east of Ribemont village. The quarry is situated off the minor road leading to 'la Férme à Chaux', south of the D12 which links Ribemont to Villers-le-Sec. The site was described by Rabelle (1893, 1902) who noted the abundance of *G.* ex gr. *quadrata* in the upper part of the section. The locality has never been worked for phosphorite but exposes three thin beds of phosphatic chalk intercalated within the soft, white, flintless chalk which forms the bulk of the sequence. The 'population', which originates from the uppermost phosphatic chalk, consists of 174 specimens (OUM KZ6281–KZ6455), of which seventy-three are near-complete guards. The sediment log (text-fig. 1) illustrates the considerable relief (up to 1.5 m) on the Ribemont Gonioteuthis Hardground, a strongly lithified and mineralized hardground which underlies the uppermost phosphatic chalk. The hardground has a bow-shaped cross-section in the central upper portion of the quarry face, which is interpreted as a synsedimentary depression in the surface of the hardground.

Villers-devant-le-Thour quarry (Ardennes) *x* 725,35 *y* 201,50 *z* 100. An intermittently worked quarry 1·5 km west-south-west of Villers-devant-le-Thour, on the south side of the D18 which joins the village to the N366. The locality is referred to by de Grossouvre (1901, p. 126), Broquet (1973), and Guérin, Maucorps, Solau, and Pomerol (1977) but no details are given. The exposure consists of 8·5 m of soft white chalk (text-fig. 1), which includes a 1-m-thick bed of phosphatic chalk towards its top. The phosphatic chalk contains abundant oyster and fish debris, frequent pectinids, and *Gonioteuthis*. The bed cuts down and thickens to nearly 2 m towards the eastern side of the quarry. Here, at its base, a 50-cm unit of large (up to 10 cm) phosphatized intraclasts and abundant *G.* ex gr. *quadrata* provides the source of the sixty nine guards (OUM KZ6480–KZ6549), including twenty four near-complete examples, analysed in this paper.

Beauval quarry (Somme) *x* 599,89 *y* 266,80 *z* 130. A large quarry on the east side of the N16, 6 km due south of Doullens and on the east side of Beauval village. Beauval is probably the best documented of all phosphatic chalk localities (Buteux 1849; Meunier 1888; de Mercey 1890; Lasne 1890, 1892, 1902; de Grossouvre 1901; Briquet 1902; Negre 1912, 1963; Tabatabaï 1977; Jarvis 1980) but despite the wealth of literature, little stratigraphical information is available, except for Tabatabaï's (1977) foraminiferal zonation. The site displays two major levels of phosphatic chalk (text-fig. 1) both resting on top of well-developed hardgrounds. The upper phosphatic chalk contains the Beauval Offaster Bed and Beauval Gonioteuthis Bed, similar to those seen at Hardivillers, towards its top. Specimens of *Gonioteuthis* have been collected from throughout the sequence, but are scarce except in the phosphatic chalk which directly overlies the upper basal hardground and the Beauval Gonioteuthis Bed itself. Insufficient well-preserved material was available for statistical analysis, but the site provides important comparative material.

Other sites. Three other specimens are included in the comparative diagrams. One (KZ6601) originates from a minor phosphatic chalk intercalated within the upper white chalk at Faucouzy quarry (Aisne) (*x* 691,75 *y* 233,63 *z* 129). The other two (KZ6788, KZ6801) come from the phosphatic chalk which directly overlies the basal hardground at Nurlu quarry (Somme) (*x* 647,65 *y* 254,60 *z* 140).

Belemnite biostratigraphy. Four genera of belemnite occur in the Santonian–early Campanian deposits of the Anglo-Paris Basin. These are *Actinocamax* Miller, 1829, *Belemnellocamax* Naidin, 1964, *Gonioteuthis* Bayle, 1879, and *Belemnitella* d'Orbigny, 1840. Of the four genera, *Belemnitella* is restricted to one species (*B. praecursor* Stolley), *Belemnellocamax* to one group (*B.* ex gr. *grossouvrei* (Janet)), and *Actinocamax* also to one species (*A. verus* Miller). The genus *Gonioteuthis*, on the other hand, is represented by an evolutionary lineage of six species and is consequently the most stratigraphically useful of the four genera.

Gonioteuthis has been studied in detail by Stolley (1897, 1916, 1930), Ernst (1963*a*, *b*, 1964, 1966, 1968), Ernst and Schultz (1974), and Christensen (1971, 1973, 1975*a*, *b*). The genus includes the evolutionary lineage *G. westfalica* (Schlüter) (oldest), *G. westfalicagranulata* (Stolley), *G. granulata* (Blainville), *G. granulataquadrata* (Stolley), *G. quadrata quadrata* (Blainville), and *G. q. gracilis* (Stolley) (youngest), and is an outstanding example of phyletic gradualism (Christensen 1976*b*). The

Gonioteuthis stock extended from the middle Coniacian to the top of the early Campanian, a period of some 10 million years (Van Hinte 1976). The genus shows three main trends during its evolution:

(1) Progressive calcification of the anterior portion of the guard, which evolves from a convexly conical, flat, or shallow alveolus in *G. westfalica* to a deep pseudoalveolus constituting up to one-third of the length of the guard in specimens of *G. q. quadrata*.

(2) The development of granulation, which is non-existent or poorly developed in specimens of *G. westfalica*, but is pronounced in *G. granulata* and stratigraphically younger species.

(3) Increasing size and stoutness of the guard, which reaches a maximum with *G. granulataquadrata* and early forms of *G. q. quadrata*.

G. westfalica is further isolated from the other species by its greater variation in guard shape and oval to pointed anterior cross-section, as compared to sub-rectangular to sub-quadrate in later species. The evolution of *G. q. gracilis* during the latest early Campanian marks a reversal of some of the general trends, with the return of slimmer, shorter guards and more shallow pseudoalveoli. The species does, however, remain distinct by the continued prominence of granulation and the presence of a notched pseudoalveolus (Ernst *in* Christensen 1975*a*, p. 37).

De Grossouvre (1894, 1899, 1901, 1907) suggested a threefold division of French phosphatic chalks based on his observations at Hardivillers. He dated the lowest phosphatic chalk at that locality as early Santonian (*Micraster coranguinum* Zone), a conclusion which is consistent with the foraminiferal evidence (Biozone e, Tabatabaï 1977). His lower unit was typified by *M. coranguinum* (Leske) and *A. verus*, the middle unit by *G.* ex gr. *quadrata* and *O. pilula*, and the upper unit by *G.* ex gr. *quadrata* and *B.* '*mucronata*'. The overlying upper white chalk also contains the latter two species together with *M. pseudoglyphus* de Grossouvre (de Grossouvre *op. cit.*).

I have confirmed this general classification, with some additional details. *G. granulata* has previously been identified from a small number of localities (Leriche 1908) and certainly this belemnite is present in the lowest phosphatic chalk at Beauval and Nurlu; furthermore, fragments of *Gonioteuthis* have been collected from a similar level at Hardivillers. De Grossouvre's record of *B. mucronata* (Schlotheim) is regarded as a misidentification of *B. praecursor* (Pl. 115, figs. 1–3, 9), which forms a minor element of the belemnite fauna in the Hardivillers Gonioteuthis Bed (3%) and in the uppermost phosphatic chalk at Ribemont (4%).

A. verus (Pl. 115, figs. 10–13) is the commonest belemnite in the lowest phosphatic chalk at Beauval, Hardivillers, and Nurlu, but proportions and relative abundancies vary. At Nurlu fifty fragments and seven complete *A. verus* (KZ 6733–6738, KZ6763; Pl. 115, figs. 10, 11), and a well-preserved guard of *G. granulata* (KZ6788; Pl.115, fig. 7) were collected from the lag on top of the basal hardground, yet at Beauval despite the larger fauna collected, no belemnites were found in the basal lag. In the lowest phosphatic chalk at Beauval, however, five specimens of *A. verus* (KZ6552–6556; Pl. 115, figs. 12, 13) and one *G. granulata* (KZ6551; Pl. 115, figs 4–6, 8) were recovered. *Belemnellocamax* ex gr. *grossouvrei* has been described from phosphatic chalks (de Grossouvre 1894, 1899, 1901, 1907; Leriche 1908, 1911), but despite the collection of several hundred belemnites, no examples of this species were recovered by the author. De Grossouvre (op. cit.) suggests that this belemnite is typical of the lower portions of phosphatic chalks.

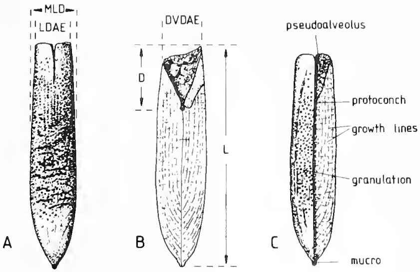
BIOMETRY OF *GONIOTEUTHIS* FROM PHOSPHATIC CHALKS

Statistical methods

The variation within belemnite 'populations' and their identification has been based on a series of univariate and bivariate statistics, histograms, and scattergrams similar to those applied by Christensen (1970, 1971, 1973, 1974, 1975*a*, 1976*a*) and Christensen, Ernst, Schmid, Schulz, and Wood (1975). Most statistical parameters were calculated utilizing an SPSS (Statistical Package for the Social Sciences) version 7 package on an ICL 2980 computer at the University of Oxford.

Guard morphology. The following characters (text-fig. 2) were measured: total length of guard (L), depth of the pseudoalveolus (D), dorso-ventral diameter at the alveolar end (DVDAE), lateral diameter at the alveolar end

TEXT-FIG. 2. Diagram showing the morphological elements of the *Gonioteuthis* guard. A, ventral view. B, left lateral view of a ground guard. C, cut-away dorsal view. MLD = maximum lateral diameter; LDAE = lateral diameter at the alveolar end; D = depth of the pseudoalveolus; L = length of guard; DVDAE = dorso-ventral diameter at the alveolar end.

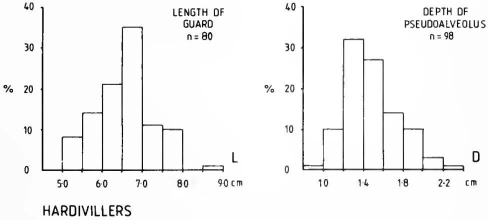


(LDAE), and maximum lateral diameter (MLD). Measurements were made with a vernier caliper to an accuracy of 0·1 mm. A number of other parameters, e.g. length of ventral fissure, have been measured by previous authors, but these have been found to be of little taxonomic value and have therefore been omitted. A small number of specimens were split to study the internal characteristics of the guard (method in Christensen 1971, p. 370), but since internal characters are of limited diagnostic use in the genus *Gonioteuthis*, no measurements were made on split material.

Univariate analysis. The following statistics were estimated: arithmetic mean ($\bar{X}$), standard deviation (SD), and coefficient of variation (CV). Histograms of two of the five characters (L, D) are shown in text-fig. 3. The frequency distributions were tested for normality using the Kolmogorov-Smirnov one sample test for goodness of fit. Clearly the univariate statistics of 'size' parameters can be effected by a large number of factors including sampling bias and *post-mortem* sorting; furthermore, a sample often contains an indeterminate number of juveniles (cf. Kermack 1954, p. 391) and in belemnites, as in Recent coleoids (Cousteau and Diolé 1973, p. 93), there are no criteria for determining the ontogenetic stage of an individual (Christensen 1975*a*). Nevertheless, the values may be of interpretative value, although bivariate statistics are regarded as being of greater taxonomic significance.

Ratios. Ratios of 'size' parameters have been widely used in the study of belemnites. Ernst (1963*a*, *b*, 1964, 1966, 1968), in particular, characterized his samples of *Gonioteuthis* by mean values of various ratios, the most diagnostic of which were the Riedel-Quotient (ratio of length of guard to depth of pseudoalveolus) and the Schlankheits-Quotient (ratio of length of guard to dorso-ventral diameter at the alveolar end). Numerous authors (e.g. Shaw 1956; Simpson, Roe, and Lewontin 1960; Sokal 1965; Sokal and Rohlf 1969) have criticized the use of ratios. The main objections are that a ratio is a secondary statistic with greater variance than either of its components, that ratios may not be normally distributed, and lastly that if the relationship between the two characters is allometric, the ratio will change during growth. Despite these mathematical limitation, Ernst's *Gonioteuthis* stratigraphy based on mean Riedel-Quotient is generally valid, since the relationship between length of guard and depth of pseudoalveolus is isometric in nearly all samples of *Gonioteuthis* (Christensen 1975*a*, *b*), and furthermore the ratio has been found to be approximately normally distributed in the present study. Consequently, Riedel-Quotients (RQ) are reported for each sample.

TEXT-FIG. 3. Histograms of length of guard (L) and depth of pseudoalveolus (D) of *Gonioteuthis* from the Hardivillers Gonioteuthis Bed.



Bivariate analysis. The five 'size' parameters and the Riedel-Quotients were correlated utilizing Pearson Correlation Matrices. Regression analysis was used to study the relationship between variable pairs during growth. Regression lines were fitted by the least-squares method primarily because of the ability to compare the slope and intercept of different samples (see Christensen 1973, pp. 115, 116 for discussion). The regression line is written $y = a+bx$ and the original measurements were used because of their rectilinear trend on arithmetically scaled scatter-plots. The following statistical parameters were calculated: the percentage of variance explained by the linear relationship (r^2), the standard error of the y-intercept (SE_a), the standard error of the slope (SE_b), the standard error of the regression line (SE_{yx}), and the value of t (t_a), and the associated probability was calculated by t-testing the intercept on the y-axis to determine whether the intercept differed significantly from zero (Hald 1957). This final test has important biological implications since only a regression line passing through the origin represents isometric growth (i.e. $y = bx$). Other possible equations ($y = a+bx$; $y = bx^a$) represent allometric growth (the latter equation is often referred to as simple allometry, e.g. Christensen 1975*a*). The regression lines were compared with each other, and with comparable 'populations' from Germany, by the methods described by Hald (1957, pp. 571–579).

Results

The results of the univariate statistical analyses of the three 'populations' are given in Table 1. Although histograms of the various 'size' parameters show a slight assymmetry (text-fig. 3), statistical analysis utilizing the Kolmogorov-Smirnov one-sample test (Table 2) shows that all characters in all three 'populations' correspond well to a normal distribution. It was noted, however, that the probability associated with the length of guard for the Ribemont 'population' was considerably lower than that for the other two samples. Although no further specimens were available for detailed measurement, two parameters, length of guard and maximum lateral diameter, could be measured to a lower precision ($\pm$ 0·25 and $\pm$ 0·05 cm respectively) on a further forty-three guards. The resulting histograms (text-fig. 4) are strongly bimodal, a K-S test giving D statistics of 0·1958 ($P = 0{\cdot}03$) and 0·1891 ($P = 0{\cdot}04$) respectively, both of which are significant at the 0·05 level. The mean length of the guards studied in detail from Ribemont is 6·30 cm, a value which lies in the trough between the two modes of the larger sample, indicating that the 'population' studied in detail is a mixture of two distinct components.

EXPLANATION OF PLATE 115

Figs. 1–3. *Belemnitella praecursor* Stolley, from the Hardivillers Gonioteuthis Bed, early Campanian, *Offaster pilula* Zone. The anterior portion of the guard KZ6272 is missing. 1—dorsal, 2—left lateral, 3—ventral views, all × 1.

Figs. 4–6 *Gonioteuthis granulata* (Blainville). Lower phosphatic chalk, Beauval, early–middle Santonian, *Micraster coranguinum* Zone. The specimen is coated in a thin shiny phosphate patina, typical of basal lag preservation. Granulation is minimal. KZ6551. 4—dorsal, 5—left lateral, 6—ventral views, all × 1.

Fig. 7. *Gonioteuthis granulata* (Blainville). Base of phosphatic chalk, Nurlu, early–middle Santonian, *M. coranguinum* Zone. Anterior end of specimen KZ6788 with a pronounced rhombohedral anterior cross-section. Note the concentric growth rings, × 1·5.

Fig. 8. *Gonioteuthis granulata* (Blainville). Anterior view of KZ6551 (figs. 4–6). The guard has a circular cross-section. Note the shallow pseudoalveolus, × 1·5.

Fig. 9. *Belemnitella praecursor* Stolley. Uncoated right lateral view of KZ6272 (figs. 1–3). The specimen is honeycombed by *Entobia cretacea* Portlock, a clionid sponge boring. The fine (0·15–0·50 mm) surface pores can be seen in figs. 1–3, × 1.

