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Pp. 1–28; 9 *Plates*, 2 *Text-figures*

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SOME EARLY ARENIG BRACHIOPODS AND TRILOBITES FROM WALES

By DENIS EDWIN BEECHING BATES

CONTENTS

SYNOPSIS

Brachiopods and trilobites from the Lower Arenig Series of Ramsey Island, Carmarthen and Arenig are compared. *Lenorthis alata* (Sowerby), *Orthambonites* sp., *Monorthis menapiensis* (Hicks), *Neseuretus ramseyensis* Hicks, *Megalaspidella* (?) *murchisoniae* (Murchison) and *Megalaspidella* (?) *whittardi* sp. nov. are described, the last species being from the Shelve area.

I. INTRODUCTION AND ACKNOWLEDGMENTS

THE lower Arenig (*D. extensus* zone) shelly faunas of South Wales were very early described, by Murchison (1839) from Carmarthen and from Ramsey Island by Hicks (1873). During collection by the writer of the Ramsey Island fauna it became evident that comparison was necessary with topotype material from Carmarthen, where the species *Spirifer alatus* Sowerby and *Ogygia murchisoniae* Murchison had been described in Murchison's Silurian System. It also became necessary to re-examine species of " *Ogygia* " from Dolgellau (*O. selwyni* Salter) and the Shelve region (Whittard 1964).

The writer wishes to acknowledge the help of a number of colleagues and friends in collecting material, especially Dr. A. S. G. Jones, who provided mountaineering assistance on the cliffs of Ramsey Island, Mr. K. Alpress, the owner of the island, and Mr. R. A. Straton, warden of the bird sanctuary at the time of collecting the material. I also wish to thank Professor H. B. Whittington and Professor Alwyn Williams for discussion on some of the trilobites and brachiopods. I am grateful

to the following for the loan of museum specimens and for the opportunity to examine collections in their care: Dr. D. A. Bassett, Dr. L. R. M. Cocks, Dr. M. C. Eagar, Mr. J. M. Edmonds, Dr. C. L. Forbes, Dr. A. W. A. Rushton and Dr. I. Strachan.

Specimens whose numbers are prefixed by " BB." and " It." are in the British Museum, by " NMW." in the National Museum of Wales, by " LL." in the Manchester Museum, by " OUM." in the Oxford University Museum, by " SM.A." in the Sedgwick Museum, Cambridge, and by " GSM." in the Geological Survey Museum.

II. STRATIGRAPHY

In South-west Wales there appears to be a break everywhere at the base of the Ordovician, except possibly in the Carmarthen region (Crosfield & Skeat 1896); on Ramsey Island and in the St. David's region the basal Arenig sediments rest disconformably on Lingula Flags. At least the lower part of the *D. extensus* zone is represented everywhere by arenaceous sediments, followed by the graptolitic Tetragraptus shales. The shelly faunas are best seen today on Ramsey Island, though the succession crops out at Llanveran, Porth Gain and Abercastle on the mainland. At Tremanhire, near St. David's, Hicks (1873 : 41) described a yellow sandstone, not now exposed, containing a shelly fauna, in which the fossils are undistorted.

Pringle (1930), in his description of Ramsey Island, erected the succession:

Tetragraptus Shales	*D. extensus* & *D. hirundo*
Porth Gain Beds	Blue-grey sandy shales with orthids dominant, also lamellibranchs, trilobites, crinoids and asteroids (60 m.)
Abercastle Beds	Grey sandy shales with trilobites and few orthids (27 m.)

These divisions were made following Cox's divisions (1916) in the Abercastle region, mainly on palaeontological differences, though he noted a gradual decrease in grain size from the coarser Abercastle Beds to the chocolate-weathering *Tetragraptus* Shales.

The base of the Abercastle Beds, on the north-east tip of Ramsey Island, was believed by Pringle to be a fault, but Cox *et al.* (1930 : 422) considered the junction to be a disconformity with a thin conglomerate containing *Bolopora undosa* resting on cleaved shales at the top of the Lingula Flags. The succession as measured by the writer is given in Text-fig. 1. Collecting has shown that the palaeontological differences listed by Pringle cannot be used to separate the Abercastle and Porth Gain Beds, and accordingly these divisions should not be used for the beds on Ramsey Island, and the term Ogof Hên Formation is proposed for the strata between the base and the topmost shelly bed. While the writer agrees with Cox *et al.* (1930) that the base of the Arenig is probably marked by a disconformity, there is some shearing along that plane which precludes a categorical assertion of this. Sandy shales lie above the plane, beneath which are cleaved mudstones without bedding planes, regarded as the topmost preserved beds of the Lingula Flags. About 30 cm. up from the plane a 2 cm. bed of coarse sandstone contains *Bolopora*-like masses (Pl. 1a); it was probably from this horizon that the *Bolopora* recorded by Cox *et al.* was collected. The lower part of the succession is marked by fine current bedded siltstone and sandstone bands, with some evidence of worm burrowing, load casting and convolute bedding (Pl. 1b).

The lowest shelly horizon is about 3 m. above the unconformity, and contains only *Orthambonites* sp. All the other elements in the fauna, with the exception of *Monorthis menapiae*, come in about 30 cm. higher up, where the coarser basal sandstones are succeeded by finer shales. *M. menapiae* is found only in the highest accessible shales, together with *Lenorthis alata* and possibly *Ramseyocrinus* (Bates 1968*b*). No specimens of *Uranaster* were found, and its range is therefore unknown.

At Carmarthen Murchison's type locality for *Spirifer alatus* and *Ogygia murchisoniae* is the old Roman Road at Pensarn, of which the lower 100 m. south-east from Capel y Babell (N.G.R. 41341920) are cut in soft grey shales. A new excavation, on the north-east side of the Roman Road at its lower end, 30 m. east of the Chapel, has furnished the material described here.

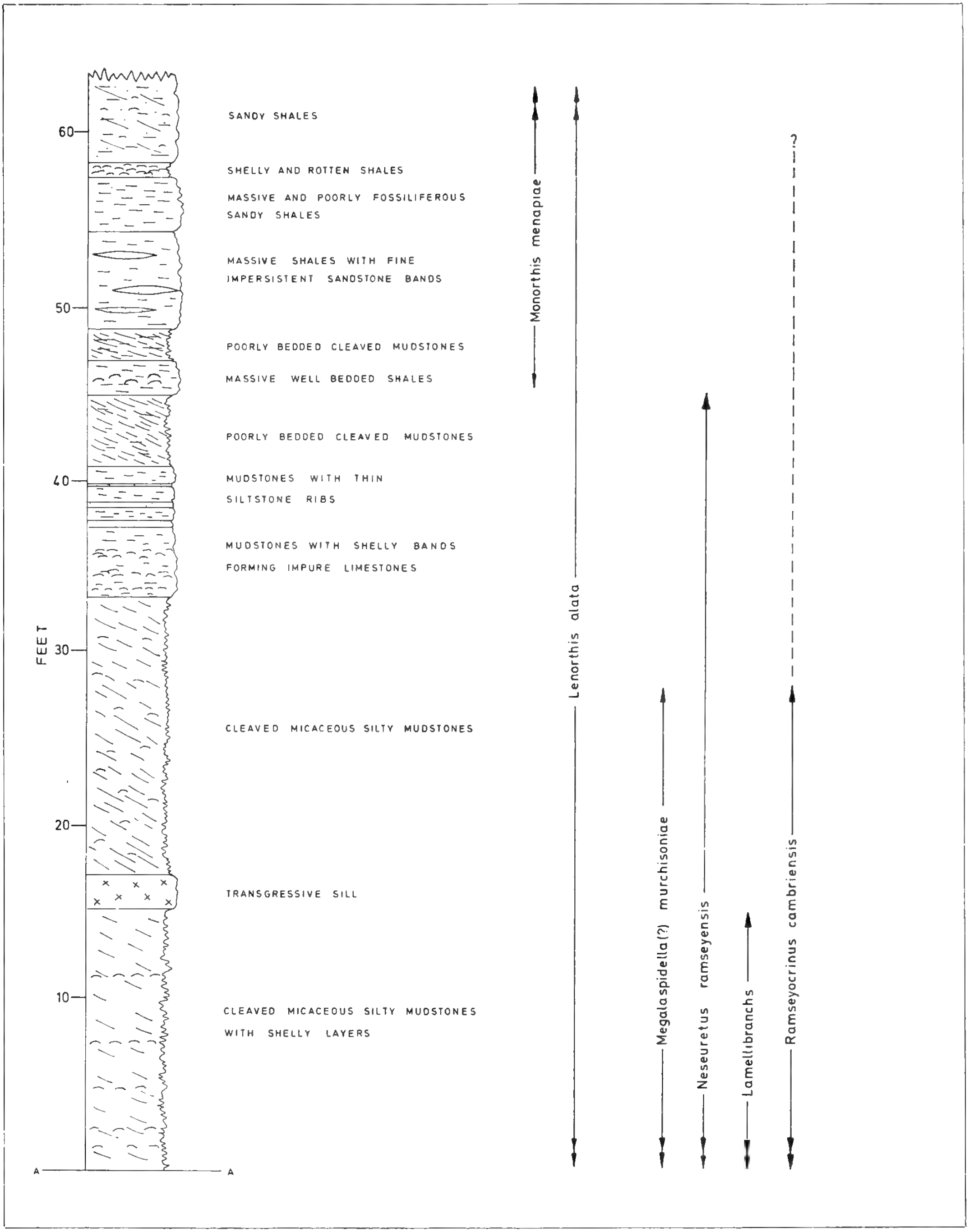
A collection of brachiopods and trilobites was made from the Henllan Ash of the Arenig District, from localities 2 and 4 of Whittington (1966 : 492). In both localities *Neseuretus parvifrons* was much more common than *N. murchisoni*, as noted by Whittington (1966 : 503), disarticulated pieces numbering about eight to one in favour of the former. *Lenorthis proava* (Salter) was common in both localities, particular in locality 4, where it out-numbered all other fossils. An analysis of the fauna collected is given in Table 1.

TABLE 1

Analysis of the fauna of the Henllan Ash from localities 2 and 4 of Whittington (1966).

	Locality 2	Locality 4
Megalaspidella (?) *murchisoniae*		
cranidium	7	3
thorax	0	1
pygidium	11	10
Neseuretus (both species)		
cranidium	16	0
thorax	7	0
pygidium	9	3
Lenorthis proava		
pedicle valve	9	13
brachial valve	6	15
conjoined valves	6	8
Inarticulate brachiopods	1	0
Orthocone nautiloid	3	3

Both species of *Neseuretus* are rare in locality 4, while *Lenorthis* is relatively more abundant. Analysis of the ratio of brachial to pedicle valves, and of the proportion


SANDY SHALES
SHELLY AND ROTTEN SHALES
MASSIVE AND POORLY FOSSILIFEROUS SANDY SHALES
MASSIVE SHALES WITH FINE IMPERSISTENT SANDSTONE BANDS
POORLY BEDDED CLEAVED MUDSTONES
MASSIVE WELL BEDDED SHALES
POORLY BEDDED CLEAVED MUDSTONES
MUDSTONES WITH THIN SILTSTONE RIBS
MUDSTONES WITH SHELLY BANDS FORMING IMPURE LIMESTONES
CLEAVED MICACEOUS SILTY MUDSTONES
TRANSGRESSIVE SILL
CLEAVED MICACEOUS SILTY MUDSTONES WITH SHELLY LAYERS
FEET
60
50
40
30
20
10
A
A
Monorthis menapiae
Lenorthis alata
Megalaspidella (?) murchisoniae
Neseuretus ramseyensis
Lamellibranchs
Ramseyocrinus cambriensis
?

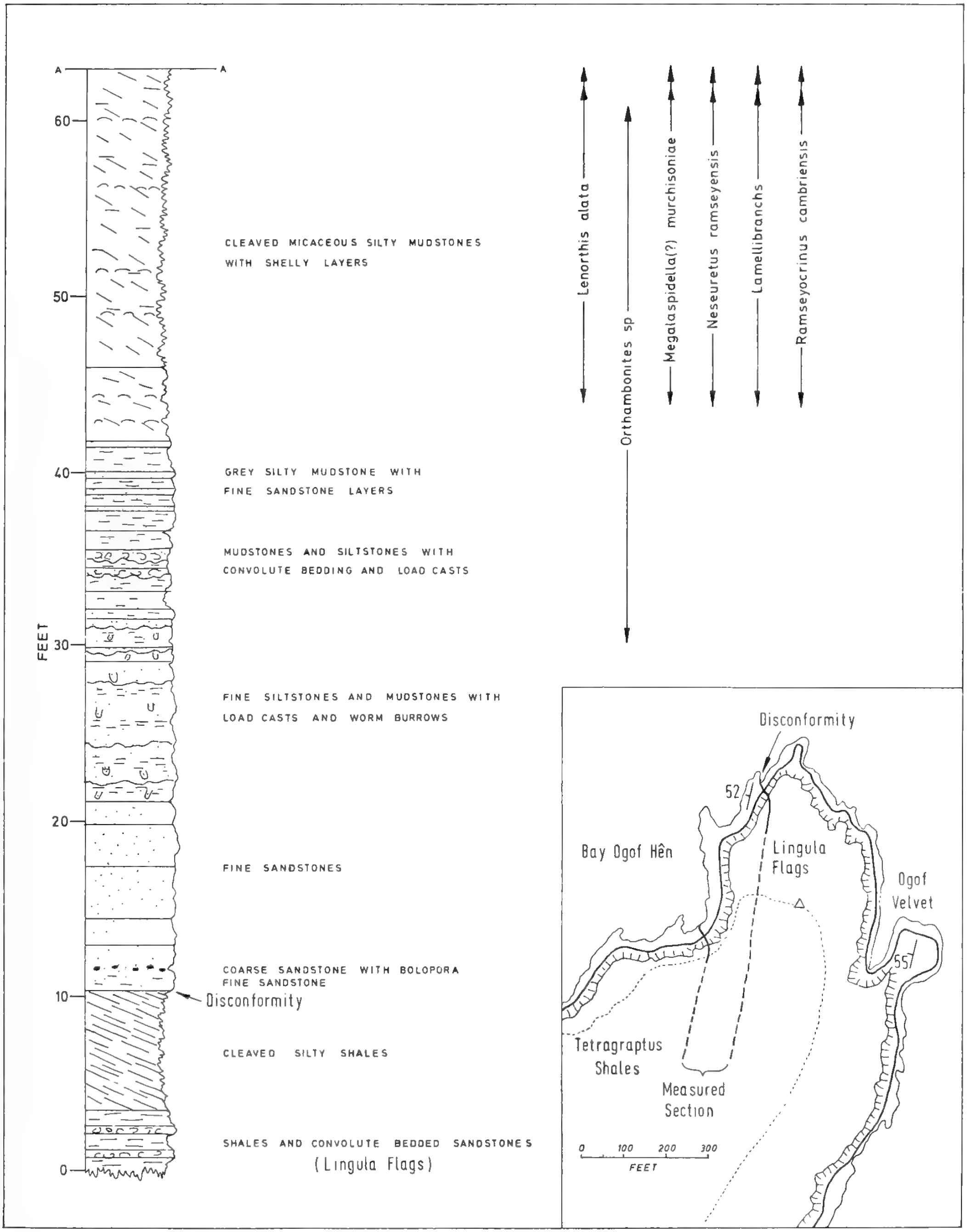


FIG. 1. Section through the Ogof Hên Formation strata at Bay Ogof Hên. Inset map shows the location of the section, at the north-east tip of Ramsey Island.

of conjoined valves present, suggests that the fauna has not suffered much *post mortem* movement. In Anglesey a count of over 500 valves from the Carmel Formation yielded only one conjoined pair.

III. FAUNAL AFFINITIES AND CORRELATION

The faunas of Ramsey Island and Carmarthen are comparable, and have similarities with other basal Arenig faunas from the Welsh region (Bates 1968*a*). There is a distinction between those of the South-west Wales and Welsh Borders belt, and the predominantly brachiopod fauna of Anglesey and Wexford. The latter fauna (Bates 1968*a*, Brenchley *et al.* 1967) contains a number of orthoid and strophomenoid species with Baltic affinities, while the former has a fauna relatively poor in brachiopods, and, so far, without Baltic elements. *Lenorthis alata* replaces the Anglesey species *L. proava*, and *Monorthis* is common to both areas; all these are indigenous stocks, as are the trilobites.

Whittard (1964 : 236) noted that *Megalaspidella* (?) *murchisoniae* (his *Ogygiocaris selwynii*) and *M.* (?) *whittardi* (his *Ogygiocaris murchisoniae*) were found at different horizons in Shelve, the former being restricted to the Mytton Flags (*D. extensus* zone) and the latter to the top of the Tankerville Flags (*D. hirundo*). At Arenig (in the Henllan Ash), and on Ramsey Island, he identified both species at the same horizon, the two species being intermingled in contrast to their separation in the Shelve region. Whittington (1966 : 498) has, in contrast, asserted that only one species is present at Arenig, *M.* (?) *murchisoniae*, identified by him (following Whittard) as *M.* (?) cf. *selwyni*. The same holds for Ramsey Island, only one species (*M.* (?) *murchisoniae*) being found, and thus it is possible that the stratigraphic separation of the two species in the Shelve region holds good elsewhere; the two species may prove alternative zone fossils for the Arenig series. *M.* (?) *whittardi* is likely, however, to prove of limited usefulness, as the *D. hirundo* zone is often devoid of trilobites.

IV. SYSTEMATIC DESCRIPTIONS OF THE BRACHIOPODS

Family **HESPERONOMIIDAE** Ulrich & Cooper 1936

Genus ***MONORTHIS*** Bates 1968

TYPE SPECIES. *Monorthis typis* Bates

Monorthis menapiae (Davidson)

(Pl. 2, figs. 1–13).

1868 *Orthis menapiae* Davidon : 314, pl. 16, figs. 24–28.
1869 *Orthis menapiae* Davidson : 228, pl. 33, figs. 8–12.

Diagnosis. Subquadrate biconvex *Monorthis*, slightly indented anteriorly, widest at a long, straight hingeline, alate, with acute cardinal angles, lateral profile convexo-plane; pedicle valve almost flat, with well marked carinate median fold, flat or slightly concave laterally, interarea plane, strongly apsacline, short, delthyrium open; brachial valve convex, with median sulcus and swollen folds on either side, interarea shorter than the ventral one, anacline, notothyrium open; ornament of both valves multi-costellate, costellae arising by bifurcation, numbering about four per mm. at shell margins and about five per mm. at 5 mm. from the ventral umbo, growth lines visible only at shell margin where they are crowded together and imbricate; ventral interior with receding dental lamellae, teeth blunt and prominent, with well defined crural fossettes, muscle scars extending a little beyond the delthyrial cavity, of the same type as in *Hesperonomiella*, with adductors and diductors expanding linearly forwards, the adductors quadrangular in outline, the diductors crescentic and extending slightly further forwards; mantle canal system probably saccate, with divergent *vascula media*; dorsal interior with small elevated notothyrial platform, cardinal process a simple ridge, brachiophores stout ridges, slightly swollen at their outer ends; sockets rounded; muscle scars with anterior and posterior pairs the same size, both sets subcircular in outline, the anterior pair directly in front of the posterior.

Type material (All distorted). Lectotype (here chosen): Internal and external moulds of pedicle valve (BB.31873a–b). Syntype: Internal mould of brachial valve (BB.31874).

Other figured material (All distorted). Internal and external moulds of brachial valve (BB.31897a–b); Internal mould of brachial valve (BB.31898); Internal and external moulds of brachial valve (BB.31899a–b); Internal mould of two pedicle valves (GSM.11938); Internal mould of pedicle valve (BB.31902); Internal and external moulds of pedicle valve (BB.31901a–b).

Horizon and locality. Lower Arenig, Ogof Hên Formation, Bay Ogof Hên, Ramsey Island. N.G.R. 708252.

Discussion. Davidson's figures of *Orthis menapiae* are somewhat misleading, as they appear to represent two species, one alate, the other with the hinge line a little shorter than the greatest width of the shell. It thus appears at first sight that the non-alate figures are of shells of the type here referred to *Orthambonites* sp. (Pl. 5, figs. 7–12). However examination of the Davidson Collection in the British Museum shows that all the specimens seen by him were alate; his non-alate drawings were simply reconstructions, and the likeness between them and *Orthambonites* sp. is simply coincidental.

The same distortion makes it difficult to compare the Ramsey specimens with *M. typis* Bates from Anglesey, though it is possible that they are referable to different species. The Ramsey specimens appear to have the pedicle valve slightly flatter, and to have stouter cardinalia. Proportions of length and width cannot, due to distortion, be measured. The Ramsey specimens have the muscle scars, teeth and mantle canal patterns rather better preserved. Specimen BB.31898 (Pl. 2, fig. 12) shows incipient development of chilidial plates, confirming the placing of this genus in the Hesperonomiidae.

Family **ORTHIDAE** Woodward 1852

Genus ***LENORTHIS*** Andreeva 1955

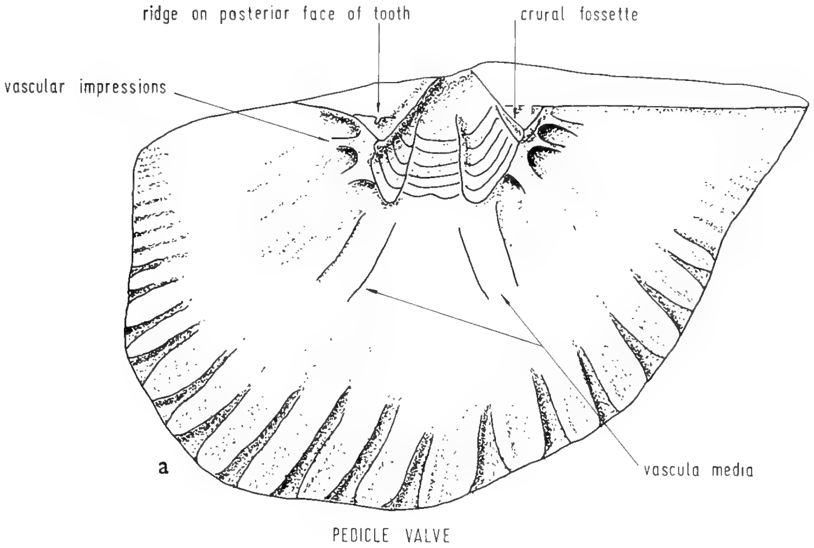
TYPE SPECIES. *Lenorthis girardi* Andreeva.

Lenorthis alata (J. de C. Sowerby)

(Pl. 2, fig. 14; Pl. 3, figs. 1–7; Pl. 4, figs. 1–10; Pl. 5, figs. 1–6)

1839 *Spirifer alatus* J. de C. Sowerby in Murchison : pl. 22, fig. 7.
1849 *Orthis alata* (J. de C. Sowerby); Salter in Murchison : 55, fig. 15, pl. 5, fig. 6.
1868 *Orthis carausii* Davidson : 315, pl. 16, fig. 23.
1869 *Orthis alata* (J. de C. Sowerby); Davidson : 232, pl. 33, figs. 17–21.
1869 *Orthis carausii* Davidson; Davidson : 229, pl. 33, figs. 1–7.
non 1883 *Orthis carausii* Davidson; Davidson : 182, pl. 14, figs. 21–26.
1911 *Orthis carausii* Davidson; Matley : 78.

DIAGNOSIS. Sub-semicircular ventro-biconvex *Lenorthis* two-thirds as long as wide (in large specimens), approximately one quarter as deep as wide, the pedicle valve being at least twice as deep as the brachial valve; widest at the hinge line, with alate cardinal angles becoming less accentuated with growth, anterior margin not indented; anterior commisure slightly sulcate; delthyrium and notothyrium open; pedicle valve convex but with concave or flattened portions adjacent to the cardinal angles, interarea slightly concave, apsacline, about one-sixth the length of the valve; brachial valve gently convex with a shallow median sulcus and concave flanks to the folds becoming flat towards the cardinal angles, interarea anacline, curved and half the length of the ventral one; ornament on both valves of approximately 40 rounded costae and equal rounded interspaces, strong in the median portion of the valves but becoming fine and crowded towards the hinge lines, with a wavelength of 0·7 mm. at 5 mm. from the dorsal umbo, the pedicle valve bearing a median costa and the brachial valve 4 costae in the sulcus; fine parvicostellae and growth lines present; ventral interior with blunt pyramidal teeth, the posterior faces parallel to the interarea and apparently bearing a central ridge aligned parallel to the edge of the delthyrium: dental lamellae vertical, receding; muscle scars approximately twice as long as the delthyrium and extending one-third the length and one-fifth the width of the pedicle valve, approximately pentagonal in outline with the adductor tracks extending linearly forward and not enclosed by the diductor tracks, the latter extending slightly further forwards than the adductor tracks and with their anterior margins running obiliquely forwards from the dental lamellae making an angle of about 50° with the hinge line; grooves present in the sides of the dental lamellae between the diductor tracks and the margin of the delthyrium; *vascula media* extend from the anterior ends of the diductor tracks and diverge at the same angle; margin of valve deeply crenulate; dorsal interior with socket ridges diverging at just under 90° from each other, short, blade-like on their postero-ventral edges, rounded at their ends, bearing faint curved striae on their outer faces; sockets excavated below the hinge line, split by a subdued median ridge whose growth forms a ridge in the interarea, outside the socket ridge, aligned on the umbo; cardinal process a simple ridge, thickened on its antero-ventral edge, flanked by low accessory ridges; notothyrial



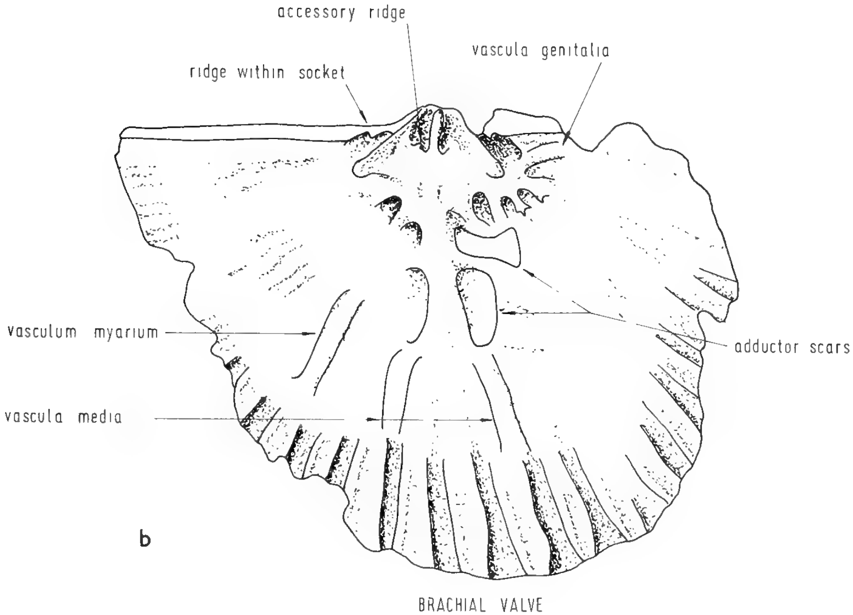


FIG. 2a. Sketch of ventral interior of *Lenorthis alata* (Sowerby), based on specimen BB.31881a (Pl. 4, fig. 2).

FIG. 2b. Sketch of dorsal interior of *Lenorthis alata* (Sowerby), based on specimen BB.31879a (Pl. 4, fig. 1).

platform extending into a thick rounded median septum running forwards for just under half the length of the valve; posterior adductor scars quadrangular, over twice as wide as long, anterior adductor scars half the width but over twice as long as the posterior adductor scars; mantle canal system digitate, *vascula media* diverge from the anterior adductor scars, *vascula myaria* and traces of *vascula genitalia* present; margin of valve deeply crenulate.

HORIZONS AND LOCALITIES. (a) Friable blue shales at the lower end of the road cutting in the Roman road at Pensarn, Carmarthen. N.G.R. 41341920.

Murchison's specimens are stated to have come from Pensarn and Mount Pleasant, Carmarthen; the Geological Survey (Strahan *et al.* 1909 : 15) lists the species from an exposure behind Capel-y-babell, at the foot of the road cutting, and from the cutting itself. The figured specimens come from a new excavation, 30 m. uphill from the Chapel, on the north-east side of the road, where the cutting begins. Davidson also records the species from the Shelve area, but according to Professor Alwyn Williams (personal communication) it has not been found there.

(b) Yellow sandstones, Tremanhire, north-east of Solva, Pembs.; exact locality not known, but probably a quarry now filled in. This is the type locality of *Orthis carausii* Davidson.

(c) Lower Arenig, Ogof Hên Formation, Bay Ogof Hên, Ramsey Island. N.G.R. 708252.

	Length (mm)	Width (mm)
TYPE MATERIAL.		
(a) Pensarn		
Lectotype of *Spirifer alatus* (here chosen):		
Internal mould of brachial valve (GSM. 6868)	9·1	24·5
(b) Tremanhire		
Lectotype of *Orthis carausii* (here chosen):		
Internal mould of brachial valve (BB.31875)	7·1	—
Syntype: External mould of pedicle valve (BB.31876)	—	—
ADDITIONAL MATERIAL		
(a) Pensarn.		
Internal mould of brachial valve (BB.31878)	8·4	14·4 (est.)
Internal and external moulds of brachial valve (BB.31879 a-b)	14·1	18·8 (est.)
Internal and external moulds of brachial valve (BB.31880a-b)	10·5	18·6 (est.)
Internal and external moulds of pedicle valve (BB.31881a-b)	12·3	19·8 (est.)
Internal mould of pedicle valve (BB.31882)	—	14·8 (est.)
External mould of brachial valve and interarea of pedicle valve (BB.31883)	—	—
External mould of brachial valve (BB.31884)	—	20·6 (est.)
External mould of brachial valve (BB.31885)	—	22·4
External mould of pedicle valve (BB.31886)	11·9	16·2 (est.)

(b) Ramsey Island (All distorted)		
Internal mould of brachial valve (BB.31887)	—	—
Internal and external moulds of brachial valve (BB.31890a-b)	—	—
Internal and external moulds of brachial valve (BB.31893a-b)	—	—
Internal mould of pedicle valve (NMW.29.308.G397)	—	—
Internal and external moulds of pedicle valve (NMW 29.308.G400 & G249)	—	—
Internal and external moulds of pedicle valve (BB.31891a-b)	—	—

DISCUSSION. The species was erected by Sowerby on account of its alate shape, and was originally placed in the genus *Spirifer*. Subsequently Salter (in Murchison 1849) and Davidson (1869) recognized it as an *Orthis*, but the interiors were not adequately figured. The only specimen from Murchison's collection now present in the Geological Survey Collection is here refigured (GSM.6868, pl. 2, fig. 14), but only shows the outline (probably distorted).

Orthis carausii was described by Davidson from Tremanhire, St. David's and Ramsey Island (1868 : 315), and refigured in 1869 (pl. 33, figs. 1–7). Through the kindness of Dr. L. R. M. Cocks, of the British Museum, the writer has been able to examine the specimens from which the figures were drawn. The blocks drawn in both papers (1868 : pl. 16, fig. 23c; 1869 : pl. 33, fig. 5) are composite drawings, not reproductions of actual blocks. The specimens used are BB.31875–7, and block B.13055. Although Davidson's figures, and texts, describe the hinge-width of the valves as being the same or a little less than the greatest width, where the specimens on these slabs can be seen to be well preserved they are definitely alate; the species is thus here accepted as a synonym of *Lenorthis alata*.

Most of the specimens of *Lenorthis* from Ramsey Island can be referred to *L. alata*. They show an alate outline, with the larger specimens tending to be less alate than the smaller, although in some specimens the distortion due to the cleavage has resulted in either accentuation or suppression of the cardinal angles. Their suppression makes it difficult to identify some specimens, and accounts for some of the confusion between this species and *L. proava* (Matley 1912 : 78). Rib-counts of the Ramsey Island specimens also show, where the preservation is good, counts of up to 40, with smaller costae close to the hingeline, and similar muscle scars and mantle canal impressions to topotype specimens of *L. alata*.

In *L. alata* the shape of the shell changes with growth, the outline becoming more quadrate as the alae become less prominent, and the cardinal angles less acute. Statistics of growth lines show that the increase in length relative to width is significantly allometric (Table 2), and this is easily seen from the growth lines in some valves (e.g. Pl. 3, fig. 1).

Muscle scars are well developed and distinctive in both valves. In the pedicle valve the diductor scars are partly impressed on the sides of the dental lamellae, and their anteromedian corners project forwards farther than the adductor scars.

Beneath the margins of the delthyrium and above the diductor tracks are two grooves expanding forwards, either the tracks left by the crural fossettes, or the tracks of pedicle adjustor muscles. In the brachial valve the posterior adductor scars are larger than the anterior scars, wider than long, and with anterior and posterior margins which are both concave inwards towards the centre of the scar.

The teeth and sockets are unusual in the development of double sockets, the outer of which apparently interlocks with a ridge on the tooth, and the inner, which is bounded medianly by the socket ridge, with the inner edge of the tooth (Text-fig. 2). The median partition of the socket leaves a ridge on the inter-area marking its track, diverging slightly anteriorly from the boundary of the notothyrium. This complication in the dentition does not seem to be common, though it may be present in *Lenorthis subconvexus* (Cooper) (Cooper 1956 : pl. 34, fig. 22). A similar ridge is indicated at least in the right hand socket of the specimen illustrated by Cooper, and its track across the interarea is visible. The teeth of *L. alata* may also bear ridges.

The mantle canal system is partially indicated by scars in both valves. The ventral *vascula media* diverge from the anterior ends of the diductor scars, but are only faintly indicated, as are the proximal ends of the *vascula genitalia*, beneath the sockets. It cannot, however, be determined whether the canal system is saccate or digitate, though the system is generally saccate within the *Orthinae*. Traces of the dorsal canal system are more extensive, and elements of the system described by Öpik (1934), figured in Moore (1965, fig. 134), can be recognized in specimen BB.31879 (Pl. 4, fig. 1). The *vascula media* diverge anteriorly from the anterior adductor scars, and are roughly parallel to the *vascula myaria* which originate at the anterolateral corners of the posterior adductor scars. Between the posterior adductor scars and the notothyrial platform the median ridge thickens to twice its anterior width, while small branches from it may represent the transmyarian apophyses of Öpik. Beneath the ends of the socket ridges is a group of three radiating ridges, probably part of the digitate *vascula genitalia*.

TABLE 2

Statistics of length (l) and width (w) of 15 pedicle valves (A) and 30 brachial valves (B) of *Lenorthis alata* (J. de C. Sowerby) from Pensarn, Carmarthen.

	A	B
$\overline{l}$	7·807	7·018
var. l	10·543	9·285
$\overline{\log_e l}$	1·9640	1·8390
var. $\log_e l$	0·1862	0·3016
$\overline{w}$	14·013	14·993
var. w	13·952	27·990
$\overline{\log_e w}$	2·5922	2·6229
var. $\log_e w$	0·0831	0·2032
r_e	0·9092	0·9087
α	1·498	1·219
var. α	0·01296	0·008628
$\log_e \beta$	1·4364	1·1135
var. $\log_e \beta$	0·01645	0·01459

The values of α and β refer to the equation $\log_e w = \log_e \beta + \alpha \log_e l$.

Genus ***ORTHAMBONITES*** Pander 1830

TYPE SPECIES. *Orthambonites transversa* Pander 1830.

Orthambonites sp.

(Pl. 5, figs. 7–12)

DIAGNOSIS. Sub-semicircular *Orthambonites*, as wide as long(?), width at hinge line less than width of shell, biconvex; pedicle valve with the greater convexity, with rounded median fold, interarea apsacline, curved, delthyrium open; brachial valve with a rounded median sulcus, interarea anacline, shorter than the ventral one, notothyrium open; ornament on both valves multicostellate with the costellae increasing by bifurcation and numbering about three per mm. at 5 mm. from the dorsal umbo; ventral interior with diverging dental lamellae descending vertically to the floor of the valve, teeth not seen, muscle scars extending beyond the lamellae, with crescentic diductors not enclosing triangular adductors and extending farther than them; dorsal interior with simple cardinal process on a raised notothyrial platform, socket ridges short, bladelike, thickened on their outer sides in front of the sockets, supported by bases which converge to the sides of rounded median ridge, sockets mainly excavated in hinge line, muscle scars quadripartite, with anterior pair slightly larger than the posterior pair.

HORIZON AND LOCALITY. Ogof Hên Shales, Bay Ogof Hên, Ramsey Island. N.G.R. 708252.

FIGURED SPECIMENS:—(All distorted). Internal mould of brachial valve (LL.3182); Internal mould of brachial valve (LL.3184); Internal mould of brachial valve (NMW.29.308.G360); Internal mould of brachial valve (NMW.29.308.G31); Internal mould of pedicle valve (BB.30900).

DISCUSSION. Externally the species is very similar to *Nanorthis* Ulrich & Cooper, though this genus has a rudimentary cardinal process and a poorly developed notothyrial platform. *Nothorthis* Ulrich & Cooper is similar but more transverse, and has a rudimentary cardinal process and a well developed notothyrial platorm. The closest species are from the Upper Pogonip of Nevada, *Orthambonites bifurcatus* Cooper, and *Orthambonites eucharis* (Ulrich & Cooper). Differences are few; in particular the distinctions between the two American species seem very finely drawn, and are mainly in the shape of the costellae. The Welsh species does not have a median ridge anterior to the ventral muscle scars, and the brachial valve may be more convex.