Figs. 10–13. *Actinocamax verus* Miller. Base of phosphatic chalk, Nurlu (10, 11) and lower phosphatic chalk, Beauval (12, 13). Early–middle Santonian *M. coranguinum* Zone. 10, KZ6738, left lateral view of a juvenile guard, × 2. 11, KZ6736, left lateral view of an adult guard, × 2. 12, left lateral and 13, ventral views of a large specimen, KZ6556. Note surface wrinkling and tapering, pyramidal anterior termination to the guard, × 2.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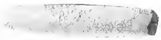
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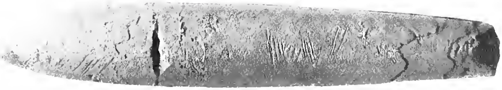
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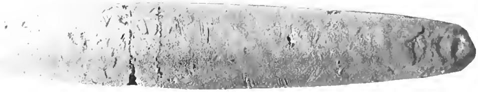
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JARVIS, Cretaceous belemnites

All three samples, like *Gonioteuthis* 'populations' collected from other facies (e.g. Christensen 1974, p. 5; 1975, p. 32), are presumably an accumulation of several generations and consist of a growth series which both juveniles and adults (Pl. 116, figs. 1–15). The approximation of the length of guard size-distributions to normality results in mean length roughly corresponding to the size which most specimens had reached when they died. This is not true of the Ribemont sample, which shows two mortality peaks—around 5·0 and 6·8 cm. The second of these two maxima approximates to the mortality peaks of the 'populations' from Hardivillers and Villers-devant-le-Thour (Table 1) and from the early Campanian *O. pilula* Zone of south-west Münsterland (Ernst 1964, p. 126); material from Höver (Lower Saxony) (Ernst 1964, p. 132) has a lower mean length, approximately 6 cm, at this level. Comparisons with Ernst's results must be treated with caution, however, since he sorted out specimens of less than 4 cm length.

TABLE 1. Univariate analyses of the 'size' parameters of three 'populations' of *Gonioteuthis* from phosphatic chalks.

HARDIVILLERS

Character	N	$\bar{X}$	σ	CV	OR
L	80	6·537	0·701	10·72	5·00–8·67
D	98	1·475	0·257	17·42	0·93–2·26
DVDAE	94	1·032	0·158	15·31	0·71–1·45
LDAE	94	0·955	0·148	15·50	0·63–1·37
MLD	86	1·099	0·168	15·29	0·74–1·61
RQ	79	4·437	0·531	11·97	3·38–6·08

RIBEMONT

Character	N	$\bar{X}$	σ	CV	OR
L	12	6·303	0·678	10·76	5·43–7·21
D	10	1·608	0·322	20·02	1·15–2·11
DVDAE	5	1·162	0·134	11·53	1·05–1·38
LDAE	9	1·091	0·140	12·83	0·87–1·29
MLD	12	1·148	0·159	13·85	0·90–1·40
RQ	10	4·038	0·539	13·35	3·33–4·92

VILLERS-DEVANT-LE-THOUR

Character	N	$\bar{X}$	σ	CV	OR
L	8	6·749	0·603	8·93	5·94–7·62
D	10	1·649	0·300	18·19	1·23–2·05
DVDAE	9	1·256	0·196	15·61	0·91–1·52
LDAE	10	1·134	0·164	14·46	0·83–1·35
MLD	9	1·194	0·155	12·98	0·97–1·39
RQ	8	4·074	0·445	10·92	3·59–4·88

The smallest guard for which detailed measurements were obtained comes from Hardivillers and has an over-all length of 5 cm (Pl. 116, figs. 5–7); the smallest specimens from Ribemont lie within the range 3·5–4·0 cm. A number of guards with damaged pseudoalveoli and lengths of < 5 cm were also collected from Hardivillers, but the proportion of individuals within this size range is small. The rarity of small guards in most samples and the total absence of guards of less than 3·5 cm length may be attributed to the interaction of low juvenile mortality rate and high initial growth-rate. Such an interaction will also control the shape of the size-frequency distributions (Craig 1967; Surlyk 1972).

TABLE 2. Results of the Kolmogorov-Smirnov test for goodness of fit to a normal distribution for three 'populations' of *Gonioteuthis* from phosphatic chalks.

HARDIVILLERS

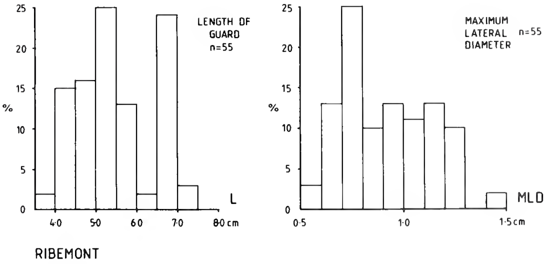
Character	N	D	Probability
L	80	0·0620	0·92
D	98	0·0783	0·59
DVDAE	94	0·0777	0·62
LDAE	94	0·0863	0·49
MLD	86	0·0559	0·95
RQ	79	0·1033	0·37

RIBEMONT

Character	N	D	Probability
L	12	0·2480	0·45
D	10	0·1384	0·99
DVDAE	5	0·2175	0·97
LDAE	9	0·1984	0·87
MLD	12	0·1075	1·00
RQ	10	0·1701	0·94

VILLERS-DEVANT-LE-THOUR

Character	N	D	Probability
L	8	0·1964	0·92
D	10	0·1324	1·00
DVDAE	9	0·1075	1·00
LDAE	10	0·0933	1·00
MLD	9	0·1395	1·00
RQ	8	0·2534	0·68



TEXT-FIG. 4. Histograms of length of guard (L) and maximum lateral diameter (MLD) of *Gonioteuthis* from the phosphatic chalk overlying the Ribemont Gonioteuthis Hardground.

The means of 'size' parameters of samples of *Gonioteuthis* have been used successfully for the analysis of time trends in evolutionary lineages (Ernst 1964), and similar studies have been applied to *A. verus* (Reyment and Naidin 1962), but such studies are only viable with normally distributed characters. Since the mortality peak for early Campanian *Gonioteuthis* is apparently between 6·5 and 6·8 cm length, the lower mortality peak of the Ribemont sample requires explanation. There are several possible interpretations which include:

(1) the peaks represent different species;
(2) 'size' parameter distributions are normally bimodal for 'populations' of *Gonioteuthis*;
(3) the 'population' has been current sorted or;
(4) the bimodality is the result of a catastrophic event.

There is no morphological evidence to support the occurrence of more than one species of *Gonioteuthis* within the Ribemont 'population'; however, stratigraphically close but specifically distinct *Gonioteuthis* 'populations' would, once mixed, be impossible to separate on morphological criteria alone. No *Gonioteuthis* 'population' has been described with a mean length as low as 5 cm and with appropriate mean Riedel-Quotient, but it should be noted that the value for *G. q. gracilis* from Misburg (Ernst 1964) does approach this value. Thus the possibility of specific mixing in the Ribemont phosphatic chalk cannot be totally dismissed although it is unlikely in my opinion.

Bimodality of 'size' parameters may result from annual or biannual mortality peaks of a species, but since no other 'populations' exhibit a bimodal distribution it must be concluded that such an explanation is invalid. Current sorting may lead to a reduction rather than an enhancement of the proportion of juveniles within a population, but transport of smaller individuals into the area of deposition remains a possibility. Bimodal distributions of this type frequently result from catastrophic events which cause the death of abnormally young 'populations', which are overprinted on the normal mortality curves. A storm deposit is the commonest example although Red-Tides provide a further possibility; the concentration of fauna into what is apparently a depression in the hardground accords most favourably with the storm-event hypothesis.

On the basis of univariate analysis the samples of *Gonioteuthis* from Hardivillers and Villers-devant-le-Thour may be considered homogenous, while the 'population' from Ribemont is heterogenous. Consequently, interpretations made from the bivariate analysis of the small number of complete specimens available from this latter locality can only be regarded as tentative.

Ratios. In general, ratios have not been utilized in this study but the validity of the Reidel-Quotient is recognized (see above) as a method of species discrimination in specimens of *Gonioteuthis*. Mean values of the Quotient for all three 'populations' (Table 1) lie within the range of values for *G. q. quadrata* (Ernst 1964, 1968), but individual specimens from Hardivillers (Pl. 156, figs. 1–15) may be referred to *G. granulata* (one specimen only), *G. granulataquadrata*, *G. q. quadrata*, or *G. q. gracilis*. Specimens from the other two localities may all be identified as either *G. granulataquadrata* or *G. q. quadrata* (or possibly *G. q. gracilis*). This range of possible 'species' within a single bed illustrates the importance of the study of 'populations' rather than individuals for the reliable identification of *Gonioteuthis* species.

Regression analysis. All five 'size' parameters and the Riedel-Quotient were compared by means of Pearson correlation matrices (Table 3). The correlation coefficients for the Hardivillers 'population' were all highly significant ($P < 0{\cdot}001$) except for the correlation between L and RQ which was less significant ($P < 0{\cdot}03$). Probabilities associated with matrices from the other localities were generally higher, although all correlations remained significant at the 0·05 level in the Villers-devant-le-Thour sample, and only probabilities associated with RQ were not significant at this level for the Ribemont sample.

Since all five 'size' parameters are very closely related, four regression analyses were made for each 'population'. The plots chosen follow the useage of Christensen (1975*a*):

(1) length of guard (x) versus depth of pseudoalveolus (y);
(2) length of guard (x) versus dorso-ventral diameter at the alveolar end (y);

(3) dorso-ventral diameter at the alveolar end (x) versus lateral diameter at the alveolar end (y);
(4) maximum lateral diameter (x) versus lateral diameter at the alveolar end (y).

With three exceptions (Table 5) the relationships of the characters in the twelve analyses were isometric.

Length of guard (x) *versus depth of pseudoalveolus* (y). A regression analysis of these two characters provides an analogous but more comprehensive quantity than Ernst's Riedel-Quotient and is specifically the most diagnostic of the four regression analyses, partly because of the greater number of comparative analyses in the literature (e.g. Christensen 1971, 1973, 1975*a*). Christensen (1975*a*) has published regression analyses of Ernst's (1964, 1968) original measurements of six species of *Gonioteuthis*. The statistical parameters for these six 'populations' are given in Table 4 and the regression lines are plotted on the relevant scattergrams (text-figs. 5–7).

Hardivillers. The statistical parameters are given in Table 5 and the values plotted on text-fig. 5A. The 'population' was compared to *G. granulataquadrata* and was found to differ significantly in slope ($0\cdot01 > P > 0\cdot001$). A comparison with *G. q. quadrata* from the early Campanian *Inoceramus* ex gr. *lingua-G.* ex gr. *quadrata* Zone of Höver gave a highly significant correlation between slopes ($0\cdot70 > P > 0\cdot60$), but the position of the lines are different ($P < 0\cdot001$). However, when compared with a stratigraphically younger 'population' of the same species (from the *Echinocorys conica-Galeola papillosa* Zone), the variances, slopes

TABLE 3. Pearson correlation matrices of the 'size' parameters of three 'populations' of *Gonioteuthis* from phosphatic chalks.

HARDIVILLERS

	L	D	DVDAE	LDAE	MLD	RQ
L	1·000	—	—	—	—	—
D	0·763	1·000	—	—	—	—
DVDAE	0·839	0·808	1·000	—	—	—
LDAE	0·825	0·810	0·980	1·000	—	—
MLD	0·814	0·711	0·955	0·940	1·000	
RQ	−0·219	−0·786	−0·434	−0·426	−0·334	1·000

RIBEMONT

	L	D	DVDAE	LDAE	MLD	RQ
L	1·000	—	—	—	—	—
D	0·773	1·000	—	—	—	—
DVDAE	0·870	0·923	1·000	—	—	—
LDAE	0·817	0·785	0·985	1·000	—	—
MLD	0·800	0·631	0·992	0·952	1·000	—
RQ	−0·344	−0·850	−0·877	−0·530	−0·287	1·000

VILLERS-DEVANT-LE-THOUR

	L	D	DVDAE	LDAE	MLD	RQ
L	1·000	—	—	—	—	—
D	0·916	1·000	—	—	—	—
DVDAE	0·720	0·854	1·000	—	—	—
LDAE	0·794	0·900	0·970	1·000	—	—
MLD	0·916	0·900	0·946	0·959	1·000	—
RQ	−0·717	−0·931	−0·853	−0·943	−0·906	1·000

TABLE 4. Statistical relationship between depth of pseudoalveolus and length of guard for six species of *Gonioteuthis* from Germany. $y = a+bx$ (modified from Christensen 1975*a*).

G. westfalica westfalica from the lower 'westfalica beds', Essen-Vogelheim (Ernst 1964*a*, p. 118; Christensen 1975*a*, p. 38)
$D = 0·1150+0·0597\ L$; $N = 196$; $r = 0·2826$; $r^2 = 7·99\%$; $SE_a = 0·0828$; $SE_b = 0·0145$; $SE_{yx} = 0·1089$; $t_a = 1·3882$ $(0·20 > P > 0·10)$

G. westfalicagranulata from Bülten (Ernst 1968, p. 278; Christensen 1975*a*, p. 38
$D = 0·0102+0·1106\ L$; $N = 51$; $r = 0·4809$; $r^2 = 23·13\%$; $SE_a = 0·1611$; $SE_b = 0·0279$; $SE_{yx} = 0·1146$; $t_a = 0·0633$ $(P > 0·90)$

G. granulata from Gleidingen (Ernst 1968, p. 278; Christensen 1975*a*, p. 38)
$D = 0·0701+0·1299\ L$; $N = 45$; $r = 0·7311$; $r^2 = 53·45\%$; $SE_a = 0·0920$; $SE_b = 0·0185$; $SE_{yx} = 0·1083$; $t_a = 0·7620$ $(0·50 > \mathrm{P} > 0·40)$

G. granulataquadrata from Weinberg (Ernst 1968, p. 278; Christensen 1975*a*, p. 38)
$D = 0·1030+0·1760\ L$; $N = 45$; $r = 0·7404$; $r^2 = 54·82\%$; $SE_a = 0·1623$; $SE_b = 0·0244$; $SE_{yx} = 0·1370$; $t_a = 0·6342$ $(0·60 > P > 0·50)$

G. quadrata quadrata from the *I.* ex gr. *lingua*-*G.* ex gr. *quadrata* Zone of Höver (Ernst 1964*a*, p. 119; Christensen 1975*a*, p. 39)
$D = -0·0888+0·2685\ L$; $N = 24$; $r = 0·7982$; $r^2 = 63·71\%$; $SE_a = 0·2640$; $SE_b = 0·0432$; $SE_{yx} = 0·2166$; $t_a = 0·3364$ $(0·80 > P > 0·70)$

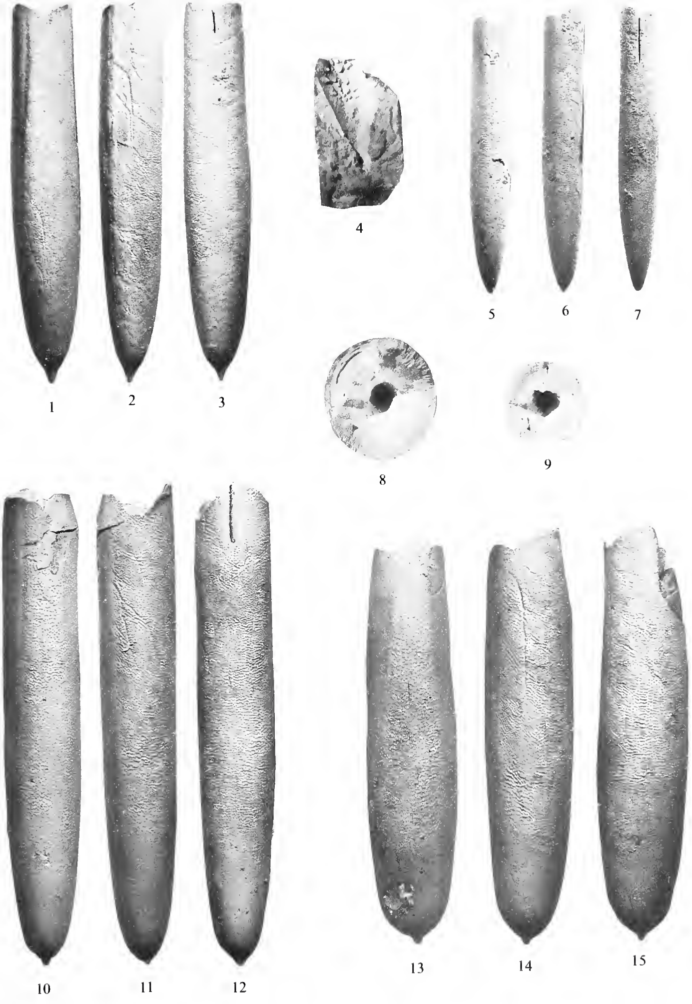
G. quadrata quadrata from the *E. conica*-*G. papillosa* Zone of Höver (measurements by Ernst, statistics after W. K. Christensen, pers. comm.)
$D = -0·3776+0·2917\ L$; $N = 65$; $r = 0·7649$; $r^2 = 58·51\%$; $SE_a = 0·1772$; $SE_b = 0·0309$; $SE_{yx} = 0·1711$; $t_a = 2·0977$ $(0·05 > P > 0·02)$

G. quadrata gracilis from the Germania IV quarry (north Germany) (Christensen 1975*a*, p. 42)
$D = -0·7641+0·3620\ L$; $N = 47$; $r = -$; $r^2 = -$; $SE_a = 0·1820$; $SE_b = -0·0318$; $SE_{yx} = 0·1152$; $t_a = 4·1975$ $(P < 0·001)$

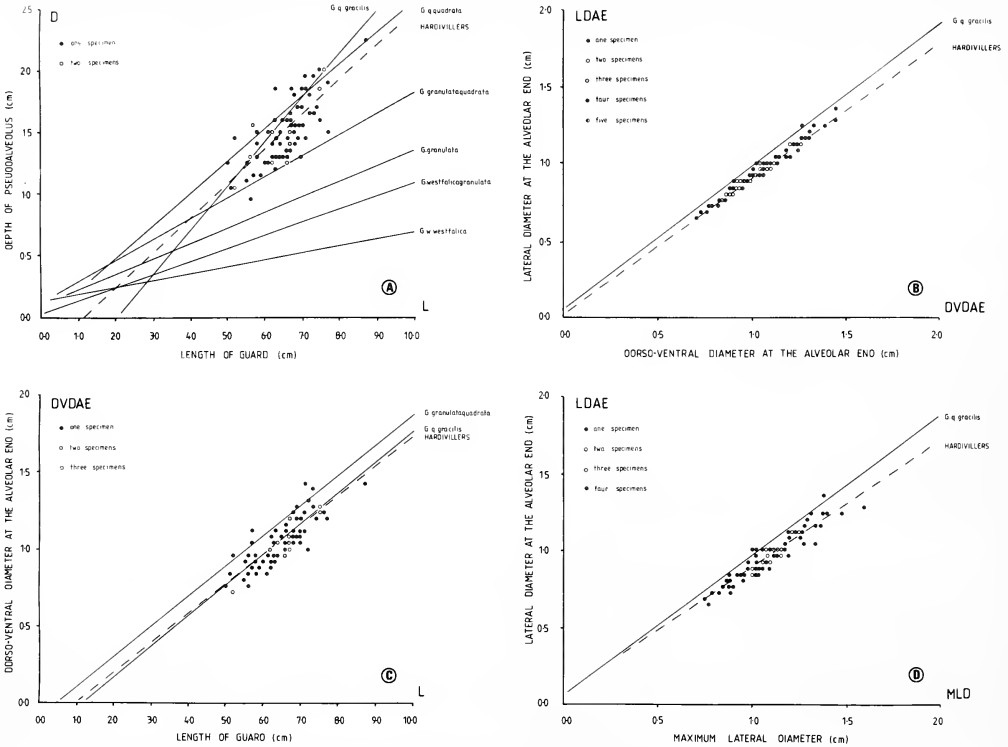
$(P > 0·90)$ and positions $(0·40 > P > 0·30)$ of the lines were found to be the same, similar results were obtained from a comparison with a 'population' of *G. q. quadrata* from the 'Smectite' of Hallembaye quarry in eastern Belgium (W. K. Christensen, pers. comm.) where *G. q. quadrata* also occurs with *B. praecursor*. When compared to *G. q. gracilis*, the variances were found to differ significantly ($F = 2·2422$ with 77 and 45 degrees of freedom; $P = < 0·01$), so the test for non-equal variances was used (Hald 1957). The correspondence between the slopes of the two lines was found to be slightly significant ($0·10 > P > 0·05$ with 106 degrees of freedom) so the positions of the lines were also tested. The test gave a probability of $0·05 > P > 0·02$ with 122 degrees of freedom, which is not significant. Clearly the regression line compares most closely with that for *G. q. quadrata* from the Hallembaye 'Smectite' and the German *E. conica*-*G. papillosa* Zone. It is noteworthy that a *t*-test on the *y*-intercept for the younger *G. q. quadrata* 'population' from Germany, *G. q. quadrata* from Belgium, and the Hardivillers 'populations' gives significant values ($0·05 > P > 0·02$), indicating an allometric relationship between the characters as seen in *G. q. gracilis* (Christensen 1975*a*).

EXPLANATION OF PLATE 116

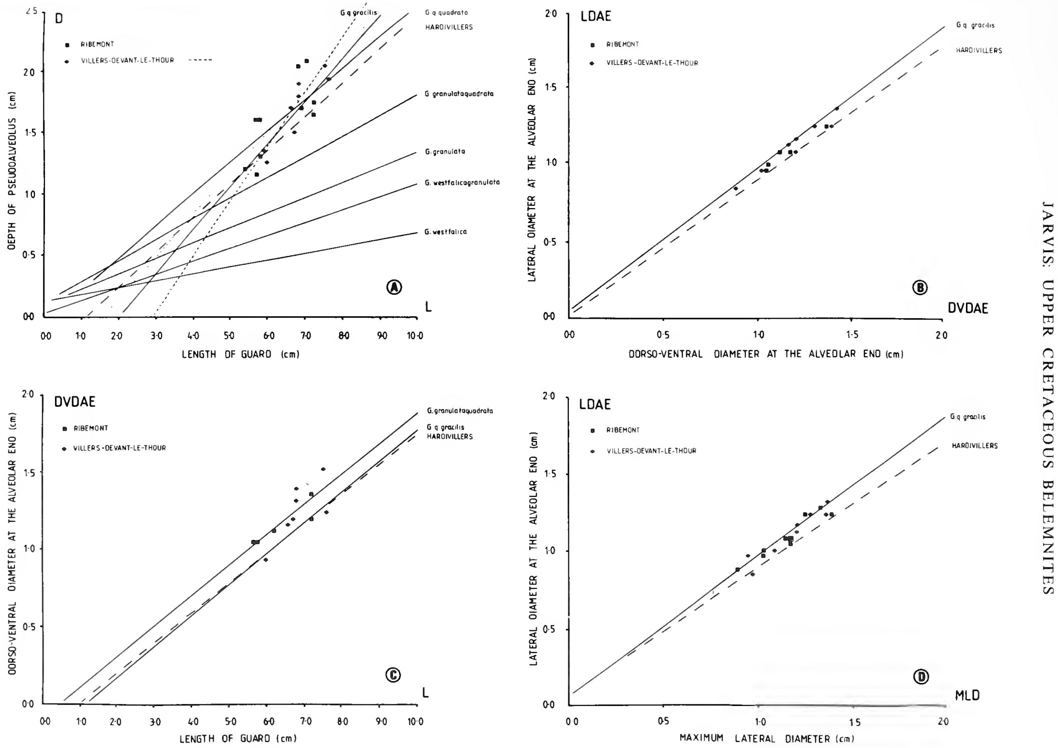
Figs. 1–15. *Gonioteuthis quadrata quadrata* (Blainville) from the Hardivillers Gonioteuthis Bed, early Campanian *Offaster pilula* Zone. 1–3, a medium-sized guard of average shape. KZ6040, dorsal, left lateral, and ventral views, × 1. 4, split anterior end of KZ6099 showing conellae, × 1. 5–7, an adolescent guard, KZ6033, the smallest complete specimen recovered from the bed, dorsal, left lateral, and ventral views, × 1. 8, anterior end of KZ6066 (figs. 13–15) showing the depth of the pseudoalveolus, × 1·5. 9, anterior end of KZ6040 (figs. 1–3) × 1·5. 10–12, the largest specimen collected, KZ6039, dorsal, left lateral, and ventral views, × 1. 13–15, the stoutest individual in the 'population', KZ6066, dorsal, left lateral, and ventral views, × 1.



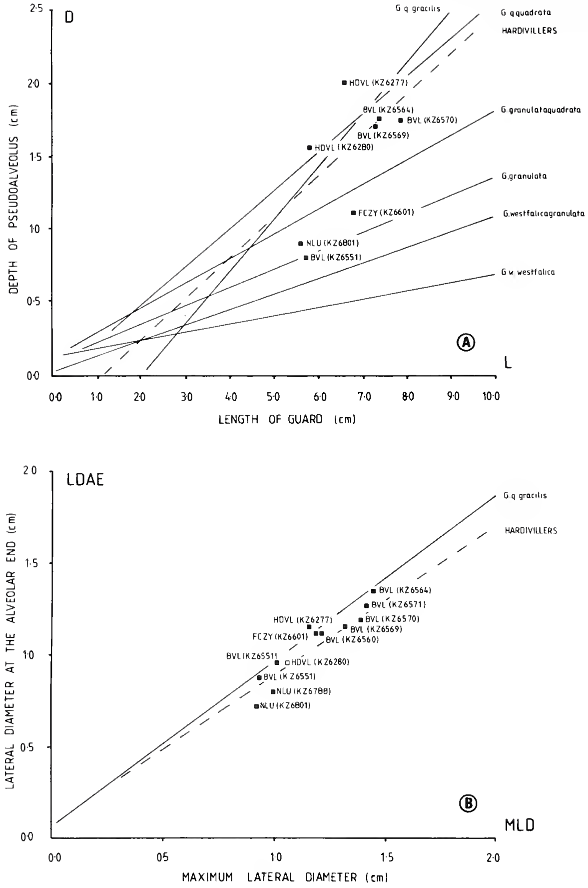
JARVIS, Cretaceous belemnites



TEXT-FIG. 5. Scatter diagrams and regression lines for *G. q. quadrata* from the Hardivillers Gonioteuthis Bed. A, length of guard (L) versus depth of pseudoalveolus (D); the regression lines of six control 'populations' from Germany (Christensen 1975*a*) are plotted for comparison (the *G. q. quadrata* line is from the older Höver 'population'). B, dorso-ventral diameter at the alveolar end (DVDAE) versus lateral diameter at alveolar end (LDAE); the regression line for *G. q. gracilis* is plotted for comparison. C, length of guard (L) versus dorso-ventral diameter at the alveolar end (DVDAE); the regression lines of *G. granulataquadrata* and *G. q. gracilis* are plotted for comparison. D, maximum lateral diameter (MLD) versus lateral diameter at the alveolar end (LDAE); the regression line of *G. q. gracilis* is plotted for comparison.



TEXT-FIG. 6. Scatter diagrams and regression lines for *G. ex gr. quadrata* from Ribemont and Villers-devant-le-Thour. The plots follow the same format as text-fig. 5.



TEXT-FIG. 7. Scatter diagrams of isolated specimens of *Gonioteuthis* collected from phosphatic chalks. A, length of guard (L) versus depth of the pseudoalveolus (D); the regression lines of the six German control 'populations' (excluding *G. q. quadrata* from the *E. conica*—*G. papillosa* Zone) and *G. q. quadrata* from Hardivillers are plotted for comparison. B, maximum lateral diameter (MLD) versus lateral diameter at the alveolar end (LDAE); the regression lines for *G. q. gracilis* from Germany and *G. q. quadrata* from Hardivillers are plotted for comparison.

Ribemont and Villers-devant-le-Thour. A comparison between the slopes and positions of the regression lines of the two 'populations' showed that they do not differ significantly ($P > 0{\cdot}40$). A comparison between the slopes of the two lines and the slope of the Hardivillers 'population' also revealed no significant differences ($0{\cdot}60 > P > 0{\cdot}50$; $0{\cdot}20 > P > 0{\cdot}10$), but a comparison between the positions of the lines indicated that although the Ribemont belemnites differed significantly from those from Hardivillers ($0{\cdot}01 > P > 0{\cdot}001$), the Villers-devant-le-Thour and Hardivillers 'populations' are apparently the same ($0{\cdot}10 > P > 0{\cdot}05$). The two samples were compared to three species of *Gonioteuthis* from Germany (text-fig. 6A) and were found to differ significantly from *G. granulataquadrata*, but could correspond with either *G. q. quadrata* or *G. q. gracilis* both in slope and position. The small number of specimens available from these two localities makes the statistical data inconclusive. Certainly the 'populations' can be assigned to *G.* ex gr. *quadrata*, but subspecific identification remains uncertain. Intuitively the 'populations' correspond more closely to stratigraphically younger 'populations' of *Gonioteuthis* (text-fig. 6A) than that from Hardivillers (text-fig. 5A).

Analytical summary and comparisons

Individual specimens from all three localities have Riedel-Quotients within the range of values typical of *G. granulataquadrata* and *G. q. quadrata*, but the mean value for all three 'populations' is within the range of *G. q. quadrata*. The high degree of scatter of values of length of guard versus depth of pseudoalveolus has led to occasionally ambiguous results, but nevertheless the Hardivillers sample shows the greatest similarity to 'populations' of *G. q. quadrata* from the Hallembaye 'Smectite' and the *E. conica–G. papillosa* Zone of Germany. Unfortunately, no further 'size' parameter regression-analyses have been published for 'populations' of *G. q. quadrata* so it has been impossible to statistically compare other parameters with control 'populations'. However, unpublished data (W. K. Christensen pers. comm.) indicate that the Hardivillers sample may be distinguished from *E. conica–G. papillosa* Zone 'populations' on plots of L *v.* DVDAE. When this additional parameter is considered the Hardivillers sample is seen to be similar to a 'population' of *G. q. quadrata* from the *I.* ex gr. *lingua–G.* ex gr. *quadrata* Zone of Ziegelei Bremer, Bottrop-Fuhlenbrock (S. Münsterland) (Ernst 1964). Unfortunately, no regression data are available for this 'population' so a more precise comparison is impossible.

G. q. quadrata from Hardivillers can be distinguished from German 'populations' of *G. granulataquadrata* on L *v.* D and L *v.* DVDAE (text-fig. 5C) and from *G. q. gracilis* on L *v.* D and MLD *v.* LDAE (text-fig. 5D). It is noteworthy that the relationship between L *v.* D, L *v.* DVDAE and MLD *v.* LDAE must be considered allometric in the sample. The Ribemont and Villers-devant-le-Thour 'populations' cannot be distinguished from one another on any character or combination of characters. Generally the values lie closer to those of *G. q. gracilis* than to those of *G. q. quadrata* from Hardivillers. This is apparent in the plots of L *v.* D, DVDAE *v.* LDAE (text-fig. 6B) and MLD *v.* LDAE (text-fig. 6D), while in the plot of L *v.* DVDAE the values are closer to those of *G. granulataquadrata*. These observations demonstrate that the *G.* ex gr. *quadrata* from these two localities have a guard morphology similar to *G. q. gracilis* but are stouter than either German *G. q. gracilis* or *G. q. quadrata* from Hardivillers. It is suggested, therefore, that these 'populations' are stratigraphically younger than those from Hardivillers but are still *G. q. quadrata*, albeit more evolved forms.

Remaining complete specimens of *Gonioteuthis* which have been collected from phosphatic chalks are plotted on text-fig. 7. In the plot of D *v.* L (text-fig. 7A) three specimens clearly lie outside the scatter of values for the three 'populations' of *Gonioteuthis* from the facies (text-figs. 5A, 6A). All three specimens are identified as *G. granulata* on their Riedel-Quotients. Two of the three (KZ6551, Pl. 115, figs. 4–6, 8; KZ6801) come from the base of phosphatic chalk sequences, while the other (KZ6601) originates from above the main phosphatic chalk at Faucouzy. Material from Beauval (BVL) on the plot of D *v.* L comes from the upper portion of the upper phosphatic chalk and it all lies very close to the regression line for the Hardivillers 'population'. The additional examples from Hardivillers (HDVL) originate from the upper white chalk. It is noteworthy that both lie in the same region of the plot as the material from Ribemont and Villers-devant-le-Thour.

The plot of LDAE *v.* MLD (text-fig. 7B) shows a high degree of scatter between the two reference regression lines. All of the material from Beauval was collected from the upper phosphatic chalk

TABLE 5. Statistical results of regression analyses of four 'populations' of *Gonioteuthis*.

HARDIVILLERS GONIOTEUTHIS BED

$y=a+bx$	N	r^2	SE_a	SE_b	SE_{yx}	t_a	Probability
D = −0·3784+0·2870 L	79	58·20%	0·1821	0·0277	0·1725	2·0775	$0·05>P>0·02$
DVDAE = −0·1974+0·1933 L	75	70·32%	0·0961	0·0147	0·0882	2·0538	$0·05>P>0·02$
LDAE = 0·0188+0·8978 DVDAE	90	96·11%	0·0202	0·0193	0·0290	0·9331	$0·40>P>0·30$
LDAE = 0·0614+0·8264 MLD	81	88·35%	0·0377	0·0338	0·0510	1·6316	$0·20>P>0·10$

PHOSPHATIC CHALK ABOVE THE RIBEMONT GONIOTEUTHIS HARDGROUND

$y=a+bx$	N	r^2	SE_a	SE_b	SE_{yx}	t_a	Probability
D = −0·5653+0·3417 L	10	59·76%	0·6343	0·0991	0·2166	0·8913	$0·40>P>0·30$
DVDAE = 0·1310+0·1604 L	5	75·54%	0·3404	0·0527	0·0768	0·3849	$0·80>P>0·70$
LDAE = 0·1894+0·7665 DVDAE	5	96·95%	0·0918	0·0786	0·0211	2·0629	$0·20>P>0·10$
LDAE = 0·0908+0·8526 MLD	9	90·55%	0·1231	0·1041	0·0459	0·7376	$0·50>P>0·40$

PHOSPHATIC CHALK, VILLERS-DEVANT-LE-THOUR

$y=a+bx$	N	r^2	SE_a	SE_b	SE_{yx}	t_a	Probability
D = −1·3240+0·4455 L	8	83·90%	0·5396	0·0797	0·1271	2·4536	$0·05>P>0·02$
DVDAE = −0·4975+0·2556 L	7	51·88%	0·7578	0·1101	0·1476	0·6565	$0·60>P>0·50$
LDAE = 0·1007+0·8331 DVDAE	9	94·01%	0·1009	0·0795	0·0440	0·9985	$0·40>P>0·30$
LDAE = −0·0287+0·9533 MLD	9	92·05%	0·1167	0·1059	0·0463	0·2459	$0·90>P>0·80$

G. q. gracilis, GERMANIA IV QUARRY, NORTHERN GERMANY (CHRISTENSEN 1975*a*)

$y=a+bx$	N	r^2	SE_a	SE_b	SE_{yx}	t_a	Probability
D = −0·7641+0·3620 L	47	—	0·1820	0·0318	0·1152	4·1975	$P<0·001$
DVDAE = −0·2428+0·2003 L	47	—	0·0693	0·0121	0·0583	3·5054	$0·01>P>0·001$
LDAE = 0·0250+0·9064 DVDAE	47	—	0·0253	0·0278	0·0290	0·9885	$0·40>P>0·30$
LDAE = 0·0506+0·9055 MLD	47	—	0·0299	0·0339	0·0351	1·6910	$0·10>P>0·05$

except KZ6551 (Pl. 115, figs. 4–6, 8) which is from the base of the lower phosphatic chalk. The Hardivillers examples are from the upper white chalk. It is clear that the specimens from Nurlu (KZ6788, Pl. 115, fig. 7; KZ6801), which are both from the base of the phosphatic chalk, lie outside the scatter of values for the three 'populations'.