V. SYSTEMATIC DESCRIPTIONS OF THE TRILOBITES

Family **ASAPHIDAE** Burmeister 1843

DISCUSSION. The most recent subdivision of the large family Asaphidae is that of Jaanusson (in Moore 1959), where seven subfamilies are recognized, on a variety of criteria.

In the Asaphinae the glabella has a pair of oblique furrows, which gives it a distinctive shape; the occipital ring is not constricted medianly, the hypostome is deeply notched, and the glabellar tubercle is far back. Of these characters, the first is confined to this subfamily. The Promegalaspidinae are unique in that the eighth thoracic segment is developed as macropleurae; also they have the occipital ring without a median constriction, the hypostome is notched, the glabellar tubercle is situated forward from the occipital ring by at least the length (sag.) of the ring. The Symphysurinae have a glabellar tubercle which is situated very far forwards, between the centres of the eyes; the occipital ring may be longest (sag.) medianly, and the hypostome appears to have a rounded posterior margin. The Thysanopyginae have a spinose pygidial border, together with a rounded posterior border to the hypostome, and a glabellar tubercle which is situated far back.

Thus these four subfamilies are distinct from each other, and the rest of the Asaphidae, in at least one character in each subfamily: oblique glabellar furrows, macropleurae, a glabellar tubercle placed very far forwards, and a spinose pygidium. All these characters are lacking in the other three subfamilies, the Isotelinae (groups A and B), Niobinae, and Ogygiocaridinae. The distinctions between these groups are less clear in the *Treatise*. The glabellar tubercle occupies a similar position in all four, the hypostomes all have triangular anterior wings, and the pygidium is rounded or bears a median spine.

Differences occur chiefly in the form of the occipital ring, and the posterior margin of the hypostome. The occipital ring in the Ogygiocaridinae and in group B of the Isotelinae is restricted medianly where seen, and has a posterior band corresponding to the articulating half ring of the first thoracic segment (Henningsmoen (1960 : 210). The posterior margin of the hypostome is strongly concave to deeply notched in the Niobinae; otherwise it is rounded, straight or pointed.

Consideration of these points suggests that Group A of the Isotelinae can be conveniently joined with the Niobinae, as comprising a subfamily with a notched or concave hypostome, and with an unrestricted occipital ring where seen (Isotelinae Angelin 1854). Group B and the Ogygiocaridinae can also be united, as comprising forms with an entire hypostome, and an occipital ring restricted where seen (Ogygiocaridinae Raymond 1937). The two groups are, however, probably closely related, and may have diverged in the Tremadoc from an ancestral form such as *Niobella*, with a rounded posterior margin to the hypostome, and an almost smooth glabella, in which the occipital ring was not restricted medianly. From this root stock the Isotelinae diverged, with progressively greater emargination of the hypostome, as in the sequences *Niobella—Niobe*, *Protopresbynileus—Presbynileus*, *Isoteloides—Isotelus—Homoteloides*. The glabella remained smooth, and all traces of the occipital ring vanished. There is also a tendency for the glabella to be parallel-sided in the early forms, and to expand in front of the eyes in later genera.

In the Ogygiocaridinae the hypostome remained rounded, or pointed, and the glabella in many of the later genera, became furrowed, and expanded forwards. The occipital ring was constricted medianly, with a well developed posterior band.

Some genera are difficult to place in this scheme. *Pseudogygites* seems, from its glabella, to be a member of the Ogygiocaridinae, but is thought by Jaanusson (in Moore 1959 : *O*343) to have a notched hypostome. *Megistaspis*, with an unrestricted occipital ring and notched hypostome, is here put in the Isotelinae, while its subgenera *Megistaspidella* and *Ekeraspis* are assigned to the Ogygiocaridinae.

Stratigraphically the Isotelinae range from the Tremadoc to the upper Ordovician, while the Ogygiocaridinae became extinct during the middle Ordovician (in a broad sense). The two subfamilies also have different geographical distributions. The Ogygiocaridinae are found in Europe and South America, and appear not to have penetrated North America. On the other hand the Isotelinae are not found in South America, but are common in North America, particularly in the Upper Ordovician.

Subfamily **OGYGIOCARIDINAE** Raymond 1937

DIAGNOSIS. Glabella tapering forwards, parallel sided or expanding in front of eyes; glabellar tubercle situated far back, well behind level of eyes; occipital ring where recognizable constricted medianly usually with a posterior band developed; hypostome with triangular anterior wings, posterior margin rounded to pointed (faintly concave in some species of *Asaphellus*); pygidium with rounded posterior margin or with median spine.

Genus ***MEGALASPIDELLA*** Kobayashi 1937

TYPE SPECIES *Megalaspidella kayseri* Kobayashi 1937.

Megalaspidella (?) ***murchisoniae*** (Murchison)

(Pl. 6, figs. 1–6; Pl. 7, figs. 1–9; Pl. 8, figs. 1, 2, 5).

1839 *Ogygia Murchisoniae* Murchison : 664, pl. 25, figs. 3a, 3b.
1852 *Asaphus Selwynii* Salter : 57.
1873 *Niobe menapiensis* Hicks : 46, pl. 4, figs. 1–9.
1873 *Niobe solvensis* Hicks : 47, pl. 4, figs. 10–16.
1896 *Ogygia marginata* Crosfield & Skeat : 538–539, pl. 26, figs. 13–26.
1906 *Ogygia marginata* Crosfield & Skeat; Evans : 603, 606, 608.
1907 *Ogygia marginata* Crosfield & Skeat; Strahan *et al.* : 10, 14–15.
1931 *Ogygia marginata* Crosfield & Skeat; Reed : 461.
1964 *Ogygiocaris selwynii* (Salter); Whittard : 232–238, pl. 34, figs. 7–13, pl. 35, figs. 1–10, pl. 36, figs. 1–7, pl. 37, figs. 1–11 (see also for earlier references).
1964 *Ogygiocaris murchisoniae* (Murchison); Whittard : 238–241, pl. 38, figs. 5–11 (see also for earlier references).
1964 *Ogygiocaris marginata* (Crosfield & Skeat); Whittard : 237, 241, pl. 36, figs. 8–10.
1966 *Ogygiocaris*? cf. *selwyni* (Salter); Whittington : 496–499, pl. 2, figs. 7–12, pl. 3, pl. 4, fig. 16.
1968a *Ogygiocaris selwynii* (Salter); Bates: 179–180, pl. 12, figs. 1, 2, 5, 6.

DIAGNOSIS. A species of *Megalaspidella*(?) with the anterior branches of the facial sutures diverging at about 100–120°; the glabella expanding slightly in front of the eyes and encroaching onto the anterior border; with or without hypostomal pits; pygidium with seven to nine axial rings and six to eight pleural furrows.

TYPE HORIZON AND LOCALITY. *Tetragraptus* Beds, Arenig Series, Roman Road, Pensarn, Carmarthen. N.G.R. 413192.

TYPE MATERIAL. (distorted). Holotype: Internal and external moulds of dorsal carapace. (GSM.18988 and counterpart).

OTHER MATERIAL.

(a). Pensarn, Carmarthen.

Internal and external moulds of cranidium (It.5805a-b); Internal and external moulds of carapace (It.5806a-b); Internal mould of hypostome (It.5807); Internal mould of pygidium (It.5808); Internal and external moulds of pygidium (It.5809a-b).

(b). Glan Pibwr, Carmarthen.

Internal mould of cranidium (SM.A.3118).

(c). Ramsey Island.

Internal mould of cranidium (OUM.B6); Internal mould of cranidium (It.5810); Internal mould of cranidium (SM.A.45141); External mould of dorsal carapace (NMW.29.308.G275); Internal mould of dorsal carapace (NMW.29.308.G219); Internal mould of hypostome (OUM.B183); Internal mould of pygidium (NMW.29.308.G28); Internal mould of pygidium (NMW.29.308.G422); Internal and external moulds of pygidium (It.5811a-b).

DESCRIPTION. Cephalon about twice as wide as long, semicircular in outline, with probably a slight change in curvature medianly. Glabella twice as long as wide, with a semicircular anterior margin and probably a slight constriction at half its length (sag.), opposite the eyes; gently convex, with a domed anterior portion. Glabella furrows if present very weakly impressed. Axial furrows weakly impressed, with shallow hypostomal pits. Fixigenae divided into two by constriction at the level of the palpebral lobes; posterior portion sub-triangular, palpebral lobes semicircular, close to glabella. Anterior border narrow medianly, possibly with a dorsally raised ridge on the midline. Occipital ring not well seen; delimited by a posterior band which is marked off by a curved furrow, convex forwards, and by very faint traces of the occipital furrow, inclined inwards and backwards from the axial furrows, commencing from in front of the posterior border furrows. Glabellar turbercle immediately in front of the occipital ring. Facial suture crosses the posterior border about midway between the axial furrow and the genal angle, inclined forwards and outwards from the margin of the cephalon, but curving immediately round to cross the posterior border furrow running directly forwards, and then describing a sigmoidal curve to the eyes. Anterior branches curve outwards and describe a similar sigmoidal curve, diverging from each other at more than 90°. The angle of divergence of the facial sutures is greatest where the sense of curvature of the suture changes from concave outwards to concave inwards. It is measured between tangents drawn to the sutures at these points. After crossing the inner margin of the anterior border the anterior branches curve round steadily to converge towards the margin, meeting it with a slight acumination at the midline, or possibly following the margin for a short distance on either side of the midline. The median suture may not therefore appear dorsally but this is difficult to verify. Librigenae large, provided with long genal spines. Lateral border broad and concave dorsally, defined by a wide shallow furrow which extends onto the fixigenae and meets the axial furrow at the hypostomal pit. Posterior border wide, defined by a furrow broader than the border itself, deepest on the fixigenae, widening and becoming shallow laterally before it fades out against the lateral border. Dorsal surface of cephalon apparently without terrace lines, but doublure of librigenae with well defined lines extending along the genal spine.

Hypostome known from poorly-preserved and incomplete specimen. Median body longer than wide. Anterior lobe much larger than posterior one, gently convex, defined by lateral furrows extending inwards towards the maculae, which are linked by a shallow median groove. Posterior lobe sickle-shaped, with indistinct maculae. Posterior border narrow medianly, rounded, with possibly a slight median point. Anterior wings small, triangular. Ornament of terrace lines parallel to the posterior border, but concave forwards across the median body and anterior wings to cross the anterior margin and become confluent with the terrace lines on the doublure of the librigenae.

Thoracic segments not well preserved, axis narrower than pleurae, convex, tapering only slightly backwards; pleurae with pleural furrows developed as broad concavities, ending in blunt spines.

Pygidium approximately as long as wide, with the posterior margin either semicircular or slightly acuminate medianly. Axis evenly tapering, of about eight axial rings and a semicircular terminal piece. Axial furrows broad and well defined. Pleurae with about six faint pleural furrows. Border broad, concave dorsally with a ridge on its inner margin, having a steep inner face. Doublure convex ventrally, with an evenly curved inner margin lying directly beneath the inner edge of the border, and bearing terrace lines parallel to its margin.

DISCUSSION. Whittard (1964 : 238) redescribed *Ogygiocaris murchisoniae* (Murchison), mainly from specimens collected in the Shelve area, but asserted that the holotype of the species, from Pensarn, Carmarthen, differed from *O. selwynii* in having anterior facial sutures diverging at about 45°, a frontal glabellar lobe which stops short of the anterior border, and in having no hypostomal pits. In addition a topotype pygidium had at least eight axial rings and five pleural pairs.

The writer has collected topotype material from Pensarn, and has re-examined the holotype; it is here claimed that *O. murchisoniae* is a synonym of *O. selwynii* as understood by Whittard. In the holotype of *O. murchisoniae*, especially in the external mould (Whittard 1964 : pl. 38, fig. 6), the anterior branches of the facial sutures diverge at about 95° (as the specimen is laterally compressed this must be an underestimate). The glabella also encroaches on the anterior border, reducing its width by at least half. Hypostomal pits have not been seen in any of the specimens, with the possible exception of It.5805 (Pl. 6, fig. 4).

The topotype pygidium figured by Whittard (1964 : pl. 38, fig. 7) as having at least eight axial rings and five pleural pairs is badly crushed and distorted. Specimen It.5806 (Pl. 6, figs. 1–2) has seven axial rings and a terminal piece, and about six pleural furrows.

The Pensarn specimens, therefore, differ significantly from *O. selwynii* of the Shelve region only in the apparent absence of hypostomal pits, and are probably conspecific with that species. The holotype of *O. selwynii* (SM.A.44425, Whittard

1964 : 236, pl. 37, fig. 1) from Hengwrt-uchaf, near Dolgellau, is, as Whittard states, poorly preserved, and shows possibly five or six axial rings followed by a relatively long terminal piece, and six or seven pleural furrows. It is possible that there may have been seven or eight axial rings present. Thus it appears probable that *O. selwynii* from its type locality is conspecific with *O. murchisoniae*, and as the earlier described species, the latter must take precedence.

The specimens identified by Whittard from the Shelve region as belonging to *O. murchisoniae* (1964 : 238–241, pl. 37, figs. 12–13, pl. 38, figs. 1–4) do, however, differ significantly from *O. murchisoniae* from Pensarn and *O. selwynii* from Shelve; they are here referred to a new species, *Megalaspidella*(?) *whittardi*.

Hicks (1873 : 46–47) described two species from the basal Arenig beds of Ramsey Island, *Niobe menapiensis* and *N. solvensis*. On re-examination of the type material, Whittard (1964 : 240) put both species into *O. murchisoniae* and considered them to be sexual dimorphs. Whittard refigured two cranidia of *N. menapiensis* (1964 : pl. 38, figs. 9–10). The original of fig. 9 (OUM.B6) is here refigured (Pl. 7, fig. 1) after further excavation from the matrix; the eye is further back than in *M.*(?) *whittardi*, the anterior branches of the facial sutures diverge at about 90° (the specimen is laterally compressed and this is therefore an underestimate), and there appear to be no hypostomal pits. The original of Whittard's fig. 10 (GSM.10174) is axially compressed, but still shows facial sutures which are widely divergent, and a glabella which encroaches on the anterior border. The writer has not seen any cranidia from Ramsey Island in which the anterior branches of the facial sutures diverge at less than 60°, and this is in axially compressed specimens; all the material from Ramsey Island is here identified as *O. murchisoniae*. Specimen SM.A.45141 (quoted by Whittard in error as SM.A.45142) is here refigured; it was identified by Whittard (1964 : 236) as a definite *O. selwynii* from Ramsey Island.

Whittard claimed that the pygidia from Ramsey Island showed a sexual dimorphism, one form being relatively longer than the other. It is difficult to check this, as the pygidia are all distorted, and their proportions may have been greatly altered. Distortion and compression also make it difficult to count the axial rings and pleural furrows on the pygidia, as these features are but faintly impressed even in well preserved specimens. A maximum of nine axial rings and a terminal piece has been observed (in NMW.29.308.G422; Pl. 8, fig. 2) and seven pleural furrows (in NMW.29.308.G148; Pl. 7, fig. 4); eight and six respectively are average figures for both measurements.

Ogygia marginata Crosfield & Skeat is here identified as a synonym of *M*(?) *murchisoniae*. Whittard recognized it as a valid species (1964 : 237, 241) in which the divergence of the anterior branches of the facial sutures is 100°, hypostomal pits occur, and the pygidium has nine axial rings and nine pleural furrows. It is thus only slightly different from *M*(?) *murchisoniae*.

The generic position of "*Ogygia*" *murchisoniae* is in some doubt (Whittington 1966 : 499). Of the genera assigned to the Asaphidae, five are close:— *Hoekaspis* Kobayashi, *Megalaspidella* Kobayashi, *Ogygiocaris* Angelin, *Ogyginus* Raymond, and *Ogygiocarella* Harrington & Leanza.

The facial sutures in "*O*" *murchisoniae* are definitely intramarginal or isoteliform

(NMW.29.308.G219; Pl. 7, fig. 7); this excludes *Ogygiocarella* and *Ogyginus*, but, as Whittard says (1964 : 232), the differences between the two types of suture are very slight, and there may not be any fundamental difference between them. Variations can be seen in the Ramsey Island specimens: in some the anterior portions are almost straight, meeting in a blunt point (It.5810; Pl. 7, fig. 3), but in others (NMW.29.308.G219; Pl. 7, fig. 7) there appears to be an even curve, which is tangential to the margin on the midline.

The glabella shows a slight expansion in front of the eyes, and a slight taper from the posterior margin to the eyes. This shape is characteristic of all the genera, with the exception of *Megalaspidella*, in which the glabella tapers evenly forwards. Glabella furrows are almost obsolete in the British species, as they are in *Megalaspidella*, and almost so in *Hoekaspis*. *Ogygiocarella*, and to a lesser extent *Ogyginus* and *Ogygiocaris*, have furrows developed.

The occipital ring is also used as a diagnostic feature. In all these genera, it is poorly developed, or not differentiated, and consists of a band, limited posteriorly against a lenticular or spindle-shaped area (the posterior band of Henningsmoen, 1960 : 210) which overlies the articulating half-ring of the first thoracic segment. The occipital ring is restricted medianly where seen in all the genera, and is defined in front by a pair of faint furrows, commencing just in front of the posterior border furrows, and running inwards and backwards, but fading out before reaching the midline. The glabellar tubercle is just in front of a line joining the two posterior border furrows. In *Megalaspidella* the occipital ring is not differentiated by these furrows, but it is faintly developed in one species of *Hoekaspis*. In the other genera it is clearly developed.

The hypostomes of the genera offer no clear cut differences between them. All have rounded or slightly acuminate posterior margins.

The pygidia of the genera are stated to differ in the following features: the number of axial rings and pleural furrows, the presence or absence of interpleural furrows, the width of the border, and the nature of the inner margin of the doublure. Whittard regarded pygidial differences of less than generic importance (1964 : 231). *Ogygiocaris*, as restricted by Henningsmoen (1960 : 216) has a scalloped margin to the pygidial doublure; all the species described by him are of middle Ordovician age (Llanvirn). Of Whittard's species from Shelve, *O. seavilli* (Whittard 1964 : 241) has a margin of this type, and is of Llanvirn age: it appears to be the only species referable to *Ogygiocaris* on these criteria from outside the Oslo region.

Thus *Hoekaspis* is close, in its glabella, facial suture and pygidium. It does, however, differ in that the librigenae have a convex border, and that the occipital furrows are better developed. *Megalaspidella* also is close, but has the glabella tapering forwards, has no glabellar furrows (as preserved), and has the anterior branches of the facial sutures diverging at a small angle (cf. "*Ogygia*" *whittardi*). Whittington (1966 : 499) compared the material from Arenig with *Megalaspidella*, pointing out that the chief differences were in the shape of the glabella and the course of the facial suture.

A generic assignation of these species is thus very difficult to make. An obvious course would be to erect a new genus for their reception, but this the writer hesitates to do: some of the differences between existing genera seem finely enough drawn. Stratigraphically *Megalaspidella* is closest to the British species.

***Megalaspidella*(?) *whittardi* sp. nov.**

1964 *Ogygiocaris murchisoniae* Whittard : 238–241, pl. 37, figs. 12–13; pl. 38, figs. 1–4 (non 5–11).

DIAGNOSIS. A species of *Megalaspidella*(?) with the anterior branches of the facial sutures diverging at about 40°; the glabella parallel sided without a definite expansion anteriorly; the frontal lobe of the glabella stopping short of the anterior border; without hypostomal pits; the pygidium having nine to ten axial rings and six pleural furrows.

TYPE SPECIMENS. Holotype: internal mould of cranidium (GSM.85363, Whittard 1964 : pl. 38 fig. 3). Paratypes: internal mould of cephalon and thorax (Wattison Coll. W. 25); internal mould of partial cephalon and thorax (GSM.85364); internal mould of thorax and pygidium (GSM.85365); external mould of cranidium, thorax and pygidium (GSM.85362); external mould of pygidium (GSM.85366).

TYPE HORIZON AND LOCALITY. Upper Arenig, *D. hirundo* zone, Tankerville Fags, Bergam Quarry, 330 yds. east-north-east of the Tankerville Mine, Shelve, Shrops.

DISCUSSION. The species was described fully, and the type specimens figured, by Whittard (see synonymy above). Reasons for erecting this species are given in the discussion of *M.*(?) *murchisoniae* (p. 20).

Family **HOMALONOTIDAE** Chapman 1890

Genus ***NESEURETUS*** Hicks 1873

1873 *Neseuretus* Hicks : 44.
1898 *Synhomalonotus* Pompeckj : 240.
1925 *Neseuretus* Vogdes : 106.
1960 *Neseuretus* Whittard : 138–141.
1966 *Neseuretus* Whittington : 499–500.

TYPE SPECIES. *Neseuretus ramseyensis* Hicks 1873.

DISCUSSION. *Neseuretus* has generally been treated as a synonym of *Synhomalonotus* Pompeckj, but Whittard (1960 : 138) showed that it takes precedence over the latter. He designated *Calymene parvifrons* as the type species, as he identified the first of Hicks's species, *N. ramseyensis* (Hicks 1873 : 44) as being conspecific with that species. However it is here claimed that *N. ramseyensis* is specifically distinct from *N. parvifrons*, and thus it should become the type species, as selected by Vogdes (1925 : 106).

Neseuretus ramseyensis Hicks

(Pl. 8, figs. 3, 4, 6–12; Pl. 9, figs. 1–3, 6).

1873 *Neseuretus ramseyensis* Hicks : 44–45, pl. 3, figs. 7–10, 16–22.
1873 *Neseuretus quadratus* Hicks : 45, Pl. 3, figs. 11, 13, 23–26, non fig. 12.
1873 *Neseuretus recurvatus* Hicks : 45, pl. 3, figs. 5–6.
1873 *Neseuretus? elongatus* Hicks : 45, pl. 3, figs. 1–3.
1873 *Neseuretus elongatus* var. *obesus* Hicks : pl. 3, fig. 4.
?1900 *Neseuretus recurvatus*? Hicks; Reed : 305, pl. 12, fig. 4.
?1900 *Neseuretus quadratus*? Hicks; Reed : 305–306, pl. 12, fig. 6. (quoted in error as fig. 5.).
?1900 *Neseuretus* sp. Reed : 306, pl. 12, fig. 5 (quoted in error as fig. 6).
1911 *Calymene tristani* (*Neseuretus ramseyensis*) Pringle : 558.
1918 *Calymene* (*Neseuretus? elongatus*) sp. Reed : 319.
1930 *Calymene* (*Neseuretus? elongatus*) sp. Pringle : 9.
1930 *Calymene tristani* Brongniart; Pringle : 12.
?1960 *Neseuretus grandior* Whittard : 141–142, pl. 20, figs. 1–2.
1960 *Neseuretus paryifrons* (Salter); Whittard : 145–146.
1960 *Neseuretus murchisoni* (Salter); Whittard : 148–150, pl. 21, figs. 1–2, *non* pl. 20, figs. 6–15.

DIAGNOSIS. A species of *Neseuretus* with probably a thin upturned anterior brim and border furrow, bearing canals on the border which may spread onto the preglabellar area; a distinct furrow in front of the glabella, indistinct glabellar furrows and well defined semicircular alae; the pygidium bearing eight to nine axial rings and a semicircular terminal piece, and eight pleural furrows, with faint interpleural furrows present towards the lateral borders.

TYPE HORIZON AND LOCALITY. Lower Arenig, Ogof Hên Formation, Bay Ogof Hên, Ramsey Island. N.G.R. 708252.

TYPE MATERIAL. Lectotype (selected by Whittard 1960 : pl. 21, fig. 1): GSM. 10166 (Hicks 1873 : pl. 3, fig. 10), cranidium. Syntypes are cranidium SM.A.45277 (Hicks 1873 : pl. 3, fig. 9; Whittard 1960 : pl. 21, fig. 2); cranidium SM.A.45276.

OTHER FIGURED MATERIAL. Cranidium (OUM.B9) (Hicks 1873 : pl. 3, fig. 12, syntype of *N. quadratus*); cranidium (It.5812); cranidium (It.5813); cephalon and thorax (NMW.29.308.G240a-b); pygidium (NMW.29.308.G168); pygidium (NMW. 29.308.G211); cranidia (SM.A.16732–3) (Hicks 1873 : 45, pl. 3, figs. 2–3, syntypes of *N.? elongatus*); dorsal carapace (L.10172) (Hicks 1873 : 45, pl. 3, fig. 1, syntype of *N.? elongatus*).

DESCRIPTION. Cranidium roughly trapezoidal in outline, original proportions not known. Glabellar outline nearly trapezoidal, with anteriorly convergent lateral margins and frontal margin slightly curved forwards; convexity variable (due to distortion), but longitudinally with a steep anterior profile. Two pairs of glabellar furrows commonly preserved; the posterior pair (1p) steeply inclined backwards from the axial furrow; second pair (2p) less steeply inclined, less deep, and not extending so far across the glabella. Faint median longitudinal ridge occasionally developed, and indications of subcircular muscle scars on the second glabellar lobes (2p) faintly preserved. Axial furrows well marked; hypostomal pits present at the antero-lateral corners of the glabella, preglabellar furrow well marked. Preglabellar area appreciably less than the length (sag.) of the glabella, inflated (probably due to distortion), marked off by the curving back of the anterior border furrows to the front of the glabella, with a variably accentuated marginal furrow and border. Border upturned, and sharply deflected downwards to define a thin brim as in *N. murchisoni* (Whittard 1960 : 149). Canal system present on the brim, occasionally also on the preglabellar area. Fixigenae about equal to half width of glabella at the level of the eyes. Paraglabellar areas faintly outlined, semicircular in outline and about the same size as the basal glabellar lobes. Occipital furrow well marked, flexed forward medianly; posterior border furrow broad (exsag.); occipital ring convex, widest medianly; posterior borders widening laterally. Facial suture gonatoparian, posterior branch sigmoidally curved; palpebral lobe crescentic in outline, probably spanning the interval between the centres of the 2p and 3p glabellar lobes, but distortion makes this very difficult to check; anterior branch extending slightly inwards to the anterior border.

Thorax of thirteen segments, axis approximately one third the total width. Articulating furrow deepening distally (cf. *N. parvifrons*, Whittington 1966 : 502, pl. 5, fig. 2). Pleural furrows deep and narrow broadening distally; tip rounded, with a broad facet. Apodemes prominent pits on internal mould.

Pygidium oval in outline, broader than long. Axis tapers uniformly to a semicircular terminal piece which does not reach the posterior margin. Articulating half-ring and furrow followed by eight to nine axial rings. Axial furrows converge uniformly to the last axial ring, then become almost parallel for a short distance before curving round the terminal piece. Pleural regions divided by seven to eight pleural furrows, including the anterior border furrow, all of which curve forwards slightly at the margin. Occasionally faint interpleural furrows present distally (seen on internal moulds). Doublure narrow and convex ventrally.

DISCUSSION. When Hicks erected *Neseuretus*, from Ramsey Island and Tremanhire, he described the pygidium as having eight to ten axial rings, as this was characteristic of all the species included by him (Hicks 1873 : 44, pl. 3). Whittard (1960) re-examined Hick's types, redefined *Neseuretus*, and referred *N. quadratus*, *N. elongatus obesus*, *N. ramseyensis* and *N. recurvatus* to *N. murchisoni* (Salter). *N.? elongatus* he identified as *N. parvifrons* (M'Coy). Whittard stated that he did not study the pygidia in detail (1960 : 139), as the species of *Neseuretus* are mainly defined on the cephala.

An accurate description of the Ramsey Island specimens is difficult, particularly in terms of relative proportions, as the specimens are all distorted, and this distortion has affected the preservation of the glabellar furrows, the anterior furrow, and the palpebral lobes. The cranidia found are mostly similar to *N. murchisoni*, in that an anterior border furrow is present, with a thin and forwardly projecting border in front. The glabella is trapezoidal in outline, though the amount of taper cannot be directly compared with either *N. murchisoni* or *N. parvifrons*, due to the distortion. Two pairs of glabellar furrows are present, and are similar in attitude to those in both *N. murchisoni* and *N. parvifrons*; the third pair, which is very faint in both those species, may be present but obliterated. The facial sutures converge anterior to the eyes, and the palpebral lobes extend from the level of the 2p glabellar lobes to the presumed level of the 3p lobes, but again this is only an estimation. In general the width of the fixigenae (tr.) at the level of the eyes is less than or equal to half the width of the glabella.

The preglabellar furrow is deeper than in either *N. parvifrons* or *N. murchisoni*, though it is in many specimens accentuated by distortion. It is also probable that the glabellar furrows were less accentuated than in those species, as even in specimens where other transverse furrows have been deepened with the distortion they still remain faint.

In several specimens (e.g. It.5813, Pl. 8, fig. 10) the internal moulds have a peculiar pattern of furrows on the glabella, representing original ridges on the ventral surface of the carapace, though the glabellar furrows cannot be fully made out. Two longitudinal furrows in the anterior half of the glabella enclose a lenticular area, while the rear half, apparently on the 2p glabellar lobes, is marked by two furrows with circular outlines, parts of which may be made by the glabellar furrows. The paired appearance of these furrows suggests that they are an original feature, perhaps accentuated by the compression and distortion of the fossil, although the glabellar furrows have apparently been obliterated. Whittard (1960 : 148) has described similar features in *N. murchisoni*, in the form of a faint median glabellar ridge, and in oval or nearly circular depressed areas on the second lobes. The latter he suggested were muscle scars.

A few *Neseuretus* cranidia from Ramsey Island have been found without the anterior border furrow, including the types of *N.*? *elongatus* (Hicks 1873 : 45–46, pl. 3, figs. 1–3; Whittard 1960 : 145). These Whittard referred to *N. parvifrons*, though in other respects they cannot be separated from specimens bearing an anterior furrow, and referred to *N. ramseyensis*. No pygidia referable to *N. parvifrons* have been found.

The pygidia referred to *N. parvifrons* and *N. murchisoni* both have a small number of axial rings and pleural furrows. *N. parvifrons* (Whittington 1966 : 502, pl. 4, fig. 9) has five axial rings, followed by a terminal piece which is distended in front, and parallel-sided where it runs down the steep posterior slope. Six pleural furrows are present, with interpleural furrows abaxially. In *N. murchisoni* (Whittard 1960 : 149, pl. 20, fig. 9) there are four or possibly five axial rings, followed by a tapering terminal piece which reaches the posterior border. Four or five pleural furrows are present, without interpleural furrows. All the well preserved pygidia from Ramsey Island have eight to nine axial rings, followed by a semi-circular terminal piece, which does not reach the posterior border, which is formed medianly by the confluence of the pleural fields. Seven to eight pleural furrows are present, with occasional faint interpleural furrows.

Of Whittard's other species, only *N. grandior* (1960 : 141, pl. 20, figs. 1, 2) is comparable, the pygidium having ten axial rings and a terminal piece, and eight to nine pleural furrows. Whittard states that it is much larger than the pygidia of either *N. parvifrons* or *N. murchisoni*, but some of the pygidia collected from Ramsey Island approach it in size.

Neseuretus murchisoni (Salter)

Pl. 9, figs. 8, 11)

1966 *Neseuretus murchisoni* (Salter); Whittington : 503, pl. 4, figs. 14, 15, 17–19.

MATERIAL. External mould of cranidium (It.5820a-b).

HORIZON AND LOCALITY. Henllan Ash, at and above the south end of the highest wall of Moel Llyfnant, Arenig (Whittington 1966 : 492, locality 2). N.G.R. 812357.

DISCUSSION. A well preserved cranidium of *N. murchisoni* is figured for comparison with *N. parvifrons* and *N. ramseyensis*. The anterior border is a rounded rim, upturned and forwardly projecting, and apparently bearing pits. The glabella has a faint median ridge, extending from the level of the 1p to the 3p glabellar furrows, widening forwards and having the outline of an exclamation mark.

Neseuretus parvifrons (McCoy)

(Pl. 9, figs. 4, 5, 7, 9, 10, 12–16)

1966 *Neseuretus parvifrons* (McCoy); Whittington : 500–503, pl. 4, figs. 1–13; pl. 5, figs. 1–10.

MATERIAL: External mould of cranidium (It.5816); External mould of enrolled carapace (It.5817); Internal mould of carapace (It.5818); Internal and external mould of pygidium (It.5819a-b).

HORIZON AND LOCALITY. Henllan Ash, at and above the south end of the highest wall on Moel Llyfnant, Arenig (Whittington 1966 : 492, locality 2). N.G.R. 812357.

DISCUSSION. Some new material, collected by the writer, is here figured for comparison with that illustrated by Whittington (1966 : 500–503, pl. 4, figs. 1–13; pl. 5, figs. 1–10), chiefly to show the nature of the external ornament. The larger pits present on the anterior margin of the cranidium are each surrounded by a raised rim, forming an incipient tubercle. Similar pits are present around the posterior margin of the pygidium, particularly over the midline. The internal openings of the pits, which are really canals through the carapace, can be seen on the internal cast of the pygidium (Pl. 9, fig. 13). The anterior portion of the rostral plate, and the ventral facing surfaces of the librigenae, have a distinct tuberculate appearance, well preserved in specimen It.5818 (Pl. 9, figs. 4, 10, 14). This specimen has been excavated to show the hypostome (cf. Whittington 1966 : pl. 5, figs. 5, 6, 8, 10). The relationship of the main body of the hypostome to the anterior wings and the subtrapezoidal anterior extension is not clear, as the hypostome may be fractured at this point, and the anterior wings are missing. The anterior plate is almost rectangular in outline, wider than long, with its antero-lateral corners produced into horns, which project ventrally. These horns may have interlocked with the pygidium during enrolment, or simply formed part of the suture with the rostral plate.

The enrolled specimen (Pl. 9, figs. 15, 16) shows that the pygidium probably tucked beneath the doublure of the cephalon, exposing the main part of the doublure, i.e. that part with the tubercular ornament.

Two small specimens, probably referable to *Neseuretus parvifrons* have been collected from Murchison's Locality at Pensarn, Carmarthen. The more complete of the two (It.5815) includes the cephalon and possibly 13 thoracic segments, but the anterior border is missing. The other specimen, a cranidium (It.5814), includes the preglabellar area and anterior border, which is not apparently marked by a marginal furrow, but is abruptly deflected ventrally. Unfortunately the specimen is crushed and the furrow may have been suppressed. The fixed cheeks in both specimens are narrow (trans.): their width at the level of the eyes being half that of the glabella at the same level. The palpebral lobes run from opposite the centre of the 2p glabellar lobes to almost the front of the glabella. The specimens are thus probably referable to *N. parvifrons,* as the anterior border furrow is apparently lacking. They differ from *N. monensis* (Shirley) in the position of the palpebral lobes.

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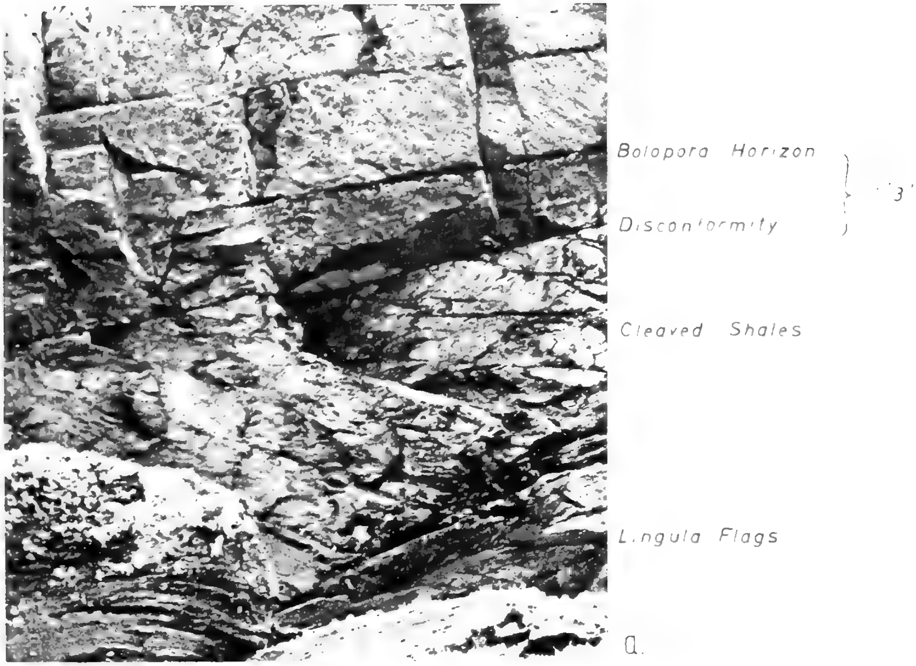
PLATE 1

a. Disconformity between the Lingula Flags and Ogof Hên Formation at Bay Ogof Hên, Ramsey Island.

b. Slumped and current bedded sandstones, siltstones and shales near the base of the Ogof Hên Formation, Bay Ogof Hên, Ramsey Island.


Bolopora Horizon
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Disconformity
Cleaved Shales
Lingula Flags
a.