Scatterplots of DVDAE *v.* L and LDAE *v.* DVDAE do not have sufficient resolution to differentiate species of *Gonioteuthis* on the small amount of comparative material available. These comparisons highlight the necessity for large collections in the identification of *Gonioteuthis* species, but they also show that material from the base of phosphatic chalks may be attributed to *G. granulata* and that this species is readily distinguished on plots of LDAE *v.* MLD as well as Reidel-Quotient and D *v.* L plots.

Factor analysis

Since factor analysis requires listwise deletion of missing values, only the 'population' from Hardivillers was regarded as being of sufficient size to enable a statistically valid application of factor analysis. A total of sixty-nine guards were utilized in the analysis, results of which are given in Table 6.

The first principal component accounts for 87·2% of the variation and possesses a strong positive correlation with all of the 'size' parameters. It is interpreted as representing guard size, which is consistent with similar results from biological studies (Blackith and Reyment 1971, pp. 147–150) and for a 'population' of *A. plenus* from England (Christensen 1974). Clearly size is intimately related to age in marine invertebrates such as belemnites, although food availability may become an overriding factor in Recent coleoids (Mangold-Wirz 1963).

The second principal component accounts for 6·8% of the total variance. It shows a strong positive correlation with D, a moderate negative relationship with MLD, and negative correlations of approximately equal magnitude with DVDAE and LDAE. The factor is consequently interpreted as representing the evolutionary stage reached by each individual within the total 'population'. It reflects the increasing depth of the pseudoalveolus combined with a progressive increase in the slenderness of the guard from the maximum robustness reached in *G. granulataquadrata*.

The third principal component only allows for 4·6% of the observed variation. It shows a strong positive correlation with L and a weak negative interrelationship of approximately equal magnitude with the remaining characters. The factor may be interpreted as a shape effect which results in the production of elongate guards. Alternatively, it may be due to an indeterminate taphonomic control, perhaps sorting of material prior to deposition.

TABLE 6. Eigenvalues and Eigenvector matrix from a principal component factor analysis of *G. q. quadrata* from the Hardivillers Gonioteuthis Bed.

Eigenvector:	1	2	3
Eigenvalue:	4·361	0·342	0·228
Variance:			
% total	87·2	6·8	4·6
cumulative	87·2	94·0	98·6
Character			
L	0·902	0·043	0·429
D	0·860	0·492	−0·125
DVDAE	0·984	−0·099	−0·097
LDAE	0·974	−0·104	−0·116
MLD	0·943	−0·279	−0·077

Calculated from a 'population' of 69 guards.

TAPHONOMY AND DEPOSITIONAL ENVIRONMENT

Some degree of taphonomic bias will inevitably be present in any fossil assemblage. Consequently it is necessary to examine and if possible remove or 'allow for' any bias before zoological or stratigraphical conclusions can be reached. Furthermore, an assemblages' taphonomy, together with its associated sedimentology, may provide valuable insights into the depositional environment of that assemblage.

The majority of guards from the Hardivillers Gonioteuthis Bed are in excellent preservation and complete. A summary of the encrustation is given in Table 7. Although pycnodonteine oysters, octocorals, and serpulids are the major encrusters, a small number of cemented foraminiferids were present on some guards. Clionid sponge borings are present in many specimens (Pl. 115, figs. 1–3, 9) but they rarely form extensive networks. A second common form of boring consists of a radiating pattern of small (<0·1 mm) ramifying bores which occur just below the surface of the guards. These may be attributed to algae or fungi. Oysters are the dominant encruster (Pl. 116, fig. 13) but only 5% of specimens bear more than two individuals, and where larger numbers are present they are generally small and have identical orientations of their hinge-lines. Only four specimens exhibit more than a single generation of encrustation, octocorals and serpulids following the pattern displayed by the oysters. The small size of the majority of the epifauna (oysters only reaching a few millimetres across) suggests that it is mostly juvenile. Examination of all specimens, including fragmentary guards, demonstrates that few, if any, show signs of mechanical abrasion, the poor preservation of the small number of broken guards being due predominately to the activities of boring sponges. Many belemnites display fine, subparallel scratch marks, (Pl. 115, figs. 12, 13; Pl. 116, fig. 13), generally oriented in a dorso-ventral direction and probably produced by the rasping action of a marine organism grazing the surface of the guards. Several guards show late-stage compactional effects, including partial crushing of their pseudoalveoli and *in situ* fracturing, occasionally accompanied by recementation of the dislocated fragments. Recent solution and partial decalcification, particularly in the area of the pseudoalveolus, has occurred in some material, but in general the guards are complete.

Specimens from the other localities display similar features to those seen in the Hardivillers sample. Most guards from Ribemont and Villers-devant-le-Thour are severely etched and corroded by weathering due to the proximity of the phosphatic chalk to the soil. Consequently, the data on the encrustation (Table 7) are less reliable for these sites. The guard from the basal lag at Nurlu (KZ6788), and hardground-associated guards from Faucouzy and Hallencourt display thin, shiny phosphate surface veneers (Pl. 115, figs. 4-6, 8) underlain by a portion of phosphatized calcite. In contrast to the opinion expressed by Tabatabaï (1977, p. 212), extensive phosphatization of belemnite guards was found to be uncommon.

TABLE 7. Summary of encrustation exhibited by three 'populations' of *Gonioteuthis* from phosphatic chalks.

Locality	Number of guards	Number encrusted (%)				
		Total	Oyster	Octocoral	Serpulid	>1 species
Hardivillers	136	53	32	31	10	20
Ribemont	73	40	30	3	6	6
Villers-devant-le-Thour	24	6	6	0	0	0

The different proportions of encrusters and encrustation are not necessarily of environmental significance since they are too readily affected by the proximity of a 'spat' source. The well-preserved nature of the guards, the juvenile stage of the majority of the epifauna, and the lack of extensive boring suggest that burial was rapid. Furthermore, the general lack of more than one generation of encrustation indicates that re-exhumation was rare. These observations have important implications concerning the environment of deposition. The sedimentology indicates that the phosphatic chalk lithofacies was a relatively high-energy environment, within which the sediment was being winnowed by current action (Jarvis 1980). Yet the taphonomy of the belemnites suggests rapid burial and lack of re-exhumation. Clearly this removes the possibility of a low sedimentation rate due to continual winnowing as this would result in the belemnites being exposed on the sea floor for extended periods. Intermittent current action with rapid winnowing events followed by periods of quiescence and burial, therefore, seems a more likely mechanism. Such a cyclic process may also explain the apparent paradox between oxic bottom waters and sediment as demonstrated by the epi- and infauna and the subsurface anoxia associated with contemporary phosphorites (Baturin and Bezrukov 1979). It can be postulated that phosphatization took place during quiescent periods, and colonization and bioturbation during times of stronger current activity.

FACIES AND ECOLOGY

The abundance of belemnites within the phosphatic chalk lithofacies *vis-à-vis* soft white chalks requires some consideration. Both *Gonioteuthis* and *A. verus* occur very frequently in shallow-water deposits situated close to ancient massifs, such as the biocalcarenites and glauconitic sands of the Balto-Scandian area (Christensen 1976). Furthermore, *Gonioteuthis* from near-shore facies are characterized by the presence of all ontogenetic stages, while 'populations' from offshore chalks only contain adult specimens (Ernst 1964). This general trend also applies to other genera of belemnites, e.g. *Belemnitella* and *Belemnella*. It must be concluded that the occurrence of juveniles in phosphatic chalk 'populations' is indicative of a near-shore and therefore shallow-water environment for the facies.

In both facies belemnites are common just below, and particularly above, hardgrounds. The formation of Chalk hardgrounds is frequently accompanied by evidence of shallower-water conditions (Bromley 1965; Kennedy 1970; Kennedy and Garrison 1975; Jarvis 1980). This explains the occurrence of hardground associated belemnites in offshore chalks, but it does not explain their concentration in the phosphatic chalk environment which is initially also presumably shallow-water (Jarvis 1980).

It has been suggested (Surlyk and Birkelund 1977) that belemnites found in offshore chalks may be considered as straying adult individuals buried outside their normal habitat. Christensen (1976) has postulated that this apparent facies control may be causally related through the food-chain. Belemnites probably preyed upon small fish, crustaceans, and cephalopods, as do their Recent relatives (Naef 1922), and such prey would be more readily available in a shallow-water environment.

The association with hardgrounds results from the interaction of two independent factors. Firstly, hardgrounds are generally regarded as representing levels of faunal condensation whether due to omission (Kennedy and Garrison 1975) or active erosion coupled with winnowing (Jarvis 1980), or a combination of both processes. Either process would be expected to result in above-average concentrations of belemnites, but the taphonomy of the material indicates that the guards were not exposed on the sea floor for extended periods. The Ribemont sample, which originates from above a hardground, does have a greater proportion of bored fragments, but the proportion is considered insufficient to confirm the condensation hypothesis. Furthermore, the bimodality of the 'population' suggests deposition following a catastrophic event rather than long-term addition of material.

The second factor is the change in ecology which would be expected after sea-floor lithification. The new environment would embrace a mixed hard-soft substrate ecosystem, which might be expected to lead to an increase in diversity, and probably increased abundance of organisms. The increase in the sea-floor dependent biota would provide a food source for animals higher in the food chain, including the fish and crustaceans which are assumed to have been the main prey of belemnites. The two factors are not mutually exclusive and undoubtedly act in concert in the majority of cases, but I consider, on taphonomic grounds, that the second of the two factors predominates in phosphatic chalks.

The Recent coleoid *Loligo opalescens* generally inhabits water depths of 120–330 m but enters shallower water for mating and at night to feed. *L. opalescens* congregates in vast numbers to mate and reproduce, after which the majority of individuals die. An estimated 20 million dead have been observed on a small area off Baja California after such an event (Cousteau and Diolé 1973). Clearly this feature of the life cycle of a Recent coleoid, similar in size and morphology to the belemnites, provides one mechanism for the formation of the so-called 'Belemnitenschlachtfeld' (Belemnite battlefield) of the literature (e.g. Naef 1922).

The Gonioteuthis beds are around 1 m thick and contain belemnites scattered throughout, although patches of larger numbers of individuals occur. The higher concentrations are not at a particular level within the Beds nor are they on top of recognizable omission surfaces. It can be postulated, therefore, that these beds are the result of a series of mass mortalities following reproduction. The reproductive cycle of *L. opalescens* has another important aspect; after mating the squids attaches its eggs to epibenthic organisms and other suitable anchorage points on the sea floor (Cousteau and Diolé 1973; Recksiek 1978). It is suggested that hardgrounds would provide a greater number of potential attachment sites than a soft substrate and would therefore be preferred as a breeding area.

It is not necessary to assume that the 'populations' of the Gonioteuthis beds were buried in the immediate area of their death. During the later stages of cuvette evolution, hardgrounds would be concentrated at the cuvette margins, where areas of lithified white chalk remained uncovered. These areas would provide preferred living/breeding sites for belemnites but, on death, individuals would be swept into the central portions of the cuvette and deposited. Subsequent bioturbation would remove the identity of individual mortality events and tend to disseminate guards throughout an interval of sediment. A further factor to be considered is the suggestion (Jarvis 1980) that phosphatic chalk formation was in part the result of upwelling of deep ocean water in the Anglo-Paris Basin, which provided the quantities of phosphate necessary for the deposition of such extensive phosphorites. Such an increase in orthophosphate would undoubtedly lead to higher plankton abundances which, as the base of the marine food-chain would result in increased numbers of higher animals including belemnites.

The Gonioteuthis beds occur at the top of the phosphatic chalks and perhaps represent an acme prior to the change in environment which resulted in the cessation of phosphatic chalk deposition. Such an acme might result from any of the factors discussed when considering the range of *A. verus* in phosphatic chalks (see below).

STRATIGRAPHICAL AND ENVIRONMENTAL CONTROLS

The facies model does not explain all aspects of the occurrence of belemnites in phosphatic chalks. The best-developed hardgrounds are at the base of phosphatic chalks, yet no basal hardground shows the concentration of *Gonioteuthis* guards typical of hardgrounds higher in the sequences. *A. verus* ranges from the Santonian to the early Campanian in Yorkshire (Jukes-Browne and Hill 1904; Wright and Wright 1942), Norfolk (Peake and Hancock 1961), and Germany (Schmid 1956; Ernst 1963*a*), but in southern England (Rowe 1901; Jukes-Browne and Hill 1904; Griffith and Brydone 1911) and northern France (de Grossouvre 1899) the species is apparently restricted to the Santonian, being particularly characteristic of the *Uintacrinus socialis* Zone. *Gonioteuthis*, on the other hand, appears infrequently in the Coniacian (as *G. westfalica*) chalks of northern France (de Grossouvre 1899, 1901, 1907) and southern England (Rowe 1901; de Grossouvre *in* Rowe 1901). Rare *G. westfalicagranulata* and *G. granulata* occur with *A. verus* in the mid-late Santonian of both areas (de Grossouvre 1899; Jukes-Browne and Hill 1904; Rowe 1904; Peake and Hancock 1961) but *G. granulata* is most abundant in the late Santonian *Marsupites testudinarius* Zone where *A. verus* is uncommon. The base of the early Campanian *Echinocorys depressula* Subzone of the *O. pilula* Zone is typified by forms intermediate between *G. granulata* and *G. q. quadrata*, i.e. *G. granulataquadrata* (Jukes-Browne and Hill 1904; Griffith and Brydone 1911), and *Belemnitella* (probably *B. praecursor*) makes its first appearance at this level (Jukes-Browne and Hill 1904). *G. q. quadrata* appears above the base of the Campanian in the 'Abundant *O. pilula*' Subzone of the *O. pilula* Zone and continues into the overlying *G. quadrata* Zone, where it becomes the index fossil (e.g. Griffith and Brydone 1911). Thus throughout the Anglo-Paris Basin *Gonioteuthis* is only relatively common in chalks where *A. verus* is rare or absent. This relationship is clearly shown by phosphatic chalks where the occurrence of the two genera is almost antipathetic. Explanations for this phenomenon must be sought from environmental, evolutionary, or provincial controls since it is not due to the relative ranges of the two fossils.

Firstly, the current regime which originally produced the cuvettes must have been of a higher order than that which accompanied their infill. This is demonstrated by the transition from erosion to deposition and may be reflected in the coarser and generally higher phosphate content of the lowest phosphatic chalks. In turn, changes in regime may be reflected in substrate and biota both within the cuvettes and elsewhere in the basin. Secondly, the major increase in the abundance of *Gonioteuthis* coincides with the evolution of *G. q. quadrata*. It might be suggested therefore that evolutionary changes in the *Gonioteuthis* stock may have enabled the genus to diversify and occupy previously unfavourable niches. Broader environmental tolerances or changes in food requirements, for example, would provide a mechanism. Lastly, Jarvis (1980) has suggested that the initiation of phosphatic chalk sedimentation was in part due to major changes in oceanic circulation during the Santonian, which accompanied the opening of the Atlantic Ocean. Later changes in the distribution of water masses during the period of phosphatic chalk sedimentation may have enabled populations of *Gonioteuthis* to enter an area which, because of oceanographical conditions, was dominated previously by *A. verus* and *B.* ex gr. *grossouvrei.* Similarly, *A. verus* might have been excluded from that area. Any one, or a combination of these factors, can be invoked to explain the observed changes in belemnite distribution during the evolution of the lithofacies.

CONCLUSIONS

(1) The phosphatic chalks of northern France provide rare examples of Santonian–early Campanian 'populations' of *Gonioteuthis*. This enables the application of statistical analysis in the identification of species.

(2) These phosphatic chalks can be divided into three biostratigraphical subdivisions on their belemnite assemblages:
   - (*a*) a lower unit characterised by *A. verus* with *Micraster coranguinum*, occasional *G. granulata* and rare *B.* ex gr. *grossouvrei*;
   - (*b*) an intermediate division typified by *G. q. quadrata* with *O. pilula*;
   - (*c*) an upper unit with *G. q. quadrata* and occasional *B. praecursor*.

(3) A combination of univariate and bivariate statistics demonstrates that the 'populations' from the Hardivillers Gonioteuthis Bed and the phosphatic chalk at Villers-devant-le-Thour are homogenous, whereas the 'population' from above the Ribemont Gonioteuthis Hardground is inhomogenous. Inhomogeneity in the latter sample is the result of a catastrophic event, probably a storm, which has resulted in the concentration of a mixed 'population' of young and old individuals.

(4) Mean Riedel-Quotients for all three 'populations' fall within the range of *G.* ex gr. *quadrata* but subspecies cannot be identified on Riedel-Quotient alone.

(5) *G. q. quadrata* has been identified as the subspecies present in the Hardivillers Gonioteuthis Bed. This 'population' of the subspecies shows an allometric relationship of L *v.* D, L *v.* DVDAE and MLD *v.* LDAE.

(6) The Ribemont and Villers-devant-le-Thour 'populations' cannot be distinguished from each other but are distinct from that studied from Hardivillers. The subspecies at the former localities shows affinities to both *G. q. quadrata* and *G. q. gracilis*.

(7) Principal component factor analysis illustrates that the major controls on *Gonioteuthis* guard morphology are:
   - (*a*) the size of the guard, which accounts for 87·2% of the observed variation;
   - (*b*) the evolutionary stage of the individual within the *Gonioteuthis* gradualistic series, 6·8% of the variation;
   - (*c*) a shape factor which produces elongate guards (or perhaps a taphonomic factor), 4·6%.

(8) The well-preserved nature of the guards, the juvenile nature of the epifauna, and the absence of extensive boring suggest relatively rapid burial, while the general lack of more than one generation of epifauna implys that re-exhumation was rare.

(9) Guard taphonomy suggests that the environment of deposition was one of intermittent current activity with rapid winnowing, followed by periods of quiescence and burial.

(10) The occurrence of juveniles in the 'populations' indicates a shallow-water environment which was the belemnites' normal habitat because of the greater availability of food.

(11) Belemnites are concentrated at hardground levels because of:
   - (*a*) a concentration of potential prey associated with the hardgrounds;
   - (*b*) the possibility that they may be preferred breeding sites and would therefore be the recipients of the large numbers of dead individuals following the mass mortalities which accompany reproduction.

(12) The virtual mutually exclusive relationship between *A. verus* and *Gonioteuthis* in phosphatic chalks may be controlled by:

(*a*) the decline in the current regime during cuvette evolution favouring *Gonioteuthis*;
(*b*) evolutionary changes in *Gonioteuthis* allowing the genera to occupy a previously unfavourable niche and to oust *A. verus*, or
(*c*) changes in provincial boundaries which accompanied changes in oceanic circulation.

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A NEW LABYRINTHODONT AMPHIBIAN FROM THE CARBONIFEROUS OF SCOTLAND

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ABSTRACT. Cranial remains of a labyrinthodont amphibian *Doragnathus woodi* gen. et sp. nov., from localities in the Viséan and Namurian of the Scottish Carboniferous, are described. The structure of the lower jaw resembles that of the earliest known Amphibia, but its dentition is unusual, comprising large numbers of strongly incurved, closely spaced marginal teeth together with a row of small needle-like coronoid teeth. The relationships of *Doragnathus* are discussed. A specimen of *Doragnathus* from Pitcorthie represents the earliest recorded labyrinthodont in the British Carboniferous.

THE Scottish Midland Valley is one of the few areas in the world from which fossil Amphibia have been found in Carboniferous sediments older than those equivalent in age to the British Coal Measures (Westphalian and Stephanian). Thirteen pre-Coal Measure genera have so far been described from a total of eleven Scottish localities. Most discoveries were made in the latter half of the last century, but recently a diverse amphibian fauna was discovered in a bone bed at the Dora Opencast Site, near Cowdenbeath, Fife (Andrews, Browne, Panchen, and Wood 1977; Smithson, in press). With the exception of an almost complete skeleton of *Crassigyrinus scoticus* (Panchen, in press) the Cowdenbeath fauna is represented by dissociated skeletal elements of at least six amphibian genera. The most common of these is a hitherto undescribed labyrinthodont represented by a large number of incomplete jaw specimens. The new form has also been found at Pitcorthie and Niddrie (Smithson, in press) and recently by Mr. Stanley Wood and the author on the island of Inchkeith, in the Firth of Forth.

Labyrinthodonts are rare components of the Scottish Lower Carboniferous amphibian assemblage, and until recently they had been recorded at only three of the eight Lower Carboniferous localities. The recognition that a jaw specimen from Pitcorthie in the collection of the Royal Scottish Museum was that of a labyrinthodont and not, as had previously been thought, a lepospondyl, and the discovery of similar material on the Island of Inchkeith, has improved this position. Although these new specimens are incomplete and poorly preserved, material from the Upper Carboniferous deposits at Cowdenbeath and Niddrie allows a description of a number of aspects of the cranial anatomy of the new labyrinthodont to be given.

The fossiliferous deposits on the island of Inchkeith and at Pitcorthie occur in strata of Viséan age. The middle of the exposed sequence on Inchkeith is thought to be equivalent to the horizon of the Burdiehouse Limestone (Davis 1936). The fossiliferous sediments at Pitcorthie almost certainly occur within the Anstruther Beds (Forsyth and Chisholm 1973). These lie below the Cuniger Rock Marine Band which has been placed, on palynological evidence, well below the Burdiehouse Limestone (Neves *et al.* 1973). Thus the amphibian remains from Pitcorthie are older than those from the Burdiehouse Limestone, and the labyrinthodont remains are the earliest recorded in the British Carboniferous.

Where necessary material was prepared with a dental mallet and industrial 'Airbrasive' unit, and a solution of 'Perspex' dissolved in chloroform was used to repair breaks in specimens.

The following abbreviations are used for the institutions owning the material: NUZ, Department of Zoology (University of Newcastle upon Tyne); RSM, Department of Geology (Royal Scottish Museum).

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SYSTEMATIC PALAEONTOLOGY

Class AMPHIBIA
Subclass LABYRINTHODONTIA
Order and Family Undesignated
Doragnathus gen. nov.

Type species. Doragnathus woodi gen. et sp. nov.

Etymology. The name refers to the large number of jaw specimens from the Dora Opencast Site.

Diagnosis. Labyrinthodont amphibian with a long, shallow lower jaw which terminates with a distinct retroarticular process; small Meckelian fenestra at the mesial exposure of the splenial/post splenial suture; dentary with room for more than eighty closely spaced, strongly incurved teeth, labyrinthine unfolding of enamel found only below the margin of the gums; a row of slim needle-like replaceable teeth on the coronoid series.

Doragnathus woodi gen. et sp. nov.

Text-figures 1–3

Etymology. The animal is named after Mr. Stanley Wood, who discovered the bonebed at the Dora Opencast Site which has yielded the majority of the material attributed to *Doragnathus.*

Diagnosis. As for genus.

Holotype. NUZ 77.5.26 incomplete left ramus of lower jaw.

Type horizon and locality. Localized seatrock, beneath a coal seam below the Lochgelly Blackband Ionstone, upper part of the Limestone Coal Group (Namurian A, Upper Carboniferous), Dora Opencast Site, Cowdenbeath, Fife, Scotland.

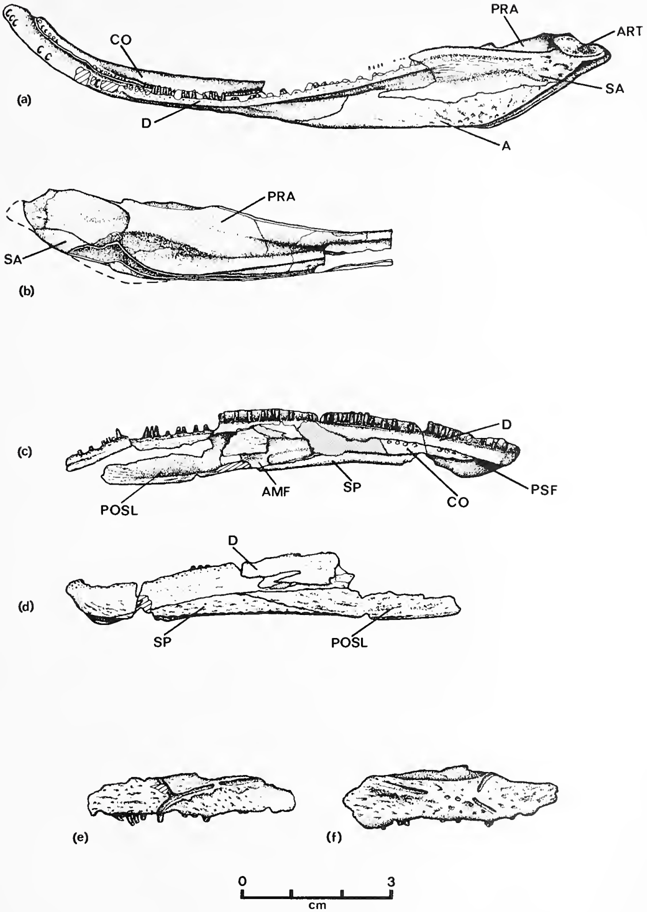
Distribution. Scottish Midland Valley (Lothian and Fife regions).

Range. Middle Calciferous Sandstone Measures (Anstruther Beds) to Upper Limestone Group (South Parrot Coal Shale). C_2S_1? zone of Viséan stage (Lower Carboniferous) to E_2 zone of Namurian A (Upper Carboniferous).

Description. The description of *Doragnathus* is based on the most complete specimens in the collections of the Royal Scottish Museum and the University of Newcastle upon Tyne. All have suffered *post-mortem* compression and only RSM GY 1898.107.51 is preserved in any degree of completeness (text-fig. 1*a*, *b*). A complete list of attributed material is deposited in the Department of Geology, Royal Scottish Museum.

Lower jaw. In its over-all construction the lower jaw is similar to that of early labyrinthodonts, e.g. *Ichthyostega* (Säve-Söderbergh 1932; Jarvik 1952) and *Metaxygnathus* (Campbell and Bell 1977). Each ramus is relatively shallow throughout its length, tapering slightly towards the synphysis in lateral view. In dorsal view each ramus curves gently towards the midline and, when articulated, the two jaws describe a distinct U. The majority of specimens are from animals with lower jaws approximately 12 cm long. A number of specimens, notably RSM GY 1975.5.3, have been found at Cowdenbeath which are considerably larger; the estimated lower jaw length of the largest of these is approximately 30 cm. The smallest recorded specimen, RSM GY 1881.43.24 from Pitcorthie, has a lower jaw approximately 6 cm long. (All measurements included in this description have been taken from specimens approximately 12 cm in length.)

A well-defined mandibular lateral line canal follows the ventral edge of the jaw ramus. At regular intervals it is partially or completely bridged with bone and appears as a series of ovoid pits approximately 1·5 mm long along their antero-posterior axis and approximately 1 mm wide. The adductor fossa is preserved in RSM GY 1898.107.51 and RSM GY 1975.5.3. It is a steep-sided cavity, approximately 2·8 cm long, walled laterally by the surangular and mesially by the prearticular. The dorsal surface of the surangular is slightly convex but is not developed into the high surangular crest of anthracosaurs and certain temnospondyls. Anteriorly the fossa tapers and is bounded by the posterior coronoid at the level of the back of the tooth row. Half-way along the floor of the fossa in RSM GY 1898.107.51 is a small raised rugosity which probably acted as a point of



TEXT-FIG. 1. *Doragnathus woodi* lower jaw and premaxillary, natural size. (*a*) lateral, (*b*) mesial view of lower jaw RSM GY 1898.107.51; (*c*) mesial, (*d*) lateral view of holotype NUZ 77.8.28; (*e*) external view right premaxillary NUZ 77.5.26; (*f*) external view left premaxillary NUS 78.1.26. Damaged bone surfaces, hatched; matrix, regular stipple. A, angular; AMF, anterior Meckelian fenestra; ART, articular; CO, coronoid; D, dentary; POSL, postsplenial; PRA, prearticular; PSF, postsymphysial foramen; SA, surangular; SP, splenial.

attachment for a mass of the adductor mandibulae musculature. In the tunnel formed between the inner and outer walls of the ramus the cavity extends as the Meckelian space, which may have been partially occupied by Meckel's cartilage (Nilsson 1944).

The Meckelian fenestrae are small and restricted to the ventral margin of the mesial surface of the jaw. They are preserved only in the holotype (text-fig. 1*c*). The most anterior fenestra perforates the jaw at the junction of the splenial and the postsplenial bones. A second, smaller fenestra may be present approximately 1 cm behind the first. Unfortunately, this region is badly damaged and interpretation is difficult. The posterior Meckelian fenestra normally found at the junction of the postsplenial and angular is absent.

The mesial surface of the symphysial region is comparatively smooth and exhibits none of the roughened areas for ligamentous attachment normally expected. The apparent absence of strong points of ligament attachment suggests that the symphysis was comparatively weak and a certain degree of movement of the jaw rami relative to one another was possible. Immediately behind the symphysis the dentary is roughly triangular in section, one side forming the lateral surface of the jaw, a second the mesial wall, and the third a tooth-bearing shelf. Directly below the tooth-bearing shelf, the mesial wall is pierced by the postsymphysial foramen. Posterior to this, the infradentary bones are incorporated into the mesial and lateral surfaces of the jaw and to the mesial edge of the tooth-bearing shelf are attached the coronoids. The greatest exposure of the dentary is in the lateral wall. Anteriorly it is approximately 5 mm deep, gently deepening posteriorly to reach its maximum depth towards the end of the tooth row. Extending along its dorsal edge is a finely ornamented border. Below this the dentary is almost smooth: only behind the symphysis is the dentary ornamented with irregular ridges and grooves. In dorsal view the tooth-bearing shelf extends from the symphysis to terminate immediately in front of the adductor fossa. Throughout its length the shelf maintains an almost constant width. It has room for more than eighty closely spaced, strongly incurved teeth. Details of the dentition are discussed separately.

The coronoids extend from behind the symphysis to the adductor fossa and form an almost horizontal roof to the Meckelian space. Small replaceable needle-like teeth extend along the lateral edges of the coronoids and form a single row of teeth lying parallel to those on the dentary. The series widens posteriorly eventually forming the anterior border of the adductor fossa. Unlike some later labyrinthodonts, the posterior coronoid is not incorporated into the lateral wall of the fossa. It was not possible to trace the sutures between the individual coronoids.

The Meckelian space is floored by the two splenials and the angular. The (pre-)splenial contacts the dentary behind the symphysis. Laterally the suture between the two bones is long and straight and runs parallel with the ventral jaw margin.

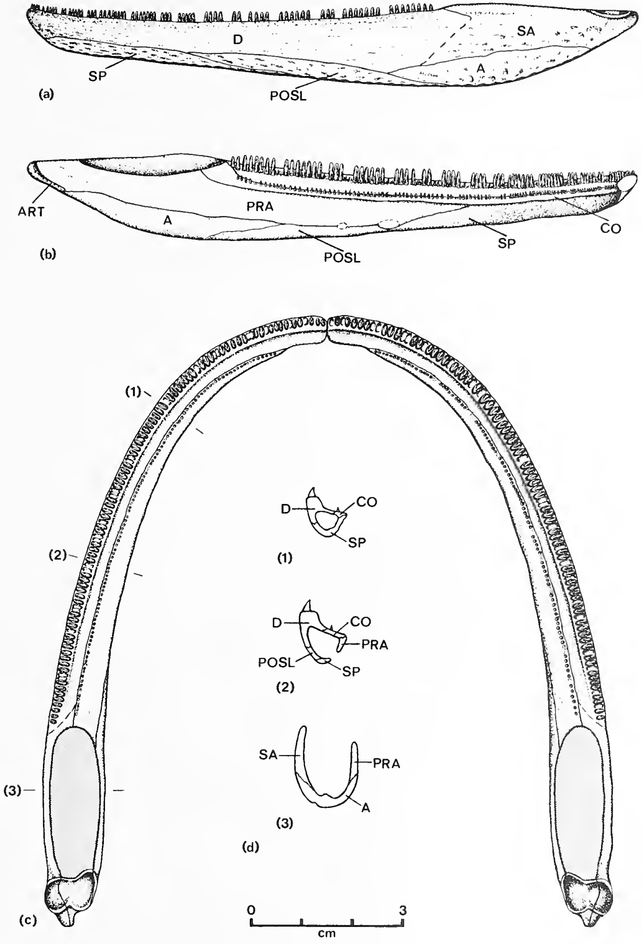
Posteriorly the splenial contacts the postsplenial along an oblique suture which passes under the ventral edge of the jaw. Both elements are ornamented with the irregular ridges and grooves found on the dentary. In mesial exposure it contacts the anterior coronoid under the mesial border of the coronoid shelf. Along the length of the suture the angle between the two bones is approximately ninety degrees. Posteriorly the dorsal edge of the splenial gently tapers away from the coronoid shelf to form a broad suture with the prearticular which contacts the postsplenial at the jaw margin. Lying at the junction of the three elements is the anterior Meckelian fossa. The postsplenial is a narrow strip of bone which, in lateral exposure, contacts the dentary along most of its length and posteriorly sutures with the angular. It contacts the prearticular along a broad suture mesially and posteriorly continues to contact the angular. Between the postsplenial and prearticular a second small Meckelian fenestra may be present lying approximately 1 cm behind the first.

The posterior part of the lateral wall of the ramus is formed by the angular and surangular. Both are ornamented with a system of ridges and pits which are less well defined than those on the two splenials. The angular wraps around the posterior edge of the ramus to present a relatively narow exposure on the mesial surface where it has a long straight suture with the prearticular.