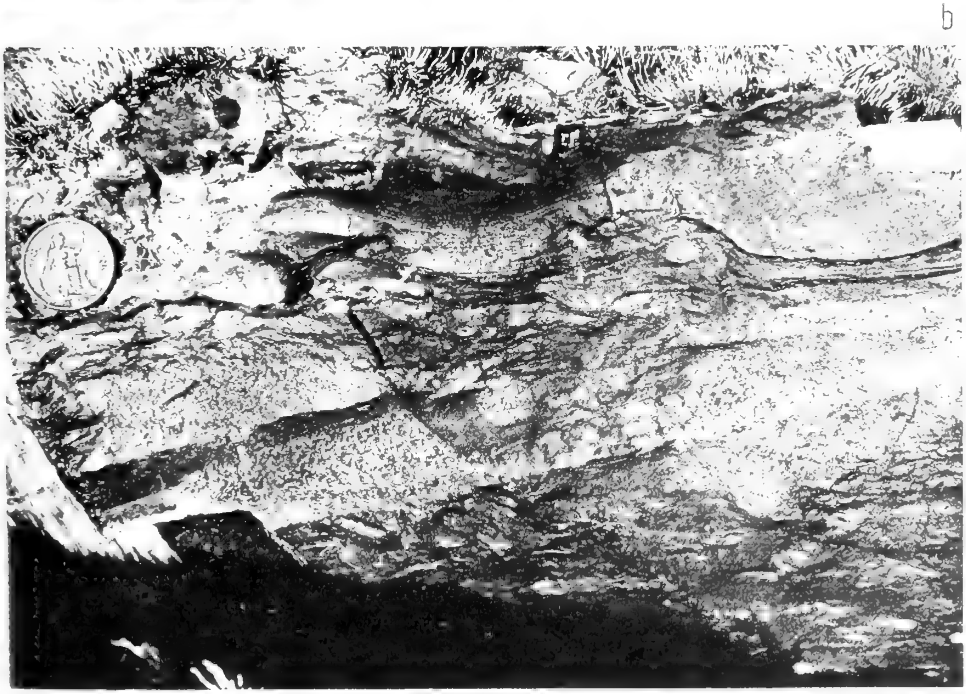
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PLATE 2

Monorthis menapiensis (Davidson)

Lower Arenig, Ogof Hên Formation, Bay Ogof Hên, Ramsey Island.

FIGS. 1–3. BB.31873 a-b. Lectotype. Internal mould of pedicle valve, latex cast of interior, latex cast of exterior. Figured Davidson 1869: pl. 33, figs. 12, 12a. × 2·8.

FIGS. 4–5. BB.31874. Syntype. Latex cast of dorsal interior, internal mould, cardinalia. Figured Davidson 1869, pl. 33, figs. 11, 11a. × 2·8, × 4·6.

FIG. 6. BB.30902a. Latex cast of ventral interior. × 2·8.

FIG. 7. GSM.11938. Latex cast of ventral interior. × 3·4.

FIG. 8. BB.30897a. Latex cast of dorsal interior. × 3·5.

FIGS. 9–10. BB.30901. Latex cast of ventral exterior and interior. × 3·3.

FIG. 11. BB.31899a. Latex cast of dorsal interior. × 3·3.

FIG. 12. BB.31898. Latex cast of dorsal interior. × 3·3.

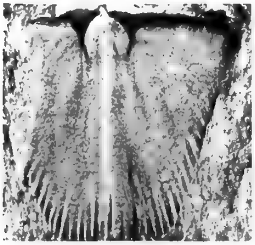
FIG. 13. GSM.11938. Latex cast of ventral interior. × 2·9.

Lenorthis alata (Sowerby)

Lower Arenig Shales, Pensarn, Carmarthen.

FIG. 14. GSM.6868. Lectotype. Internal mould of brachial valve. Figured by Murchison 1839 pl. 22, fig. 7. × 2·5.

PLATE 2



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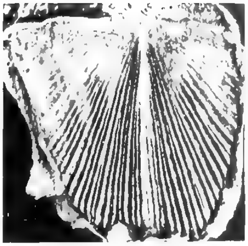

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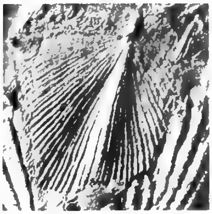

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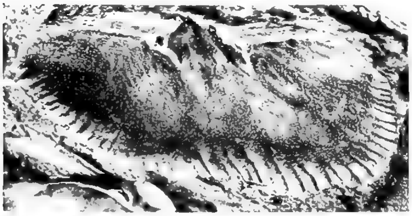

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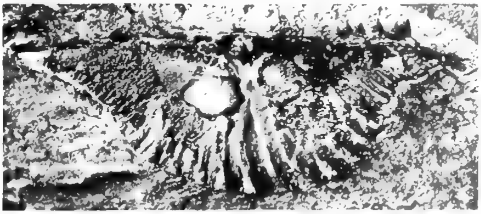

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PLATE 3

Lenorthis alata (Sowerby)

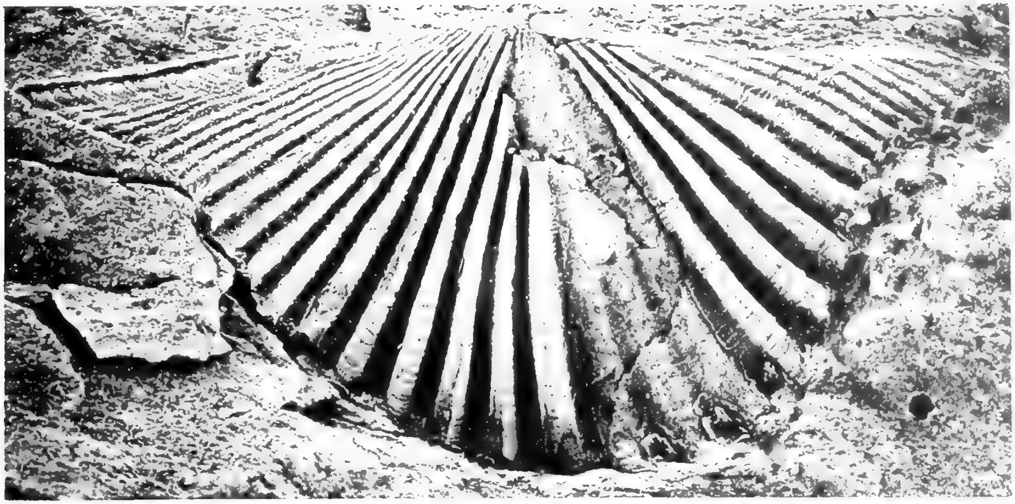
Lower Arenig Shales, Pensarn, Carmarthen.

FIG. 1. BB.31885. External mould of brachial valve. × 6·2.

FIGS. 2, 4, 6. BB.31880. Latex cast of dorsal interior, postero-ventral view of cardinalia, latex cast of exterior. × 3·0, × 13·0, × 2·4.

FIG. 3. BB.31882. Latex cast of ventral interior. × 3·0.

FIGS. 5, 7. BB.31883. Latex cast of conjoined valves, posterior and dorsal views. × 2·5.



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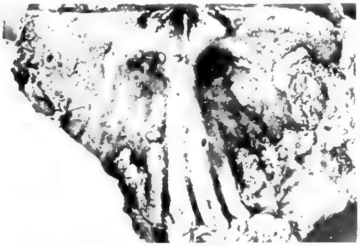

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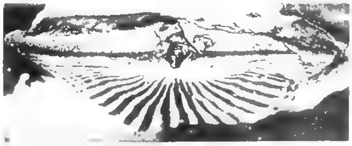

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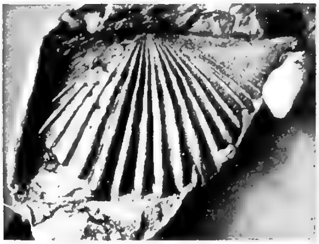

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PLATE 4

Lenorthis alata (Sowerby)

Lower Arenig Shales, Pensarn, Carmarthen.

FIGS. 1, 3. BB.31879a. Latex cast of dorsal interior, postero-ventral view of cardinalia. × 2·5, × 15·0.

FIG. 2. BB.31881a. Latex cast of ventral interior. × 2·5.

FIG. 4. BB.31878. Latex cast of dorsal interior. × 3·1.

FIG. 7. BB.31886. Latex cast of ventral exterior. × 2·3.

Lower Arenig Sandstone, Tremanhire, Solva.

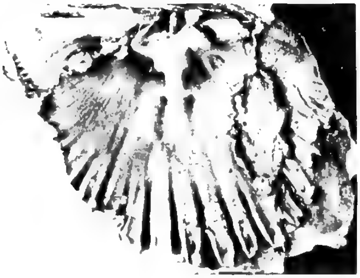
FIG. 5. BB.31875. Lectotype of *Orthis carausii* Davidson. Internal mould of brachial valve. Figured Davidson 1869 pl. 33, fig. 5, specimen at left side of block. × 2 8.

FIG. 6. BB.31876. Syntype of *Orthis carausii* Davidson. Latex cast of ventral exterior. Figured Davidson 1869. pl. 33, fig. 3. × 2·8.

Lower Arenig, Ogof Hên Formation, Bay Ogof Hên, Ramsey Island.

FIG. 8. BB.31893a. Latex cast of dorsal interior. × 3·8.

FIGS. 9, 10. BB.31887. Latex cast of dorsal interior, postero-ventral view of cardinalia. × 2·5, × 5·5.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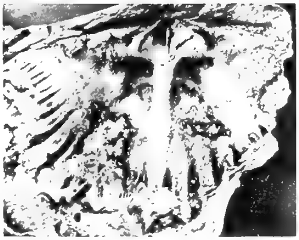
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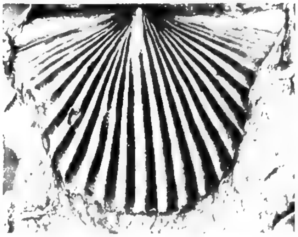
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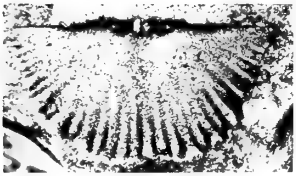
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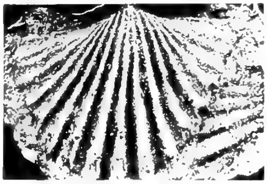
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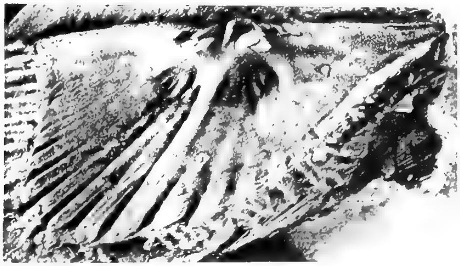
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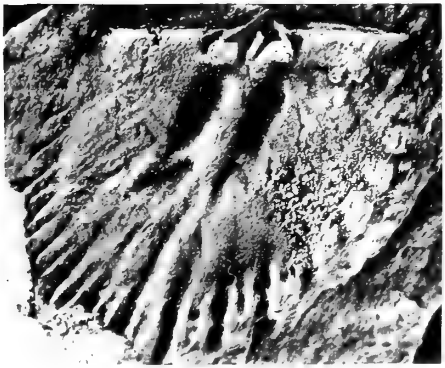
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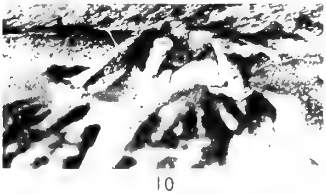
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PLATE 5

Lenorthis alata (Sowerby)

Lower Arenig, Ogof Hên Formation, Bay Ogof Hên, Ramsey Island.

FIGS. 1, 2. BB.31891. Internal mould of pedicle valve, latex cast of exterior. × 2·5.

FIGS. 3, 5. NMW.29.308.G400. Latex cast of ventral interior. × 2·5, × 5·5.

FIG. 4. BB.31890b. Latex cast of dorsal exterior. × 3·6.

FIG. 6. NMW.29.308.G397. Internal mould of pedicle valve. ×3·5.

Orthambonites sp.

Lower Arenig, Ogof Hên Formation, Bay Ogof Hên, Ramsey Island.

FIGS. 7, 8. NMW.29.308.G31. Latex cast of dorsal interior, ventral and anterior views. × 3·3, ×4·1.

FIG. 9. BB.30900. Internal mould of pedicle valve. × 3·3.

FIG. 10. LL.3182. Latex cast of dorsal interior. × 3·3

FIG. 11. LL.3184. Latex cast of dorsal interior. × 4·4.

FIG. 12. NMW.29.308.G360. Latex cast of dorsal interior. × 3·3.

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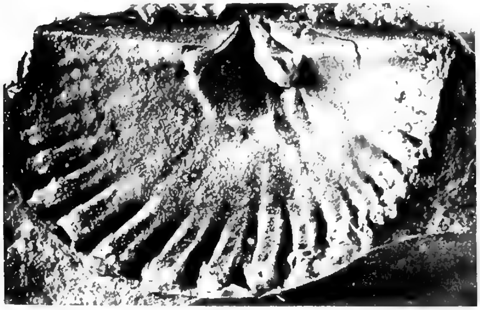

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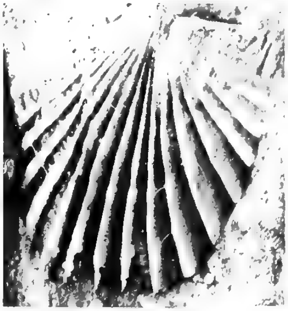

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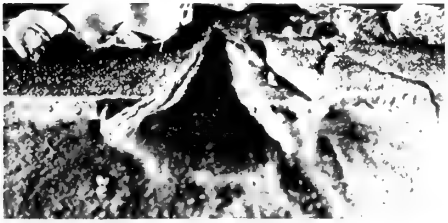

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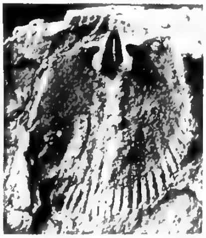

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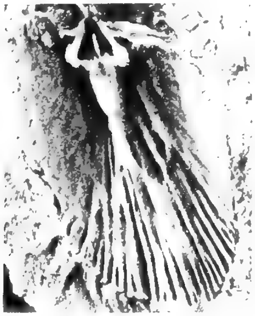

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PLATE 6

Megalaspidella*(?) *murchisoniae (Murchison)

Lower Arenig Shales, Pensarn, Carmarthen.

FIGS. 1, 2. It.5806 a-b. Dorsal carapace, internal and external moulds. × 1·8.

FIG. 3. GSM.18988. Holotype. Internal mould. Figured Murchison 1839, pl. 25, fig. 3. × 1·3.

FIG. 4. It.5805a. Cranidium. × 1·6.

FIG. 5. It.5809b. Latex cast of dorsal surface of pygidium. × 2·0.

FIG. 6. It.5808. Internal mould of pygidium. × 2·6.


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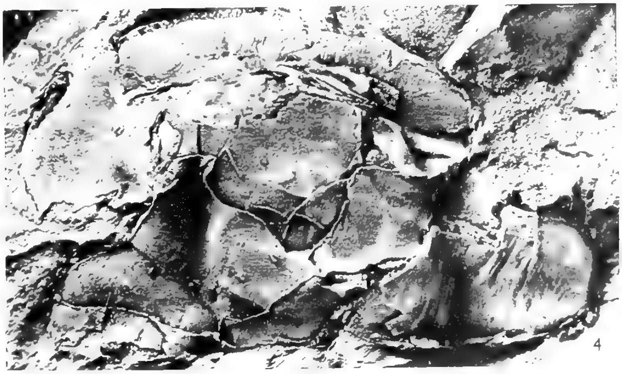
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PLATE 7

Megalaspidella*(?) *murchisoniae (Murchison)

Lower Arenig, Ogof Hên Formation, Bay Ogof Hên, Ramsey Island.

FIG. 1. OUM.B6. Syntype of *Niobe menapiensis* Hicks. Ventral mould of cranidium. Figured Hicks 1873, pl. 4, fig. 3. × 1·4.

FIG. 2. OUM.B183. Internal mould of hypostome. × 1·3.

FIG. 3. It.5810. Internal mould of cranidium. × 1·2.

FIG. 4. NMW.29.308.G148. Internal mould of pygidium. × 1·3.

FIG. 5. SMA.45141. Internal mould of cranidium. Identified by Whittard 1964 p. 236 as *Ogygiocaris selwynii* (specimen no. quoted in error as SMA.45142). × 1·3.

FIG. 7. NMW.29.308.G219. Internal mould of dorsal carapace. × 1·4.

FIG. 8. NMW.29.308.G.275. Internal mould of dorsal carapace. × 1·4.

Lower Arenig Shales, Pensarn, Carmarthen.

FIG. 6. Internal mould of hypostome. × 3·6.

Lower Arenig Shales, Glan Pibwr, Carmarthen.

FIG. 9. SM.A.3118. Syntype of *Ogygia marginata* Crosfield & Skeat. Internal mould of cranidium. Figured Crosfield & Skeat 1896 pl. 26, fig. 26. × 1·0.


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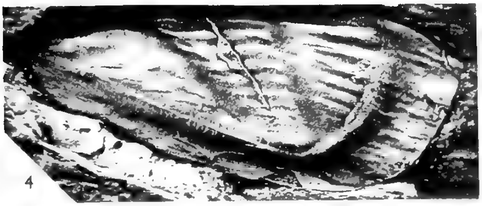
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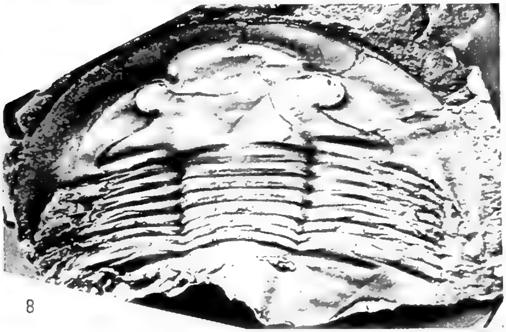
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PLATE 8

Megalaspidella*(?) *murchisoniae (Murchison)

Lower Arenig, Ogof Hên Formation, Bay Ogof Hên, Ramsey Island.

FIG. 1. It . 5811b. Latex cast of external surface of pygidium. × 1·9.

FIG. 2. NMW.29.308.G422. Internal mould of pygidium. × 1·4.

FIG. 5. NMW.29.308.G28. Internal mould of pygidium. × 0·8.

Neseuretus ramseyensis Hicks

Lower Arenig, Ogof Hên Formation, Bay Ogof Hên, Ramsey Island.

FIGS. 3, 4. It.5812. Internal mould of cranidium, lateral and dorsal views. × 3·9. × 3·0.

FIG. 6. OUM.B9. Syntype of *Neseuretus quadratus* Hicks. Internal mould of cranidium. Figured Hicks 1873 pl. 3, fig. 12. × 1·3.

FIGS. 7, 11. OUM.B11. Internal mould of cranidium. × 2·4.

FIG. 8. SM.A.16733. Syntype of *Neseuretus elongatus* Hicks. Internal mould of cranidium. Figured Hicks 1873 pl. 3, fig. 3. × 3·8.

FIGS. 9, 11. SM.A.16732. Syntype of *Neseuretus elongatus* Hicks. Internal mould of cranidium, lateral and dorsal views. Figured Hicks 1873, pl. 3, fig. 2. × 3·8.

FIG. 10. It.5813. Internal mould of cranidium. × 1·3.

FIG. 12. OUM.B186. Internal (dorsal) mould of hypostome. × 2·5.


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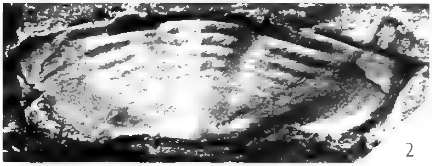
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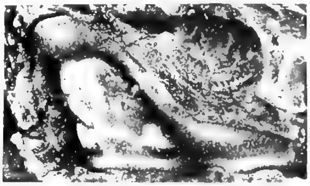
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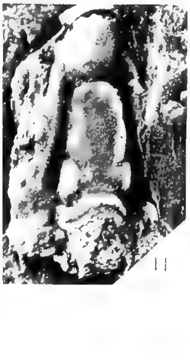
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PLATE 9

Neseuretus ramseyensis Hicks.

Lower Arenig, Ogof Hên Formation, Bay Ogof Hên, Ramsey Island.

FIG. 1. NMW.29·308.G211. Internal mould of pygidium. × 1·7.

FIGS. 2, 3. NMW.29.308.G168. Internal mould of pygidium, dorsal and lateral views. × 2·4.

FIG. 6. SM.A.16734. Internal mould of pygidium. Figured Hicks 1873 pl. 3, fig. 19. × 1·4.

Neseuretus parvifrons (McCoy)

Lower Arenig, Henllan Ash, Moel Llyfnant, Arenig.

FIGS. 4, 10, 14. It.5818. Latex cast of internal mould of carapace, with hypostome in place; ventral view, hypostome, rostral plate and doublure of librigenae. × 2·3, × 3·5, × 5·8.

FIGS. 5, 7. It.5816. Latex cast of external mould of cranidium, dorsal and anterior views. × 2·9, × 9·7.

FIGS. 9, 12, 13. It.5819. Latex cast of external mould of pygidium, dorsal and posterior views, and latex cast of ventral surface of pygidium, internal view to show the openings of the canals. × 4·7, × 11·0, × 11·0.

FIGS. 15, 16. It.5817. Latex cast of enrolled carapace, lateral and dorsal views. × 2·3.

Neseuretus murchisoni (Salter)

Lower Arenig, Henllan Ash, Moel Llyfnant, Arenig.

FIGS. 8, 11. It.5820b. Latex cast of external mould of cranidium, dorsal and lateral views. × 3·0.


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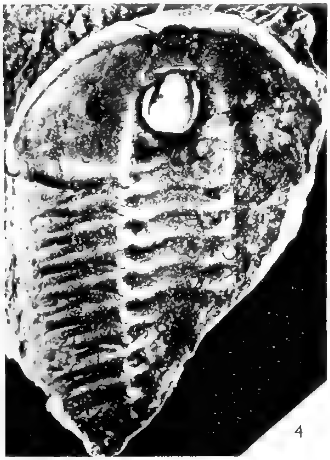
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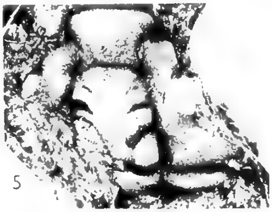
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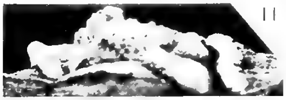
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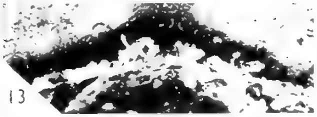
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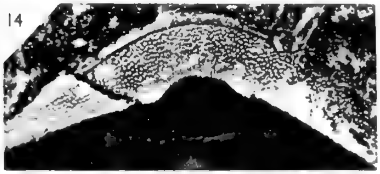
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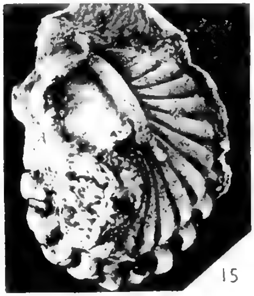
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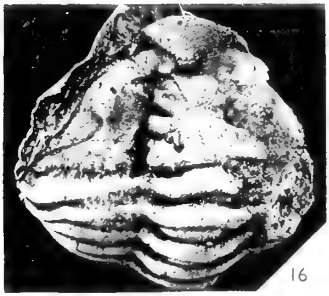
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THE POLYZOA OF SOME BRITISH JURASSIC CLAYS

L. J. PITT
&
H. D. THOMAS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 18 No. 2
LONDON: 1969

THE POLYZOA OF SOME BRITISH JURASSIC CLAYS

BY

LESLIE JOHN PITT
&
the late HENRY DIGHTON THOMAS

Pp. 29–38; 4 *Plates*

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THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 12 *August*, 1969 *Price Eleven Shillings*

THE POLYZOA OF SOME BRITISH JURASSIC CLAYS

By L. J. PITT & the late H. D. THOMAS

ABSTRACT

Two new species of Polyzoa from Hampen Marly Beds (Bathonian) are described and figured, and Gregory's figured types of *Berenicea parvitubulata* are re-described. *Berenicea spatiosa* Gregory *non* Walford is discussed.

INTRODUCTION

COMPARED with the faunas of the Lias and the Bradford Clay the number of species of Polyzoa recorded from other Jurassic clays is small.

Three species of Polyzoa, *Stomatopora dichotoma*, *Berenicea diluviana* and *B. archiaci*, were found at Woodham's Brick Pit about six miles west of Aylesbury (National Grid Reference 42/707186). This pit is in the *mariae* zone of the Lower Oxfordian and the *athleta* and *lamberti* zones of the *Callovian* somewhat above the more carbonaceous shales sought by the Fletton brickmakers. We were unable to find Polyzoa in the more carbonaceous shales of the *coronatum* zone in the London Brick Co.'s Pit at Calvert, a few miles to the West. There appeared to be a possible connection between the presence of much carbon and the absence of Polyzoa. With the aid of a grant from the Godman Exploration Fund many pits were visited from the Dorset Coast to Warboys in Huntingdonshire. Unfortunately we found few exposures in the higher zones but at Warboys the pit is worked in both the highly carbonaceous shales and the less carbonaceous Upper Oxford Clay. (This pit belongs to the London Brick Co. and the National Grid Reference is 52/309818). None of the highly carbonaceous shales yielded Polyzoa but in the upper part of the Warboys Pit we found the same two species of *Berenicea* as we had recorded from Woodham. They were encrusting *Gryphaea*, which was abundant in both the upper and the lower parts of the exposure. No Polyzoa were found on the *Gryphaea* from the lower part. The absence of Polyzoa could not therefore be accounted for by the lack of suitable hosts but could be attributed to the depositional conditions which caused the high carbon content.

We had found poorly preserved *Berenicea parvitubulata* encrusting *Ostrea hebridica* at Temple Mill Quarry, Sibford Ferris, Oxfordshire (National Grid Reference SP 347362), in a thin seam of clay above the Great Oolite White Limestone. Dr. W. S. McKerrow suggested we should look at a temporary exposure in the Hampen Marly Beds at Enstone, where abundant *Ostrea hebridica* had been found in a silage pit in a field opposite the reservoir (National Grid Reference SP 377237). This is lower in the succession and slightly older than the Great Oolite White Limestone. These proved extremely interesting as they were encrusted with Polyzoa in a much better state of preservation than is usual in the Jurassic. Only four species were found, including two new species described here for the first time, but the number of specimens was large and included all states of development.

ACKNOWLEDGMENTS

Our thanks are due to the Trustees of the Godman Exploration Fund for a grant to facilitate the collection of further material, to Dr. W. S. McKerrow for information regarding the Enstone exposure, to the Sedgwick Museum, Cambridge, for the loan of the specimen of *Stomatopora dichotoma* described by Haime and his type of *S. waltoni*, and the owners and managers of the many quarries visited. Especially we would thank Dr. A. B. Hastings for her help and advice, particularly in connection with the brood-chambers in *Stomatopora*, for reading the manuscript and making useful criticisms.

Order STENOLAEMATA Borg 1926

Sub-order CYCLOSTOMATA Busk

Family **TUBULIPORIDAE** Johnston

STOMATOPORA Bronn 1825

Stomatopora dichotoma (Lamouroux) 1821

(Pl. 4, fig. 1)

1821 *Alecto dichotoma* Lamouroux : 86, pl. 81, figs. 12–14.
1896 *Stomatopora dichotoma* Gregory : 43, pl. 1, figs. 1, 2 *Cum. syn.*
1940 *Stomatopora dichotoma* Orieux : 3–13, pls. 1–4.
1963 *Stomatopora dichotoma* Illies : 75, pl. 3, figs. 1–4, pl. 4, figs. 1–5, pl. 5, figs. 1–3, pl. 6, figs. 1–3.

DIAGNOSIS. *Stomatopora* typically forming a loose irregular radiating, many branched zoarium. Zooecia cylindrical, peristomes well raised, surface punctate and transversely wrinkled. The zooecia increase in diameter after the second or third dichotomy.

MATERIAL. D 41608, D 41609 and D 41610 from the Oxford Clay, Woodham's Pit, near Aylesbury. D 51465 and D 51466 from the Hampen Marly Beds, Enstone, Oxfordshire.

REMARKS. All the mature specimens of *Stomatopora* collected from the above localities come within the definition of *S. dichotoma* (Lamouroux) given by Gregory (1896) and the measurements given by Illies (1963). Lang (1904) commented that species of *Stomatopora* could not be differentiated unless whole zoaria were compared. Some specimens we collected were in an early stage of development and quite indistinguishable from the type of *S. waltoni* Haime (1854) specimen J. 5828 in the Sedgwick Museum, Cambridge. Zoaria which attain maturity are quite distinct. After the second or third dichotomy the zooecia are larger and less regular than those of *S. waltoni*. As all the mature zoaria collected are *S. dichotoma* we conclude that the immature colonies belong to this species also.

Canu & Bassler (1920 : 652), placed the genus *Stomatopora* in the Inovicellata when only Gregory's somewhat dubious brood-chambers had been described and figured. Since then brood-chambers in recent *Stomatopora* have been described and figured by Borg (1926 : 358, text-fig. 66, *S. eburnea*; text-figs. 67 and 68, *S. granulata*, and

1944 : 24, pl. 1, fig. 2, *S. eburnea*), and by Osburn (1953 : 45, pl. 65, fig. 2, *S. granulata*). They are typical Cyclostome brood-chambers of the simplest kind, consisting of a single zooid, inflated distally to form a chamber which may be slightly lobed and has finely punctate walls.

After cleaning by modern methods the " hemispherical tubercle " of Gregory's figured specimen proved to be the peristome of a lateral branch from an adjacent series of zooecia that had been overgrown by its neighbour. The apparent lateral branch on the right of the figure is in fact this underlying branch. We made a careful scrutiny of all our material for possible brood-chambers and the few structures picked out for closer examination all proved to have been produced in ways comparable to Gregory's specimen. So far no fossil brood-chambers have been found in this genus.

STRATIGRAPHY. This is a long ranging species recorded in Great Britain from the Lower Lias to the Cornbrash. The Woodham's Pit specimens are interesting as they extend this range up into the Oxford Clay.

BERENICEA Lamouroux 1821

Berenicea enstonensis sp.nov.

(Pl. 1, fig 1; Pl. 4, figs 2–3.)

DIAGNOSIS. *Berenicea* with transversely ribbed zooecia, the transverse ribs forming prominent concentric ridges on the zoarium, apertures longitudinally elongate, with slightly raised, well defined, peristomes; brood-chambers transversely triangular.

HOLOTYPE. D 51452 and paratype D 51453, encrusting valves of *Ostrea hebridica* from the Hampen Marly Beds, Enstone, Oxfordshire.

Other material examined D 51449, 51450 and 51451 from the same locality.

DESCRIPTION. Zoarium thin, encrusting, flabelliform in the young stages, becoming irregularly discoidal in adult stages. Zooecia slender, visible practically throughout their length, not very inflated, cylindrical, front wall with narrow, transverse ribs which are continuous across adjacent zooecia (except where interrupted by brood-chambers) forming concentric ridges on the zoarium. The zooecial apertures are oval, elongated in the proximal-distal direction, peristomes slightly raised, arranged mainly in quincunx.

The brood-chambers are transversely triangular, widest at the distal edge, with rounded corners, slightly inflated, smooth, enveloping several zooecial tubes, the openings of which are arranged almost symmetrically, ooeciostome median, placed nearly on the distal margin of the brood-chamber, slightly smaller than the normal zooecial apertures.

MEASUREMENTS.

Width of zooecia	0·13 mm.
Width of aperture	0·07 mm.
Width of brood-chamber . . .	0·8 mm.
Separation of transverse ribs . .	0·045 mm.

REMARKS. In all the Enstone specimens the measurements are remarkably constant. It was not possible to make measurements of the zooecial length as the ribbing masks the initiation of the zooecia. The largest zoarium examined, D 51450 is 6 mm. in diameter.

This species is well characterized by its strong transverse ribs. Similar ribbing is found in *Berenicea portlandica* Gregory (1896 : 83, pl. 3, fig. 5) but its zooecia are larger. Gregory compared that species with *B. striata* Haime (1854 : 179, pl. 7, figs. 8a, b,) to which he also doubtfully referred two British specimens (1896; pp. 84–85). Haime described his species as having fine and numerous ribs, and his figure indicates that these were much finer than those of *B. enstonensis*. Of the two specimens referred to by Gregory, one, D 1785 is very much worn and is specifically indeterminate. The other specimen, D 2215, lacks strong ribs and is neither *B. striata* nor *B. enstonensis*. *Proboscina rigauxi* (Sauvage, 1889 : 42, pl. 3, figs. 6–8), from the Bathonian of Hydrequent, Boulonnais, also has transverse ribs but the Cornbrash specimen figured by Gregory (1896 : 69, pl. 2, fig. 6) not only has the Proboscinoid habit but also has larger zooecia. The material referred to *B. microstoma* (Michelin) by Reuss (1867 : 8, pl. 1, figs. 6a, b,) appears to have similar ribbing but its zooecia are bottle shaped. Similar ribbing occurs in some species of *Reptomultisparsa* d'Orbigny but that genus is distinguished at once from *Berenicea* by its multilamellar zoarium. *Reptomultisparsa undulata* Michelin sp. (1846 : 242, pl. 56, figs. 15a, b) demonstrates these features, see also Gregory, 1896 : 115, pl. 6, figs. 2, 3, and Canu, 1913 : 270).

The transversely triangular brood-chamber is a diagnostic character of those species of *Berenicea* for which Canu introduced the genus *Plagioecia* (1918 : 327). Although the nature of the brood-chamber in the Cyclostomata is of value, its importance as a generic criterion is by no means certain, and hence we prefer to use the term *Berenicea* (cf. Borg, 1926 : 468–470).

Berenicea cobra sp.nov.

(Pl. 3, figs. 1, 3.)

DIAGNOSIS. *Berenicea* with a large irregular zoarium, zooecia variable in length, peristomes circular, prominent, with circular aperture, brood-chambers long, resembling a cobra head in shape, widest at the distal third, gently convex, the oeciostome terminal or nearly so, prominent, transversely elliptical.

HOLOTYPE. D 51459 from the Hampen Marly Beds, Enstone, Oxfordshire, encrusting *Ostrea hebridica*.

DESCRIPTION. The holotype is a broken specimen, now semicircular, with a diameter of 14 mm. and encrusts an *Ostrea hebridica*. It abuts against a smaller, nearly circular colony of the same species. The holotype includes two complete and at least two incomplete brood-chambers. On the same shell there are also remains of a younger, flabelliform zoarium, the ancestrular disk is lost and is represented only by a circular scar.

MEASUREMENTS.

	All material examined (mm.)	D 51459 (mm.)
Length of zooecia	0·4 –0·9	0·6–0·9
Width of zooecia	0·125–0·15	0·15
Diameter of aperture	0·085–0·09	0·09
Brood-chamber:		
Length	1·4 –2·35	2·35*
Max. width	0·30 –0·45	0·45*
Ooeciostome:		
Width of aperture	0·11 –0·13	0·13
Height of aperture	0·08 –0·11	0·10

* The best developed brood-chamber.

REMARKS. This species is well characterized by its long brood-chambers, which distinguish it from all other known *Berenicea*. The non-fertile zooecia are similar in size to those of *B. diluviana* Lamouroux (1821 : 81, pl. 80, figs. 3, 4), but the brood-chamber of that species, as figured by Canu (1898 : 267, figs. 1–4), is short but wide. Gregory, however, refers certain English specimens to Lamouroux's species and states that the brood-chamber (= gonocyst) is "pyriform; rather narrow; usually but slightly broader than the zooecia". Gregory's material is therefore probably not conspecific with *B. diluviana* as interpreted by Canu. Canu refers *B. diluviana* to *Plagioecia* (1918 : p. 327), because of the shape of the brood-chambers. *B. cobra* would fall into *Oncousoecia* if the nature of the brood-chamber is a diagnostic generic character.

Most of the specimens of *B. cobra* are mauve in colour in contrast to the other species found at Enstone.

Berenicea parvitubulata Gregory 1896

(Pl. 1, fig. 2; Pl. 2, figs. 1–3; Pl. 3, fig. 2)

1896 *Berenicea parvitubulata* Gregory : 45.
1896a *Berenicea parvitubulata* Gregory: Gregory : 95, pl. 4, figs. 5, 6.

DIAGNOSIS. Zoarium encrusting, flabelliform or irregularly discoidal. Zooecia narrow, cylindrical, distinct, the central zooecia visible throughout their entire, length, surface plain, peristomes small, slightly raised. Brood-chambers elongated, the width of several zooecia, inflated, ooeciostome median, at or close to the distal border, circular, slightly raised and smaller than the zooecial apertures.

LECTOTYPE. (Here chosen): B.M.(N.H.) No. 60535, Cornbrash, Rushden, Northamptonshire.

We regard the syntype as specifically distinct.