Behind the tooth row, the lateral dorsal margin of the jaw is formed by the gently convex rim of the surangular. Posteriorly it sheathes the articular, extending behind the glenoid to form the lateral wall of a short retroarticular process. Passing down the posterior edge of the process is the surangular articular suture. In dorsal view, the rim of the surangular which sheathes the articular is thickened and incorporated into the glenoid fossa. The suture between the surangular and dentary could not be traced.

The mesial wall of the adductor fossa is formed principally by the prearticular, a long narrow element which extends forward to fill much of the inner surface of the jaw. Posteriorly it sheathes the articular and is incorporated into the glenoid, but unlike the surangular does not form part of the retroarticular process. It sutures with the angular and splenial bones ventrally and its dorsal edge contacts the posterior coronoid to form the anterior margin of the adductor fossa.

The remaining element in the lower jaw is the articular which represents the only ossification of Meckel's cartilage. It is embraced on its lateral and mesial surfaces by the surangular and prearticular respectively, but



TEXT-FIG. 2. *Doragnathus woodi* lower jaw. Composite restoration, natural size. (*a*) lateral, (*b*) mesial, (*c*) dorsal view, (*d*) transverse sections of jaw at positions indicated in (*c*). Abbreviations as in text-fig. 1.

only on its mesial surface is it exposed where it extends posteriorly to form the internal surface of the retroarticular process. The shape of the glenoid fossa, when viewed dorsally, resembles a distorted figure of eight. This is clearly seen in RSM GY 1975.5.3. The articular surface is divided into two subcircular depressions by a ridge oriented along the anterior posterior axis of the jaw. The mesial depression extends slightly further forward than that on the lateral surface of the fossa. Both are bounded anteriorly by a well-defined precondyloid process. The postcondyloid process is not clearly defined since the posterior margin of the fossa is incorporated into the retroarticular process. The foramen for the chorda tympani (mandibular) branch of the seventh nerve, which in most Amphibia pierces the lower jaw just below the glenoid fossa, could not be traced.

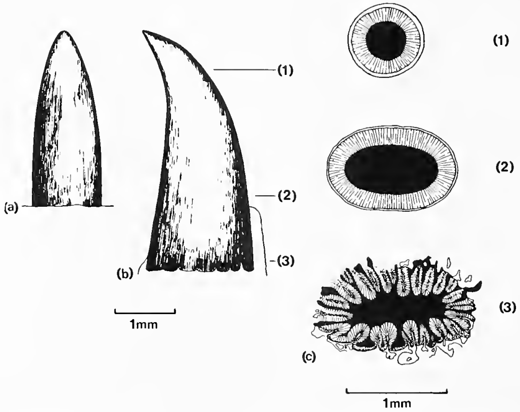
Premaxilla. A number of isolated, partially complete, premaxillae containing marginal teeth of the type described from the lower jaw of *Doragnathus* have been found at Cowdenbeath. All are thought to be from skulls with a lower jaw length of approximately 12 cm. In antero-lateral view the premaxilla is a narrow elongate element ornamented with irregular ridges and grooves as found on the splenials of the lower jaw. In ventral aspect it is gently curved and mirrors the shape of the anterior region of the mandible. There is room for more than twenty-five teeth. The premaxillary margin of the choana is not preserved on any specimen.

The supraorbital lateral line canal passes across the exterior surface of the premaxilla. It extends over the posterior dorsal edge onto the nasal and along the antero-lateral edge to join the second half of the supraorbital canal on the opposite premaxilla. The canal is manifest in a variety of ways. In NUZ 77.5.26 it appears as an open groove which is bridged over with bone at one point only. In NUZ 78.2.26, however, it is bridged over much of its length and is visible as an irregular series of pits (text-fig. 1*e*, *f*). Only where it runs over onto the nasal and opposite premaxillary does it appear in an open groove.

In palatal aspect, the premaxilla extends posteriorly as a broad shelf of bone to suture with the vomers. The presence of a palatal fenestra is improbable.

Maxilla. An incomplete maxilla has been found at Pitcorthie (RSM GY 1881.43.24). Apart from showing that the maxillary teeth are of the type found on the dentary and premaxilla, it yields little information.

Dentition. The marginal teeth in the upper and lower jaws of *Doragnathus* are identical. They are of uniform size along most of the tooth row becoming smaller towards its posterior end. There is no parasymphysial tusk on the lower jaw and no peaking along the dentary or maxillary. In lateral view the teeth are bullet-shaped and in posterior aspect strongly incurved (text-fig. 3*b*). Their bases are twice as wide as long and narrow towards the apex of the tooth, becoming almost circular in section just below the tip.



TEXT-FIG. 3. *Doragnathus woodi* teeth. (*a*) lateral, (*b*) posterior view of marginal tooth × 12; (*c*) transverse sections through tooth as positions indicated in (*b*), × 20.

Labyrinthine infolding of the enamel is only found at the base of the teeth below the margin of the gums. In section they show the characteristic infolding of the external primary dentine, but whereas in many osteolepiform crossopterygians and most labyrinthodonts the infoldings meander and some cases are branched (Schultze 1969), those of *Doragnathus* appear as straight, nonconvolute unbranched folds (text-fig. 3*c*). The majority of teeth from which histological sections have been taken in fish and in other labyrinthodonts have been the large tusk teeth on the palate and the coronoids. However, the marginal dentition of most crossopterygians comprises teeth considerably smaller than the tusk teeth and these exhibit simple folding, e.g. *Megalichthys* (Schultze 1969, p. 94), of a type very similar to that found in *Doragnathus*. The tortuous infolding often taken to typify labyrinthodont teeth is undoubtedly a size-related phenomenon, a fact clearly demonstrated by Bystrow and Efremov (1940, p. 46).

The teeth are arranged in the jaw as a series of 'clusters and gaps'. Normally approximately seven teeth are grouped together as a cluster and separated from a similar cluster by one or two replacement pits. However, groups of smaller than seven occur particularly in the middle of the tooth row and the over-all pattern of tooth replacement is unclear.

The coronoid dentition comprises a single row of small, replaceable, needle-like teeth which lie parallel to the marginal row. The palatal dentition is unknown.

DISCUSSION

The paucity of complete or partially complete specimens of *Doragnathus* prevents a satisfactory analysis of its relationships, but certain features of its lower jaw allow a number of points to be considered. The over-all structure of the jaw resembles that of the earliest known Amphibia. It differs from those of rhipidistian fishes in a number of respects, notably the largest teeth in the jaw are found in the dentary, the coronoid teeth are small and there are no coronoid fangs. The prearticular fails to reach the symphysis and the mesial surface of the jaw is perforated anteriorly by at least one Meckelian fenestra.

The position of *Doragnathus* within the Amphibia seems clear. Its average skull size (represented by specimens with lower jaws 12 cm long) is larger than that found in the majority of non-labyrinthodont amphibians, and the largest specimens are considerably larger than any known 'lepospondyl'. The infolded internal structure of the marginal teeth suggest its inclusion within the Labyrinthodontia, but infolded teeth have been found in the microsaur *Trihecaton* (Vaughn 1972), and it is possible that infolding is primarily a function of tooth size (Thomson and Bossy 1970). However, one additional feature which suggests affinity with the labyrinthodonts is the presence of an anterior Meckelian fenestra. No non-labyrinthodont is known in which the mesial exposure of the splenial/postsplenial suture is perforated.

The position of *Doragnathus* within the Labyrinthodontia is less certain. In most respects its lower jaw is primitive and resembles that of *Ichthyostega* (Säve-Söderbergh 1932; Jarvik 1952), and *Metaxygnathus* (Campbell and Bell 1977). Each has a retroarticular process and an extensive prearticular which forms much of the mesial wall of the jaw. A single row of teeth is present on the coronoids lying parallel to the marginal row on the dentary. However, the parasymphysial tusks present in *Ichthyostega* (Campbell and Bell 1977) are absent in *Metaxygnathus* and *Doragnathus*. Parasymphysial tusks are present in the majority of early labyrinthodonts, e.g. colosteids (Panchen 1975), loxommatids (*sensu* Beaumont 1977), *Crassigyrinus* (as '*Macromerium*' Panchen 1973; see Panchen, in press) and *Caerorhachis* (Holmes and Carroll 1977), and their absence in *Metaxygnathus* and *Doragnathus* may be significant. However, in forms in which the dentition is irregular and the teeth numerous and of uniform size and shape, tusks are usually lost completely, e.g. the loxammatoid *Spathicephalus* (Tilley 1971). This principle may also apply to *Doragnathus*, and the absence of parasymphysial tusks need not necessarily indicate close relationship. In addition a number of differences in the structure of the lower jaw suggest that the two genera are not closely related, notably the absence in *Metaxygnathus* of an anterior Meckelian fenestra, the shallow lateral extent of the dentary, and the high elevation of the articular above the tooth row.

Both *Doragnathus* and *Spathicephalus* occur at Cowdenbeath (Smithson, in press) but are easily distinguished by differences in their dentition. The marginal teeth of *Spathicephalus* are chisel-shaped in lateral view and are not incurved (Smithson in press, text-fig. 2) and coronoid teeth are restricted to the anterior coronoid (E. H. Beaumont (*née* Tilley) pers. comm.). Whilst differences in the dentition of the two forms indicate a clear generic distinction, the possibility of close relationship cannot be ruled out. Unfortunately the lower jaw of *Spathicephalus* is inadequately known and little direct comparison can be made to clarify the problem.

In a recent review of the Namurian amphibian fauna I tentatively suggested that *Doragnathus* be included within the Trimerorhachoidea (Smithson, in press). This suggestion now seems untenable. Although the lower jaws bear superficial resemblance, the presence of a posterior Meckelian fenestra in trimerorhachids and the posterior extension of the posterior coronoid, either incorporated into the surangular crest (e.g. in *Trimerorhachis* Williston 1914) or forming a distinct coronoid process (e.g. *Dvinosaurus* Bystrow 1938), almost certainly precludes close relationship.

It is clear that the position of *Doragnathus* within the Labyrinthodontia is uncertain. Those features which it shares with other forms are almost certainly primitive for labyrinthodonts as a whole and, until more complete material is available, the taxonomic position of *Doragnathus* will remain obscure. Only in the arrangement of the dentition, notably the uniform structure and large number of marginal teeth, does the lower jaw of *Doragnathus* differ significantly from those of other early labyrinthodonts.

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A LYSOROPHID AMPHIBIAN FROM THE COAL MEASURES OF NORTHERN ENGLAND

by M. J. BOYD

ABSTRACT. A description is given of the presacral vertebrae and ribs of a lysorophid amphibian from the Middle Coal Measures (Westphalian B) of Northumberland. The specimen is the earliest lysorophid yet described and is the first certainly identifiable member of the group to be recorded from any horizon outside North America. An isolated presacral vertebra from an unknown Coal Measures horizon at Low Moor, West Yorkshire, may represent additional evidence of lysorophids in the British Carboniferous. Lysorophids appear to have been present in both lacustrine and coal swamp pool environments in the Upper Carboniferous as well as surviving in 'red bed' environments in the Lower Permian in North America.

THE Lysorophidae is a family of small 'lepospondyl' (*sensu* Romer 1966) amphibians hitherto known with certainty only from Upper Carboniferous and Lower Permian freshwater deposits in North America. The lysorophids have in the past been assigned to a number of different amphibian taxa, including the Orders Apoda (Moodie 1909) and Urodela (Sollas 1920; von Huene 1956). Romer (1966) regarded the lysorophids as constituting a family of aberrant microsaurs; in a recent discussion of lysorophid structure and relationships, however, Carroll and Gaskill (1978, p. 186) have suggested that the members of the group are sufficiently distinct from typical microsaurs to warrant exclusion from the Order Microsauria.

The type genus of lysorophid, *Lysorophus*, was first described by Cope (1877) on the basis of three isolated vertebrae from the Upper Pennsylvanian of Danville, Illinois. Unfortunately the absence of more diagnostic material makes it impossible to distinguish *Lysorophus* from other Carboniferous lysorophids (Carroll and Gaskill 1978). One of the most fully known of described Carboniferous lysorophids is *Cocytinus* Cope 1871, from the Westphalian D horizon of Linton in Ohio. An articulated specimen of *Cocytinus* from Linton has recently been figured by Carroll and Gaskill (1978, fig. 132B). A lysorophid referable to *Cocytinus* has also been reported by Baird (1964) from the lower Westphalian D of Mazon Creek, Illinois. Relatively abundant lysorophid material, usually referred to the genus *Lysorophus*, is known from the Lower Permian of Texas. Many of these last specimens are preserved in a matrix which renders preparation difficult, but serial-sectioning techniques enabled Sollas (1920) to give a detailed account of the skull and the anterior postcranial skeleton of one specimen. Further Lower Permian lysorophid material has, more recently, been described by Olson (1971) from the Hennessey Formation of Oklahoma.

No description has hitherto been published of a lysorophid from any locality outside North America. Although lysorophids have been reported from the Westphalian A ox-bow lake site of Jarrow in Co. Kilkenny, Eire (Thomson and Bossy 1970), the very poor state of preservation of most of the specimens from this locality (Rayner 1971) makes definite identification difficult. A small amphibian from the late Stephanian or early Autunian of Nièvre in France, tentatively identified as an aïstopod by Thevenin (1910), may also possibly be a lysorophid (Baird 1964) but, as at Jarrow, preservation is very poor and certain identification is not possible.

MATERIALS

The following description is of a previously undescribed lysorophid specimen which was collected, probably during the latter half of the nineteenth century, from the Coal Measures of Northumberland. The specimen, registered in the collections of the Hancock Museum, Newcastle upon Tyne, as

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G91.15, is from the black shale immediately overlying the Low Main Seam at the colliery of Newsham near Blyth. This horizon lies within the Upper Modiolaris zone of the Middle Coal Measures (Land 1974) and is Westphalian B in age. Because the specimen lacks a skull, it is impossible to diagnose it at generic or specific level, and the specimen is therefore not named. However, it merits description as the first certainly identifiable lysorophid to be recorded from outside North America.

A single presacral vertebra, until recently housed in the Geology Museum of the Wigan College of Technology in Wigan, Lancashire, but now registered as G152.04 in the Hancock Museum collections, may represent additional evidence of the presence of lysorophids in the British Upper Carboniferous and is also described below. The vertebra was collected between 1880 and 1920 from the Coal Measures of Low Moor, near Bradford in west Yorkshire. Unfortunately, its precise horizon is not recorded. However, the holotype specimen of the large eogyrinid embolomere *Pholiderpeton scutigerum* Huxley 1869, which is also from the Low Moor area, was collected from the shale overlying the Black Bed Coal at Toftshaw and this horizon lies in the Lower Communis zone of the Lower Coal Measures (Westphalian A) (Panchen 1970). It is possible that vertebra G152.04 was collected from the same horizon.

DESCRIPTION

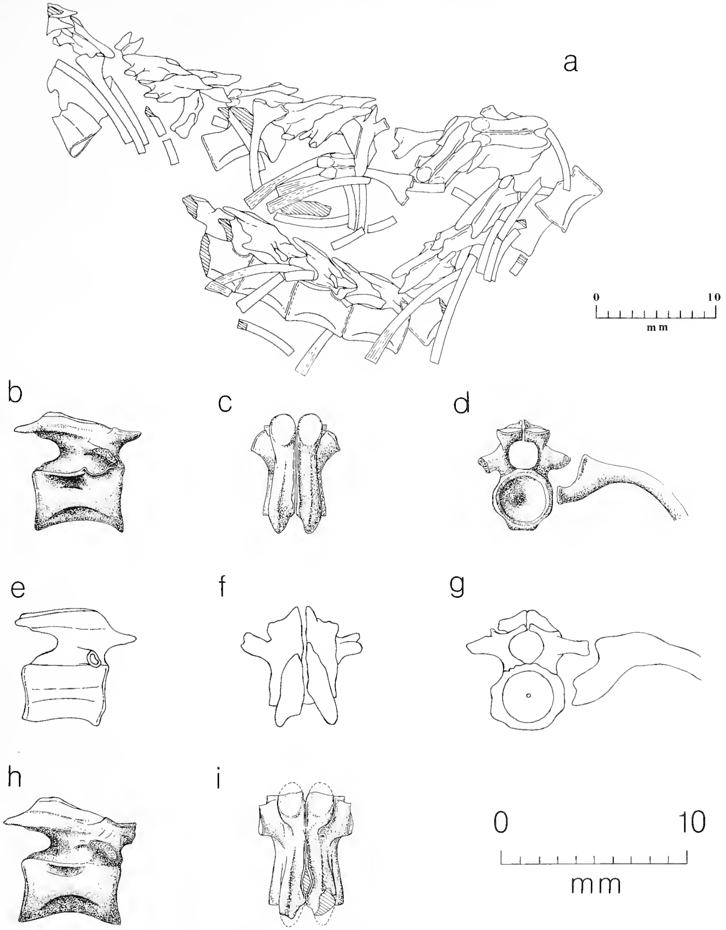
As preserved, specimen G91.15 (text-fig. 1*a*) consists of a small slab of shale bearing an articulated series of eighteen well-preserved presacral vertebrae, in addition to the fragmentary and incomplete neural arches of the three preceding vertebrae. Most of the neural arches present have become detached from their respective centra but the component parts of almost all vertebrae still lie closely adjacent to one another and exhibit few traces of distortion or crushing. Trunk ribs are associated with the majority of the twenty-one vertebrae represented in G91.15. There is no obvious variation in the structure of either vertebrae or ribs within the preserved series. This uniformity of structure would seem to suggest that the complete animal possessed an, at least moderately, elongated presacral vertebral column, and it is of interest to note that *Cocytinus* is known to possess approximately seventy-two presacral vertebrae (Carroll and Gaskill 1978).

In a typical anterior presacral vertebra the centrum is holospondylous, spool-shaped and deeply amphicoelous. It is probable that, as in *Lysorophus* (Sollas 1920), the centrum is perforated for passage of the notochord. There is no evidence of the presence of distinct intercentra in G91.15. The external surface of the centrum is excavated ventro-laterally to form a pair of longitudinally elongate depressions which extend almost the full length of the element. A pair of similar depressions is present dorso-laterally but these are restricted to the posterior half of the centrum. In the anterior one-third of the centrum is situated a pair of dorsally directed depressed facets for articulation with the neural arch pedicels. The articulation between neural arch and centrum is clearly sutural in all the vertebrae present in G91.15. The most notable feature of the neural arch is its ossification in two separate halves, with the line of separation running along the length of the neural spine. The presence of a longitudinally divided neural arch and spine in the trunk vertebrae was clearly demonstrated in *Lysorophus* by Sollas (1920). Although occurring in very immature microsaurs (Carroll and Gaskill 1978) and the adults of some 'labyrinthodont' amphibians, this phenomenon is not known in adult 'lepospondyls' except in the lysorophids. The neural spine is very much reduced and consists of a scarcely perceptible ridge running the length of the dorsal surface of the neural arch. Both pre- and postzygapophyses possess horizontally orientated articular surfaces. In the anterior one-third of the neural arch, at the level of the neurocentral articulation, is situated a pair of elongate, antero-laterally directed diapophyses. A similar orientation of the diapophyses is present in the anterior dorsal vertebrae of *Lysorophus* described by Sollas (1920, fig. 42).

The ribs of G91.15 (text-fig. 1*a*, *d*) are dichocephalous and possess long, curved shafts which are compressed antero-posteriorly. None of the vertebrae show any evidence of a facet to receive the rib capitulum. The probable original relationships of neural arch, centrum and rib are shown in text-fig. 1*d*.

DISCUSSION

The vertebrae of G91.15 are typically lysorophid in structure and very closely resemble those of *Lysorophus* as described by Sollas (1920). A series of Sollas's restorations of the dorsal vertebrae of *Lysorophus*, based upon serial sections, is figured (text-fig. 1*e*–*g*) for comparison with those of



TEXT-FIG. 1. Presacral vertebrae of lysorophids. *a*, semi-diagrammatic representation of Hancock Museum specimen G91.15 as preserved; *b–d*, restoration of an anterior trunk vertebra of specimen G91.15 in *b*, right lateral view; *c*, dorsal view and *d*, anterior view articulated with proximal part of trunk rib; *e–g*, anterior trunk vertebra of *Lysorophus* in *e*, right lateral view; *f*, dorsal view and *g*, anterior view articulated with proximal part of trunk rib (*e–g* after Sollas); *h–i*, Hancock Museum specimen G152.04 in *h*, right lateral view as preserved and *i*, dorsal view with probable original extent of zygapophyses restored. Cross-hatching indicates broken bone surface.

G91.15. Among the more significant resemblances between described lysorophids and specimen G91.15 may be cited the following:

1. Dorsal vertebrae with a neural arch ossified in separate lateral halves.
2. A sutural, rather than fused, neurocentral articulation.
3. A neural spine reduced to a low ridge on the neural arch.
4. Prominent zygapophyses with horizontally orientated articular surfaces.
5. A holospondylous and deeply amphicoelous centrum.
6. The possession of elongate, dichocephalous trunk ribs, the tuberculum of which articulates with a diapophysis.

Whilst characters 2–6 are all parallelled in other 'lepospondyl' taxa and 3–5 are present simultaneously in aïstopods (e.g. Baird 1964), character 1 and hence the combination of all six listed characters is apparently unique, amongst described 'lepospondyl' amphibians, to the Lysorophidae.

Hancock Museum specimen G152.04, from an unknown Coal Measures horizon at Low Moor (text-fig. 1*h–i*) is less certainly lysorophid. Although resembling the vertebrae of G91.15 in the possession of a holospondylous, deeply amphicoelous centrum, and a neural arch with a much-reduced neural spine and horizontally orientated zygapophyseal articular surfaces, G152.04 differs in two respects. The neural arch is ossified as a single structure and would appear to be firmly united, and possibly fused, to the centrum. It is possible, however, that both characters may be age-related or may represent regional variation within the vertebral column, and G152.04 is, therefore, here very tentatively attributed to the Lysorophidae. The relative shortness of the diapophyses compared with those of the vertebrae of G91.15 and their directly lateral, rather than antero-lateral, orientation may indicate that vertebra G152.04 derives from a more posterior region of the presacral vertebral column than is present in the former specimen.

In addition to representing the first certain record of lysorophid amphibians outside North America, specimen G91.15 is the earliest recognizable lysorophid yet described. The stratigraphic range of previously described members of the Lysorophidae extends from the Upper Freeport Coal of Linton, Ohio (Upper Allegheny or lower Westphalian D), where the group is represented by the genera *Cocytinus* Cope 1871 and *Molgophis* Cope 1868 (Steen 1931), to the Choza Formation of the Texas Clear Fork Group (Leonardian, Lower Permian) which has yielded specimens referable to *Lysorophus* Cope 1877 (Olson 1958). The presence of specimen G91.15 in the black shale overlying the Low Main coal seam at Newsham extends the known range of the lysorophids down into the Upper Modiolaris zone of the Middle Coal Measures (Westphalian B).

The uncertainties as to the horizon and relationships of the amphibian represented by the isolated vertebra G152.04 must debar it from consideration in any discussion of the stratigraphic range of the Lysorophidae. Of greater importance is the possibility of the presence of lysorophids in the small tetrapod assemblage from Jarrow in Co. Kilkenny. The Jarrow Seam lies in the lower part of the Communis zone (Eagar 1964) of the Lower Coal Measures (Westphalian A) and, should the reported material prove to be diagnostically lysorophid, this would considerably antedate the Newsham specimen described above.

The fact that the, approximately 200, amphibian specimens from Newsham in the collections of the Hancock Museum include only the single lysorophid described in this present study suggests that G91.15 may possibly be a transported specimen rather than a normal member of the Newsham fauna. Romer (1930) reported only four lysorophid specimens amongst approximately 170 tetrapod fossils from Linton, and it may be that lysorophids were atypical members of permanent water-body communities in the Carboniferous and possibly erratics from small ponds and streams of a more temporary nature. If, however, G91.15 is interpreted as a genuine member of the Newsham amphibian community (previously described members of which have been listed by Land 1974, p. 61) the nature of its environment in life is of some interest. The black shale at Newsham is usually considered to represent the sapropel deposited in a large and deep, possibly coastal or deltaic, lake (Panchen 1970) which was almost certainly the original environment of most of the larger fish and amphibians known from this site. Milner (1978) has noted that Coal Measures lake deposits such as that at Newsham appear to be characterized by a rather limited assemblage of amphibians including eogyrinid embolomeres, loxommatids, the nectrideans *Keraterpeton* and *Batrachiderpeton*, and the aïstopod genus *Ophiderpeton*, all of which taxa are scarcely or not at all represented in the pond or small pool faunas such as those of Linton or Nýřany in Czechoslovakia. Pointing out that, unlike the small tetrapod assemblages of the latter sites, the member groups of the Coal Measures lacustrine fauna appear to have no representatives in the Permian, Milner (1978) suggested that the demise of this assemblage was due to reduction in number, and loss in continuity, of large lakes in Euramerica as a result of the late Carboniferous Armorican orogeny. In view of this hypothesis it is interesting to note the possibility that lysorophid amphibians inhabited both lacustrine (Newsham) and coal swamp pool (Linton) environments in the Coal Measures, and that the group also survived into the Lower Permian in North America. Olson (1958) has described lysorophid aestivating burrows from the Texas Clear Fork Group, and it seems not unlikely that the acquisition of the ability to aestivate under dry conditions may have been an important factor in the adaptation of the lysorophids to the conditions of life prevailing in the early Permian.

Acknowledgements. My thanks are due first to Mr. A. M. Tynan, Curator of the Hancock Museum, and Dr. Robin Grayson of the Geology Section of the Wigan College of Technology for permission to describe the specimens in their care. I would also like to thank Miss Susan Turner (Hancock Museum) for her kindness and assistance during the period of preparation of this work and Dr. A. R. Milner (Birkbeck College, University of London) for his most helpful advice.

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FLOATING ORIENTATIONS OF CEPHALOPOD SHELL MODELS

by R. A. REYMENT

ABSTRACT. Accurately constructed models of ammonoid shells were used in experiments on floating orientations. These experiments show that inflated shells of the cadicone type float stably, with or without liquid in the final chambers. Highly compressed involute shells are unstable unless the last two chambers contain liquid. The highly evolute shell type, represented by *Dactylioceras*, floats on its side when empty and vertically when the last four chambers contain liquid.

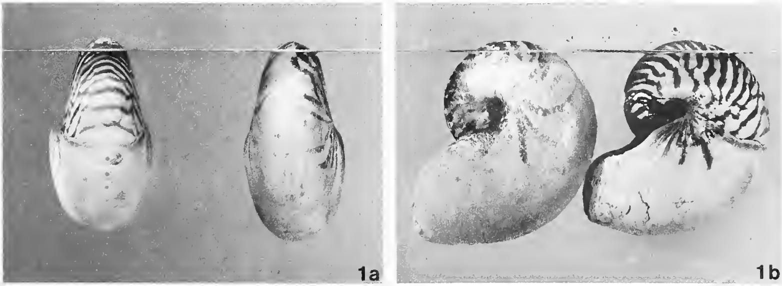
THE present note is a continuation of a series of studies by the writer on the nekroplanktic properties of cephalopod shells (Reyment 1958, 1968, 1970, 1973). The observations summarized here are based on the behaviour of four exact models of ammonoid species; namely, the early Turonian *Hoplitoides ingens* (von Koenen), *Paravascoceras hartti* (White), and *Pseudaspidoceras*? sp., and the Toarcian *Dactylioceras* sp. The first three forms were selected from Brazilian specimens in the Palaeontological Museum of Uppsala University; the *Dactylioceras* comes from the Jurassic of Great Britain.

In order to test the accuracy of the techniques used for making the models, as well as the structural assumptions involved, a model of *Nautilus pompilius* was made. Motion pictures were made of all experiments.

METHOD OF CONSTRUCTION OF THE MODELS

The models were made from actual specimens in the following manner. The ammonoids were dissected, and the component parts for the models prepared by means of a commercial vacuum-moulding apparatus. The technique of vacuum-moulding consists of quickly sucking a preheated sheet of plastic of suitable thickness around a plaster-of-Paris mould. Vacuum-moulding is a widely used method for making children's toys. The required specific gravity (here taken as 2·89) was obtained by copper-plating the plastic parts until the desired weight had been obtained.

Although the models were produced in as accurate a way as possible, it is difficult to be absolutely sure how close to the original shell a particular replicate may be. In order to test the reliability of the method of construction used, a shell of *N. pompilius* was made as a control. The resulting model is shown in text-figs. 1*a–b*, floating alongside a real shell of the pearly nautilus of about the same size.



TEXT-FIG. 1*a–b*. Model of *Nautilus pompilius* floating alongside an actual specimen. In 1*a*, the model is to the right, in 1*b* it is to the left.

[Palaeontology, Vol. 23, Part 4, 1980, pp. 931–936.]

The experiments were made on empty and weighted shells thereby simulating the effect of the animal in the body chamber. Salt water at a concentration of thirty-three parts per thousand was used.

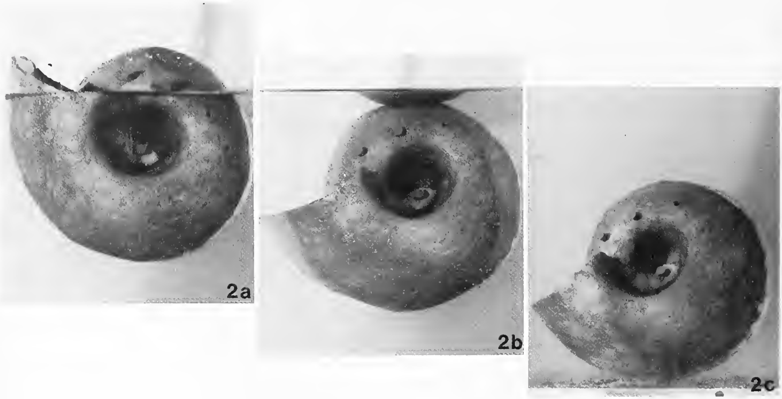
INFLATED SHELLS

Two kinds of moderately evolute, inflated shells, with square to broadly oval whorl sections, were made for studying the properties of this kind of ammonoid. Both were found to possess quite similar buoyancy properties.

Cadicone shell

The species *P. hartti* (White) is a typical cadicone, with whorls in adults appreciably wider than they are high (depressed whorl section). The specimen on which the model was based has a diameter of 20 cm. The following observations were made on the model and simulated ammonoid animal.

1. All chambers empty: the shell floats with 20% of it above the water, measured in terms of the diameter at right angles to the water surface. The aperture faces upwards (text-fig. 2*a*).
2. Three chambers liquid-filled: the shell is just in contact with the water surface but does not break it (text-fig. 2*b*). The aperture is lower than for the orientation shown in text-fig. 2*a*.
3. Fourth chamber quarter-filled: the shell sinks to the bottom. The resting position taken up by the cadicone is shown in text-fig. 2*c*.



TEXT-FIG. 2. *Paravascoceras hartti* (White), Early Turonian (Cretaceous). *a*, floating orientation of empty shell. *b*, floating orientation with the last three chambers liquid-filled. *c*, with some liquid in the fourth last chamber, the shell sinks, showing resting position of the model. Weight of 'animal' added to model (uplift compensated).

A highly ornamented evolute shell

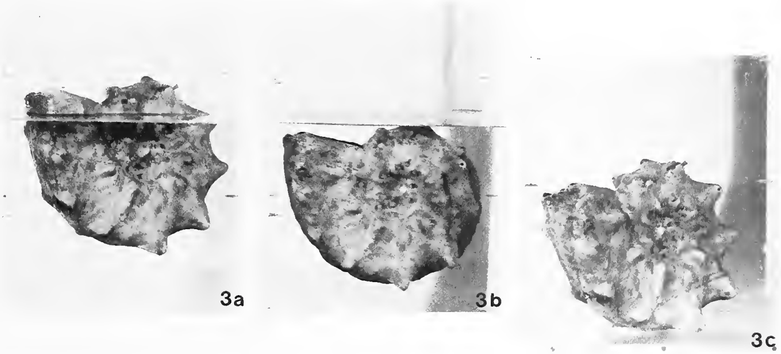
The form here determined as *Pseudaspidoceras*? sp. has a diameter of 32 cm. Its whorl section is square to rectangular and the prominent tubercles are hollow and open to the chambers. The question of whether tubercles are hollow, open or floored, or solid, is of consequence in buoyancy studies. The ammonoid animal was not simulated in the experiment recorded below.

1. The empty shell: this model floats with 26% of the shell above water; the aperture faces upwards (text-fig. 3*a*).

2. Three chambers liquid-filled: a small part of the shell remains above water; the aperture is still directed upwards.

3. Four chambers liquid-filled: the shell is just buoyant; the aperture is now lower than that shown in text-fig. 3*a*. The orientation for this stage of the experiment is shown in text-fig. 3*b*.

4. Fifth last chamber quarter-filled: this slight increase brings about an immediate loss of buoyancy. Prior to this, the shell floated with the body chamber directed upwards (text-fig. 3*c*).



TEXT-FIG. 3, *Pseudaspidoceras*? sp., Early Turonian (Cretaceous). *a*, floating orientation of empty shell. *b*, floating orientation with last four chambers filled. *c*, loss of buoyancy occurs when a small amount of liquid is added to the fifth last chamber.

COMPRESSED INVOLUTE SHELL

The oxynote variety of shell

This was studied by means of a model of *H. ingens* (von Koenen), based on a very large specimen with a diameter of 49 cm. The ammonoid animal was not simulated in the experiment recorded below.

1. Floating position of the empty shell: this is unstable and the shell floats at an angle to the water surface, with 17% of the shell above water (text-fig. 4*a*).

2. Three chambers liquid-filled: a small fraction of the shell remains above water; the aperture of the body chamber is lower than for the empty shell (text-fig. 4*b*).

3. Four chambers liquid-filled: the shell sinks when four chambers are entirely full of liquid, and the resting position adopted is shown in text-fig. 4*c*.