DESCRIPTION OF LECTOTYPE. Zoarium nearly circular, embracing the ancestrula, with two young zoaria budded from it. Zooecial tubes slender, cylindrical, visible throughout their length, surface plain, peristomes somewhat raised, apertures circular. The measurements of the earlier zooecia are smaller than those of later zooecia. Brood-chambers numerous, elongate triangular, relatively broad, rather inflated, widest at the distal end, ooeciostome median, at or close to the distal border, about half the width of the zooecial tubes; the ends of two or more zooecia covered by the brood-chamber project symmetrically on either side of the ooeciostome; one or two zooecia, symmetrically placed about the mid-line, recline on the proximal ends of the brood-chambers. A few transverse ridges cross the brood-chambers.

MEASUREMENTS.

	Lectotype (mm.)	Enstone material (mm.)
Width of zooecia in small zoaria or early stages of large zoaria	0·080	0·075
Width of zooecia in later stages of large zoaria	0·135	0·125
Diameter of aperture in small zoaria or early stages of large zoaria	0·038	0·038
Diameter of aperture in later stages of large zoaria	0·060	0·057
Width of brood-chamber at distal end	0·4–0·8	0·22–0·66

REMARKS. Most of the Enstone material had smaller zoaria than the lectotype and the measurements were slightly smaller. The ancestrula is well preserved in several specimens as a circular disk from which the protozooecium is budded, giving rise in turn to two or possibly three other zooecia. Distal to these the zoarium takes up its normal shape (see Pl. 2, figs. 2, 3). The preservation is exceptionally good and in a few specimens the growing edge is preserved (see Pl. 2, fig. 1). Brood-chambers were very numerous in the Enstone material, up to six in a zoarium. They vary markedly in shape. All are inflated and all expand in width distally, the majority to a broadly triangular shape but some, after the initial expansion become more or less semi-cylindrical, even in the same zoarium.

The Enstone specimens illustrate very well the gradual increase in size of the zooecia with the growth of the zoarium.

The material obtained from Temple Mill Quarry, Sibford Ferris was worn and crushed and included many immature zoaria. The zooecia were filled with iron pyrites which emphasizes the porous nature of the frontal walls, a feature not seen in the Enstone specimens, presumably because of the calcification.

Although specimen no. 60535 is somewhat worn we designate it as lectotype since D 1912, the other figured syntype of *B. parvitubulata* is, we consider, a different species, possibly *B. spatiosa* (Walford). Fortunately there are a number of zooecia in 60535 which are practically unworn and which show the specific characters. A feature not sufficiently stressed by Gregory is the clear demarcation of the zooecia from one another and their slight elevation distally.

Note on *Berenicea spatiosa* Gregory non Walford

Tubulipora spatiosa Walford (1889 : 567, Pl. 8, figs. 10–12) was referred to *Berenicea* by Gregory (1896 : 86), who included several specimens in the species. As described by Walford, the species is not a *Berenicea* but appears to be a *Tubulipora*. We have examined a number of Gregory's specimens, which are certainly *Berenicea*. Further, they are not all conspecific, e.g. D 30 and D 2174 are markedly different from one another in their characters, and, moreover, D 30, figured by Gregory (1896 : 86, pl. 3, fig. 1) does not agree with his diagnosis.

In specimen D 30, the zoarium encrusts the cylindrical branches of another Polyzoan. The frontal walls of the zooecia are flat and flush with one another. The lines of contact between the zooecia are obscure, but in water are seen to be straight. The peristomes are all well raised and circular and average 0·04 mm. in diameter, the apertures are circular and average 0·025 mm. in diameter.

Specimen D 1912, a figured syntype of *B. parvitubulata* (see note under that species), closely resembles D 30. The measurements of the peristomes and apertures (0·084 mm. and 0·50 mm. respectively) are however about twice those of D 30.

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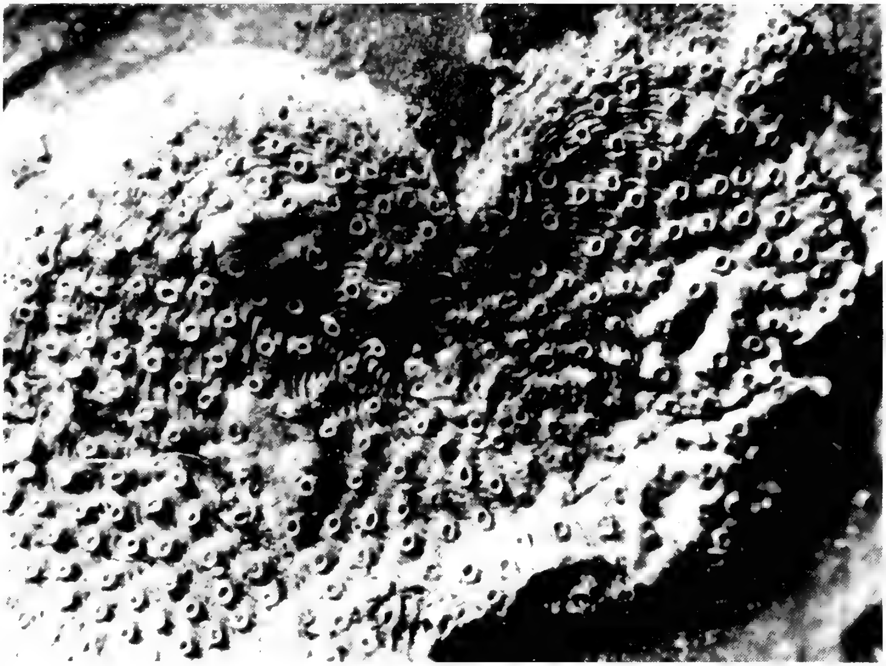
PLATE 1

Berenicea

FIG. 1. ***Berenicea enstonensis*** sp. nov. × 20. Hampen Marly Beds, Enstone, Oxfordshire. The type specimen showing the brood-chambers enveloping several zooecial tubes. The much smaller distal ooeciostome is clearly visible.

FIG. 2. ***Berenicea parvitubulata*** Gregory. × 20. Hampen Marly Beds, Enstone, Oxfordshire. Showing the peristomes well raised distally, part of the growth margin at the bottom of the figure and a brood-chamber, top left, with ooeciostome.



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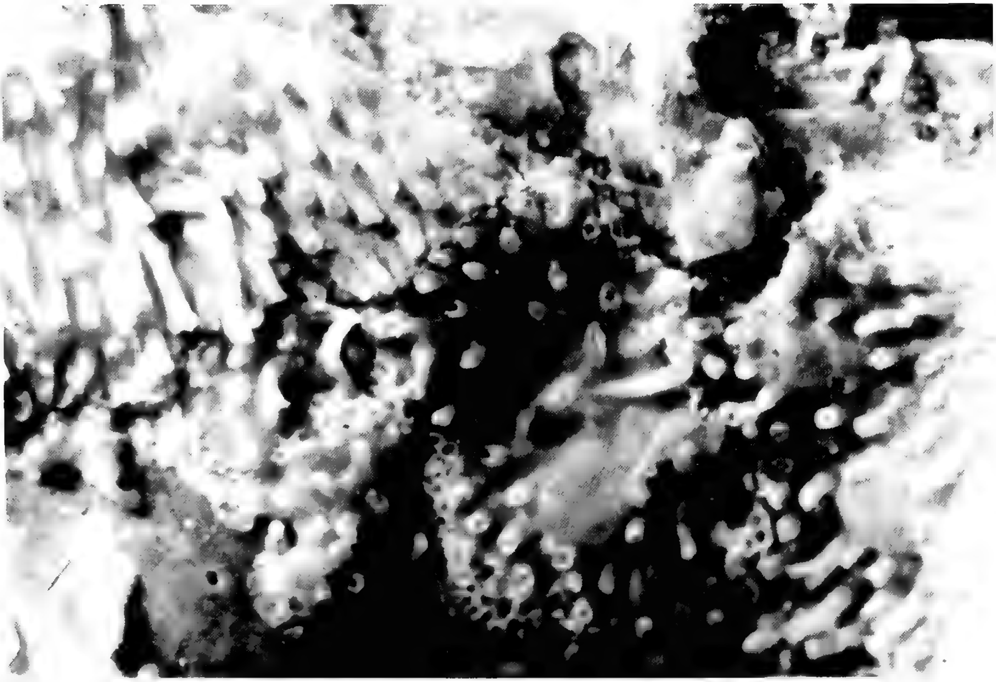

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PLATE 2

Berenicea parvitubulata Gregory

FIG. 1. A specimen × 20 from the Hampen Marly Beds Enstone, Oxfordshire showing the variation in shape of the brood-chambers, and the growth margin. No. D 51468.

FIG. 2. Another specimen from Enstone, × 20 showing the growth margin and the ancestrula. No. D 51469.

FIG. 3. Two immature specimens from Enstone, × 20, showing the ancestrulae. No. D 51455.

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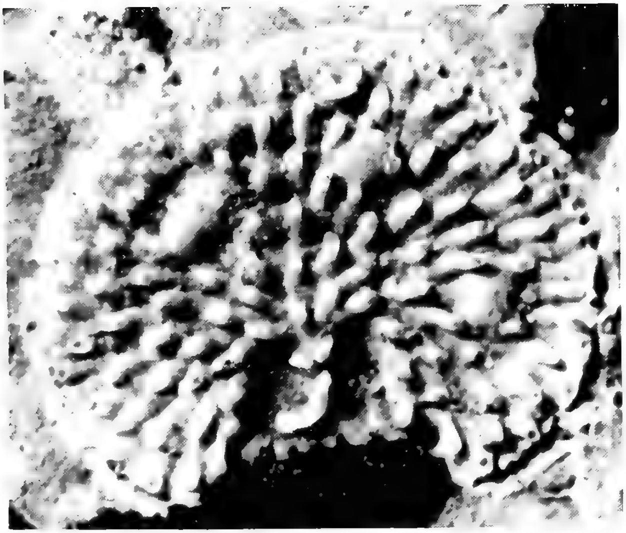

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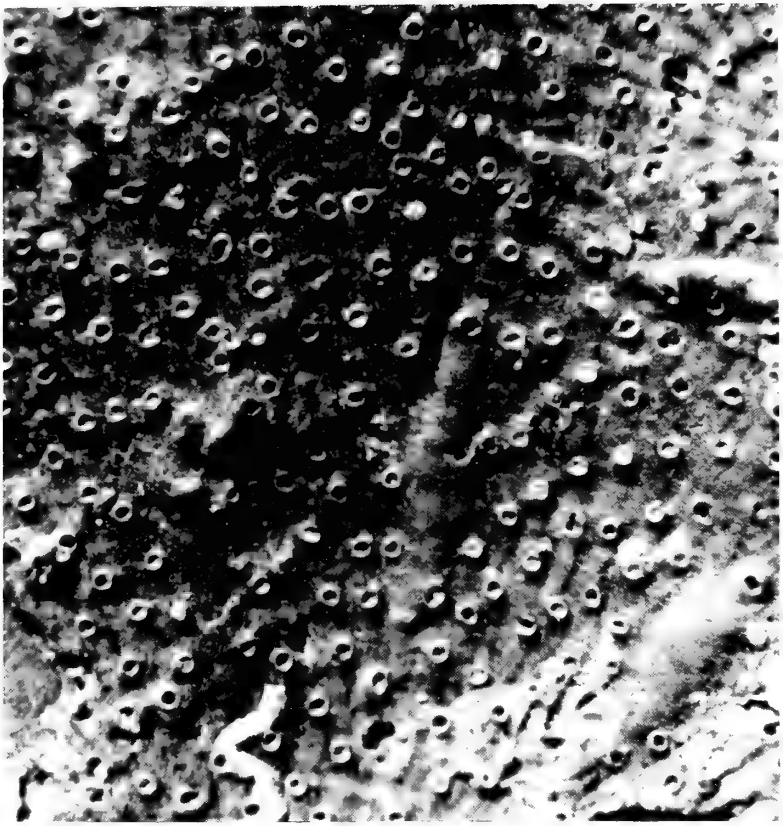
PLATE 3

Berenicea

FIG. 1. ***Berenicea cobra*** sp. nov. × 20. Part of the type specimen showing the long "cobra" shaped brood-chambers, the elliptical oeciostomes and the well defined circular peristomes. Hampen Marly Beds, Enstone. No. D 51459.

FIG. 2. ***Berenicea parvitubulata*** Gregory. × 20. An unusual zoarium with an apparent double origin, Hampen Marly Beds, Enstone. No. D 51456.

FIG. 3. ***Berenicea cobra*** sp. nov. × 20. A young zoarium showing the ancestrula, also from the Hampen Marly Beds, Enstone. No. D 51464.



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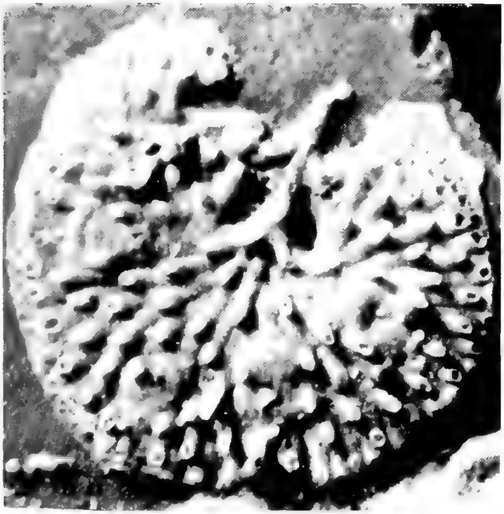

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PLATE 4

Stomatopora and ***Berenicea***

FIG. 1. ***Stomatopora dichotoma*** (Lamouroux). × 20. Several overgrowing zoaria showing ancestrulae and the increase in size of the zooecia with the growth of the zoarium. From the Hampen Marly Beds, Enstone. No. D 51465.

FIG. 2. ***Berenicea enstonensis*** sp. nov. × 10. The paratype, from the Hampen Marly Beds, Enstone, showing one complete and several broken brood-chambers. No. D 51452.

FIG. 3. ***Berenicea enstonensis*** sp. nov. × 20. A young zoarium, also from the Hampen Beds, Enstone, showing one complete and several broken brood-chambers. No. D 51452.

All plates photographed by the senior author and untouched.

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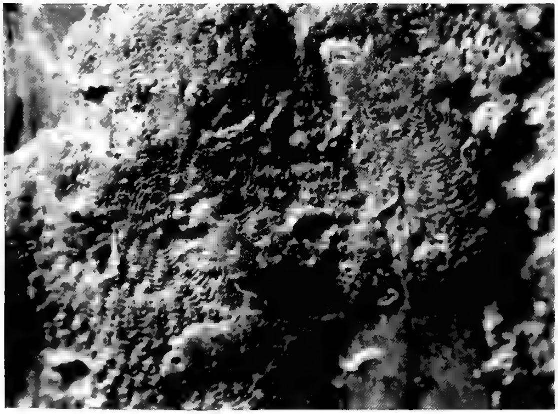

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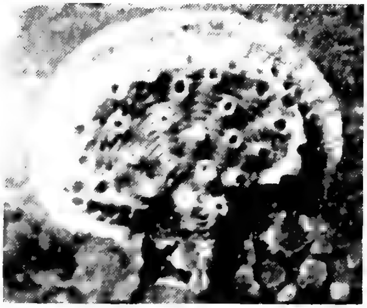

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THE ORDOVICIAN TRILOBITE FAUNAS OF THE BUILTH-LLANDRINDOD INLIER, CENTRAL WALES. PART I

C. P. HUGHES

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 18 No. 3
LONDON: 1969

THE ORDOVICIAN TRILOBITE FAUNAS OF THE BUILTH-LLANDRINDOD INLIER, CENTRAL WALES. PART I

BY

CHRISTOPHER PAUL HUGHES

Pp. 39–103; 14 *Plates*, 6 *Text-figures*

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THE ORDOVICIAN TRILOBITE FAUNAS OF THE BUILTH-LLANDRINDOD INLIER, CENTRAL WALES. PART I.

By CHRISTOPHER PAUL HUGHES

CONTENTS

SYNOPSIS

This paper is the first of a series in which the Ordovician trilobite faunas of the Builth-Llandrindod Inlier are to be described using biometrical techniques. The families Agnostidae, Raphiophoridae, Cheiruridae, Colpocoryphidae and Eohomalonotidae are described here and the following new species and subspecies erected: *Cnemidopyge parva, Flexicalymene aurora, Platycalymene tasgarensis* Shirley *simulata, Placoparina sedgwickii* (M'Coy) *shelvensis.* A short review of the stratigraphy and previous faunal studies is included, together with a general discussion on the use of biometrical techniques in trilobite studies.

I. INTRODUCTION AND ACKNOWLEDGMENTS

THE trilobites to be described in this series of papers are from the Ordovician rocks forming an inlier between the towns of Llandrindod Wells and Builth Wells[1] in the southern part of Radnorshire and the northern tip of Brecknock. The inlier, about nine miles long and five miles across at its widest point, is elongated from north-east to south-west (see Text-fig. 1). To the north-west the inlier appears to have a faulted contact with Ashgillian rocks which link the inlier to the main Ordovician outcrop of Central Wales. Little research has been done on that region and it is beyond the scope of this work.

The relationship between this inlier and the other Ordovician outcrops of Wales and the Borderlands is shown in Text-fig. 2. From this it is apparent that the inlier

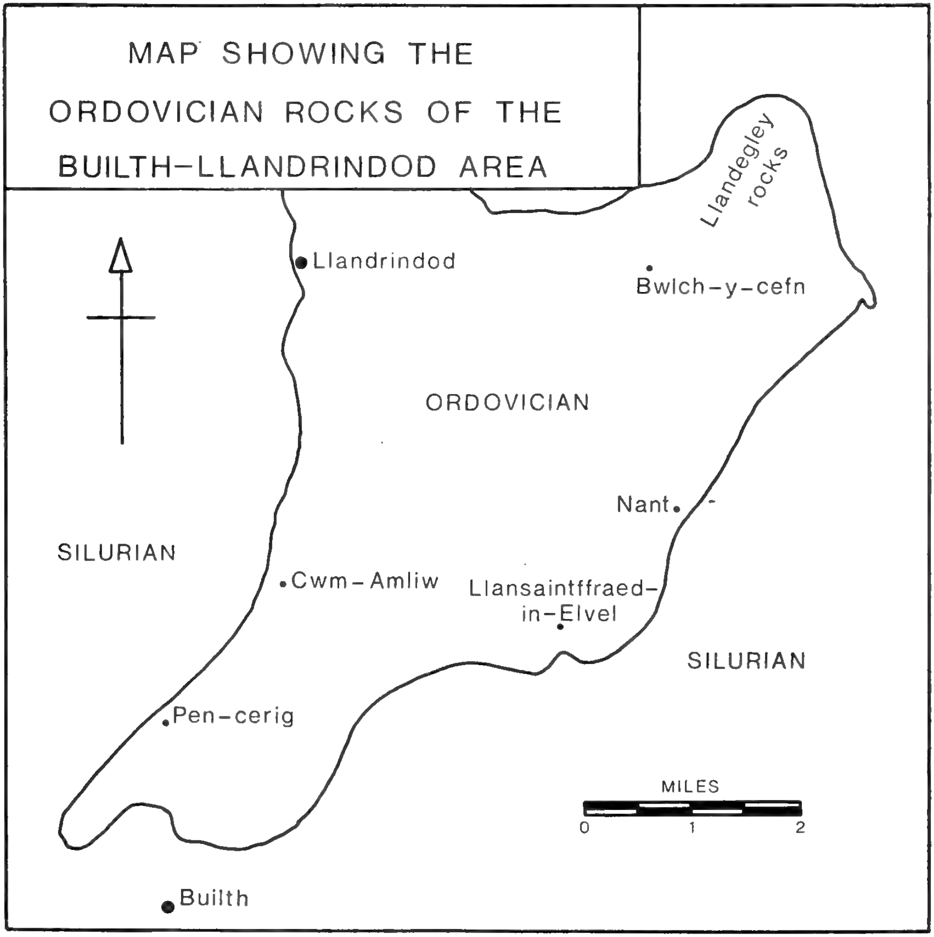

FIG. 1. Map showing the distribution of Ordovician rocks in the Builth-Llandrindod area. After Jones & Pugh 1941.

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[1] Hereafter referred to as Llandrindod and Builth.

is situated approximately half-way between the well-known shelly Ordovician outcrops at Llandeilo (Williams 1948, 1953) and Shelve (Whittard 1931, 1940, 1940*a*, 1955–67).

Due to the presence of volcanic and intrusive rocks, the Ordovician inlier contrasts strongly with the gentler topography of the surrounding Silurian strata. Although the intrusive and volcanic rocks of the inlier are well exposed, the sedimentary rocks are rarely seen in continuous section. In spite of numerous streams, surprisingly few are sufficiently free from superficial deposits to provide more than isolated outcrops, thus limiting the knowledge of the sedimentary succession which ranges from Lower Llanvirn (*murchisoni* Zone) to basal Caradoc (*gracilis* Zone).

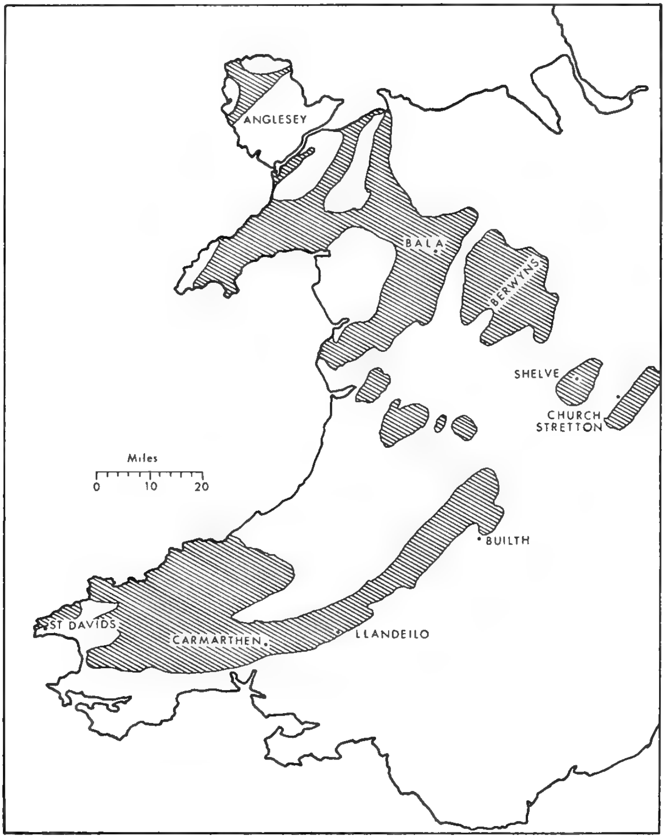

FIG. 2. Map showing the Ordovician outcrops of Wales and the Welsh Borderland together with the main localities yielding shelly faunas.

The bulk of the material used for this study was collected by the author during the tenure, at the Queen's University of Belfast, of a research studentship awarded by the Natural Environment Research Council to whom I am grateful for financial

assistance. All type and figured material is deposited in the collections of the British Museum (Natural History), London, together with some further specimens. I am much indebted to Professor Alwyn Williams and Dr. A. D. Wright for their supervision and encouragement whilst the work was in progress and for critically reading much of the manuscript. My thanks are also given to Professor H. B. Whittington of the Sedgwick Museum, Cambridge, for much helpful advice and discussion in the later stages of the work. I am also indebted to Sir William Pugh and the late Professor O. T. Jones for generously supplying information concerning fossiliferous localities.

I thank Dr. D. A. Bassett and Mr. D. E. Evans, National Museum of Wales, Cardiff; Mr. A. G. Brighton and Dr. C. L. Forbes, Sedgwick Museum, Cambridge; Dr. D. L. Bruton, University of Oslo; Dr. F. M. Broadhurst, University of Manchester; Dr. W. T. Dean, British Museum (Nat. Hist.); Dr. V. Jaanusson, Naturhistoriska Riksmuseet, Stockholm; Mr. C. W. Newman, Radnorshire County Museum, Llandrindod Wells; Mr. W. J. Norton, Shropshire County Museum, Ludlow; Mr. H. P. Powell, University of Oxford; Dr. A. W. A. Rushton, Institute of Geological Sciences; Dr. I. Strachan, University of Birmingham; and Mr. J. T. Wattison, Stoke-on-Trent, for the loan of specimens in their care.

II. HISTORICAL REVIEW

The occurrence of trilobites in the Ordovician rocks of the Builth region has been known for a long time, being referred to by Murchison as long ago as 1833 (p. 476) when he recorded the occurrence of *Asaphus Buchii* in the dark trilobite flags of the Lower Silurian. A list provided subsequently by Murchison (1839 : 660, 662, 664) comprised the following five species from the region: *Agnostus pisiformis* Brongn.; *Asaphus Buchii* Brongn.; *Trinucleus? Asaphoides* (n.s.); *Trinucleus fimbriatus* (n.s.); *Trinucleus nudus* (n.s.).

In 1849 the faunal list was increased by M'Coy, who in describing some new fossils in the Cambridge University Collections, erected five species on specimens from the inlier, as follows: *Ampyx latus; Barrandia Cordai; Cryphaeus Sedgwickii, Ogygia radians; Trinucleus gibbifrons* var. Also in that year Salter recorded *Ogygia Portlockii* and *Asaphus Tyrannus* from Builth, and redescribed *Ogygia Buchii*, while *Ampyx nudus* was redescribed by Forbes.

In the period 1851–55 Sedgwick & M'Coy published their " Synopsis of the Classification of the British Palaeozoic rocks " in which the following eleven trilobite species were recorded from the Builth region: *Ampyx latus* (M'Coy); *Ampyx nudus* (Murch. Sp.); *Barrandia cordai* (M'Coy); *Diphlorhina triplicata* (Hawle and Corda)?; *Eccoptochile Sedgwickii* (M'Coy); *Isotelus* (*Basilicus*)? *laticostatus* (Green Sp.); *Isotelus* (*Basilicus*) *Powesii* (Murch.); *Ogygia buchii* (Brong. Sp.); *Ogygia radians* (M'Coy); *Tretaspis fimbriatus* (Murch. Sp.); *Trinucleus gibbifrons* (M'Coy).

Sedgwick & M'Coy's work was followed in 1864–83 by Salter's unfinished Monograph of the British Trilobites in which he described only eight trilobites from the Builth region, the following three being recorded for the first time: *Calymene duplicata* Murchison; *Ogygia angustissima* Salter; *Ogygia* (*Ptychopyge*) *corndensis* Murchison.

Ogygia portlockii, originally placed on the faunal list by Salter (1849), but omitted by Sedgwick & M'Coy (1851–55), was formally removed from the Builth faunal lists in this work.

Subsequent to 1866 no work on the trilobite fauna appeared until 1940 when Elles published her paper on the stratigraphy and faunal succession of the inlier. In this study Elles recorded 22 trilobites of which seven (denoted in the following list by an asterisk) were new: *Agnostus m'coyi* Salter; *Ampyx bisectus**; *Ampyx nudus* (Murchison); *Ampyx salteri* Hicks; *Barrandia cordai* (M'Coy); *Barrandia homfrayi* Hicks; *Barrandia* (*Homalopteon*) cf. *portlocki* Salter; *Barrandia* (*Homalopteon*) *radians* (M'Coy); *Calymene* (*Flexicalymene*) *aldonensis* (Reed); *Calymene* (*Platycalymene*) *duplicata* (Murchison); *Eccoptochile* (?) *sedgwicki* M'Coy; *Ogyginus corndensis* (Murchison); *Ogyginus corndensis* mut. *intermedius**; *Ogygiocaris buchi* (Brongniart); *Trinucleoides reticulatus**; *Trinucleus chamberlaini**; *Trinucleus fimbriatus* s.s. Murchison; *Trinucleus fimbriatus* mut. *primus**; *Trinucleus fimbriatus* mut. *ultimus**; *Trinucleus* cf. *foveolatus* Angelin; *Trinucleus* (*Cryptolithus*) *gibbosus**; *Trinucleus* (*Cryptolithus*) *lloydi* Salter.

Elles's paper is the most recent description of the Builth trilobites, although Whittard (1955–67) made some reference to the Builth fauna in his Monograph of the Shelve Trilobites.

The works cited above are concerned essentially with the trilobites and graptolites, the other faunal elements having received little attention. This is no doubt a reflection on the paucity of the other fossil groups, although brachiopods, bryozoa, conulariids, gastropods, lamellibranchs, ostracodes and sponges do occur in small numbers.

From the above lists it would appear that forms such as the cyclopygids, illaenids, marrolithinids and odontopleurids are absent from the Builth region. However, whilst the present study shows the Builth fauna to be less restricted than was formerly thought, it is still quite distinct from other Anglo-Welsh assemblages.

III. STRATIGRAPHICAL SUMMARY

The rocks of the inlier outcrop in a series of folds trending north-east to south-west. The plunge of the folds is variable and may be related to the numerous intrusions. The outcrops have been affected by faulting, particularly wrench faults, and this, together with the extraordinary burst of Llanvirn vulcanicity has led to complications in determining the succession and correlating from one part of the inlier to another. The stratigraphical succession as outlined by Elles (1940) and modified by Jones & Pugh (1941, 1948, 1949) has been used as the basis for the stratigraphical control of the fauna, although current field studies have necessitated some slight modifications. The dominant sedimentary types are mudstones and shales, which are interbedded with ashes and numerous doleritic intrusions. An exception to this is the Newmead Group with its more arenaceous deposits.

The thicknesses listed below are those given by Jones & Pugh (1948, 1949) and only include the thicknesses of the shale-mudstone sequence in the Lower Llanvirn, Llandeilo and Basal Caradoc. As indicated by these authors, if the thicknesses of the interbedded ashy beds are included then up to 10,000 feet of rocks are present in the southern part of the area, and slightly less in the northern part due to the thinning of the Upper Llanvirn sequence (see Text-fig. 3).

Stratigraphical Succession

		Approximate thickness in feet
CARADOC	*Nemagraptus gracilis* shales with dolerite intrusions.	1,000
LLANDEILO	Shales and mudstones with occasional limestone and ash bands.	2,000
	UNCONFORMITY	
UPPER LLANVIRN	Upper *Didymograptus murchisoni* shales	0–400
	Cwm Amliw Ash	
	Rhyolitic Ash and ashy mudstones	150
	Newmead Group	
	Flinty mudstones	30
	Pyritiferous feldspar sands and boulder beds	160
	Grey feldspar sands and boulder beds	330
	UNCONFORMITY	
UPPER LLANVIRN	Builth Volcanic Group	
	Spilites, Keratophyres and Felsitic agglomerate	1,200
	Lower *Didymograptus murchisoni* shales	250
	Red agglomerate and Ash	500
	UNCONFORMITY	
	Llandrindod Volcanic Series	
	UNCONFORMITY	
LOWER LLANVIRN	*Didymograptus bifidus* shales with some ashy and more arenaceous bands	3,000

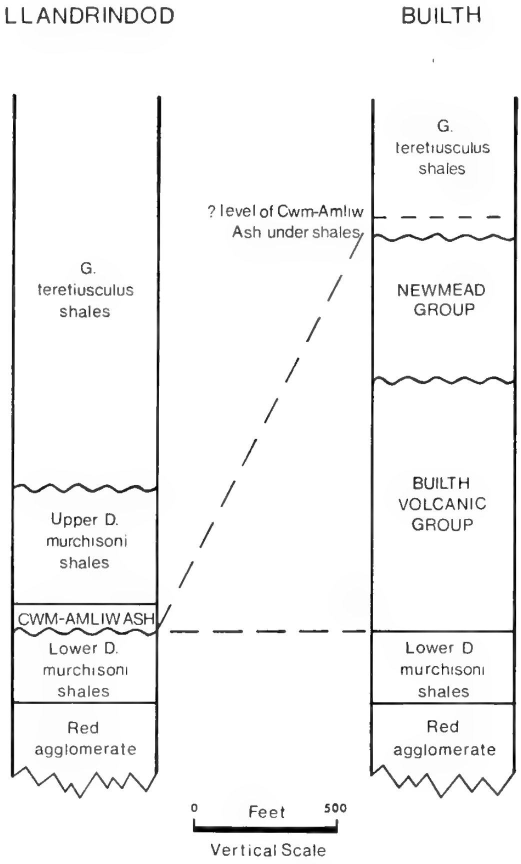

FIG. 3. Diagram showing the variation in the Llanvirn succession in the inlier. Modified after Jones & Pugh 1949.

Lower Llanvirn

This subseries consists of a thick sequence of about 3,000 feet, composed mainly of shales and mudstones, which are commonly micaceous, together with some more arenaceous bands. About 1,000 feet from the top of the subseries there is a widespread, almost continuous horizon of dolerite intrusions, with the beds above the dolerite becoming more ashy. The lower part of the succession, in general, is only sparingly fossiliferous, the fauna being restricted to a few trilobites and graptolites and occasional inarticulate brachiopods and small lamellibranchs. The beds near the top of the sequence yield a rich fauna of trilobites with some graptolites, brachiopods, sponges and larger lamellibranchs; these beds were assigned to the *Didymograptus speciosus* Subzone by Elles (1940).

Upper Llanvirn

This subseries may be considered as a shale-mudstone succession with a widespread development of volcanics and associated sediments in the middle of the sequence. Such a simple picture, however, is considerably modified because in the northern part of the inlier the great bulk of the volcanics were never developed; while to the south the upper part of the volcanics, together with the overlying shales, are overstepped by the *Glyptograptus teretiusculus* shales. Thus the Upper Llanvirn succession shows considerable variation within the inlier, the changes being summarized in Text-fig. 3. The fauna of the Upper Llanvirn consists basically of graptolites, which are exceedingly abundant at some localities. Trilobites are generally extremely rare, although some ogygiocaridinids appear towards the top of the succession. In the southern part of the inlier, the fauna of the Newmead Group reflects the different facies for it is made up almost exclusively of articulate brachiopods and sponge remains.

Llandeilo

This series is represented by about 2,000 feet of shales and mudstones with an occasional thin limestone and calcareous ash band. Numerous small doleritic intrusions are present, being most likely confined to two horizons, one in the lower and the other in the upper part of the succession (Jones & Pugh 1946). As in the higher Lower Llanvirn, trilobites are more common than graptolites; inarticulate brachiopods, lamellibranchs, ostracodes and sponges also occur sporadically throughout the succession but only as a minor element of the fauna.

Basal Caradoc

Where exposed this succession almost invariably consists of dark indurated shales and mudstones, near, or in contact with the numerous dolerite intrusions. Jones & Pugh (1948) estimated the thickness of the *N. gracilis* shales to be about 1,000 feet although the upper part is poorly exposed. While the trilobites continue to form a prominent part of the fauna, the graptolites are also very abundant at several horizons. Inarticulate brachiopods, gastropods, and less commonly articulate brachiopods, nautiloids and sponges are also present.

IV. THE USE OF BIOMETRICAL TECHNIQUES

Since the early pioneer work on the application of biometrical techniques in palaeontological studies by such workers as Burma (1948), Kermack & Haldane (1950), Kermack (1954) and Imbrie (1956), the use of statistical procedures in the study of fossil populations is being slowly accepted in many branches of palaeontology. There has however been a general reluctance, with a few notable exceptions, on the part of trilobite workers to adopt these techniques. This may be due, as Williams (1962 : 70) pointed out, to a general belief among many palaeontologists that the use of statistical techniques is unnecessary in assessing the degree of morphological similarity, as that can be done effectively by the experienced systematist without recourse to statistics. While this may be true in certain cases, depending on the individual worker, no verbal description can communicate the amount of variation in characters so precisely as a statistic or series of statistics. Another reason for the non adoption of biometric techniques in trilobite studies may be the fragmentary nature of so much trilobite material; this, however, cannot be used as a valid argument against the use of statistical methods whenever the available material permits.

In considering continuously variable parameters, such as length and width, bivariate analyses have been generally found, by workers on differing phyla, to be satisfactory. This form of treatment was fully described by Kermack & Haldane (1950) and Kermack (1954). Apart from its comparative simplicity, this form of analysis has the advantage over multivariate analyses of indicating precisely which characters are similar and which show differences. This identification of changes affecting single characters is important in dealing with temporal as well as spatial variations because it provides a means of unravelling evolutionary trends. Bivariate analysis is also a well-tested method for taxonomic discrimination, although it is more cumbersome than the multivariate techniques which give an overall idea of similarity or dissimilarity. By means of various biometric techniques adopted here, it has been possible: firstly to supplement the specific diagnoses with measures of variation affecting many characters; secondly to investigate growth patterns typical of fossil trilobite populations and the occurrence of holaspid instars.

Before the normal biometric techniques can be applied to the Trilobita however, the possible effects of the discontinuous mode of skeletal growth found in the arthropods must be considered. It is clear, since increase in size of a typical arthropod can only take place between the shedding of one exoskeleton and the hardening of the next, that the theoretical growth curve relating any two size parameters will never be realized in the life-history of any single individual. Instead, both parameters, based on exoskeletal dimensions, will increase in size by a series of jumps, although the points thus arrived at will all be on the theoretical curve.

Although moulting of many arthropods, including some trilobites, tends to occur at each doubling of weight (Przibram 1931; Hunt 1964, 1967), the natural variation within a sample, coupled with variations in initial post-larval weight are in some instances sufficient to obscure any recurrent modality in the sizes at which moulting occurs. In a large population of such a species, moulting will thus take place randomly at any size, and the measurements of exoskeletal parameters should fall on a continuous curve. In those cases where a recurrent modality in moult size is apparent, the measurements obtained of exoskeletal parameters in any sample will still lie along the theoretical growth curve, and will differ from the former case only in that there will be intervals along the curve in which no measurements occur.

It is thus seen that the mode of growth of trilobites presents no reasons against using the bivariate techniques proposed by Kermack & Haldane (1950) and Kermack (1954), although there may be some bias towards the smaller individuals due to the presence of exuviae in a sample.

Owing to the periodic renewal of the entire exoskeleton, growth lines are absent and no indication of the former shape of an individual can be obtained. Thus damaged specimens cannot be utilized to give measurements for an individual when at an earlier growth stage as is possible, for instance, with brachiopods. This fact can often seriously reduce the amount of data obtainable from a sample. The lack of growth lines also means that in a water-sorted sample the data obtainable are strictly limited to the size of the individuals present and no data can be deduced for individuals smaller than those represented in the sample. Although the mechanics of hydrodynamical sorting are still not adequately understood, it is safe to assume that the variability of characters in a water-sorted sample will be less than in a natural population. Williams (1962 : 72) considered that the effect of water sorting on systematic studies of brachiopods could be disastrous were it not for the preservation of growth lines which record the development of the exoskeletons of most individuals. Whilst this does not rule out the use of biometric techniques in trilobite studies, it does, in certain cases restrict knowledge of the growth and development to a relatively small size range. Great caution must therefore be exercised in distinguishing between forms which are inferred from samples to be of different absolute size.

Thus it is seen that neither the discontinuous nature of the skeletal growth nor the absence of growth lines on the exoskeleton precludes the use of statistical treatments already in use for organisms like echinoderms and brachiopods which are subject to continuous skeletal growth. The lack of growth lines does however mean that more assiduous collecting is necessary to obtain a sufficient sample size, and even in moderately large samples, knowledge may be restricted to a limited size range. This need for protracted collecting is still not a valid reason against using biometrical techniques whenever possible. In the present study the various techniques and notation have been used as originally outlined by Kermack & Haldane (1950) and Kermack (1954) and subsequently adopted and enlarged on by Williams (1962).

Unless some care is taken in collecting, faunal samples from any particular outcrop or region may show a considerable degree of " collector's bias ". This has been discussed by Kermack (1954) and Simpson, Roe & Lewontin (1960) and in the present study an effort was made to reduce this to a minimum. In only two localities were fossil remains sufficiently abundant to make bulk sampling possible. These were the cliff section in the Howey Brook where the so-called " *Trinucleus* " band consists of little other than trilobite remains and in the upper reaches of the Camnant Brook where a rotten stone band crops out which is largely fossil debris. Where the dispersed distribution of trilobites rendered the collection of bulk samples impracticable every trilobite fragment was retained to avoid the necessity of making field selections of the " best " specimens. At certain localities however, like the middle quarry at Llanfawr where trilobites are very common, some selection inevitably occurred. It is thus felt that the samples obtained are reasonably free from bias.

The single orientation method of measurement proposed by Shaw (1957) has been adopted throughout. In those measurements involving distances between, or to, furrows, the measurements have been taken from the deepest (dorsoventrally) point in the furrow. A micrometer ocular was used for all measurements under 2 cm. Larger measurements were made using vernier calipers.

Although the notation proposed by Shaw (1957) and adopted by Hunt (1967) for various measurements is useful, particularly in standardizing measurements of various species, it is rather unwieldy if applied too rigidly. Consequently it has been decided to define the measurements made for each family independently, although standard " code letters " have been retained throughout. Thus " A " always refers to measurements of cephalic length; " K " to glabellar width; " Z " to pygidial length measurements.

The selection of parameters for measurement must be to some extent subjective. This introduces a contradiction, for the aim of using statistical techniques is to be as objective as possible (see Olson & Miller 1951 : 218). In respect to trilobites, selection of the most suitable measurements is not always clear due to a general lack of knowledge of growth mechanisms. Moreover selection is often strongly influenced by the amount, and state of preservation, of the material available. All the data given in the present study are taken from internal moulds and have been selected, as far as possible, to define the major elements of the exoskeleton. However it must be stressed that this selection is subjective and it is for future research to judge which are the most important and useful parameters, both taxonomically and for our understanding of trilobite growth and evolution. By limiting measurements to those which may be termed " basic " characters it is hoped that growth patterns within the trilobites may be found, although the limited coverage of the present work does not reveal any such patterns.

V. TERMINOLOGY

The morphological terms proposed by Harrington, Moore & Stubblefield *in* Moore (1959) have been adopted throughout with the exception of a few terms either in use or introduced since that date, together with certain new terms here introduced. Such terms applied only to particular families or other taxa will be listed in the appropriate part of this series.

Intra-axial furrow—This term is proposed for the furrow between the middle and lateral lobe of the thoracic axial ring of agnostids.

Occiput—This term introduced by Stäuble (1953 : 87) and adopted by Whittington (1959 : 441) is here accepted.

Pleural ridge—This term is used for any ridge running in a general transverse direction across the thoracic pleura.

Terminal area (of pygidium)—This term is introduced in species having a ribbed pleural field for that part of the pleural field posterior to the last furrow.

VI. DEFINITION OF MEASUREMENTS

Measurements taken on agnostids (see Text-fig. 4)

A	maximum cephalic length—measured in the sagittal line.
A_1	intraborder cephalic length—measured in the sagittal line between the posterior margin of the cephalon and the anterior border furrow.
B	glabellar length—measured in the sagittal line from the posterior of the glabella to the preglabellar furrow.
B_1	the distance from the posterior of the glabella to the intersection of the axial furrow and the transglabellar furrow, as projected onto the sagittal line.
B_2	the distance from the posterior of the glabella to the transglabellar furrow as measured in the sagittal line.

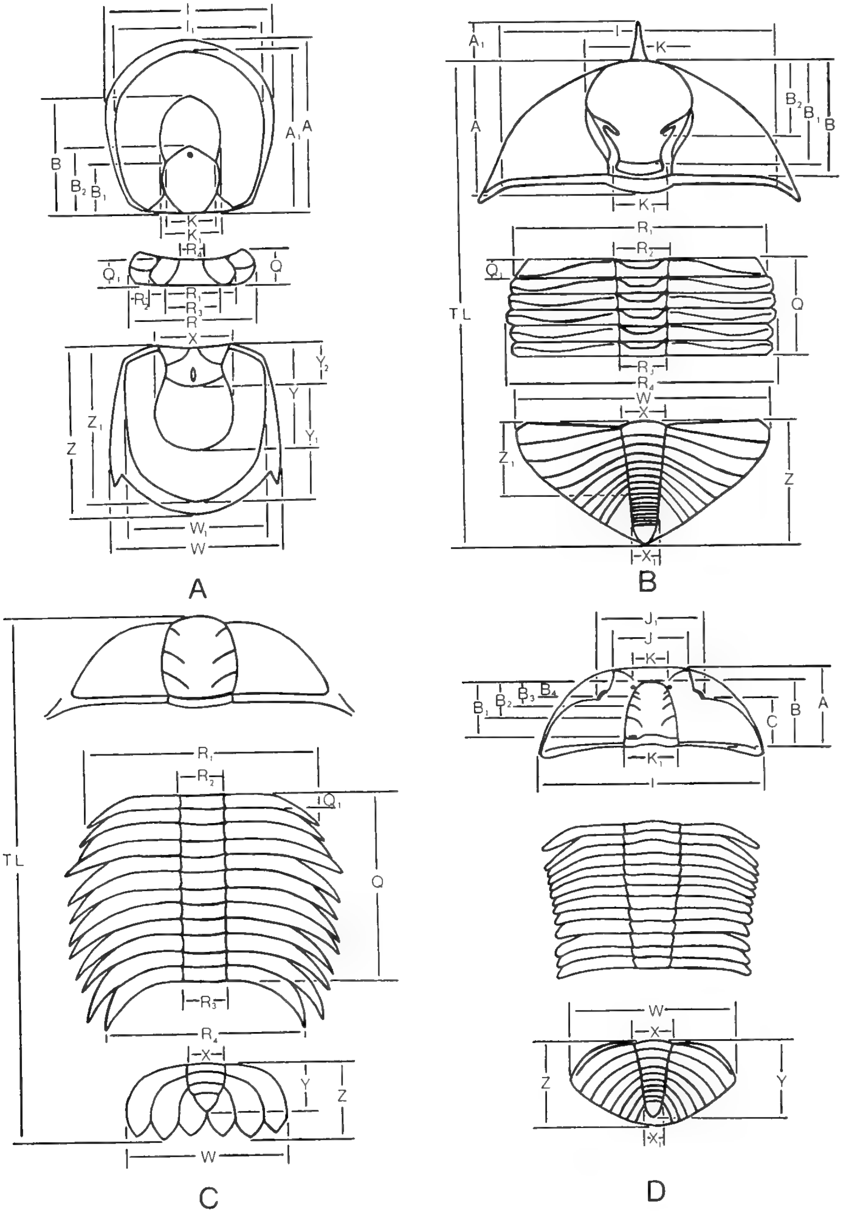

FIG. 4. Diagram showing the measurements taken on agnostids, raphiophorids, *Placoparina* and calymenids.

I	maximum cephalic width—measured in a transverse direction.
I_1	maximum intraborder cephalic width—measured in a transverse direction between the lateral border furrows.
K	transverse furrow glabellar width—measured in a transverse direction between the axial furrows at the intersections of the transglabellar furrow and the axial furrows.
K_1	maximum glabellar width—measured in a transverse direction between the axial furrows.
Q	anterior thoracic segment length—measured between the most anterior and posterior portions of the segment as projected onto an exsagittal line.
Q_1	axial length of anterior thoracic segment—measured in the sagittal line.
R	maximum anterior thoracic segment width—measured in a transverse direction.
R_1	maximum width of thoracic axis—measured in a transverse direction between the lateral extremities of the axial ring.
R_2	pleural width of anterior thoracic segment—measured between the lateral extremity of the pleura and the posterolateral extremity of the axis as projected onto a transverse line.
R_3	posterior width of median axial lobe—measured in a transverse direction along the posterior of the segment between the intra-axial furrows.
R_4	anterior width of median axial lobe—measured in a transverse direction along the anterior of the segment between the intra-axial furrows.
W	maximum pygidial width—measured in a transverse direction.
W_1	maximum intraborder pygidial width—measured in a transverse direction between the lateral border furrows.
X	maximum axial width—measured in a transverse direction.
Y	axial length—measured in the sagittal line from the anterior margin to the postaxial furrow.
Y_1	the distance from the transverse axial furrow to the posterior border furrow, as measured in the sagittal line.
Y_2	the distance between the anterior margin of the pygidium and the transverse axial furrow as measured in the sagittal line.
Z	pygidial length—measured in the sagittal line between the anterior and posterior margins of the pygidium.
Z_1	maximum intraborder pygidial length—measured in the sagittal line between the anterior margin of the pygidium and the posterior border furrow.

Measurements taken on raphiophorids (see Text-fig. 4)

A	cephalic length—measured in the sagittal line from the posterior margin to the anterior of the glabella, excluding the frontal glabellar spine.
A_1	length of frontal glabellar spine—measured in the sagittal line.
B	glabellar length—measured in the sagittal line between the occipital furrow and the anterior of the glabella.
B_1	the distance between the " posterior lateral glabellar furrows " and the anterior of the glabella as measured in the sagittal line.
B_2	the distance between the posterior extremity of the " anterior lateral glabellar furrows " and the anterior of the glabella, as projected onto the sagittal line.
I	cephalic width—measured in a transverse direction between the points of deflection of the posterior margin.
K	anterior glabellar width—measured in a transverse direction between the axial furrows at the maximum width of the glabella.
K_1	posterior glabellar width—measured in a transverse direction between the axial furrows at the maximum width of the " basal glabellar lobe ".
Q	thoracic length—measured in an exsagittal line between the anterior margin of the anterior segment and the posterior margin of the posterior segment.

Q_1	length of anterior thoracic segment—measured in an exsagittal line between the anterior and posterior margins of the anterior thoracic segment.
R_1	anterior thoracic width—measured in a transverse direction between the lateral extremities of the posterior margin of the anterior thoracic segment.
R_2	anterior thoracic axial width—measured in a transverse direction between the axial furrows along the anterior of the anterior axial ring.
R_3	posterior thoracic axial width—measured in a transverse direction between the axial furrows along the posterior of the posterior axial ring.
R_4	midthoracic width—measured in a transverse direction between the lateral extremities of the posterior margin of the third thoracic segment.
W	maximum pygidial width—measured in a transverse direction.
X	anterior pygidial axial width—measured in a transverse direction between the axial furrows along the anterior margin.
X_1	posterior pygidial axial width—measured in a transverse direction between the axial furrows at the posterior of the parallel-sided portion of the axis.
Z	pygidial length—measured in the sagittal line between the anterior margin and the posterior of the axis.
Z_1	the distance between the anterior margin and the join of the hindmost furrow on the pleural field with the axial furrows, as measured in an exsagittal line.
T.L.	total length—measured in the sagittal line between the anterior of the glabella (excluding the frontal glabellar spine) and the posterior of the pygidial axis.

Measurements taken on *Placoparina* (see Text-fig. 4)

Q	thoracic length—measured in an exsagittal line between the anterior margin of the anterior thoracic segment and the posterior margin of the posterior thoracic segment.
Q_1	anterior thoracic segment length—measured in an exsagittal line between the anterior and posterior margins of the anterior thoracic segment.
R_1	anterior thoracic width—measured in a transverse direction between the distal extremities of the anterior thoracic segment.
R_2	anterior thoracic axial width—measured in a transverse direction along the posterior of the anterior thoracic axial ring between the axial furrows.
R_3	posterior thoracic axial width—measured in a transverse direction along the posterior of the posterior thoracic axial ring between the axial furrows.
R_4	posterior thoracic width—measured in a transverse direction between the distal extremities of the posterior thoracic segment.
W	maximum pygidial width—measured in a transverse direction.
X	anterior pygidial axial width—measured in a transverse direction along the anterior margin between the axial furrows.
Y	pygidial axial length—measured in the sagittal line between the articulating half ring furrow and the posterior of the axis.
Z	pygidial length—measured between the articulating half ring furrow and the posterior tip of the second pair of pleural terminations, as projected onto the sagittal line.
T.L.	total length—measured between the anterior margin of the glabella and the posterior tip of the second pair of pleural terminations, as projected onto the sagittal line.

Measurements taken on calymenids (see Text-fig. 4)

A	cephalic length—measured in the sagittal line between the anterior and posterior margins of the cephalon.
B	cephalic axial length—measured in the sagittal line between the posterior margin of the cephalon and the preglabellar furrow.
B_1	glabellar length—measured in the sagittal line between the occipital furrow and the preglabellar furrow.

B_2	the distance between the preglabellar furrow and the intersection of the 1p lateral glabellar furrows and the axial furrows, as projected onto the sagittal line.
B_3	the distance between the preglabellar furrow and the intersection of the 2p lateral glabellar furrows and the axial furrows, as projected onto the sagittal line.
B_4	the distance between the preglabellar furrow and the intersection of the 3p lateral glabellar furrows and the axial furrows, as projected onto the sagittal line.
C	postpalpebral length—measured between the posterior of the palpebral lobe and the posterior margin of the cephalon, as projected onto the sagittal line.
I	maximum cephalic width—measured in a transverse direction.
J	anterior cranidial width—measured in a transverse direction between the anterior extremities of the cranidium.
J_1	mid cranidial width—measured in a transverse direction between the posterior of the palpebral lobes.
K	anterior glabellar width—measured in a transverse direction between the anterior fossulae.
K_1	posterior glabellar width—measured in a transverse direction between the axial furrows along the posterior cephalic margin.
W	maximum pygidial width—measured in a transverse direction.
X	anterior pygidial axial width—measured in a transverse direction between the axial furrows along the anterior margin.
X_1	posterior pygidial axial width—measured in a transverse direction between the axial furrows at the posterior of the axis.
Y	pygidial axial length—measured in the sagittal line between the anterior pygidial margin and the posterior of the axis.
Z	pygidial length—measured in the sagittal line.

VII. SYSTEMATIC DESCRIPTIONS

Family **AGNOSTIDAE** M'Coy 1849

Genus ***GERAGNOSTUS*** Howell 1935

1939 *Geragnostella* Kobayashi.

DIAGNOSIS. Agnostids with transglabellar furrow and axial furrows variously developed; no longitudinal preglabellar furrow. Pygidial axis generally slightly more than half pygidial length; trilobed; short posterolateral spines present. Dorsal surface smooth.

TYPE SPECIES. *Geragnostus sidenbladhi* (Linnarsson 1869).

DISTRIBUTION. The genus ranges from the Tremadoc to Llandeilo Series and is widely distributed throughout Europe, North and South America and China.

DISCUSSION. Considerable difficulties are encountered in distinguishing between *Geragnostus* and *Trinodus* M'Coy 1846 and both Ross (1958 : 563–564; 1967 : 8–9) and Whittington (1963 : 28; 1968) have discussed this question. Until recently it seemed possible that within the genus there were two groups, of possible subgeneric or even generic rank, one characterized by a well-developed transglabellar furrow and the other by the poor development or complete absence of such a furrow. Ross (1967 : 8–9) has followed Whittard (1966 : 265) in stressing the importance of this furrow, advocating that those forms with no transglabellar furrow be referred to

Trinodus, and those with, to *Geragnostus*. This subdivision would appear to be straightforward but for Dean's (1966 : 275–276) discovery that *Geragnostus occitanus* Howell 1935 shows considerable variation in the degree of development of the transglabellar furrow and axial furrows which are clearly present in some specimens any almost completely absent in others. Thus it would now seem unwise to consider and possible generic separation based on the development of these furrows. Dean (1966 : 274) has suggested that further research may show *Geragnostus* to be a junior synonym of *Trinodus*; however, until new material of the type species of *Trinodus*, *T. agnostiformis* M'Coy is described, some confusion between these genera will continue.

Having shown that the axial furrows may not always be developed around the posterior of the pygidial axis in *Geragnostus*, Dean (1966 : 273) placed *Geragnostella* Kobayashi 1939 in synonymy with *Geragnostus* on the grounds that the pygidial axis of *Geragnostella* could no longer be held as different from that of *Geragnostus*.

Although many of the species of *Geragnostus* are of limited geographical range, the wide occurrence of the genus makes it of particular use in the study of faunal provinces.

Geragnostus mccoyii (Salter *in* Murchison)

(Pl. 1, figs. 1–12)

1839 *Agnostus pisiformis* (Wahlenburg); Murchison : 650, 664, 704, pl. 25, figs. 6a, 6b.
1851 *Diplorhina triplicata* M'Coy *in* Sedgwick & M'Coy : 142, pl. 1E, fig. 11.
1854 *Agnostus McCoyii* Salter *in* Murchison : pl. 3, fig. 8.
1859 *Agnostus maccoyii* Salter *in* Murchison : pl. 3, figs. 7, 8, Foss. 10, fig. 5.
1939 *Geragnostus* (*Corrugatagnostus*) *maccoyi* (Murchison); Kobayashi : 173.
1955 *Geragnostus maccoyi* (Murchison); Whittard : 8, pl. 1, figs. 5, 6.
1966 *Geragnostus maccoyii* (Murchison); Whittard : 265–266, pl. 46, fig. 2. Includes full synonymy.

DIAGNOSIS. *Geragnostus* with glabella approximately bisected by chevron-shaped transglabellar furrow, with small median glabellar node immediately to posterior; lateral occipital lobes present. Pygidial axis with anterior lateral lobes and two segments, posterior one being about two-thirds of axial length; median node present on anterior segment; axial furrows sinuous with axis constricted opposite transverse furrow.

LECTOTYPE. GSM. 8710 (Stokes Coll.). (Pl. 1, figs. 1, 2.) Internal mould of cephalon. Figured by Murchison 1839, pl. 25, fig. 6b as *Agnostus pisiformis*. Designated and refigured by Whittard 1955 : 8, pl. 1, fig. 5.

DIMENSIONS.

A	A_1	B	B_1	B_2	I	I_1	K	K_1
3·1	2·8	2·1	1·1	0·9	3·4	3·0	1·2	1·1

All measurements in mm. For explanation of symbols see Text-fig. 4.

TYPE LOCALITY AND HORIZON. The precise locality for the lectotype is not certain, but it is most likely the small quarry at the south-western end of Pen-cerig Lake, in beds of uppermost Llandeilo age.

Other figured material. It. 2670 (Pl. 1, figs. 4, 8); It. 2671 (Pl. 1, fig. 3); It. 2673 (Pl. 1, fig. 12); It. 2675 (Pl. 1, fig. 9); It. 2677 (Pl. 1, fig. 10); It. 2680 (Pl. 1, fig. 11); GSM. 8709 (Pl. 1, figs. 5, 6); Wattison Coll. H1 (Pl. 1, fig. 7).

Distribution. The species is virtually confined to the Builth-Llandrindod inlier where it occurs in beds of the Llandeilo and basal Caradoc Series (*teretiusculus* and *gracilis* Zones). A single specimen, however, has also been recorded from the Meadowtown Beds (Llandeilo) of the Shelve district (Whittard 1966 : 266).

Description. The roundedly subquadrate cephalon tends to be slightly wider than long. The subcylindrical glabella, rounded in front and smooth, is moderately convex, occupies, in general, a little over two-thirds of the cephalic length and is defined by deep axial furrows. A single conspicuous transglabellar furrow, present at about the mid-glabellar length, is markedly convex forwards, giving a concavo-convex outline to the anterior glabellar lobe; the anterior lobe being in general fractionally wider than the posterior lobe. On external moulds a small median glabellar node is present immediately behind the transglabellar furrow (Pl. 1, fig. 10); there is also a suggestion of its development on many well-preserved internal moulds (Pl. 1, figs. 1, 11). Prominent triangular lateral occipital lobes are developed. The genae are smooth, gently and evenly convex, commonly narrowing slightly in front of the glabella. The border is separated by a deep, moderately wide border furrow with moderately sloping sides, becoming steeper and narrower at the posterolateral corners and along the posterior edge of the genal regions (Pl. 1, fig. 11). Although the posterolateral corners are rarely well preserved, the small spines described by earlier authors (e.g. Salter 1864*a*) are not present, although there may be a slight swelling of the border.

The thorax consists of two segments, the anterior one being the larger (Pl. 1, figs. 5, 7). The axis of the anterior segment is broad and divided into a median trapezoidal lobe and a pair of oval lateral lobes with major axes directed inwards and forwards at about 45°; the pleurae are divided by pleural furrows into nearly equal bands. The posterior segment is similar, differing chiefly in that the major axes of the oval lateral lobes lie in a transverse direction. The pleurae of both segments are curved forwards.

The subquadrate pygidium, like the cephalon, is typically slightly wider than long. The axis, rounded posteriorly, is slightly over one-half of the pygidial length and is slightly constricted just to the anterior of the transverse furrow. This furrow is well developed, gently concave anteriorly, and occurs at about one-third the length from the anterior of the axis. Immediately anterior of this is an elongated median node. At the anterolateral corners of the axis are a pair of prominent lobes. The pleural lobes are smooth, more or less constant in width and convexity and are limited by a deep border furrow. A convex border is present laterally and posteriorly, becoming steeply upturned along the anterior margin of the pleural lobes. Small spines are present at the posterolateral corners (Pl. 1, fig. 4).

Ontogeny. Small holaspid individuals appear to differ little from the largest. Specimen It. 2673 (Pl. 1, fig. 12) however most likely represents a meraspid degree one. This specimen is similar to the one figured by Whittington (1965 : pl. 2, figs.

14, 18) as a meraspid degree one of *Geragnostus fabius* (Billings 1865) in that it shows the pleural region of what is to become the pleura of the second thoracic segment. Unfortunately the axial portion of the embryo thoracic segment is not preserved in the Builth specimen. Unlike Whittington's specimen, the remainder of the axis of the transitory pygidium is divided into two nearly equal lobes, the posterior one being slightly larger. Thus the axis is very similar to the glabella of a small holaspid and the possibility that this specimen represents a very small cephalon with a particularly wide posterior border must remain. The dimensions of this individual are; length 1·14 mm; width 1·32 mm. Four other small pygidia varying in length from 1·4–1·9 mm. all appear to be small holaspids.

BIOMETRICAL DATA. Sample populations from the Llandeilian rocks exposed in the stream section east of Bach-y-graig 40 yards east of the point where the footpath enters the wood at the western end of the section and the small quarry at the south-western end of Pencerig Lake were tested for differences in the growth ratios (a or α) and initial growth shape (b or β); no statistically significant differences were found. The following Tables have been compiled by using the combined samples.

TABLE 1

x : y	$\bar{x}$	var. x	y	var. y	r	r_e	α	var. α	a	var. a	n
$A_1 : I_1$	3·14	0·44	3·06	0·45	0·93	0·94	1·04	0·0037	1·02	0·0047	33
$A_1 : B$	3·15	0·55	2·27	0·31	0·99	0·99	1·03	0·0006	0·74	0·0001	43
$B : B_2$	2·26	0·27	1·24	0·09	0·97	0·98	1·05	0·0004	0·58	0·0012	47
$Z : W$	2·85	0·68	2·86	0·78	0·94	0·94	1·07	0·0050	1·07	0·0052	28
$Y : Z$	1·91	0·30	2·92	0·62	0·99	0·99	0·94	0·0006	—	—	40
$Y_2 : Y$	0·73	0·05	1·86	0·30	0·81	0·81	0·94	0·0080	2·41	0·0544	39

Bivariate statistics for the cephalon and pygidium of *G. mccoyii* (Salter *in* Murchison). All measurements in mm. For explanation of symbols see Text-fig. 4.

TABLE 2

Q	Q_1	R	R_1	R_2	R_3	R_4
1·0	0·6	3·1	2·0	0·6	1·1	0·4
0·9	0·5	—	—	—	—	—
—	0·6	—	—	—	—	—

Thoracic measurements of three specimens of *G. mccoyii* (Salter *in* Murchison). All measurements in mm. For explanation of symbols see Text-fig. 4.

In view of the use of various ratios in discriminating certain species within this genus the means and variance for various ratios along with their observed ranges are given in Table 3.

The relatively large variation in the ratio $Y_2 : Y$ may be due to the fact that its variance is dependent on the variance of both Z_1 and Y_1 ($Y_2 = Z_1 - Y_1$).

An attempt has been made to see whether the shape of the transglabellar furrow altered with size. As expected the value of $B_2 - B_1$ increases with the value of B

TABLE 3

Ratio	Mean	var.	Observed range	n
$B_2 : B$	0·55	0·001	0·47–0·60	47
$B : A$	0·66	0·001	0·55–0·72	31
$Y_2 : Y$	0·39	0·005	0·27–0·56	39
$Y : Z$	0·59	0·002	0·47–0·69	34

Statistical data for various ratios for *G. mccoyii* (Salter *in* Murchison). For explanation of symbols see Text-fig. 4.

(see Table 4), but the ratio $B_2 - B_1 : B$ does not show a similar increase (see Table 5). Thus it is seen that the amount of forward convexity increases more or less proportionately with increase in glabellar length.

TABLE 4

B in mm.		1·5–1·9	2·0–2·4	2·5–2·9	3·0–3·5
$B_2 - B_1$ in mm.	0·1	5	—	—	—
	0·2	3	10	3	—
	0·3	—	4	6	4

Data showing the increase in the value of B_2–B_1 with increase in B for *G. mccoyii* (Salter *in* Murchison). For explanation of symbols see Text-fig. 4.

TABLE 5

B in mm.	1·5–1·9	2·0–2·4	2·5–2·9	3·0–3·5
Range in value of $B_2 - B_1 : B$	0·056 to 0·13	0·083 to 0·15	0·074 to 0·12	0·097 to 0·10

Ranges in the value of the ratio B_2–B_1 : B for corresponding values of B for *G. mccoyii* (Salter *in* Murchison). For explanation of symbols see Text-fig. 4.

DISCUSSION. In the past there has been some confusion over the spelling of *mccoyii*, but the original spelling of Salter *in* Murchison 1854 should be retained.

As was pointed out by Whittard (1966 : 266) the radial ornament on the genae described by Salter (1864*a* : 6, pl. 1) is simply due to cracking of the exoskeleton and Kobayashi (1939 : 173) was mistaken in placing the species in *Corrugatagnostus* Kobayashi 1939.

G. mccoyii may be distinguished from many other species of the genus, including *G. sidenbladhi*, by its well-developed axial and transglabellar furrows. Of those species with a transglabellar furrow well developed, it resembles most closely *Geragnostus hirundo* (Hicks 1875) from the " Middle Arenig " of Whitesand Bay. *G. mccoyii* differs however in the squarer cephalic outline and the greater anterior convexity of the transglabellar furrow; the pygidium of *G. mccoyii* is distinguished by the transverse furrow occurring at about one-third, instead of one-half, the distance along the pygidium as measured from the anterior margin. *G. caducus* (Barrande 1872) from the Dd_1 beds at Sancta Benigna is easily distinguished by the development of a second transverse glabellar furrow and its more prominent median glabellar node. Tjernvik (1956 : 188 ff.) erected four new species of *Geragnostus*: *G. crassus*, *G. lepidus*, *G. wimani* and *G. explanatus*. *G. mccoyii* differs from all these in that the transglabellar furrow is more strongly developed. *G. mccoyii* is distinguished from *G. occitanus* Howell 1935, and *G. mediterraneus* Howell 1935, by its better and more constantly developed axial and transglabellar furrows and also in the shorter axis of the pygidium.

The internal and external moulds are very similar and apart from the lateral pygidial borders, differ only in that the furrows are somewhat deeper and broader on the internal moulds than on the external ones. This is in general agreement with Whittington's findings on *Geragnostus clusus* Whittington (Whittington 1963 : 30) and also with Dean's work on *G. occitanus* Howell 1935 (Dean 1966 : 274–276). However variation in the development of the transglabellar and axial furrows as found by Dean in *G. occitanus* is unknown in *G. mccoyii*. It is noted that a furrow is present on some internal moulds on the outer portion of the lateral pygidial borders, anterior to the posterolateral spines and subparallel to the lateral margin (Pl. 1, fig. 4). No trace of such a furrow is to be found on external moulds (Pl. 1, fig. 8) and it is believed that the furrow may indicate the presence on the ventral side of the doublure of a structure for interlocking the cephalon and pygidium on enrollment. Similar though not identical structures are known in *Trinodus elspethi* (Raymond 1925) (Hunt 1964, pl. 2, fig. 9), and in *Baltagnostus eurypyx* Robison 1964 and *Peronopsis interstricta* (White 1874) (Robison 1964, pl. 80, fig. 14; pl. 82, fig. 14).

The thoracic segments are of the usual agnostid pattern. Their general form supports Whittington's conclusion that the oval lateral lobes are axial and not pleural structures, although they do differ in certain respects from those of *G. clusus* as described by Whittington (1963 : 29, 32, text-fig. 3). The most striking difference is in the size of the median and lateral axial lobes of the anterior segment. In *G. clusus* they occupy only the posterior part of the segment, whereas in *G. mccoyii* they occupy the whole of the axis; the anterior margin of the segment, too, is concave forwards, whereas in *G. clusus* it is more or less straight; and no median notch is seen in *G. mccoyii*. The posterior segments are in general very similar in the two species, although the form of the articulating half ring is not known in *G. mccoyii*.

Out of the eight complete or nearly complete specimens known, three show rotation of the cephalon and thorax relative to the pygidium (Pl. 1, fig. 3); the other five, although they may be slightly disarticulated, show no rotation of the various elements relative to one another. It is tentatively suggested that the specimens showing rotation may be the exoskeletons of moults and those showing no rotation, individuals that died.

Apart from its occurrences in the Builth area the species has in the past (Hicks 1875 : 180) been recorded from South Wales, but the poor preservation of these specimens makes his identifications questionable. The species has also been recorded from the Upper Lingula Flags at Malvern, although as was pointed out by Groom (1902 : 103) these specimens are almost certainly *Agnostus trisectus*.

Genus ***SPHAERAGNOSTUS*** Howell & Resser 1936

DIAGNOSIS. Cephalon smooth, convex, without furrows. Pygidium somewhat smaller than cephalon, with subcircular axis occupying over half the area of the exoskeleton.

TYPE SPECIES. *Sphaeragnostus similaris* (Barrande 1872).

DISTRIBUTION. Known from the Upper Tremadoc of Kendykyas (USSR), Llandeilo of Bohemia and Britain, Middle Ashgill of Poland, Quebec and Sweden and also possibly from the Lower Ashgill of Ireland.

DISCUSSION. Despite its wide geographical distribution the genus is extremely rare, being known from only a few specimens of each of the species. Its occurrence in the Builth district is of interest as it is the first record of the genus from the Llandeilo Series of the British Isles.

Sphaeragnostus sp.

(Pl. 1, figs. 13–15)

FIGURED MATERIAL. It. 2681 (Pl. 1, figs. 13, 15). Internal mould of pygidium. It. 2682 (Pl. 1, fig. 14). Internal mould of pygidium.

DIMENSIONS.

	W	X	Y	Z
It. 2681	*c.* 2·8	1·6	1·6	2·7
It. 2682	*c.* 3·1	1·8	1·7	2·8

All measurements in mm. For explanation of symbols see Text-fig. 4.

LOCALITIES AND HORIZON. The species is known from the old quarry 350 yards west of Maesgwynne (It. 2682); the stream section 15 yards south-west of this quarry; and the left bank of the stream section in the Dulas Brook 150 yards south-west of this quarry and 60 yards north of spot height 727 (It. 2681). All these occurrences are in the Llandeilo Series.

DESCRIPTION. The cephalon and thorax are unknown.

The subcircular pygidium is truncated anteriorly and slightly elongated sagittally. The subcircular axis, occupying about three-fifths of the pygidial length, is moderately convex, and possesses a median node slightly anterior of its centre. The axial furrows are deep and of constant width. The smooth pleural lobes become narrower and more steeply inclined anteriorly. The border is narrow anterolaterally, widening to about 0·2 mm. at the posterior. Posterolateral spines are not developed.

DISCUSSION. *Sphaeragnostus* is poorly known, the only other possible occurrence in the British Isles being *Sphaeragnostus* sp. from Co. Clare, Ireland (Whittington 1968). However, the presence of the unfurrowed, subcircular, tubercled pygidial axis, and the anterior narrowing of the pleural lobes, would seem to indicate that the Builth specimens belong to this genus.

The species may be distinguished from *Sphaeragnostus similaris* (Barrande 1872) by its more rounded axis. Furthermore, the border, as figured by Barrande (1872, pl. 14, fig. 18), is uniform in width in *S. similaris* whereas it increases in width posteriorly in the Builth specimens. *Sphaeragnostus gaspensis* Cooper & Kindle 1936, differs in that it is appreciably more elongate, the length : width ratio being 1·2 : 1. It also differs in that the axis is more oval; the border however is similar to the Builth specimens in that it increases in width posteriorly. *Sphaeragnostus cingulatus* (Olin 1906) is known from a single poorly preserved specimen in Olin's collection at Lund, and also from one other very poorly preserved specimen probably referrable to this species in the collection at Copenhagen Museum (see Kielan 1960 : 57). The specimens are similar to the Builth ones in that they are less elongate than *S. gaspensis* and have a circular axis, but appear to differ in that the median node is situated very near the anterior margin in *S. cingulatus*. However, until such time as better material is available from Sweden no proper comparison can be made. *Sphaeragnostus* sp. described by Lisogor (1961 : 61) from the Tremadoc of Russia is distinguished in being wider than long, the length : width ratio being 3 : 4. *Sphaeragnostus*? sp. from the Ashgill of Co. Clare, Ireland, is not well documented, but it appears to be more elongate than the Builth form.

The genus exhibits a trend for the pygidium to become more elongate. The earliest-known specimens, from the Upper Tremadoc of Russia, have a length : width ratio of 0·75, whereas in the Ashgill species the ratio is approximately 1·2. The new British species from the Llandeilo together with Barrande's single specimen from Bohemia fit into this trend well with a length : width ratio of about 1·0.

Family **RAPHIOPHORIDAE** Angelin 1854

Genus ***CNEMIDOPYGE*** Whittard 1955

DIAGNOSIS. Cephalon subtriangular to subsemicircular, glabella pyriform with four pairs of muscle areas (these tend to appear as two pairs of " lateral glabellar furrows " on compressed shale specimens); frontal glabellar spine circular in cross section or triangular with ventral side convex and dorsal sides concave, apex running medianly; facial suture just transgresses onto dorsal surface. Thorax rectangular, of six segments, anterior one slightly macropleural. Pygidium triangular, approximately same size as cephalon; axis and pleural fields strongly segmented.

TYPE SPECIES. *Cnemidopyge nuda* (Murchison).

DISTRIBUTION.—The genus has its maximum development in Britain in the Builth district, being recorded in rocks from lowest Llandeilo to Basal Caradoc age; its only other confirmed British occurrence being as an extreme rarity from the Shelve district. The genus is also present in Sweden and Southern Norway where it ranges in age from Upper Llanvirn (Vikarby Lst.) to Caradoc (Dalby Lst.) (Jaanusson 1960, 1963, 1964). The genus has also been recorded from ?Caradoc rocks of Canada (Norford 1964).