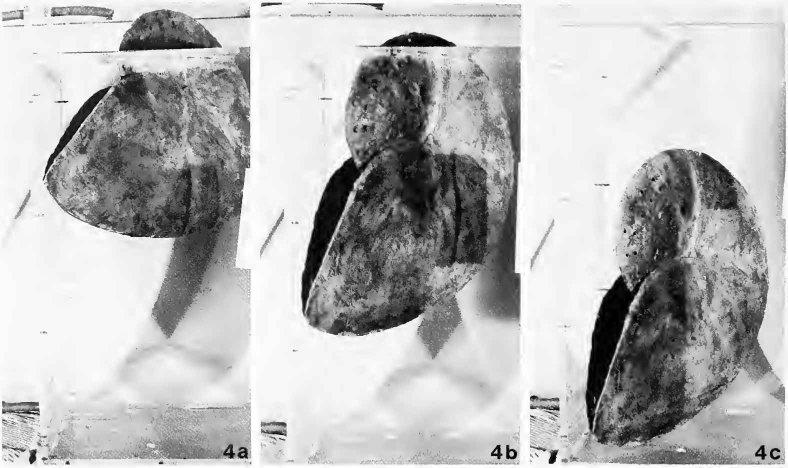
SERPENTICONE SHELL

The highly evolute shell

This type was investigated by a model of a specimen of *Dactylioceras* sp. with a diameter of 23 cm. The weight of the ammonoid animal was allowed for in the experiment described below (text-figs. 5*c*–*f*).

1. The floating position of an empty shell is illustrated in text-fig. 5*a*.

2. Three chambers liquid-filled: the shell just breaks the surface of the water but remains horizontally oriented (text-fig. 5*b*).

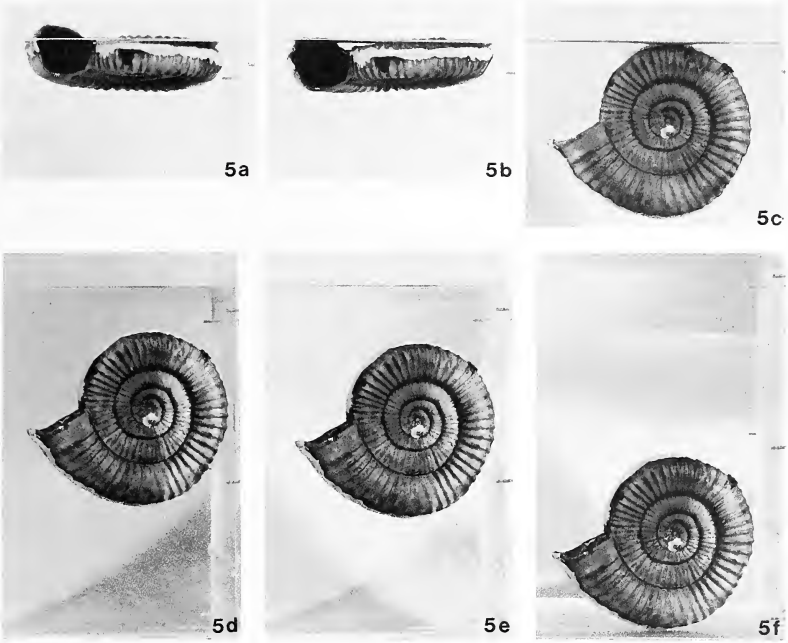


TEXT-FIG. 4. *Hoplitoides ingens* (von Loenen), Early Turonian (Cretaceous). *a*, floating position of empty shell. *b*, floating orientation with three last chambers liquid-filled. *c*, the shell sinks when the fourth chamber contains liquid.

3. Last four chambers liquid-filled: there is an abrupt change in orientation, and the shell becomes vertical. It floats upright and is reasonably stable; this is presumably the living position of the dactylioceratid animal. About 6% of the shell remains above water.
4. Last four and a half chambers liquid-filled: the shell does not break the surface of the water and sinks gradually to the bottom if struck sharply (text-fig. 5*c*).
5. If held at the depth indicated in text-fig. 5*d*, the shell rises slowly to the surface.
6. If held at the depth indicated in text-fig. 5*e*, the shell sinks slowly. In both stages (5) and (6) the shell contains the same amount of liquid. A motion picture is available of this part of the experiment. Careful frame-by-frame study shows that the serpenticone type of shell, as represented by *Dactylioceras*, reacts sluggishly to movement when in a state of buoyancy equilibrium. On the other hand, it appears to be as stable as, for example, the cadicone with respect to its vertical orientation.
7. Resting position of the model on the bottom of the tank (text-fig. 5*f*).

CONCLUDING REMARKS

The suite of experiments briefly reported here indicates the variability in stability shown by various kinds of ammonoid shell. The most stable of the types studied is represented by shells with depressed whorl sections; next, are shells with a sub-quadrate whorl section and a moderate degree of evolution. A highly compressed and involute shell form, such as possessed by many species of *Hoplitoides*, does not float in a vertical position when empty. The same observation applies for highly evolute, serpenticone shells of dactylioceratid type, which when empty float in a horizontal position. Serpenticones, when normally weighted with cameral liquid, appear remarkably sluggish when forces are applied to them.



TEXT-FIG. 5. *Dactylioceras* sp. Toarcian (Jurassic). *a*, horizontal floating position of the empty shell. *b*, with the last three chambers liquid-filled, the shell just breaks the surface, remaining horizontally oriented. *c*, with the last four and a half chambers liquid-filled the shell is in hydrostatic equilibrium. *d*, held at 6 cm below the surface of the water, the shell floats to the surface. *e*, held at 7·5 cm below the surface of the water, the shell sinks slowly to the bottom. *f*, the resting position of *Dactylioceras* on the bottom of the tank.

In an earlier study (Reyment 1973), the effect of varying the length of the body chamber on the floating orientation of empty shells was the main topic of interest. In the present paper the body chamber was allowed to remain a constant length, the experiments being directed towards studying the relationships between the amount of liquid in the last chambers of the final whorl and the floating orientation of the shells.

Compared with Reyment (1958, 1973) and Mutvei and Reyment (1973), the work here summarized gives answers to several questions which could not be treated with the cruder models used in the earlier investigations.

Acknowledgements. Very special thanks are due to Mr. Bertil Annell for his interest and skill in making the ammonoid models. The entire method for producing them was worked out by him in consultation with Mr. Eric Ståhl. Mr. Annell also actively assisted with the experiments. My thanks also to Mr. Gustav Andersson, who photographed the experiments, including the cinematography. All the above are at Uppsala University.

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THE PALAEONTOLOGICAL ASSOCIATION

ANNUAL REPORT OF COUNCIL FOR 1979

MEMBERSHIP AND SUBSCRIPTIONS. Membership totalled 1,554 on 31 December 1979, a decrease of 8 over the previous year. There were 986 Ordinary Members (an increase of 6); 218 Student Members (a decrease of 8); and 350 Institutional Members (a decrease of 6). The number of institutions subscribing to *Palaeontology* via Blackwell's agency was 420. Subscriptions to *Special Papers in Palaeontology* numbered 158 individual and 116 Institutional members, decreases of 16 and 1 respectively since 31 December 1978. Subscriptions to *Special Papers* through Blackwell's agency rose from 109 to 131. Sales of back parts of *Palaeontology* to members via the Membership Treasurer showed a sharp drop from 33 to 15 transactions in 1979. Sales of back copies of *Special Papers* to members rose to 95 transactions, realizing £1,657. Thirty-two members took advantage of the special offer of A. M. Davies's *Tertiary Faunas* negotiated between the Association and the publishers.

FINANCE AND PUBLICATIONS. During 1979 the Association published Volume 22 of *Palaeontology* in four parts at a total cost of £37,203 (including £4,267 postage and distribution). It contained 42 papers totalling 982 pages and 130 plates. *Special Paper 22* (for 1978): 'Curation of Palaeontological Collections' and *Special Paper 23*: 'The Devonian System', were published in June and August 1979 respectively at a total cost of £19,679. Changes in page format were introduced in *Special Paper 23*; text area was increased by approximately 10% and the type-size used for most of the text was slightly reduced. This has reduced the number of pages which in turn has lowered production and distribution costs. The changes will be extended to *Palaeontology* in 1980. Sales of Devonian Symposium field guides during 1979 resulted in an income of £814, which more than covers costs of production and distribution. The Association is very grateful to all those who have made donations. However, costs continue to rise, and subscription rates for *Palaeontology* and *Special Papers* will have to be increased in 1981.

MEETINGS. Eight meetings were held during 1979. The Association is indebted to the organizers and hosts, and to those who led field excursions.

a. *The Twenty-second Annual General Meeting* was held in the Lecture Theatre of the Geological Society of London on 21 March 1979. Dr. J. H. Callomon (London) delivered the Twenty-second Annual Address on 'Jurassic Ammonites in Time and Space'.

b. *A Symposium on the Terrestrial Environment and the Origin of Land Vertebrates*, jointly organized with the Systematics Association, was held on 18–19 April 1979 at the University of Newcastle upon Tyne. Approximately seventy people attended the meeting. Dr. A. L. Panchen was local secretary.

c. *A Field Meeting* was organized by the Carboniferous Group on the 'Lower Carboniferous of Dovedale, Manifold Valley and Weaver Hills area of N.E. Staffordshire', and led by Dr. N. Aitkenhead and Mr. J. I. Chisholm. Eighty-six people attended the excursion which was held on 20–23 April 1979.

d. *A Field Meeting* on the 'Cambrian of the Harlech Dome, North Wales' was held on 27–29 April 1979 and led by Dr. A. W. A. Rushton and Dr. P. M. Allen. Fifteen members attended.

e. *A Field Meeting* on 'Caradoc benthic communities; Shropshire, Berwyn Hills and Bala' was held on 14–16 September 1979 and led by Dr. P. J. Brenchley and Dr. M. J. Lockley. Ten members attended.

f. *A Symposium on Evolutionary Lineages and Selection Pressures*, jointly organised with the British Micropalaeontological Society, was held on 22 September 1979 as part of the Fourth Meeting of the Geological Societies of the British Isles at Sheffield, 19–23 September 1979. Dr. R. J. Aldridge organized the symposium and about fifty members attended.

g. *A Working Group* on 'Facies and faunas of the Tethyan Tertiary' was held on 31 October 1979 at Bedford College, London. Thirty attended the meeting and the local secretary was Dr. E. P. F. Rose.

h. *The Annual Christmas Meeting*, was an open meeting held at University College, Cardiff, on 17–19 December 1979 and jointly hosted by University College and the National Museum of Wales. One hundred and twenty members attended, and the President's Awards were presented to Dr. J. A. Crame and Dr. A. C. Scott. Joint field excursions with the British Sedimentological Research Group visited the Carboniferous, Triassic, and Jurassic at Ogmore-by-Sea (leaders: Professor D. V. Ager and Ms. W. Glanvill), the Triassic and Jurassic of Barry and Penarth (leaders: Mr. M. Mayall and Dr. M. Tucker), and the Silurian and Devonian of southern Powys (leaders: Dr. D. Edwards and Dr. I. Tunbridge). The local secretary was Mr. E. W. Nield.

COUNCIL. The following members of the Association served on Council following the A.G.M. on 21 March 1979: *President*: Professor H. B. Whittington, F.R.S.; *Vice-Presidents*: Dr. E. P. F. Rose, Dr. C. T. Scrutton; *Treasurer*: Mr. R. P. Tripp; *Membership Treasurer*: Dr. J. C. W. Cope; *Secretary*: Dr. R. Riding; *Editors*: Professor C. B. Cox, Dr. M. G. Bassett, Dr. K. C. Allen, Dr. R. A. Fortey; *Other members*: Dr. R. J. Aldridge, Dr. M. C. Boulter (Circular Reporter), Dr. M. D. Brasier, Dr. P. J. Brenchley, Dr. D. E. G. Briggs, Dr. C. H. C. Brunton (Institutional Membership), Dr. S. Conway Morris, Dr. M. B. Hart, Dr. P. M. Kier, Dr. S. C. Matthews, Dr. I. E. Penn, Dr. M. Romano, Dr. D. J. Siveter, Dr. J. Watson.

CIRCULARS. Four Circulars, 95–98, were distributed to Ordinary and Student Members and on request to over 100 Institutional Members during 1979.

COUNCIL ACTIVITIES. During 1979 Council decided to institute a new category of membership for those who have been Ordinary members of the Association for at least fifteen years, and who have retired from employment. This 'Retired Member' category will commence in January 1980 and should provide a stimulus for longstanding members to remain in the Association despite the effects of rising costs on pensions and savings.

A presentation copy of *Special Paper 23* 'The Devonian System' was awarded to Academician D. V. Nalivkin, to whom the volume is dedicated, at a ceremony in Leningrad.

Plans for future meetings of the Association include a symposium on 'Life in the Precambrian' at Leicester in April in addition to the established programme of events. It is also proposed to introduce more one-day meetings on specialist topics. A field meeting on Malta is planned for January 1981 and will be followed soon afterwards by an excursion to West Germany by the Carboniferous Group.

Professor C. B. Cox completed his term as representative for the Association with the International Palaeontological Association and his place has been taken by Dr. L. R. M. Cocks. Thanks are due to Professor Cox.

BALANCE SHEET AND ACCOUNTS FOR THE YEAR ENDING 31 DECEMBER 1979

Balance Sheet as at 31 December 1979

1978				
£	£		£	£
		Current Assets		
	26,508	Investments at cost (see schedule)	36,904	
	–	Stock of paper	480	
	581	Devonian Symposium Guides	–	
	1,401	Sundry debtors	4,078	
	6,145	Cash at bank	7,768	
34,635				49,230
		Current Liabilities		
	500	Royal Society loan	–	
	1,410	Subscriptions received in advance	1,891	
	–	Provision for cost of publication of *Palaeontology*	10,491	
	7,000	Provision for printing *Special Paper* No. *23*	11,383	
	1,236	Sundry creditors	881	
10,146				24,646
£24,489				£24,584

Represented by:

Publications Reserve Account

	17,780	Balance brought forward	24,489	
	6,709	Excess of income over expenditure for the year transferred from Income and Expenditure Account	95	
£24,489				£24,584

Income and Expenditure Account for the Year Ended 31 December 1979

1978 £	INCOME	£	£
	Subscriptions for 1979	25,468	
	Subscriptions for 1977/78	1,703	
26,585			27,171
	Palaeontology—Sales	12,482	
	—Donations	1,153	
14,800			13,635
	Special Papers—Sales	6,535	
	—Donations	562	
7,684			7,097
–	Profit on sale of *Tertiary Faunas*		216
281	Offprints—loss		(414)
200	Profits on sale of investment		376
–	Receipt from Adelaide University		505
4,292	Investment Income (see Schedule)		5,009
£53,842			£53,595
	EXPENDITURE		
	Cost of publication of *Palaeontology*:		
	Volume 22, Part 1	8,974	
	Part 2	8,723	
	Part 3	9,016	
	Part 4	10,490	
34,341			37,203
	Cost of publication of *Special Papers*:		
	Provision for No. *23*	11,351	
	Under provision for No. *22*	1,297	
8,771			12,648
	Cost of Circulars:		
	Preparation	1,336	
	Postage	609	
2,271			1,945
	Administrative Expenses		
	Postage and stationery.	694	
	Editorial expenses	253	
	Secretarial help	–	
	Meeting expenses	483	
	Membership of Societies	10	
	Audit fee	190	
	Grant and awards	25	
1,750			1,655
	Devonian Symposium Guides: Net loss		49
£47,133			£53,500
£6,709	Excess of income over expenditure for the year transferred to Publications Reserve Account		£95

Schedule of Investments and Investment Income as at 31 December 1979

		Cost £	Gross Income for Year £
£12,000	13.¼% Exchequer Stock 1987	11,520	518
£1,000	9% Treasury Stock 1992/1996	991	90
£1,000	9% Treasury Stock 1994	955	90
£4,000	8% Treasury Stock 2002/2006	2,192	320
£5,357	13.¼% Treasury Stock 1997	5,000	710
£3,000	13.¼ Exchequer Stock 1996	3,000	435
£2,000	Agricultural Mortgage Corporation Ltd. 9.¼% Debenture 1980/1985	1,938	185
£1,500	Bootle Corporation 7.¾% Redeemable Stock 1977/1979—(Redeemed)	–	116
5,270	M. & G. Charifund units	4,073	785
£2,000	Imperial Group Ltd. 8% Convertible Unsecured Loan Stock 1985/1990	1,405	160
10,000	New Throgmorton Trust Ltd. 25p Income Shares.	1,706	299
1,600	Commercial Union Assurance Co. Ltd. 25p Shares	2,157	233
600	Consolidated Gold Fields Ltd. 25p Shares	1,012	117
1,000	Clarke, Nicholls & Coombs Ltd. 25p Shares	954	33
			4,091
	Bank interest (net)		922
	Holding charges		(4)
		£36,903	£5,009
	Market value at 31 December 1979 (1978—£31,212)	£40,654	

Report of the Auditors to the Members of The Palaeontological Association. In our opinion the accounts as set out on pages 2 to 4, give a true and fair view of the state of the affairs of the Association at 31 December 1979 and of its income and expenditure for the year ended on that date.

D. J. Carey & Co.
Chartered Accountants

Chislehurst, Kent, February 1980

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The Association was founded in 1957 to further the study of palaeontology. It holds meetings and demonstrations as well as publishing *Palaeontology* and *Special Papers in Palaeontology*. Membership is open to individuals and to institutions on payment of the appropriate annual subscription. Rates for 1980 are:

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