Discussion. Whittard's separation of the genus from *Ampyx* appears well justified, for although the pygidial ribs commonly show irregularities in development, they are persistent throughout all the known species; in addition these form a useful character for species differentiation. However due to the slightly compressed nature of the British material a full definition of the cephalic characters cannot be obtained until the study of the better preserved Scandinavian material at present in hand is completed.

Present knowledge of the genus suggests that it was derived from some, as yet unknown, *Ampyx* in Balto-Scandia by the development of ribs on the pygidium in early Ordovician time, migrated to the Welsh Borderland in Llandeilo time and finally onto N. America in Caradoc time; such migrations are known in Brachiopods (Williams 1969). The differences between some *Ampyx* and *Cnemidopyge* are marginal and there are two species currently placed in *Ampyx*, *A. lobatus* Cooper 1953 from the Porterfield of N. America and *A. salteri* Hicks 1875 from the Arenig of S. Wales, which have some ribs present on the pleural fields. It may be that *A. salteri* was near the ancestral form from which *Cnemidopyge* arose, and that the North American species represents a second, independent development.

Whilst the British representatives of the genus show a progressive increase in the number of pygidial ribs with time, preliminary studies of the Scandinavian forms suggest that this is not the case throughout the genus.

Cnemidopyge nuda (Murchison)

(Pl. 2, figs. 1–8, 10, 12; Pl. 3, figs. 1–5)

1839 *Trinucleus nudus* Murchison : 660, pl. 23, fig. 5.
1849 *Ampyx nudus* (Murchison); Forbes : 1–4, pl. 10, figs. 1–6.
1849 *Ampyx latus* M'Coy : 410.
1851 *Ampyx latus* M'Coy; Sedgwick & M'Coy : 147, pl. 1E, fig. 13.
1851 *Ampyx nudus* (Murchison); Sedgwick & M'Coy : 148.
1925 *Ampyx nudus* (Murchison); Raymond : 31.
1940 *Ampyx nudus* (Murchison); Elles : 406–408, 410–412, 414–419, 421, 432.
1940 *Ampyx nudus* (Murchison); Whittard : 161–162, pl. 5, figs. 9–10.
1940 "*Ampyx*" *latus* M'Coy; Whittard : 162.
1955 *Cnemidopyge nuda* (Murchison); Whittard : 20–21.
1955 *Ampyx latus* M'Coy; Whittard : 21.
1960 *Ampyx latus* M'Coy; Dean : 80.

Diagnosis. *Cnemidopyge* with no median glabellar ridge. Pygidium generally with seven or eight ribs on pleural fields and up to twenty axial rings; pygidia commonly show asymmetrical development of ribs. External surface ornamented with tiny pustules.

Lectotype. GSM. (GSc) 6835 (Pl. 2, fig. 2). Internal mould of cephalon and thorax.

Paralectotype. GSM. (GSc) 6835 (Pl. 2, fig. 1). Internal mould of nearly complete specimen.

Prior to this study, GSM. (GSc) 6835 (originally figured by Murchison 1839, pl. 23, fig. 5), which incorporates two specimens of *C. nuda*, has been loosely referred to as the holotype (Whittard 1940 : 162). It is here proposed to select the specimen consisting of the cephalon and thorax as lectotype and the more complete specimen as paralectotype. Both these specimens are internal moulds and show no trace of the dorsal ornament.

DIMENSIONS.

	A	B	B_1	B_2	I	K	K_1	T.L.
Lectotype	6·7	6·0	4·7	3·9	—	3·5	*c.* 1·8	—
Paralectotype	—	—	—	—	11·8	4·0	*c.* 2·0	17·5

	Q	Q_1	R_1	R_2	R_3	R_4
Lectotype	5·3	1·1	11·3	2·3	2·1	11·7
Paralectotype	5·8	1·3	12·0	2·5	2·0	12·3

	W	X	X_1	Z	Z_1	No. of axial rings	No. of ribs Left	No. of ribs Right
Paralectotype	11·3	1·8	0·8	5·9	3·2	11+	7	7

All measurements in mm. For explanation of symbols see Text-fig. 4.

TYPE LOCALITY AND HORIZON. The species was originally described by Murchison (1839 : 660) as from " Gwern-y-fad " and " The Gilwern Hill, Nr. Llandrindod ". The present study however suggests that the species is not present at " Gwern-y-fad ". Forbes (1849 : 1–4) when redescribing the species, states that it was known only from the " Cardeddau Hills, Nr. Builth ", although judging from lithology GSM. 82854, which was probably that figured by Forbes, is almost certainly from Harper's Quarry, north-east of Wellfield. Murchison's original specimen, GSM. (GSc) 6835 bears a label stating that it is from " Pen Carrig, Builth ". Thus some confusion exists as to the type locality, but it is most likely that the type specimens are from the quarry at the south-western end of Pen-cerig Lake, from beds of uppermost Llandeilo age, a supposition that is supported on lithological grounds.

OTHER FIGURED MATERIAL. It. 2683 (Pl. 3, fig. 1); It. 2684 (Pl. 2, fig. 10); It. 2685 (Pl. 3, fig. 3); It. 2687 (Pl. 2, fig. 12); It. 2688 (Pl. 2, fig. 5); It. 2691 (Pl. 2, fig. 8); It. 2692 (Pl. 3, fig. 2); It. 2693 (Pl. 2, fig. 4); GSM. 35388 (Pl. 3, fig. 5); SM. A.15,620 (Pl. 2, fig. 6); BU. 365 (Pl. 2, fig. 3; Pl. 3, fig. 4); BU. 366 (Pl. 2, fig. 7).

DISTRIBUTION. The species is apparently confined to the Builth region, apart from an unconfirmed report from near Llandeilo (Sedgwick & M'Coy 1851 : 148). It is common in the upper part of the Llandeilo, and present as a rarity in the Basal Caradoc.

DESCRIPTION. Complete individuals are ovate, ranging from slightly longer than wide to about one and a half times as long as wide. The extreme cases almost certainly result from a certain amount of compression either parallel or perpendicular to the sagittal line.

The cephalon is subsemicircular in outline, the maximum width being about two and a half times the sagittal length (excluding the frontal glabellar spine). The glabella is pyriform, narrow posteriorly, expanding frontally to about twice the width to form a prominent frontal glabellar lobe. The posterior of this lobe is defined by a pair of " lateral glabellar furrows " which are directed posteromedianly at about 45° and extend about half-way to the sagittal line. Comparison with undistorted limestone material suggests that these furrows are formed by the buckling of the exoskeleton along the line of the *2*p muscle area and more anterior muscle areas (Pl. 2, figs. 9, 11). The posterior pair of " lateral glabellar furrows ", occurring about three-quarters the way along the glabella from the anterior, are continuous, though shallow, medianly, and are similarly believed to have been caused by compression in the region of the *1*p muscle area. Such compression is also believed to account for the isolation from the glabella of the lobes apparently developed laterally to the glabella (the ala of Whittard 1955 : 19, 22; 1966 : 268) (see also Whittington 1959 : 461). The occipital ring is very short (*sag.*), separated from the glabella by a wide, rather shallow furrow. Anteriorly a median glabellar spine is developed which arises from near the top of the steeply declined frontal face of the glabella. In cross section the spine is circular and is generally slightly shorter than the remainder of the cephalon, although on one specimen it is about one and a third times as long.

The genal regions are essentially gently convex, becoming steeply declined laterally and sloping steeply into the deep axial furrows medianly. The posterior border furrow is moderately wide, shallow, and is a direct continuation of the occipital furrow. Its posterior edge is sharply turned up dorsally forming the posterior border. At the genal angles both the border and the border furrow are deflected posterolaterally to form a spatulate projection, the edges of which mark the course of the facial suture where it cuts across the base of the librigenal spines (Pl. 2, fig. 4). The facial suture is marginal frontally, but curves up onto the steep outer regions of the genae laterally, becoming near marginal just before the genal angles prior to cutting across the base of the genal spines. The librigenae are thus confined to a small area on the declined outer parts of the genal regions. A straight, unbranched genal ridge is present commencing opposite the " anterior lateral glabellar furrows " and terminating in the genal angle (Pl. 3, fig. 5). The librigenal spines are long and slender, initially directed posterolaterally, but rapidly becoming more or less posteriorly directed to extend well beyond the pygidium (Pl. 3, fig. 1).

The cephalic doublure is narrow, flat and nearly parallel sided, but medianly invaginated by the hypostomal suture (Pl. 3, fig. 2). A similar structure is known in *Lonchodomas carinatus* Cooper 1953 (see Whittington 1959 : 476, text-fig. 8c, pl. 32, figs. 2, 3). No median suture is present. The hypostoma is unknown.

The thorax is approximately rectangular with the anterior of the six segments being slightly macropleural. The maximum width, generally occurring along the anterior edge of the third segment, is about twice the total sagittal length (see Table 9). The well-defined axis is transversely convex, with only slight tapering posteriorly. Prominent nodes at the anterolateral corners of each axial ring are separated from the main part of the ring by a shallow furrow which merges anteriorly with the pronounced articulating furrow (Pl. 3, fig. 5). The anterior segment is distinct from the other segments in its longer (*exsag.*) pleurae and oblique, not truncated, extremities. The pleural furrow of the anterior segment is slightly sigmoidal, as are those of the remaining segments, although these cut the lateral edge medianly rather than posteriorly. The swollen inner portion of the posterior band is most pronounced in the anterior segment.

The triangular pygidium is about twice as wide as long. The axis is convex, tapering posteriorly but becoming subparallel-sided at the rear, and extends to the posterior margin. Up to 20 axial rings may be developed, although only the anterior nine or ten are generally clearly defined. Occasional specimens (Pl. 3, fig. 5) show paired subcircular muscle scars in the outer parts of the axial ring furrows. Excluding the anterior border, the pleural fields typically possess seven ribs, but show some variation (see Tables 10 and 11). Posteriorly there is a small unfurrowed triangular terminal area. About one-quarter of the specimens show asymmetrical or irregular development of the pleural ribs (Pl. 2, fig. 10). Subparallel terrace lines are present on the ventrally deflected posterolateral borders.

With the exception of parts of the genae, the entire dorsal exoskeleton is ornamented with small pustules about 0·05 mm. in diameter (Pl. 3, figs. 3, 4).

ONTOGENY. A single meraspid specimen about 3·2 mm. long and 3·1 mm. wide most likely belongs to degree 5 (Pl. 2, fig. 7), but due to disturbance of the thorax the exact number of segments is uncertain, and although there are apparently only four segments on the axis, the pleural regions suggest five. The cephalon is similar to that of the adult form; the glabella however is carinate, a feature possibly accentuated by compression, while the "lateral glabellar furrows" are lacking. The frontal glabellar spine is about two-thirds the cephalic length. The genal regions are rather flat, and apart from the lack of genal ridges are similar to those of holaspides.

The thoracic segments are poorly preserved but appear to resemble those of the adult.

The transitory pygidium is triangular, possibly slightly more obtusely rounded posteriorly than in the holaspid. Only four, or possibly five ribs are developed on the pleural fields with only about six or seven axial rings discernible.

BIOMETRICAL DATA. Relatively few complete specimens are known and estimated length : width ratios were possible in only five specimens (see Table 6). Although the values vary considerably they provide no real evidence of the existence of two distinct forms as recorded by Whittard (1955) in some raphiophorids. It is believed that

TABLE 6

Total length	Width	Length/Width
c. 11·0	10·4	c. 1·06
c. 13·5	9·0	c. 1·50
c. 17·0	13·8	c. 1·23
17·5	11·3	1·55
c. 22·0	17·0	c. 1·30

Length and width measurements for complete specimens of *C. nuda* (Murchison).
All measurements in mm. and taken on internal moulds.

TABLE 7

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
B : K	5·47	0·9555	4·04	0·3664	0·764	0·770	0·84	0·0286	0·62	0·01597	12
K : K_1	4·07	0·5540	2·02	0·0940	0·939	0·942	0·83	0·0194	0·41	0·00502	6
B : B_1	5·84	1·5331	4·58	1·0354	0·987	0·987	1·05	0·0023	—	—	14
B : B_2	5·86	1·6508	3·68	0·7483	0·984	0·983	1·07	0·0035	0·67	0·00131	13

Bivariate statistics for the cephalon of *C. nuda* (Murchison). All measurements in mm. For explanation of symbols see Text-figs. 4.

TABLE 8

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
W : Z	14·41	8·9012	6·48	1·7050	0·928	0·932	0·97	0·0178	0·44	0·00380	9
W : X	14·11	8·8189	2·34	0·2956	0·954	0·955	1·10	0·0133	0·18	0·00038	10
Z : X	6·25	1·5400	2·42	0·2000	0·850	0·850	0·93	0·0172	0·36	0·00257	16
X : X_1	2·54	0·2400	1·22	0·1178	0·914	0·918	1·44	0·0408	0·22	0·00124	10
Z : Z_1	6·12	1·9543	3·77	0·9464	0·942	0·943	1·13	0·0108	0·70	0·00419	15

Bivariate statistics for the pygidium of *C. nuda* (Murchison). All measurements in mm. For explanation of symbols see Text-fig. 4.

TABLE 9

Q	Q_1	R_1	R_2	R_3	R_4
—	—	*c.* 15·4	3·4	2·7	*c.* 15·6
—	1·3	—	4·0	—	—
7·3	1·5	—	—	—	—
—	1·3	—	3·3	—	—
10·2	1·2	—	—	—	—
5·3	1·1	11·3	2·3	2·1	11·7
5·8	1·3	12·0	2·5	2·0	12·3

Thoracic measurements for *C. nuda* (Murchison). All measurements in mm. For explanation of symbols see Text-fig. 4.

TABLE 10

Complete specimens

Number of ribs . . .	6	7	8	Asymmetrical	Irregular
Number of specimens . .	0	13	7	5	2

Left pleural fields

Number of ribs . . .	6	7	8	Irregular
Number of specimens . .	1	18	10	0

Right pleural fields

Number of ribs . . .	6	7	8	Irregular
Number of specimens . .	2	20	8	3

Full data of rib counts on the pleural fields of *C. nuda* (Murchison).

TABLE 11

Number of ribs	6	7	8
Number of specimens . . .	2	21	12

mean = 7·29; var. = 0·3276; n = 35

Frequency distribution of the number of ribs on the pleural fields of *C. nuda* (Murchison), together with the mean and variance.

the variation in the length : width ratios are due to the combination of individual variation coupled with the effects of slight compression.

From Table 10 it is seen that only 5% of the total number of pleural fields show irregularities in rib development. Counts on complete pygidia reveal that 7·5% show irregularities in rib development, while a further 18·5% of the total number of specimens show more ribs on one pleural field than on the other. In order to calculate the mean number of ribs developed using as large a sample as possible, the data for the right field alone were considered, except in cases where data were only available for the left field; thus only one field was considered on any given specimen. The data obtained are given in Table 11. A 2 × 2 probability test shows that there is no significant correlation between the number of ribs developed and the length of the pygidium, and thus there is no necessity to relate rib counts to the size of the individual.

DISCUSSION. *C. nuda* is characterized by the number of ribs on the pygidium and the lack of a median glabellar ridge and may be distinguished from other *Cnemidopyge* by these two characters. *C. nuda granulata* Whittard 1955 has a slightly more coarsely developed surface ornament. The various Scandinavian forms appear to have a different surface ornament, possibly a reflection of a differing environment, and also generally possess a weak median glabellar ridge.

Re-examination of specimen SM. A.15620, described as *Ampyx latus* by M'Coy (1849 : 410) and Sedgwick & M'Coy (1851, pl. 1E, fig. 13), shows that six thoracic segments are present and not five as had previously been thought. The slight overlap of the pygidium onto the posterior of the thorax partially obscures the sixth segment, but the sixth axial ring and part of the right pleura are clearly visible (Pl. 2, fig. 6). The specimen is identical to the small specimens of *C. nuda* found at the eastern end of the stream exposures east of Tre coed, north of Builth, and *A. latus* M'Coy is accordingly included here in the synonymy of *C. nuda*.

Although recorded from the Shelve region in the past, Whittard (1955 : 20) has given reasons for supposing these to be due to mis-labelling of specimens and thus the species appears to be restricted to the Builth region.

Slight swellings on the genal ridge described by Sedgwick & M'Coy (1851 : 148) and thought by them to be rudimentary eyes have not been observed. However the preliminary studies of the Scandinavian species reveals the presence of a genal caecal system based on a main caeca correspondingly situated to the genal ridge of *C. nuda*, and any swellings along the ridge are presumed to be related to this caecal system rather than to visual organs.

The species varies considerably in size, being significantly larger (size represented by pygidial length) at the exposures above the right bank of the stream 200 yards east of Pen-cerig Lodge, and significantly smaller at the eastern end of the stream section 160 yards south-east of Tre coed than at the type locality (holaspid specimens only taken into consideration).

Cnemidopyge nuda (Murchison) ***granulata*** Whittard

(Pl. 4, figs. 1–6; Pl. 5, figs. 1, 5)

1940 *Ampyx nudus* (Murchison); Elles : *pars*. 408, 412.
1955 *Cnemidopyge granulata* Whittard : 22, pl. 2, figs. 9–12.
1966 *Cnemidopyge granulata* Whittard; Whittard : 268–269, 299, pl. 46, fig. 7.

Diagnosis. *Cnemidopyge nuda* generally with eight ribs on pleural fields. External surface ornamented with small granules.

Type material. Holotype. GSM. 92950 (Pl. 4, fig. 1; Pl. 5, fig. 5). Internal and external moulds of cranidium.

Paratype. GSM. 92951 (Pl. 4, fig. 3). Internal and external moulds of incomplete thorax and pygidium.

Dimensions. Owing to the incomplete and distorted nature of the type specimens very few measurements can be made. However, estimates of various measurements have been made as follows:

	A	B_1	I	K	K_1
Holotype	11·0	8·0	24·0	8·5	4·0

	Q	Q_1	R_1	R_2	R_3	R_4	W	Z
Paratype	11·1	2·7	33·5	7·5	6·0	33·0	32·0	12·5

All measurements in mm. For explanation of symbols see Text-fig. 4.

Type locality and horizon. Both specimens are from near the base of the Rorrington Beds of the Holywell Burn, the holotype from The Mount, near Rorrington, Shropshire, and are of Upper Llandeilo age (see Williams 1969a).

Other figured material. It. 2702 (Pl. 4, fig. 4); It. 2703 (Pl. 4, fig. 6); It. 2704 (Pl. 4, fig. 2); It. 2705 (Pl. 4, fig. 5; Pl. 5, fig. 1).

Distribution. The subspecies is known from both the Shelve and Builth regions. At Shelve it is exceedingly rare, being known from only three specimens ranging in age from Upper Llandeilo to lowest Caradoc. Although by no means common, the subspecies is slightly more abundant at Builth being known from about twenty specimens from beds of probable Upper Llandeilo age.

Description. On account of the close affinity to *C. nuda s.s.* only a comparative description is given together with some revision of Whittard's original definition.

Whittard's description was based on very limited material, and it is now known that several features described by him are liable to some variation. The cephalon is extremely similar to that of *C. nuda*, the protuberant glabella described by Whittard is considered to be the result of slight buckling of the steep outer portions of the genal regions. Further, the cephalic width may vary from just under two and a half times to about two and three-quarter times the length, while the axial furrows may be as deep, or deeper than the posterior border furrow. Unlike *C. nuda* no trace of any genal ridge has been detected. A granular surface ornament is developed and as in *C. nuda* this is most coarsely developed on the glabella; the granules are, however, somewhat larger than in *C. nuda*, ranging from 0·06 mm. to 0·08 mm. in diameter (Pl. 5, fig. 1). This coarser granulation typifies the thorax and pygidium (Pl. 4, fig. 5).

The pygidium shows some interesting minor differences from *C. nuda*, for although the numbers of ribs on the pleural fields overlap, the mean is slightly, though significantly higher in *C. nuda granulata* (see Table 13). Further, although relatively few specimens are available, irregular rib development is so far unknown in *C. nuda granulata*.

ONTOGENY. Meraspis ?Degree 3. One poorly preserved specimen (Pl. 4, fig. 6) about 1·6 mm. long and 1·9 mm. wide appears to have only three thoracic segments. The associated left genal region is smooth and without a genal ridge. The thoracic segments appear to conform to the general raphiophorid pattern. The triangular pygidium is rather shorter and more obtusely rounded posteriorly than in adult specimens. The pleural fields are furrowed, and although the total number of ribs is not discernible it is certainly less than in the holaspid form.

BIOMETRICAL DATA. Although more material is known from Builth than from the type locality, data are insufficient for formal analysis. It is worth noting that the Builth specimens are smaller than the type specimens, being more comparable in size with the third specimen from Shelve, GSM. 102174 (Whittard 1966; pl. 46, fig. 7). The few data for the ribs of the pleural fields of the Builth material are given in Table 12.

TABLE 12

Complete specimens

Number of ribs . . .	7	8	9	Asymmetrical
Number of specimens . .	1	3	1	1

Frequency distribution of the number of ribs on the pleural fields of complete specimens of *C. nuda* (Murchison) *granulata* Whittard together with the incidence of pygidia showing asymmetrical development of ribs.

No specimen has irregular development of ribs. Considering data for the right field only, except where data are only available for the left field, the distribution is as in Table 13.

A 2 × 2 probability test shows that there is no significant correlation between the number of ribs developed on the pleural fields and the length of the pygidium.

TABLE 13

Number of ribs	7	8	9
Number of specimens . . .	2	4	1

mean = 7·86; var. = 0·476; n = 7.

Frequency distribution of the number of ribs on the pleural fields of *C. nuda* (Murchison) *granulata* Whittard together with the mean and variance.

Comparison of the corresponding data for *C. nuda* and *C. bisecta* shows that the mean number of ribs for *C. nuda granulata* falls between those of the other species. Application of the " t " test however shows the difference in the means of *C. nuda* and *C. nuda granulata* to be significant at the 5% level ($0{\cdot}05 > P > 0{\cdot}01$), but that there is no significant difference between the values for *C. nuda granulata* and *C. bisecta.*

DISCUSSION. When Whittard first described this species (1955 : 22) it was not known that the other species of *Cnemidopyge* also possessed a granular surface ornament. The present study, while indicating that *C. nuda granulata* is morphologically distinct from *C. nuda s.s.* in that the surface ornament is more coarsely developed, suggests that the degree of morphological similarity is too great to warrant the continued specific separation of these two forms.

The other two species, *C. parva* sp. nov. (see below) and *C. bisecta* are readily distinguished, the former by its smaller number of pygidial ribs and fine surface ornament and the latter by its prominent median glabellar ridge.

C. nuda granulata continues the trend seen in *C. parva* and *C. nuda* for the number of pygidial ribs to increase with time. It also is the oldest British *Cnemidopyge* to exhibit the coarser ornament which becomes well developed in *C. bisecta.*

The subspecies, which occurs at approximately the same horizon both at Builth and Shelve, is short lived, apparently giving rise to *C. bisecta* with the appearance of the median glabellar ridge.

Cnemidopyge parva sp. nov.

(Pl. 4, fig. 7; Pl. 5, figs. 2–4, 6–8; Pl. 6, fig. 1; Pl. 7, fig. 4)

1940 *Ampyx nudus* (Murchison); Elles : *pars.* 406–407, 410, 412.

DIAGNOSIS. *Cnemidopyge* generally with only five or six ribs developed on pleural fields. Glabella with no median ridge.

TYPE MATERIAL. Holotype. It. 2694 (Pl. 6, fig. 1). Internal mould of nearly complete specimen.

Paratypes. It. 2695 (Pl. 5, figs. 4, 8). External mould of damaged cephalon. It. 2696 (Pl. 7, fig. 4). Internal and external moulds of damaged, nearly complete specimen. It. 2697 (Pl. 4, fig. 7). Internal mould of cephalon with frontal glabellar spine. It. 2698 (Pl. 5, fig. 7). Internal mould of pygidium.

DIMENSIONS.

	A	A_1	B	K	Q	Q_1	R_1	R_2	R_3	R_4
Holotype	—	—	—	c. 5·0	5·3	1·2	13·0	3·6	2·7	13·0
It. 2697	5·3	4·4	4·8	3·5	—	—	—	—	—	—

						No. of axial rings	No. of ribs		
	W	X	X_1	Z	Z_1		Left	Right	T.L.
Holotype	11·8	2·4	1·3	5·2	3·0	14+	5i	6	c. 16·5
It. 2698	10·6	2·2	0·8	5·0	2·8	12+	5	5	—

All measurements in mm. For explanation of symbols see Text-fig. 4. "i" indicates an additional incipient rib.

TYPE LOCALITY AND HORIZON. Shales of Llandeilo age in the left bank of the stream section east of Bach-y-graig, 40 yards east of the point where the footpath enters the wood at the western end of the section.

OTHER FIGURED MATERIAL. It. 2699 (Pl. 5, fig. 2); It. 2700 (Pl. 5, fig. 3); It. 2701 (Pl. 5, fig. 6).

DISTRIBUTION. Apart from the type locality the species is also known from the stream section west of Wellfield Lodge immediately below the point where the stream is piped under the road; age similar to that of the type locality.

DESCRIPTION. A full description of this species is superfluous as it differs from *C. nuda* (Murchison) described above mainly in the pygidium, which has only five or six ribs on the pleural fields with 14 or 15 axial rings (Pl. 6, fig. 1). A possible difference in the thorax is that the axis of the new species may be relatively wider anteriorly than in the other British species (cf. Tables 9, 14, 19).

A solitary librigena (Pl. 5, fig. 2) is very like that deduced for *C. nuda* being small, fused posteriorly into the librigenal spine and clearly restricted to a small area on the lateral portions of the genal regions.

ONTOGENY. Degree unknown. A disarticulated specimen of a compressed cephalon and a small transitory pygidium is known (Pl. 5, fig. 6). The transitory pygidium is smaller than that of a possible meraspid degree 2 specimen, but is essentially similar to the adult form. The posterior is however more obtusely rounded, and fewer axial rings are developed.

?Degree 2. A single poorly preserved specimen (Pl. 5, fig. 3) has apparently only two thoracic segments. It appears very similar in basic morphology to the adult form, but preservation is insufficient to allow detailed comparisons. Four and five pygidial ribs are developed on the left and right pleural fields respectively.

BIOMETRICAL DATA. Relatively few specimens of this new species are known and thus few data are available; such as are, are included in Tables 14–17.

As regards the rib counts it is seen that of the specimens upon which complete counts were possible, one-quarter are asymmetrical, with equal numbers of the

TABLE 14

Q	Q_1	R_1	R_2	R_3	R_4
5·3	1·2	13·0	3·6	2·7	13·2
—	1·3	11·3	*c.* 3·0	2·4	11·5
—	0·8	9·5	2·5	—	9·7

Thoracic measurements on *C. parva* sp. nov. All measurements in mm. For explanation of symbols see Text-fig. 4.

TABLE 15

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
W : Z	9·22	7·7200	3·87	2·3171	0·990	0·992	1·29	0·00438	—	—	8
W : X	9·22	7·7200	1·89	0·3214	0·988	0·990	0·98	0·00346	0·20	0·00166	8
Z : X	3·87	2·3171	1·89	0·3214	0·985	0·988	0·78	0·00239	—	—	8
Z : Z_1	4·25	2·2767	2·55	0·6967	0·992	0·993	0·93	0·00599	0·55	0·00214	4

Bivariate statistics for the pygidium of *C. parva* sp. nov. All measurements in mm. For explanation of symbols see Text-fig. 4.

TABLE 16

		Right pleural field	
Number of ribs	4	5	6
Number of specimens	—	5	4
		Left pleural field	
Number of ribs	4	5	6
Number of specimens	1	5	3
		Complete specimens	
Number of ribs	5	6	Asymmetrical
Number of specimens	3	3	2

Full data on rib counts on the pleural fields of *C. parva* sp. nov.

TABLE 17

Number of ribs	4	5	6
Number of specimens	—	6	4

mean = 5·40; var. = 0·267; n = 10

Frequency distribution of the number of ribs on the pleural fields of *C. parva* sp. nov., together with the mean and variance.

remainder having five or six ribs. Data obtained by considering counts on the right pleural field, except where data are only available for the left, being given in Table 17.

The few cephalic measurements obtained show no obvious difference from those of *C. nuda*. The various thoracic measurements for *C. parva*, *C. nuda*, and *C. bisecta* show that there are virtually no differences between these species with regard to the overall outline, relative length (*exsag.*) of the anterior segment or the tapering of the axis. Despite the general lack of data, it appears that the anterior of the axis may be relatively wider in *C. parva* than in the other species. Analysis of data for the pygidium shows that although no difference is recognizable in shape *C. parva* is readily distinguished by having significantly fewer ribs.

DISCUSSION. This new species represents the earliest *Cnemidopyge* known from the British Isles. It may be distinguished from *C. bisecta* (Elles) by its lack of median glabellar ridge, and from both *C. nuda* and *C. nuda granulata* by the smaller number of ribs developed on its pleural fields. It is also noteworthy that of a total of eighteen counts, no examples of irregular ribbing have been observed in *C. parva*, although one-quarter of individuals have one more rib on one pleural field than on the other. In *C. nuda* 5% of pleural fields show irregular development of ribs, and in *C. bisecta* the figure is as high as 28%.

Cnemidopyge bisecta (Elles)

(Pl. 6, figs. 2–9; Pl. 7, figs. 1–3, 5; Pl. 8, fig. 3)

1940 *Ampyx bisectus* Elles : *pars*. 416–419, 421–422, 432, pl. 29, figs. 1–5.
1955 *Cnemidopyge bisecta* (Elles); Whittard : 15, 21.

DIAGNOSIS. *Cnemidopyge* having median glabellar ridge, merging anteriorly with frontal glabellar spine. Pygidium with generally eight or nine pleural ribs commonly showing asymmetrical or irregular development of ribs. Dorsal surface of exoskeleton ornamented with small granules.

TYPE MATERIAL. Holotype. SM. A.10,073 (Pl. 8, fig. 3). Internal mould of nearly complete specimen.

Paratypes. SM. A.10,074 (Pl. 6, fig. 4). Internal mould of large cephalon. SM. A.10,075. Internal mould of damaged specimen lacking pygidium. SM. A.10,076. Internal mould of damaged specimen lacking pygidium. SM. A.10,077. Internal mould of cephalon.

DIMENSIONS.

	A	A_1	B	B_1	B_2	I	K	K_1
Holotype	8·1	—	7·6	5·6	4·4	17·9	6·5	3·9
SM. A.10,074	14·4	—	12·7	10·1	8·2	27·3	9·7	5·7
SM. A.10,075	10·0	*c.* 7·0	9·0	6·6	5·1	—	7·5	—
SM. A.10,076	8·4	—	7·9	6·0	4·9	—	5·8	3·8
SM. A.10,077	7·8	—	6·8	5·4	4·4	16·6	6·5	3·9

	Q	Q_1	R_1	R_2	R_3	R_4
Holotype	7·1	1·6	18·5	4·4	3·6	19·5
SM. A.10,075	9·1	2·0	—	—	—	—
SM. A.10,076	6·9	1·6	—	4·3	3·3	—

	W	X	X_1	Z	Z_1	No. of axial rings	No. of ribs Left	No. of ribs Right
Holotype	18·0	3·3	1·5	6·9	4·9	9+	8*	7

All measurements in mm. For explanation of symbols see Text-fig. 4.

* Pleural furrow separating 7th and 8th ribs developed only at lateral and axial extremities.

TYPE LOCALITY AND HORIZON. Dark shales beneath the dolerite in the middle quarry, Llanfawr, Llandrindod, of Basal Caradoc age (*gracilis* Zone).

OTHER FIGURED MATERIAL. It. 2707 (Pl. 6, fig. 9); It. 2708 (Pl. 6, fig. 5); It. 2710 (Pl. 6, fig. 2); It. 2711 (Pl. 6, fig. 6); It. 2712 (Pl. 7, fig. 1); It. 2713 (Pl. 6, fig. 7); It. 2714 (Pl. 7, fig. 3); It. 2715 (Pl. 7, fig. 5); It. 2716 (Pl. 6, fig. 8); It. 2717 (Pl. 7, fig. 2); I. 4289 (Pl. 6, fig. 3).

DISTRIBUTION. The species is apparently confined to the Builth-Llandrindod region. Despite records by Elles (1940 : 408, 412, 432) of its occurrence in the highest Llandeilo, the present study indicates that it is restricted to the Basal Caradoc.

DESCRIPTION. Although readily distinguished, this species is similar to *C. nuda* except for a few features, and requires only a comparative description.

The few known complete specimens are about one and a quarter times as long as wide and are thus comparable to *C. nuda*.

The most striking difference in the cephalon is the presence of the median glabellar ridge commencing immediately in front of the " *1*p furrows " and fusing frontally with the base of the frontal glabellar spine. The " *1*p furrows " are shallow medianly (Pl. 6, fig. 4) resulting in the " basal glabellar lobe " being less clearly defined anteriorly than in *C. nuda*. The posterior border furrow deepens distally to form a shallow depression at the base of the librigenal spine. The librigenal spines are long, slender and gently curved initially, becoming straight and posteriorly directed, extending well beyond the pygidium (Pl. 6, fig. 3). The course of the facial suture is a little obscure but it may not encroach very high on to the dorsal surface laterally. The cephalic doublure and hypostoma are not known.

The granular surface ornament is distributed in a basically similar manner to that in *C. nuda*, but an extra band of tiny pustules, about 0·04 mm. in diameter, is developed just anterior of the posterior border furrow (Pl. 7, fig. 5). The granules on the glabella are about 0·09–0·10 mm. in diameter, while those on the genae are only about 0·05–0·07 mm.

Apart from the surface ornament the thorax is similar to that of *C. nuda*. The granular ornament is coarser and also is well developed along the anterior edge of the anterior pleural band and on the posterior pleural band, but is absent in the pleural furrow (Pl. 6, fig. 9).

The pygidium is similar to that of *C. nuda* but differs in that the mean number of ribs is significantly higher in *C. bisecta*. There is also a much higher incidence of irregularities in the rib development than in *C. nuda* (28 %, 5 %; see also pages 68, 77). In common with the remainder of the dorsal exoskeleton the ornamentation is more coarsely developed in *C. bisecta*.

BIOMETRICAL DATA. More data are available for *C. bisecta* than for other species of *Cnemidopyge*. Although the species is abundant, complete individuals are very rare, two only providing length : width ratios of between 1·2 and 1·3.

The relatively complete data have enabled a number of bivariate analyses to be carried out on the cephalon, thorax and pygidium. The statistics obtained from these are given in Tables 18–22.

TABLE 18

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var α	a	var. a	n
1 : B	17·60	28·5200	7·73	7·2140	0·994	0·994	1·14	0·0039	0·50	0·00076	6
B : K	8·10	2·4855	6·44	1·5427	0·915	0·914	0·99	0·0161	0·79	0·01010	12
K : K_1	6·40	1·7133	3·53	0·8533	0·949	0·951	1·27	0·0193	0·71	0·00619	10
B : B_1	8·10	2·2385	6·29	1·4831	0·984	0·984	1·05	0·0029	0·81	0·00175	14
B : B_2	8·19	2·2958	5·08	1·0267	0·972	0·972	1·08	0·0058	0·67	0·00224	13

Bivariate statistics for the cephalon of *C. bisecta* (Elles). All measurements in mm. For explanation of symbols see Text-fig. 4.

TABLE 19

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
R_1 : Q	18·70	2·0150	7·62	0·5675	0·877	0·875	1·30	0·1316	0·53	0·02167	5
R_1 : R_2	17·45	14·0270	4·05	1·2350	0·906	0·909	1·27	0·0699	0·30	0·00394	6
R_2 : R_3	4·40	0·4160	3·65	0·3310	0·963	0·963	1·07	0·0210	0·89	0·01449	6
Q : Q_1	7·73	0·8150	1·66	0·0667	0·887	0·887	1·33	0·0733	0·29	0·00349	7

Bivariate statistics for the thorax of *C. bisecta* (Elles). All measurements in mm. For explanation of symbols see Text-fig. 4.

TABLE 20

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
W : Z	17·72	11·2433	7·74	3·0875	0·941	0·942	1·19	0·0146	0·52	0·00286	13
W : X	17·72	11·2433	3·15	0·4375	0·959	0·962	1·10	0·0083	0·20	0·00028	13
Z : X	8·11	3·6041	3·23	0·4268	0·912	0·916	0·87	0·0058	0·34	0·00095	23
X : X_1	3·15	0·4539	1·32	0·0472	0·883	0·883	0·77	0·0077	—	—	19

Bivariate statistics for the pygidium of *C. bisecta* (Elles). All measurements in mm. For explanation of symbols see Text-fig. 4.

TABLE 21

	Complete specimens					
Number of ribs . . .	7	8	9	10	Asymmetrical	Irregular
Number of specimens . .	—	4	3	—	3	7
	Left pleural field					
Number of ribs . . .	7	8	9	10	Irregular	
Number of specimens . .	—	9	3	—	7	
	Right pleural field					
Number of ribs . . .	7	8	9	10	Irregular	
Number of specimens . .	2	9	5	1	5	

Full data of rib counts on the pleural fields of *C. bisecta* (Elles).

TABLE 22

Number of ribs	7	8	9	10
Number of specimens	6	13	7	1

mean = 8·11; var. = 0·6410; n = 27

Frequency distribution of the number of ribs on the pleural fields of *C. bisecta* (Elles), together with the mean and variance.

Of the total number of pleural fields for which data are available, 28% show irregularities in rib development. Of the complete specimens known 41% show some rib irregularities and a further 18%, although showing no irregular ribs, possess more ribs on one field than on the other. Table 22 shows the data for right fields only, except in cases where data are available for the left field only. A 2 × 2 probability test again reveals that there is no significant correlation between the number of ribs and the pygidial length.

Tests show that, where bivariate analyses of relative growth and shape are available, the three species of *Cnemidopyge*, *C. bisecta*, *C. nuda* and *C. parva* are fundamentally alike. Indeed *C. bisecta* differs significantly from the other two only in the number of ribs developed on the pleural fields, in the occurrence of irregularities in rib development and such non-parametric features as surface ornament.

DISCUSSION. In her original description, Elles (1940 : 422) implied that a triangular pygidium was only characteristic of *C. bisecta*. In fact the pygidial outline of *C. nuda* is indistinguishable from that of *C. bisecta*, and it is possible that reliance on this alleged difference led Elles to misidentify *Cnemidopyge* found in the uppermost Llandeilo as belonging to *C. bisecta*.

C. bisecta is easily distinguished from *C. parva* sp. nov. by its greater number of pygidial ribs and the possession of a median glabellar ridge. *C. nuda* (Murchison) may be distinguished by the lack of median glabellar ridge.

C. bisecta shows the culmination of the two trends, i.e. pygidial rib numbers and granulation. The presence of the median glabellar ridge in *C. bisecta* is of some interest as it appears to be present, though not so prominent, in the Scandinavian representatives of the genus.

Although some of the irregularities in the rib development on the pygidium may be pathological (Pl. 7, fig. 2), the incidence of irregularities is unusually high and may represent an inherited characteristic.

Raphiophorid sp. indet.

(Pl. 8, figs. 1, 2)

FIGURED SPECIMEN. It. 2718. External mould of damaged cranidium and anterior part of thorax.

LOCALITY AND HORIZON. From Lower Llanvirn shaly mudstones exposed in the Camnant Brook, probably from above Court.

DESCRIPTION. The cephalon is about two and a half times as wide as long and is similar to that of *C. nuda*. The glabella is clavate, with no median ridge and possesses a frontal spine which is circular in cross section. The glabellar segmentation appears to be similar to that of other raphiophorids. The genal regions are gently tumid except for their outer portions which are more steeply declined. No trace of any surface ornament or genal ridges is present.

The anterior three thoracic segments are present, though poorly preserved. The anterior one is slightly macropleural and they all appear to be typically raphiophorid.

The pygidium is not known.

Discussion. Although poorly preserved, this specimen is of interest as it is the only confirmed occurrence of a raphiophorid from the Llanvirn of the Builth region. Elles records *Ampyx salteri* Hicks 1875 as an extreme rarity from the "*Trinucleus*" band in the upper part of the Lower Llanvirn (Elles 1940 : 395). This specimen has not been traced and its identification is open to question.

The raphiophorid species typical of the equivalent horizon in the Shelve region is *Ampyx linleyensis* Whittard 1955, and although no proper comparison can be made, the cephalon of the Builth specimen does appear less triangular than that of *A. linleyensis*.

Family **CHEIRURIDAE** Salter 1864

Subfamily **CYRTOMETOPINAE** Öpik 1937

Genus ***PLACOPARINA*** Whittard 1940

Diagnosis. Cyrtometopinid having pedunculate eyes situated close to anterior of cephalon, associated with transverse structures very like eye ridges; long (*exsag.*) narrow (*tr.*) librigenae, almost gonatoparian facial sutures; short transversely directed fixigenal spines. Glabella with three pairs subequal lateral furrows. Thorax of twelve segments. Pygidium with three pairs of pleural spines.

Type species. *Placoparina sedgwickii sedgwickii* (M'Coy).

Distribution. The genus is not known outside England and Wales and is apparently confined to *P. sedgwickii sedgwickii* (M'Coy) from the Llandeilo of the Builth inlier and *P. sedgwickii* (M'Coy) *shelvensis* subsp. nov. from the highest Lower Llanvirn of the Shelve region. In addition it has been recorded from beds of uncertain age from Abereiddy Bay and it may also be present in the Skiddaw Slates (Whittard 1958 : 115).

Discussion. Whittard originally erected this genus for *Cryphaeus sedgwickii* M'Coy which he separated from *Eccoptochile* Hawle & Corda 1847 on account of its blindness. Prantl & Přibyl (1947 : 25) and Přibyl (1953 : 39) did not accept that the blindness of *P. sedgwickii* warranted its generic separation from *Eccoptochile* and accordingly they rejected *Placoparina*. Whittard (1958 : 113–115), however, described eyes from new material of *P. sedgwickii* and thus the status of *Placoparina* clearly demanded reconsideration. Whittard was able to show that although eyes were present, other newly discovered features, notably the long (*exsag.*) narrow (*tr.*) librigenae were clearly unlike other known cheirurid genera and warranted the retention of *Placoparina* as a distinct genus. Having regard in particular to the form of the librigenae, situation of the pedunculate eyes and the near gonatoparian condition of the facial sutures it is here proposed to follow Whittard and accord full generic status to *Placoparina*.

Placoparina sedgwickii sedgwickii (M'Coy)

(Pl. 8, figs. 4–6; Pl. 9, fig. 3)

1849 *Cryphaeus Sedgwickii* M'Coy : 406–407.
1851 *Eccoptochile Sedgwickii* (M'Coy); Sedgwick & M'Coy : 155–156, pl. 1F, fig. 14.
1852 *Cheirurus* (*Cryphaeus*) *Sedgwicki* (M'Coy); Barrande : 775.
1854 *Cryphaeus* (*Eccoptochile*) Sedgwickii M'Coy; M'Coy : 145.
1864 *Cheirurus* (*Eccoptochile*) *Sedgwicki* (M'Coy); Salter : 73, pl. 5, fig. 17.
1940 *Placoparina sedgwicki* (M'Coy); Whittard : *pars.* 168, pl. 6, figs. 5, 6; *non* figs. 7–9.
1945 *Cheirurus sedgwickii* (M'Coy); Reed : 59.
1958 *Placoparina sedgwicki* (M'Coy); Whittard : *pars.* 113–115. Includes full synonymy.

DIAGNOSIS. *Placoparina* with well developed terminal axial piece and spatulate terminations to pygidial pleurae.

HOLOTYPE. SM. A.15616a, b (Pl. 8, figs. 4, 5; Pl. 9, fig. 3). Internal and external moulds of damaged entire exoskeleton.

DIMENSIONS. Owing to the damaged nature of this specimen only a limited number of measurements are possible, the details of which are given below.

T.L.	Q	Q_1	R_1	R_2	R_3	R_4	W	X	Y	Z
c. 75·0	40·0	3·6	*c.* 58·0	12·5	8·4	*c.* 49·0	33·0	8·4	10·2	14·3

All measurements in mm. For explanation of symbols see Text-fig. 4.

TYPE LOCALITY AND HORIZON. The exact locality of the holotype is not known. It was given imprecisely by M'Coy as " Two miles north of Builth ". Elles believed that this specimen was from the stream section south-east of Tre coed (Elles 1940 : 410), but although this is possible on lithological grounds, prolonged searching has failed to reveal any further specimens. The species is known from only two other localities in the Builth district (on the right bank above the stream 200 yards east of Pen-cerig Lodge and about 80 yards west of the junction of the Cefnllys road and the lane to Gorse farm, this latter locality being no longer accessible due to road improvements) and neither of the lithologies from these localities matches that of the type specimen. Although the exact locality must remain uncertain it is thought most likely to lie within the Llandeilian outcrop.

OTHER FIGURED SPECIMEN. BU. 367 (Pl. 8, fig. 6).

DISTRIBUTION. Only three specimens of this subspecies are known all from the Llandeilo of the Builth region. *P. sedgwicki s.l.* is known from beds of uncertain age from Abereiddy Bay and may also be present in the Skiddaw Slates (see Whittard 1958 : 115).

DESCRIPTION. Complete individuals are subrectangular in outline being about one and a half times as long as wide.

The rounded cephalon is about three and a half times as wide as long. The glabella is convex, defined by deep, slightly outwardly convex axial furrows, and its maximum width is only slightly less than its length. The frontal lobe of the glabella is anterior of the maximum width and by analogy to *P. sedgwickii shelvensis* subsp. nov. (see page 80) is believed to overhang the anterior border furrow. The three pairs of lateral glabellar furrows are curved backwards, *1*p extending towards the occipital furrow; *2*p extend about one-third of the distance across the glabella; while *3*p, although parallel to *2*p, extend for a slightly shorter distance. The occipital ring is well developed and possesses no median node. The fixigenae are large, steeply declined marginally, and are assumed to extend nearly to the lateral cephalic margins, although details of the librigenae are unknown. The posterior border furrow is deep and delimits the prominent convex posterior border. Both the posterior border and the border furrow expand distally. Eyes are not certainly known but are probably situated in a position similar to those of *P. sedgwickii shelvensis*. The surface of the fixigenae is coarsely pitted and finely granular between the larger pits. The pits are lacking on the glabella, which does however retain the fine granular ornament.

The nearly parallel-sided thorax consists of 12 segments. The axis is prominent, occupying about one-fifth of the total thoracic width. The axial rings are simple with weakly developed lateral nodes and well developed articulatory furrows and half rings. The pleural regions are relatively flat, being only slightly arched between the fulcra and the axial furrows. Medianly each pleura is divided into an anterior and posterior band by a line of pits which in larger individuals may be sunken slightly below the level of the remainder of the pleura (Pl. 8, fig. 5). The pits only extend as far as the fulcrum, beyond which the pleurae trend posterolaterally, the deflection becoming progressively greater to the posterior, and terminate in a stout spine. The external surface of the thorax is covered with a fine granular ornament but the sunken granules, described by Whittard (1958 : 114) as becoming progressively more abundant to the posterior in the Shropshire specimens are not developed.

The pygidial axis consists of three prominent axial rings and a well developed triangular terminal piece which reaches the margin medianly. The anterior pleurae are similar to those of the thorax and possess a median transverse line of pits. Distally, however, they form spatulate posteriorly directed pleural terminations. The second pair are smaller, have fewer pits developed medianly, but terminate similarly. The third pair are much reduced and have only two pits developed medianly, but again possess well developed spatulate terminations. The external surface is ornamented with fine granules but as in the thorax the sunken granules described by Whittard are absent.

DISCUSSION. See discussion of *P. sedgwickii* (M'Coy) *shelvensis* subsp. nov.

Placoparina sedgwickii (M'Coy) ***shelvensis*** subsp. nov.

1940 *Placoparina sedgwickii* (M'Coy); Whittard : *pars.* 166–169, pl. 6, figs. 7–9.
1958 *Placoparina sedgwicki* (M'Coy); Whittard : *pars.* 113–115, pl. 15, figs. 6–13.

DIAGNOSIS. *P. sedgwickii* having sunken granules on external surface of thorax and pygidium, and less spatulate terminations to third pygidial pleura.

TYPE MATERIAL. Holotype. GSM. 92926a, b (figured Whittard 1958, pl. 15, figs. 6–8).

Paratypes. Wattison Collection W 3; GSM. 92927; GSM. 92928; GSM. 92929 (figured Whittard 1958, pl. 15, figs. 9, 11, 10, 12, 13 respectively).

TYPE LOCALITIES AND HORIZONS. All the type material is from the shales interbedded in the Stapelely Volcanic Group, Lower Llanvirn of Nind Quarry, Shropshire, with the exception of GSM 92929 which is from the topmost Hope Shales, Lower Llanvirn, in the path west of Brithdir, near Old Church Stoke, Shropshire.

DISCUSSION. In his redescription of *P. sedgwickii* from Shropshire, Whittard (1958 : 113–115) considered that the slight differences between the holotype from Builth and the Shropshire material to be unimportant systematically. However, the absence of sunken granules from the thoracic and pygidial surfaces and the broader, more spatulate terminations of the third pygidial pleurae, are sufficiently consistent to warrant the subspecific separation of the Builth and Shelve forms.

Family **CALYMENIDAE** Burmeister 1843

Genus ***FLEXICALYMENE*** Shirley 1936

DIAGNOSIS. Glabella outline generally subparabolic; anterior border moderately long (*sag.*) and usually inclined forwards; eyes generally approximately opposite 2p lobes. Thorax generally with 13 segments.

TYPE SPECIES. *Flexicalymene caractaci* (Salter).

DISTRIBUTION. The genus ranges from the Lower Llanvirn to the Ashgill (Zone 4, Ingham 1966) and is widely distributed throughout the British Isles, Bohemia and eastern North America. Its Llanvirn occurrences are limited to the Anglo-Welsh region.

DISCUSSION. Prior to this study the genus was not known from rocks older than the Upper Llanvirn. However, a new calymenid recovered from the Llanvirn of the Builth region is best assigned to *Flexicalymene*. The inclusion of this new species within *Flexicalymene* enlarges the concept of the genus to embrace stocks with a glabella which is rather more square anteriorly than is typical.

Flexicalymene aurora sp. nov.

(Pl. 8, fig. 7; Pl. 9, figs. 1, 2, 4, 7, 8)

1940 *Calymene* (*Flexicalymene*) *aldonensis* Reed; Elles : 396, 398, 432.

DIAGNOSIS. *Flexicalymene* with trapezoidal glabella with four pairs of lateral glabellar lobes with rounded outlines; mid-point of eyes opposite second pair. Pygidial axis broad with six axial rings and terminal piece; pleural fields with four ribs.

TYPE MATERIAL. Holotype. It. 2974 (Pl. 9, fig. 4). Internal mould of nearly complete cephalon and anterior five thoracic segments.

Paratypes. It. 2975 (Pl. 8, fig. 7). Internal mould of damaged cranidium. It. 2976 (Pl. 9, figs. 1, 2). Internal and external moulds of left librigena. It. 2977 (Pl. 9, fig. 7). Internal and external moulds of pygidium. It. 2978 (Pl. 9, fig. 8). Internal and external moulds of pygidium.

DIMENSIONS.

	A	B	B_1	B_2	B_3	B_4	C
Holotype . .	8·5	6·5	5·2	3·5	2·2	1·2	3·3
It. 2975 . .	—	5·1	4·2	2·9	1·8	0·9	2·8

	I	J_1	K	K_1
Holotype . .	17·5	10·7	3·3	5·9
It. 2975 . .	—	—	—	4·7

	W	X	X_1	Y	Z	No. of axial rings	No. of ribs Left	Right
It. 2977 . .	11·5	4·6	2·5	6·4	6·9	6	4	4
It. 2978 . .	9·2	3·0	—	—	4·8	5+	4	4

All measurements in mm. For explanation of symbols see Text-fig. 4.

TYPE LOCALITIES AND HORIZON. The holotype and paratypes, with the exception of It. 2978, are from the exposures on the north side of the track leading from Bwlch-llŵyn to Hendy Bank, 100 yards east of Bwlch-llyn. Paratype It. 2978 is from the cliff section in the left bank of the Howey Brook half a mile east-south-east of Carregwiber. Both localities lie in the *Didymograptus speciosus* Subzone of the Lower Llanvirn.

DISTRIBUTION. This new species is known only from the two localities cited above.

DESCRIPTION. No entire specimens are known, but it is estimated that the total length would be about two and a half times the maximum width occurring along the posterior cephalic margin.

The semicircular cephalon is about twice as wide as long; the glabella occupies about one-quarter of the posterior width, tapering anteriorly to about one-half of its posterior width across the frontal lobe. The glabellar length is slightly greater than its anterior width. Four pairs of rounded, clearly defined lateral glabellar lobes are developed, 1p being the largest and of oval outline. 1p furrows are deep and bifurcate axially, the major branch turning posteriorly towards the occipital furrow which it fails to reach; the other branch is short and notches the posterior of the 2p lobes. These are nearly circular in outline, about half the size of the 1p pair, and are constricted at their base anteriorly by the 2p furrows and posteriorly by the anterior branch of the *1*p furrows. The *2*p furrows are deep and similar to *1*p, with the exception that no anterior branch is developed axially. The *3*p lobes are smaller, wider (*tr.*) than long (*exsag.*), and anteriorly defined by short, more or less transversely directed *3*p furrows. The *4*p lobes are very small, similar in outline to the *3*p, though shorter (*exsag.*) and defined anteriorly by little more than tiny notches forming the *4*p furrows. The axial furrows are deep and slightly constricted opposite the *3*p lobes by a small buttress formed by an extension of the weak eye ridges (Pl. 9, fig. 4). The occipital ring is typically calymenid with the occipital furrow deflected round the posterior of the *1*p lobes. No median occipital node appears to be developed. The preglabellar field is not known.

The genal regions are moderately convex and extend very slightly anterior to the glabella. The mid-point of the eyes is situated approximately in line (*tr.*) with the centre of the *2*p lobes and about half-way across the genae. The posterior border furrow is well developed, straight and in common with the border, becomes wider laterally. The librigenae are typically calymenid in form with well-developed convex border and border furrow. The rostral plate is axe-shaped and underlies virtually the whole of the preglabellar field (Pl. 9, fig. 4).

The total number of thoracic segments is unknown but at least five are present; their form is typically calymenid.

The pygidium is rather like a taut bow in outline, being slightly less than twice as wide as long. The axis is relatively wide, anteriorly about one-third of the pygidial width, tapering posteriorly to about one-half this width. Six axial rings and a terminal piece are present in paratype It. 2977 but possibly only five in It. 2978. The pleural fields possess four furrowed ribs with a relatively large terminal area. The rib furrows are most pronounced laterally. The external surface is ornamented with small tubercles, which appear to be larger and more closely spaced in the marginal regions.

DISCUSSION. This, the earliest known *Flexicalymene*, is similar to many of the later species, such as *F. cambrensis* (Salter 1865), *F. caractaci* (Salter 1865), *F. acantha* Bancroft 1949 and *F. cobboldi* Dean 1963. However it differs from all of these in the rather square anterior of the glabella. The new species is about the same age as *Platycalymene tasgarensis* Shirley 1936 from the Hope Shales of the Shelve region, although *F. aurora* is easily distinguished by the more rounded outlines of its lateral glabellar lobes, particularly the *2*p lobes, and by the development of small buttresses opposite the *3*p furrows. The glabella also appears to be relatively longer and the eyes more posteriorly placed in *F. aurora* but the significance of this is difficult to assess until a larger sample is known.

Genus ***PLATYCALYMENE*** Shirley 1936

DIAGNOSIS. Calymenid like *Flexicalymene* but depressed and with anterior border more roll-like; eyes opposite second or third lateral glabellar lobes. Lateral glabellar lobes rather rectangular, not rounded; anterior of glabellar rather square.

TYPE SPECIES. *Platycalymene duplicata* (Salter).

DISTRIBUTION. The genus is now known from the Lower Llanvirn, Llandeilo and Basal Caradoc of the Welsh Borderland and also from the Tramore Limestone in County Waterford. It has also been recorded from the *Chasmops* Limestone of Skåne in beds approximately equivalent to the *Dicranograptus clingani* Zone.

DISCUSSION. Since Shirley's sub-division of the calymenids there has been discussion as to the validity of some of his genera. However, with the exception of Richter (1940), most workers have accepted his basic divisions, although *Reacalymene* is generally taken as a subgenus of *Flexicalymene* (see Dean 1962 : 112). The only addition to the Ordovician genera has been the introduction of *Onnicalymene* Dean 1962 for those forms previously attributed to *Flexicalymene* in which the palpebral lobes are opposite the *1*p lobes.

Shirley (1936 : 395) defined *Platycalymene* as a depressed form with parabolic outline to the glabella with three pairs of lateral glabellar lobes, and a short pregabellar field with a roll-like anterior border. At present four species are generally referred to this genus, namely the types species *P. duplicata* (Salter 1865) from the Basal Caradoc of the Welsh Borderland, *P. tasgarensis* Shirley 1936 from the Lower Llanvirn of Shropshire, *P. eire* Lamont 1949 from the Tramore Limestone of County Waterford, and *P. dilatata* (Tullberg 1882) from the *Chasmops* Limestone of Skåne. Of these, neither *P. eire* nor *P. dilatata* are well known; both may be junior synonyms of *P. duplicata*, as the only differences appear to be slight variations in glabellar proportions. Cephalic profiles of both *P. duplicata* and *P. tasgarensis* show that the anterior border is not so pronounced as Shirley indicated (1936 : 391), but is more steeply inclined and more convex than is typically found in *Flexicalymene*. This difference alone seems insufficient to distinguish between the two genera. The position of the palpebral lobes is of little use in distinguishing *Platycalymene*; they may be opposite the *3*p lobes as in the type species or opposite the *2*p as in *P. tasgarensis*, a condition typical of most *Flexicalymene*. However, there is a further difference which was not stressed by Shirley, involving the outline of the lateral glabellar lobes. In *Flexicalymene* the glabella is typically subparabolic in outline with well-rounded lateral glabellar lobes. In *Platycalymene* the glabella is better described as trapezoidal and the lateral glabellar lobes are more rectangular in outline (compare *F. aurora*, Pl. 8, fig. 7 with *P. duplicata*, Pl. 10, fig. 5). This difference, together with that of the cephalic profiles, is considered sufficient to warrant the continued separation of *Platycalymene* from *Flexicalymene*, although a full revision of the Ordovician calymenids might not uphold this. It is interesting to note that, for the Anglo-Welsh region at least, *Platycalymene* is restricted to shaly facies and *Flexicalymene* is generally confined to the more calcarenitic facies, and it may subsequently be found that *Platycalymene* is simply a facies variant of *Flexicalymene*.

Platycalymene duplicata (Murchison)

(Pl. 9, figs. 5, 6; Pl. 10, figs. 1–8; Pl. 11, figs. 1–9; Pl. 12, figs. 1, 4, 5)

1839 *Asaphus duplicatus* Murchison : 661–662, pl. 25, fig. 8.
1852 *Calymene duplicata* (Murchison); Barrande : 574.
1927 *Calymene* (*Metacalymene*) *duplicata* (Murchison); Kegel : 619.

1936 *Platycalymene duplicata* (Murchison); Shirley : 390–395, 399, 400, 403.
1940 *Calymene* (*Metacalymene*) *duplicata* (Murchison); Richter : 1031.
1960 *Platycalymene duplicata* (Murchison); Whittard : 151, 154–157, pl. 21, figs. 13–15. Includes full synonymy.
1960 *Platycalymene duplicata* (Murchison) *parallela* Whittard : 157, pl. 21, fig. 16.
1966 *Platycalymene duplicata* (Murchison); Whittard : 300.
1966 *Platycalymene duplicata* (Murchison) *parallela* Whittard; Whittard : 300.

DIAGNOSIS. *Platycalymene* with three, occasionally four lateral glabellar lobes; mid-point of eyes opposite 3p furrows. Pygidium semi-oval generally with nine axial rings and terminal piece and eight ribs. Entire exoskeleton rather depressed.

HOLOTYPE. GSM. 6847 (Pl. 9, fig. 6). Internal mould of pygidium and associated external mould of thorax.

DIMENSIONS.

W	X	X_1	Y	Z	No. of axial rings	No. of ribs Left	No. of ribs Right
16·0	3·6	1·8	6·9	7·7	9	9 + i	9 + i

All measurements in mm. For explanation of symbols see Text-fig. 4. The suffix +i indicates the development of a further incipient rib.

TYPE LOCALITY AND HORIZON. The label affixed to the holotype records it as being from the "uppermost trilobite bed, Wilmington, near Marton Pool". Whittard (1960 : 156) however has pointed out that Wilmington is located on the Aldress Shales from which no calymenids are recorded. He concludes from the known occurrences of the species in the Shelve district and also on lithological grounds that the holotype may be either from the Rorrington Beds or the Spy Wood Grit.

OTHER FIGURED MATERIAL. It. 2982 (Pl. 11, fig. 9); It. 2983 (Pl. 10, fig. 8); It. 2984 (Pl. 11, fig. 5); It. 2985 (Pl. 11, fig. 7); It. 2986 (Pl. 12, fig. 5); It. 2988 (Pl. 10, fig. 4); It. 2989 (Pl. 10, fig. 7); It. 2990 (Pl. 11, fig. 6); It. 2991 (Pl. 11, fig. 8); It. 2994 (Pl. 12, fig. 1); It. 2995 (Pl. 11, fig. 4); It. 3000 (Pl. 10, fig. 3); It. 3001 (Pl. 11, fig. 2); It. 3002 (Pl. 10, fig. 2); It. 3003 (Pl. 10, fig. 1); It. 3006 (Pl. 11, fig. 3); It. 3007 (Pl. 11, fig. 1, Pl. 12, fig. 4); It. 3008 (Pl. 10, fig. 6); It. 3009 (Pl. 9, fig. 5); Wattison Coll. H. 13 (Pl. 10, fig. 5).

DISTRIBUTION. The species is recorded only from the Shelve and Builth regions. In the Shelve region Whittard (1960 : 156) records it from high in the *Nemagraptus gracilis* Zone to probably low in the *Diplograptus multidens* Zone. In the Builth region it occurs throughout beds of the *N. gracilis* Zone, the only Caradocian rocks exposed in the Builth area.

DESCRIPTION. The maximum width of entire exoskeleton is about two-thirds of the total length and is attained across the posterior of the cephalon. Posterior to this the exoskeleton tapers gently, being only about one-half of the total length across the anterior of the pygidium. The general transverse convexity of the exoskeleton is low, although the axis is moderately convex and the lateral portions, particularly of the thorax are deflected ventrally. Small tubercles of varying size, up to 0·15 mm. in diameter, are developed over the entire dorsal surface. The larger ones, though present over all parts, show concentrations along the anterior and lateral margins (Pl. 10, fig. 4; Pl. 11, fig. 5).

The cephalon is between two and a half and three times as wide as long, with rounded margins laterally which become straight anteriorly. The trapezoidal glabella, with posterior width about equal to length, occupies about one-quarter of the posterior cephalic width and tapers gently to the anterior. Some variation in the glabella proportions is present, but the existence of distinct " wide " and " narrow " forms cannot be demonstrated (see Text-fig. 5). The variation in the glabellar proportions may or may not have been accentuated by *post-mortem* deformation; it is believed that the glabellar outline of *P. duplicata parallela* Whittard is a result of such deformation and is thus included here in the synonymy. Although convex both sagittally and transversely, the sagittal convexity of the glabella is much less than in most other calymenids. Cephalic profiles obtained from internal moulds of the Builth material (Text-fig. 6) do not show such a pronounced roll-like anterior border as figured by Shirley (1936 : 391), but they show a more convex

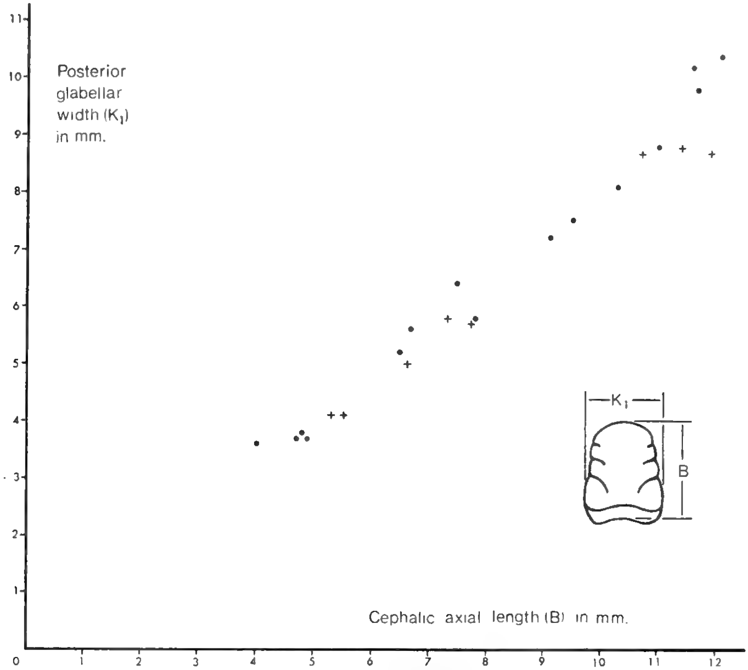

FIG. 5. Graph of cephalic axial length (B) against posterior glabellar width (K_1) of *Platycalymene duplicata* (Murchison) illustrating the lack of " wide " and " narrow " forms. • = specimens from the middle quarry, Llanfawr, Llandrindod; + = specimens from the quarry at Gwern-yfed-fâch half a mile south-east of Builth Road station.

border than is typical of *Flexicalymene.* Whilst it is conceded that the Builth material may be slightly flattened, profiles from material from the Spy Wood Grit of the Shelve region also fail to show such a pronounced roll-like border.

Three pairs of lateral glabellar furrows are developed, but occasionally traces of a fourth pair are present (Pl. 11, fig. 9). Also in some specimens only the *1*p and *2*p furrows are developed (Pl. 11, fig. 6). The *1*p furrows are the most strongly developed, extending from about one-third the way along the glabella and being curved posteromedianly, just failing to reach the occipital furrow. The slight outward convexity of the axial furrows together with the *1*p furrows impart an outline to the *1*p lobes similar to a cat's ear. The *2*p furrows situated slightly more than half-way along the glabella are shorter, directed posteromedianly and only slightly curved, giving a parallel-sided outline to the *2*p lobes. The *3*p furrows are situated between about three-quarters and four-fifths the way along the glabella and are generally rather weakly developed forming shallow, straight posteromedianly directed depressions on the flanks of the glabella (Pl. 10, fig. 5; Pl. 12, fig. 5). When *4*p furrows are developed they take the form of very shallow, short, transversely directed furrows (Pl. 11, fig. 9). The simple occipital ring is bounded by a clearly incised occipital furrow which is deflected laterally round the posterior of the *1*p lobes. About four-fifths of all internal moulds show indications of a small, though distinct, median occipital node, which is apparently absent on the remaining one-fifth. Evitt & Whittington (1953) showed that the wing process on the anterior wings of the hypostoma indents the anterior apodemes at the point of their contact. This also appears to be the case in *P. duplicata,* for the indentations, occurring as tiny spike-like structures in the anterior fossulae of internal moulds, are clearly present (Pl. 12, fig. 1). Lamont (1949 : 314; 1950 : 300) has recorded the presence of a second pair of fossulae in *P. duplicata* slightly to the posterior. These are present directly behind the eye ridge on the fixigenae (Pl. 11, fig. 9), and it is thought that Stubblefield's (1950 : 67) suggestion that they are a complimentary structure to the eye ridge is preferable to the idea that they indicate a tripart origin of the frontal lobe (Lamont 1949 : 314).

The gently convex genal regions extend slightly anterior to the glabella. The posterior border furrow is deep and straight. The posterior border is narrow axially expanding laterally to about four times its initial width. Small palpebral lobes are situated with their mid-point opposite the *3*p furrow and just over one-third the way across the genae. The visual surface of the eye is not known. A weak eye ridge extends from the palpebral lobe to the axial furrows (Pl. 10, fig. 5). The anterior branch of the facial suture is directed more or less exsagittally from the eye, curving axially towards the anterior border. The posterior branch is directed approximately transversely from the eye before curving posteriorly to cut the genal angle (Pl. 10, fig. 3). The librigenae possess a prominent convex border and a well developed border furrow (Pl. 10, fig. 4). The larger dorsal tubercles (diameter ranging from 0·10–0·15 mm.) are perforated near their summit, the pores being about 0·03 mm. in diameter. No evidence has been found of openings on the slopes of the tubercles (see Evitt & Whittington 1953 : 53). The ornamentation is absent in the lateral glabellar furrows (Pl. 11, fig. 1). Whittard (1960 : 148) described a similar feature in

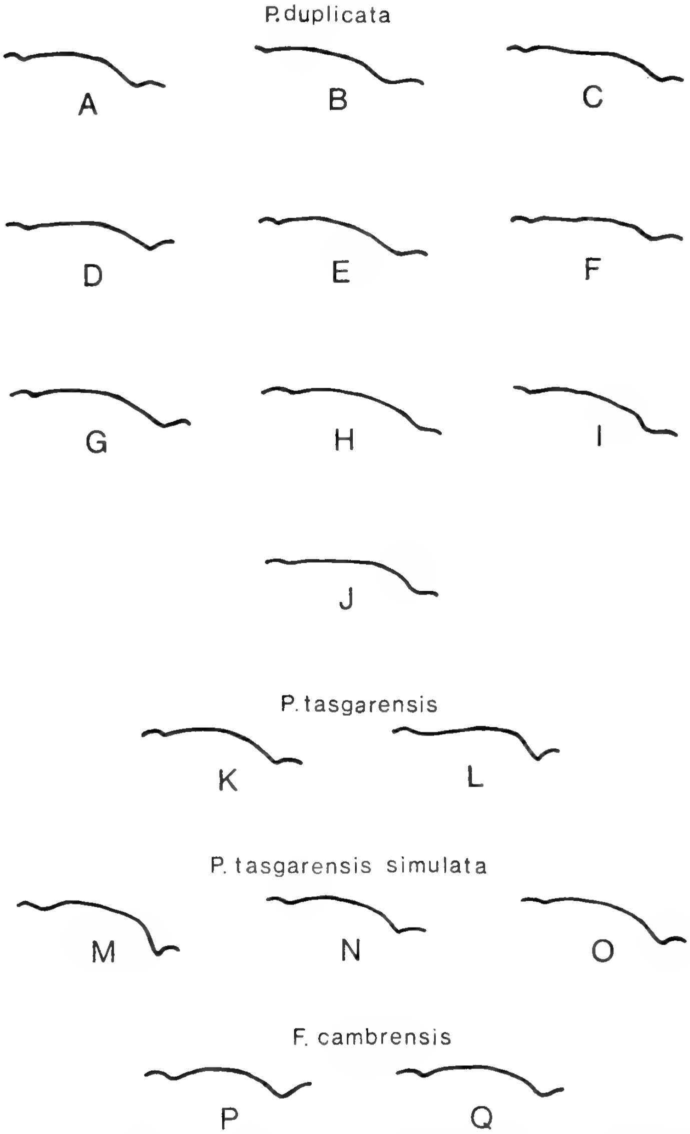

FIG. 6. Diagram showing the similarity of cephalic profiles of *Platycalymene duplicata* (Murchison), *P. tasgarensis* Shirley, *P. tasgarensis* Shirley *simulata* subsp. nov., and *Flexicalymene cambrensis* (Salter). All profiles drawn to a standard length. (A. It. 2990, B. It. 2993, C. It. 2997, D. It. 2995, E. It. 2981, F. It. 2996, G. It. 2987, H. GSM 87127, I. GSM. 87126, J. GSM. 87130, K. GSM. 87119, L. GSM. 87120, M. It. 3014, N. It. 3015, O. It. 3013, P. It. 2980, Q. It. 2979). A–G from the middle quarry, Llanfawr, Llandrindod; H, I, J from the Spy Wood Grit, Rorrington, Shropshire; K, L from the Hope Shales, Whitsburn Dingle, Shropshire, M, N from the stream section south-east of Tre coed; O from the Dulas Brook; P, Q from the east end of the Pheasantry, Dynevor Park, Llandeilo.

P. tasgarensis which he considered corresponded with muscle attachment areas on the internal surface; these areas in *P. duplicata* appear to be of a similar nature.

The subrectangular hypostoma has gently concave lateral margins with a total length of about one and a third times the maximum width. The median body is strongly convex ventrally and divided by a shallow furrow into an oval anterior lobe about three and a half times as long as the crescentic posterior lobe. Conspicuous oval maculae are present in the posterolateral regions of the anterior lobe. In some specimens the furrows bounding the anterior of the maculae are continuous medianly, though very shallow, and together with the furrow bounding the posterior of the anterior lobe give the impression of a slight ridge crossing the median body with the maculae situated at the lateral ends. The anterior border is long (*sag.*) and flexed sharply ventrally at about half-way between the anterior furrow and the margin. Well-developed anterior wings have a deep pit ventrally near the anterolateral extremity, with a corresponding boss dorsally. The lateral border furrows shallow towards the anterior and posterior, the associated borders being narrow and flexed ventrally. The posterior border is flat, forked, with the median notch extending forwards nearly to the well developed posterior border furrow. The ventral surface of the lateral and posterior borders and border furrows is ornamented with small tubercles (Pl. 10, fig. 8).

The thorax consists of 13 segments. The axial rings are transversely convex, simple, and with weak lateral nodes. The articulating furrow is well developed, deepening laterally to form deep apodemal pits. The fulcrum of the anterior segments is situated more distally than in the posterior segments and it appears that in general the posterior pleurae are more steeply deflected ventrally than the anterior ones, thus the thorax becomes slightly narrower and more convex posteriorly (Pl. 10, fig. 6). The pleural furrows are well developed axially, becoming shallower beyond the fulcrum.

The semi-oval pygidium is rather compressed anteriorly, and about twice as wide as long. The axis is well defined, transversely convex and anteriorly occupies about one-quarter of the pygidial width. It tapers posteriorly to about half its anterior width, the greater part of the tapering occurring over the anterior half of the axis. Nine axial rings are generally developed but some specimens have eight or ten (see Table 26). No evidence has been found to support Whittard's claim (1960 : 155) that where fewer rings are developed, the terminal piece is proportionately longer. The ring furrows of the anterior five or six rings deepen laterally to form apodemal pits. The pleural fields possess eight normally well-developed ribs, although nine may be present (see Table 27). The ribs have a median furrow typically present only on the distal half, but in a few specimens (Pl. 10, fig. 2) it may be traced along the entire rib length. In nearly all specimens a notch near the posterior of each rib, at its axial end, corresponds to the axial end of the furrow. Only one known pygidium shows irregularities in rib development; this is thought to have been the result of injury (Pl. 11, fig. 2).

ONTOGENY. A single tiny glabella (Pl. 11, fig. 3), 1·6 mm. long is believed to be a meraspis, degree unknown. Although basically similar to adult glabellae, it shows some minor differences. Posteriorly it is about as wide as long, but tapers slightly anteriorly. The anterior margin is slightly more rounded than is generally the case in holaspides. Three pairs of lateral glabellar furrows are developed. 1p are prominent and frontally of similar form to those of the adult; posteriorly they extend to cut the occipital furrow, thus isolating the 1p lobes. The short 2p furrows are directed posteromedianly as in adult specimens. The 3p furrows are only weakly developed, being little more than a prominent notch in the sides of the glabella. Although the occipital ring is not preserved it is evident that the occipital furrow is of the same form as in the holaspides, being deflected posteriorly round the 1p lobes. Some form of preglabellar field is present, but details are not preserved.

Dimensions

B_1	B_2	B_3	B_4	K	K_1
1·6	1·1	0·7	0·3	1·2	1·7

All measurements in mm. For explanation of symbols see Text-fig. 4.

Biometrical data. Much data is available for this species from both the Middle quarry, Llanfawr, and the quarry at Gwern-yfed-fâch. However, comparison of the bivariate statistics and pygidial data shows there are no significant differences between the two samples. The data given below are based on the larger sample obtained from the former locality.

Table 23

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
B : B_1	8·23	6·7656	6·89	4·8411	0·997	0·996	1·01	0·0005	0·85	0·00025	19
B : B_2	8·23	6·7656	4·53	2·0000	0·988	0·988	0·99	0·0014	0·54	0·00042	19
B : B_3	8·15	7·0300	2·82	0·8935	0·991	0·991	1·03	0·0012	0·36	0·00014	18
B : B_4	8·35	6·6812	1·84	0·3950	0·973	0·974	1·10	0·0041	0·24	0·00021	17

Bivariate statistics for the glabella of *P. duplicata* (Murchison). All measurements in mm. For explanation of symbols see Text-fig. 4.

Table 24

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
B : C	8·00	7·2600	5·65	3·8075	0·993	0·993	1·02	0·0013	0·72	0·00067	13
B : K_1	8·15	7·9900	6·65	5·9400	0·990	0·990	1·05	0·0017	0·86	0·00114	15
K_1 : K	6·84	5·9550	4·91	2·8105	0·984	0·985	0·96	0·0013	0·69	0·00071	23
A : B	10·62	8·9993	8·70	6·3240	0·994	0·994	1·02	0·0009	0·84	0·00060	16

Bivariate statistics for the cephalon of *P. duplicata* (Murchison). All measurements in mm. For explanation of symbols see Text-fig. 4.

Discussion. As already mentioned *P. eire* and *P. dilatata* may be synonyms of *P. duplicata*. *P. eire*, from the Tramore Limestone of County Waterford, supposedly has a slightly more convergent glabella than is typical of *P. duplicata*, but examples similar to *P. eire* are known from Builth (compare Lamont 1949, pl. 18, fig. 1 with Pl. 11, fig. 6). *P. dilatata* from the *Chasmops* Limestone of Skåne is not well known

TABLE 25

x : y	$\bar{x}$	var. x	$\bar{y}$	var. y	r	r_e	α	var. α	a	var. a	n
W : Z	20·20	94·9200	10·26	25·3325	0·996	0·997	1·02	0·0021	0·52	0·00071	5
W : X	22·84	88·5929	5·34	5·6133	0·993	0·994	1·07	0·0027	0·25	0·00018	7
Y : X	10·20	13·4512	5·13	4·0725	0·984	0·986	1·09	0·0022	0·55	0·00064	17
$X : X_1$	5·10	3·8482	2·48	0·7665	0·981	0·982	0·92	0·0019	0·45	0·00047	18
Z : Y	10·85	15·2747	9·74	12·0188	0·995	0·996	0·99	0·0005	0·89	0·00049	18

Bivariate statistics for pygidium of *P. duplicata* (Murchison). All measurements in mm. For explanation of symbols see Text-fig. 4.

TABLE 26

	Number of axial rings		
	8	9	10
Number of specimens . .	2	12	3

mean = 9·06; var. = 0·5763; n = 17

Frequency distribution of the number of axial rings developed on internal moulds of *P. duplicata* (Murchison), together with the means and variance.

2 × 2 probability tests show that there is no correlation between either the number of axial rings or the number of pleural ribs developed and the size of the pygidium as measured by the pygidial length.

TABLE 27

Number of ribs . . .	7 + i	8	8 + i	9
Number of specimens . .	1	14	3	5

mean = 8·26; var. = 0·2024; n = 23

Frequency distribution of the number of ribs developed on internal moulds of *P. duplicata* (Murchison) together with the mean and variance. The suffix " +i " indicates the development of a further incipient rib. Such a rib was counted as half a rib for the purposes of calculating the mean.

TABLE 28

mean = 8·0; var. = 0·0454; n = 12

Mean and variance for the number of ribs developed on external moulds of pygidia of *P. duplicata* (Murchison).

Comparison of these data with those for internal moulds (Table 27) shows no significant difference.

but apparently has no furrows developed on the pygidial ribs. No definite decision as to the validity of this species can be made until it is redescribed. It is considered that the different glabellar outline of *P. duplicata parallela* Whittard is due to compression and that it should not be separated from *P. duplicata s.s.*

P. tasgarensis Shirley 1936 is easily distinguished by its more posteriorly placed eyes and also the wider pygidial axis with fewer axial rings and only four ribs. *P.* cf. *duplicata* (below) from the uppermost Llandeilo of the Builth region is similar to *P. duplicata* and may be distinguished only by the fewer ribs on the pleural fields.

Although it has been shown (Text-fig. 5) that distinct " wide " and " narrow " forms are not present, two forms of cephala are distinguishable, those with, and those without a median occipital node. It has been suggested that the presence or absence of occipital structures, generally occipital spines, in forms otherwise alike may indicate male and female forms, the males lacking the spine (Hu 1963; Bell & Ellinwood 1962; Lochman & Hu 1959). If this is so, the males of *P. duplicata* would be in a minority of about one to four. In this respect it is perhaps worth noting that modern arthropod populations commonly have a considerably higher proportion of females than males.

***Platycalymene* cf. *duplicata* (Murchison)**

(Pl. 12, figs. 2, 7)

1940 *Platycalymene duplicata* (Murchison); Elles : *pars.* 411, 417, 432.

FIGURED MATERIAL. It. 3011 (Pl. 12, fig. 7). Internal mould of cranidium. It. 3012 (Pl. 12, fig. 2). Internal mould of pygidium.

DIMENSIONS.

	A	B	B_1	B_2	B_3	B_4	C
It. 3011	3·6	3·0	2·5	1·6	1·1	0·7	1·4

	I	J	K	K_1
It. 3011	8·5	2·8	1·6	2·2

	W	X	X_1	Y	Z	No. of axial rings	No. of ribs Left	No. of ribs Right
It. 3012	6·7	1·8	0·8	3·2	0·6	8	6	6

All measurements in mm. For explanation of symbols see Text-fig. 4.

LOCALITY AND HORIZON. Small quarry at the south-western end of Pen-cerig Lake, in shales of uppermost Llandeilo age.

DISCUSSION. The cranidium and pygidium differ in some respects from those of *P. duplicata* from the overlying Basal Caradoc. The cranidium, which is small, has a more convex cephalic profile; the pygidium, which again is rather small compared with the majority of specimens of *P. duplicata*, possesses only six ribs, plus an obscure seventh, on the pleural fields; that is fewer than in any specimen known from the Basal Caradoc. The close relationship between this form and *P. duplicata* cannot be denied and yet the pygidium shows some affinity to *Platycalymene tasgarensis simulata* subsp. nov. (p. 93) occurring lower in the Llandeilo of the Builth region, with its fewer number of pleural ribs and more bow-like outline. However, the pygidium differs from *P. tasgarensis simulata* in its more slender axis and slightly higher number of axial rings.

Platycalymene tasgarensis Shirley ***simulata*** subsp. nov.

(Pl. 12, figs. 3, 6, 8–10; Pl. 13, figs. 1–3)

1940 *Platycalymene duplicata* (Murchison); Elles : *pars.* 411, 412, 432.

DIAGNOSIS. *Platycalymene* with relatively high convexity, three pairs of rather angular lateral glabellar lobes and squarish glabellar anterior; mid-point of palpebral lobes opposite 2p furrows. Pygidium with seven axial rings and six well-developed pleural ribs.

TYPE MATERIAL. Holotype. It. 3013 (Pl. 13, fig. 3). Internal mould of cranidium.

Paratypes. It. 3014 (Pl. 12, fig. 3). Internal and external moulds of cranidium. It. 3015 (Pl. 12, fig. 10; Pl. 13, fig. 2). Internal and external moulds of cranidium. It. 3016 (Pl. 12, figs. 8, 9). Internal and external moulds of pygidium. It. 3017 (Pl. 13, fig. 1). Internal and external moulds of pygidium. It. 3018. Internal mould of pygidium.

DIMENSIONS.

	A	B	B_1	B_2	B_3	B_4	C
Holotype	8·3	6·8	5·6	3·6	2·2	1·4	3·2
It. 3014	4·3	3·6	3·0	2·0	1·3	0·8	—
It. 3015	5·7	4·8	3·9	2·5	1·7	1·1	2·5

	I	J	J_1	K	K_1
Holotype	17·0	6·9	9·5	3·6	6·3
It. 3014	10·3	—	—	2·3	3·2
It. 3015	—	—	—	2·6	3·6

	W	X	X_1	Y	Z	No. of axial rings	No. of ribs Left	No. of ribs Right
It. 3016	*c.* 13·5	4·3	1·8	5·6	6·5	7	6	6
It. 3017	*c.* 9·0	3·1	1·5	4·0	4·6	6	6	6
It. 3018	13·0	3·9	1·9	6·0	6·9	7	6	6

All measurements in mm. For explanation of symbols see Text-fig. 4.

TYPE LOCALITIES AND HORIZONS. The holotype is from Llandeilo shales outcropping in the left bank of the Dulas Brook, 150 yards south-west of the old quarry 350 yards west of Maesgwynne, and 60 yards north of spot height 727. Paratypes It. 3016, It. 3017 are from the stream section 15 yards south-west of the above quarry, the remaining paratypes being from the stream section south-east of Tre coed, It. 3014 from the easterly end, 160 yards south-east of the farm and It. 3015, It. 3018 from the westerly end 120 yards from the farm.

OTHER FIGURED SPECIMEN. It. 3019 (Pl. 12, fig. 6).

DISTRIBUTION. The species is rare in the Builth region where it is recorded only from the localities yielding the type material.

Description. The dimensions of the complete exoskeleton are not known. The cephalon is slightly over twice as wide as long and is roughly semicircular in outline, but rather straight anteromedianly. The glabella is convex both transversely and longitudinally. In outline it is trapezoidal and may vary from being slightly wider than long to slightly longer than wide. Three pairs of lateral glabellar furrows are developed. *1*p are the strongest and are angulated at about their mid-length, the anterior portion being directed posteromedianly at about 30° to the transverse direction and the posterior portion becoming nearly parallel to the sagittal direction, extending towards, but not reaching, the occipital furrow. The *2*p furrows are shorter, and for the greater part parallel to the anterior portion of the first pair, but axially they curve slightly to the posterior. These two pairs of furrows define rather square *2*p lobes. The *3*p furrows are even shorter and are more weakly developed, but again are parallel to the outer portions of the first two pairs. Specimen It. 3015 shows indications of a fourth pair of furrows which form little more than a notch in the glabellar sides opposite the weakly developed buttress at the end of the eye ridge (Pl. 12, fig. 10). The occipital ring is simple with a small median node generally present, though this is apparently not developed in the holotype (Pl. 13, fig. 3). The occipital furrow is well incised and laterally is deflected round the posterior of the *1*p lobes. Although the cephalic profile does not match well with that given by Shirley for the type species of *Platycalymene*, the anterior border is more steeply inclined and roll-like than is typical of *Flexicalymene* (Text-fig. 6).

The genal regions are moderately convex, and extend slightly in front of the glabella. The mid-point of the palpebral lobes is about opposite the *2*p furrows, and situated about one-third of the way across the genae. Weakly developed eye ridges (Pl. 12, fig. 10) reach the axial furrows just anterior of the *3*p furrows. The posterior border and border furrows are well developed, expanding distally and also curving gently to the anterior. The librigenae are typically calymenid with prominent border and border furrows (Pl. 12, fig. 6).

Virtually all the external surface of both cephalon and pygidium is covered with small tubercles, some slightly larger than others. However, as in many other calymenids the slopes of the lateral glabellar furrows lack tubercles and are thought to correspond to areas of muscle attachment on the internal surface of the exoskeleton (Pl. 13, fig. 2).

The thorax is not known.

The pygidium has a " taut bow " outline and is generally slightly less than twice as wide as long. The axis is relatively wide anteriorly occupying nearly one-third of the pygidial width. It tapers more or less uniformly posteriorly and possesses seven transversely convex axial rings together with a terminal piece. The pleural fields possess six well-developed ribs which are furrowed more or less along their entire length (*tr.*), the furrows becoming shallower medianly.

Discussion. This new subspecies from the Llandeilo is similar to *P. tasgarensis* from the Lower Llanvirn of the Shelve region. The only differences appear to be in the straighter cephalic axial furrows, and the slightly higher number of pygidial ribs developed in the Builth specimens. The new subspecies is readily distinguished from *P. duplicata* by its more posteriorly placed eyes and lower number of axial rings and pleural ribs developed on the pygidium. The same criteria serve to distinguish *P.* cf. *duplicata*.

Family **COLPOCORYPHIDAE** Hupé 1953

Genus ***PLAESIACOMIA*** Hawle & Corda 1847

TYPE SPECIES. *Plaesiacomia rara* Hawle & Corda.

DISTRIBUTION. Lower Llanvirn of Wales, Caradoc and possibly Llandeilo of France, Spain, Portugal, Bohemia and North Africa.

DISCUSSION. Dean (1966*a*) has recently reviewed *Plaesiacomia* together with *Colpocoryphe* Novak *in* Perner 1918 and concluded that the two genera should not be considered as synonymous as was suggested by Vaněk (1965). If the specimens from Builth described below are correctly assigned, they are of particular interest not only as the first record of this typically Mediterranean genus in Britain, but it is by far the earliest known occurrence so far recorded.

Plaesiacomia sp.

(Pl. 13, figs. 4–8; Pl. 14, figs. 1–2)

FIGURED MATERIAL. It. 3023 (Pl. 14, fig. 2). Internal mould of damaged cranidium. It. 3024 (Pl. 13, figs. 7, 8). Internal mould of damaged cranidium. It. 3025 (Pl. 14, fig. 1). External mould of damaged cranidium. It. 3026 (Pl. 13, figs. 4, 5). Internal mould of pygidium. It. 3027 (Pl. 13, fig. 6). Internal mould of pygidium.

DIMENSIONS.

	B	K		W	X	Z
It. 3023	5·0	*c.* 4·7	It. 3026	*c.* 5·5	*c.* 2·6	*c.* 3·8
It. 3024	3·9	3·6	It. 3027	*c.* 4·2	*c.* 2·0	*c.* 2·7

All measurements in mm. Where B is the sagittal glabellar length including the occipital ring; K the maximum glabellar width; W the maximum pygidial width; X the anterior pygidial axial width; Z the sagittal pygidial length.

LOCALITY AND HORIZON. Exposures on the left bank in the ravine in the upper reaches of the Camnant Brook immediately north of the prominent " S " bend 230 yards S. 13° W. of the fence crossing near the stream source in beds of Lower Llanvirn age.

DESCRIPTION. The glabella is smooth, gently convex and tapers towards the anterior. The occipital ring is narrow, but clearly differentiated from the glabella by the occipital furrow. The axial furrows and preglabellar furrow are deep and fairly steep-sided. Anteriorly a narrow border is developed (Pl. 13, figs. 7, 8), but shows little transverse convexity and only a slight notch is developed. The palpebral lobes appear to have been relatively small and situated about two-thirds the way along the glabella from the posterior. The fixigenae are gently convex, wide posteriorly with the facial sutures presumably cutting the margin in the region of the genal angles.

The two associated pygidia are diamond-shaped in outline, about one and a half times as wide as long. The axis is wide, convex and nearly parallel sided with traces of four, possibly five, axial rings and a terminal piece (Pl. 13, fig. 6). The pleural fields are small, triangular and apparently without ribs, apart from the narrow anterior border. Posteriorly the pleural fields appear not to extend as far as the axis, but this is thought to be due to the incomplete preservation of the outer thin portions of the pleural fields, the apparent margin of the pygidium marking the position of the border furrow which must lie close to and parallel to, the actual margin.

DISCUSSION. Although *Plaesiacomia* as currently understood is typically a younger genus, these specimens appear to be better placed here than in *Colpocoryphe* on account of the glabellar outline, lack of lateral glabellar furrows, lack of prominent eye ridges and the absence of a well-developed vincular notch in front of the cephalon. Of the three species currently assigned to *Plaesiacomia*, the Builth specimens are most like *P. rara* from the Caradoc of Bohemia. *P. oehlerti* (Kerforne 1900) differs in its more posteriorly placed eyes and *P.*? *brevicaudata* (Deslongchamps 1825) may be distinguished by the ill definition of the posterior of the pygidial axis and the position of the pygidial vincular furrow.

Family **EOHOMALONOTIDAE** Hupé 1953

Genus ***PLATYCORYPHE*** Foerste 1919

1865 *Homalonotus* (*Brongniartia*) Salter : *pars* 104, 220.
1918 *Eohomalonotus* Reed : *pars* 322.

DIAGNOSIS. With Whittington's (1965*a* : 486) proposed emendations, Whittard's (1961 : 163) diagnosis reads as follows: Cephalon triangular to trapezoidal in outline; glabella sharply truncated anteriorly, trapezoidal; three pairs of straight, sometimes weakly impressed lateral furrows. Facial suture gonatoparian; eyes opposite second or first lateral glabellar lobes; rostral plate axe-shaped, curved connective suture. Hypostoma divided by middle furrow into an anterior lobe much larger than posterior one; no maculae known. Thorax of 13 segments; pleural furrows moderately deep and pleural terminations rounded. Pygidial axis fails to reach posterior margin; pleural fields with up to six ribs which may be furrowed distally.

TYPE SPECIES. *Platycoryphe platycephalus* Foerste.

DISTRIBUTION. Recently the genus has been recorded from the Arenig of south-western France (Dean 1966 : 318–320). Prior to this, the earliest record was in Britain where the genus ranges from the Lower Llanvirn into the low Caradoc. In Bohemia it is restricted to the Letna Beds of early Caradoc age, whereas in N. America the genus ranges through rocks of ?Trenton to Richmond age and possibly even into the Lower Silurian (see Whittington 1965*a* : 488). The genus may also be present in the Caradoc of south-eastern Turkey (Dean 1967 : 120).

Discussion. The genus has recently been reviewed by Whittington (1965*a*) and no further discussion is necessary.

Platycoryphe vulcani (Murchison)

(Pl. 14, figs. 3–7)

1839 *Asaphus? Vulcani* Murchison : 663, pl. 25, fig. 5.
1854 *Homalonotus* (*Asaphus*) *Vulcani* (Murchison) : pl. 2, figs. 3, 4.
1961 *Platycoryphe vulcani* (Murchison); Whittard : 163–167, pl. 22, figs. 8–19. Includes full synonomy.
1961 *Platycoryphe vulcani* (Murchison); Dean : 343–344.
1965*a* *Platycoryphe vulcani* (Murchison); Whittington : 488.
1966 *Platycoryphe vulcani* (Murchison); Dean : 318–320.

Diagnosis. *Platycoryphe* with cephalic axial furrows straight or slightly convex outwards; posterior glabella width one and three-quarter times anterior width; lateral glabella furrows commonly weakly developed; fossulae absent; paraglabellar area may or may not be developed. Pygidial ribs unfurrowed.

Neotype. GSM. 87137. Enrolled specimen from the Lower Llanvirn Weston Shales, near Curscote, Shropshire. Designated and figured by Whittard (1961 : 166, pl. 22, figs. 8–11).

Locality and horizon. Exposures on the left bank in the ravine in the upper reaches of the Camnant Brook immediately north of the prominent " S " bend 230 yards S. 13° W. of the fence crossing near the stream source; coarse siltstones weathering to rotten stone of Lower Llanvirn age.

Figured material. It. 2832 (Pl. 14, figs. 3, 6); It. 2833 (Pl. 14, fig. 7); It. 2835 (Pl. 14, fig. 5); It. 2836 (Pl. 14, fig. 4).

Description. One cranidium, two librigenae and four pygidia are known from the Lower Llanvirn of the Builth district which appear to be conspecific with the form occurring in the passage beds at the top of the Stapeley Shales and in the Weston Beds of the Shelve region.

Although slightly cracked, the glabella of the Builth specimens is trapezoidal in outline as in the Shelve specimens, the posterior width being one and three-quarter times the anterior width. The lateral glabellar furrows are extremely weakly developed, but faint traces of three pairs are present. As is commonly found in homalonotids, the axial and occipital furrows are more clearly developed on internal moulds than on external moulds. The axial furrows are nearly straight, with slight outward convexity. The occipital furrow is bowed gently forwards medianly and limits the anterior of the simple, flat, narrow (*sag.*) occipital ring. As in the Shelve material, fossulae are apparently not developed. The precise nature of the preglabellar field, fixi- and librigenae is not determinable in the Builth material but as far as can be seen they are similar to those of the Shelve specimens. There is a slight indication of a paraglabellar area developed on the right fixigena.

The hypostoma and thorax are unknown from Builth.

The pygidium is essentially similar to those from Shelve, with five or six ribs present on the pleural fields and apparently with seven axial rings developed.

The external surface of both the cephalon and the pygidium is covered with a coarse, uniform granular ornament.

Discussion. Since Whittard's redescription of this species (1961 : 164–167, pl. 22, figs. 8–19), both Dean (1961 : 344) and Whittington (1965*a* : 488), while accepting Whittard's use of *Platycoryphe*, have pointed out that in some cases it is very difficult to distinguish between species of *Brongniartella* Reed 1918 and *Platycoryphe* on account of the variation in the development of the lateral glabellar furrows. Such an instance is to be found in *P. vulcani* in which the lateral glabellar furrows may be either well developed or virtually obsolete (see Whittard 1961, pl. 22, figs. 12, 16). Although similar variation is not known in the type species *P. platycephalus* (Foerste 1910) it is present in *P. christyi* (Hall 1860) (see Whittington 1965*a* : 488) and it is believed that *vulcani* was correctly placed in *Platycoryphe* by Whittard. Further support for this is given by the absence of any constriction of the anterior portion of the glabella which is characteristically present in *Brongniartella*. The lateral glabellar furrows are also very weakly developed in *P. convergens* Dean 1966 but since there is only one specimen of this, the earliest described *Platycoryphe*, it is not known if the furrows show any variation in their degree of development.

Whittard, in discussing the affinities of this species, concluded that the three European species, *P. bohemicus* (Barrande 1852), *P. foveolatus* (Prantl & Přibyl 1945) and *P. vulcani* were closely related and distinguishable from one another on their glabellar outlines. Whittington (1965*a* : 488) has since given good reasons for considering *P. foveolatus* as synonymous with *Brongniartella platynotus* (Dalman 1828). Whittard acknowledged the possibility that *P. bohemicus* might be conspecific with *P. vulcani* and Barrande's original figures (1852, pl. 34, figs. 40–42) together with Prantl & Přibyl's subsequent illustrations (1949, pl. 1, figs. 1, 2) show that there is very little difference between these two forms. However, they are from quite different horizons and it is possible that *P. bohemicus* from low in the Caradoc is a distinct morphological type with a slightly wider glabella. Apart from these species, Whittington (1965*a*) recognized *P. platycephalus* (Foerste 1910), *P. christyi* (Hall 1860), *P. dubius* (Savage 1913) and *P. dentatus* Dean 1966 has since been described. *P. platycephalus* and *P. christyi* may be distinguished by the presence of fossulae and better developed lateral glabellar furrows. *P. christyi*, *P. dubius* and *P. dentatus* may be distinguished by the presence of furrows on the pygidial ribs. *P. dentatus* is further distinguished by a distinct step in the axial furrows opposite the second lateral glabellar furrows.

Although *P. vulcani* is superficially like *P. convergens* Dean in the obsolescence of the lateral glabellar furrows it may readily be distinguished from Dean's species by its flatter anterior border, more posteriorly placed eyes and straight anterior glabellar margin.

The Builth material is apparently slightly larger than the Shelve specimens, the cranidium and largest pygidium from Builth being about 13·0 and 11·5 mm. in length respectively, compared with lengths of 11·2 and 10·4 mm. for the largest cephalon and pygidium figured by Whittard. None of the Builth specimens however approaches the size of the large isolate pygidium referred to *Platycoryphe* sp. by Whittard.

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EXPLANATION OF PLATES

Most of the trilobites figured are in the collections of the British Museum (Natural History) and their numbers are prefixed I., or It. Other specimens are in the collections of the following institutions: Birmingham University (BU.), Institute of Geological Sciences (GSM.), Naturhistoriska Riksmuseet, Stockholm (Ar.), Sedgwick Museum, Cambridge (SM.), and the private collections of Mr. J. T. Wattison (H). All specimens were whitened with ammonium chloride before photographing. All photographs are by the author and none is retouched.

PLATE 1

Geragnostus mccoyii (Salter *in* Murchison) p. 56

Uppermost Llandeilo, small quarry at south-western end
of Pen-cerig Lake. G.R. SO.043541.

FIGS. 1, 2. Lectotype. Dorsal and lateral views of internal mould of cephalon. GSM. 8710. ×9.

FIG. 3. Internal mould of complete specimen. It. 2671. ×5.

FIGS. 4, 8. Internal and external moulds of pygidium showing furrows on lateral border of internal mould but not on external mould. It. 2670. ×9.

FIGS. 5, 6. Dorsal and lateral views of internal mould of thorax and pygidium. GSM. 8709. ×9.

FIG. 7. Internal mould of complete specimen. Wattison Collection. H 1. ×5.

FIG. 9. Internal mould of small holaspid pygidium. It. 2675. ×20.

FIG. 10. External mould of nearly complete specimen. It. 2677. ×5.

FIG. 11. Internal mould of cephalon showing posterior border. It. 2680. ×6.

FIG. 12. Internal mould of ?meraspis degree one transitory pygidium. It. 2673. ×20.

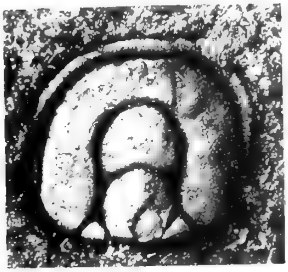
Sphaeragnostus sp. p. 61

Llandeilo, left bank of Dulas Brook, 150 yards south-west of
the old quarry west of Maesgwynne. GR. SO. 058564.

FIGS. 13, 15. Dorsal and lateral views of internal mould of pygidium. It. 2681. ×9.

Llandeilo, old quarry 350 yards west of Maesgwynne.
G.R. SO.059566

FIG. 14. Internal mould of pygidium. It. 2682. ×9.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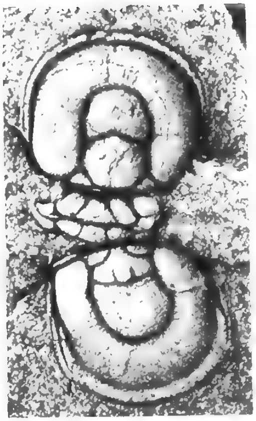
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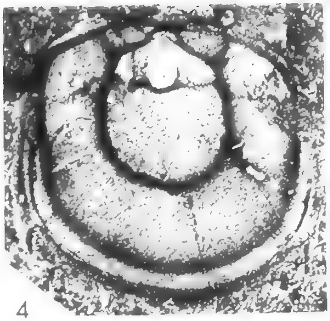
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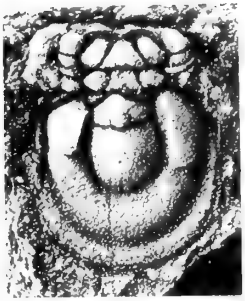
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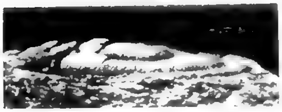
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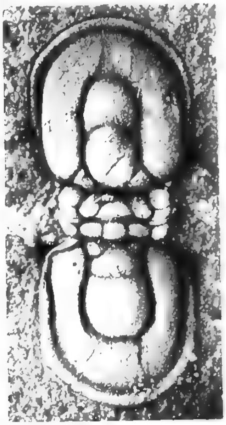
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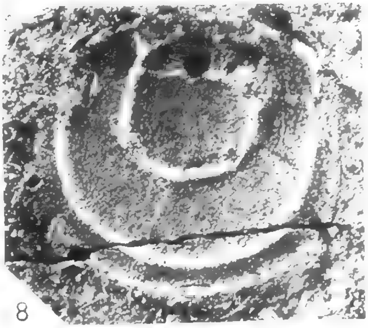
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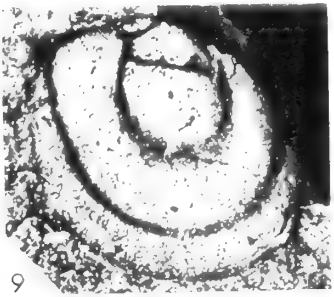
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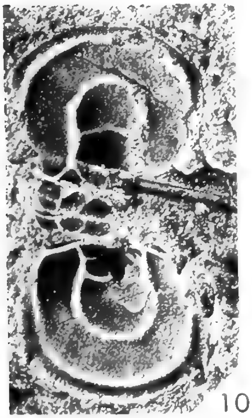
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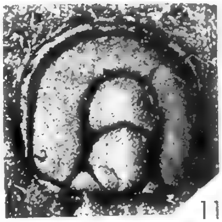
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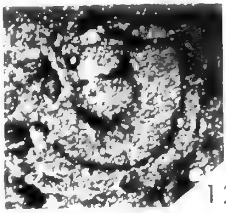
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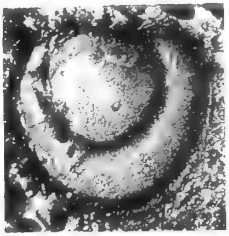
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PLATE 2

Cnemidopyge nuda (Murchison) p. 63

Uppermost Llandeilo, small quarry at south-western end
of Pen-cerig Lake. G.R. SO.043541.

FIG. 1. Paralectotype. Internal mould of nearly complete specimen. GSM. (Geol. Soc. Coll.). 6835. ×3.

FIG. 2. Lectotype. Internal mould of cephalon and thorax. GSM. (Geol. Soc. Coll.). 6835. ×3.

FIG. 5. Internal mould showing irregular rib development. It. 2688. ×3.

FIG. 10. Internal mould of incomplete pygidium showing irregular rib development. It. 2684. ×4.

FIG. 12. Enrolled specimen with cephalon folded back beneath the pygidium. It. 2687. ×3.

Llandeilo, above right bank of stream 200 yards east of
Pen-cerig Lodge. G.R. SO.047538.

FIG. 3. External mould showing frontal glabellar spine and surface ornament (for enlargement see Pl. 3, fig. 4). BU. 365. ×2.

FIG. 4. Internal mould showing course of facial suture across the genal angle. It. 2693. ×2.

Llandeiolo, stream section south-east of Tre coed;
exact locality unknown.

FIG. 7. Latex cast of meraspis ?degree 5. BU. 366. ×10.

Llandeilo, " Shales 3 miles N. of Builth ", possibly from
the stream section south-east of Tre coed.

FIG. 6. Internal mould of small holaspis. Figured as *Ampyx latus*, Sedgwick & M'Coy 1851, pl. 1E, fig. 13. SM. A.15,620. ×5.

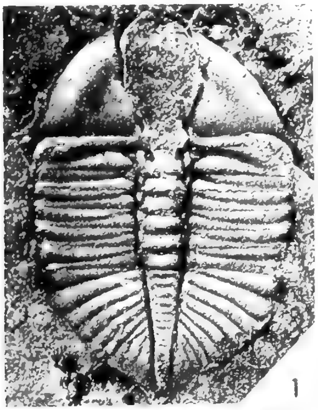
Llandeilo, 160 yards south-east of Tre coed on
left bank of stream. G.R. SO.054552.

FIG. 8. Internal mould of small holaspis. It. 2691. ×7.

Cnemidopyge sp.

Folkeslundakalk, Öland, Brunnby kanal.

FIGS. 9, 11. Lateral and dorsal views of cranidium with some exoskeleton adhering showing paired muscle depressions on the glabella. Riksm. Stockholm. Ar. 21628. ×3.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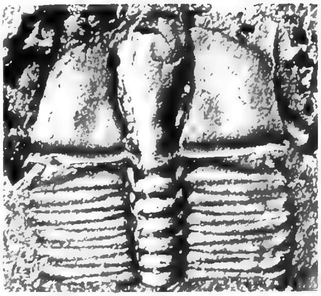
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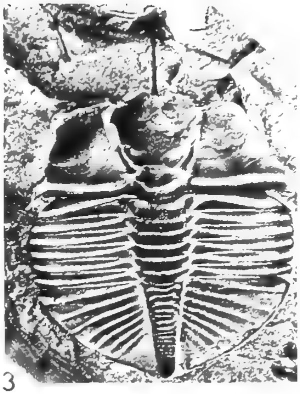
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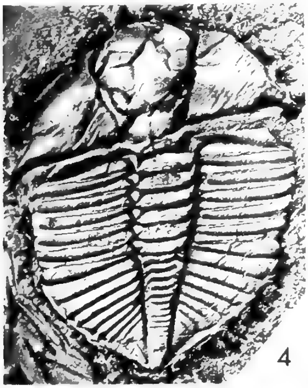
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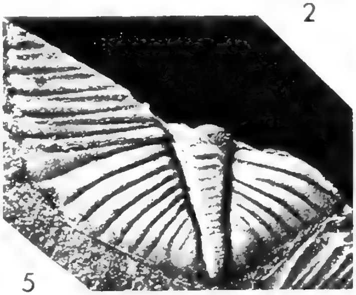
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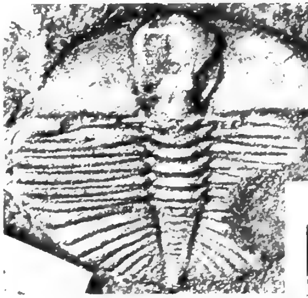
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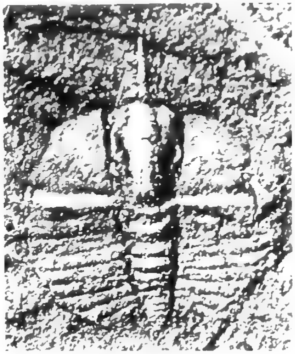
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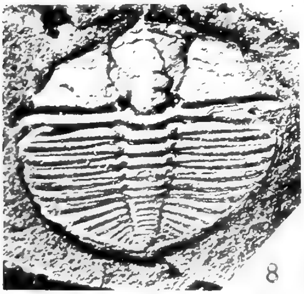
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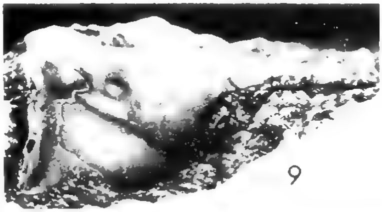
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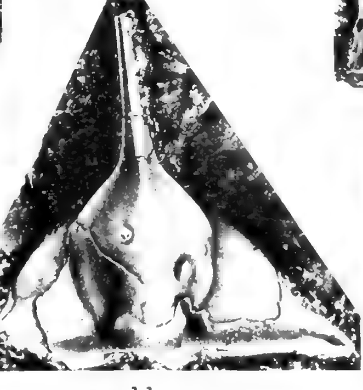
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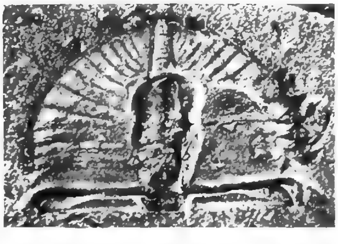
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PLATE 3

Cnemidopyge nuda (Murchison) p. 63

Uppermost Llandeilo, small quarry at south-western end
of Pen-cerig Lake. G.R. SO.043541.

FIG. 1. External mould showing long curved genal spine. It. 2683. × 3.

FIG. 3. External mould showing granular ornament on part of thorax and on pygidium. It. 2685. *c.* × 10.

Llandeilo, 160 yards south-east of Tre coed on
left bank of stream. G.R. SO.054552.

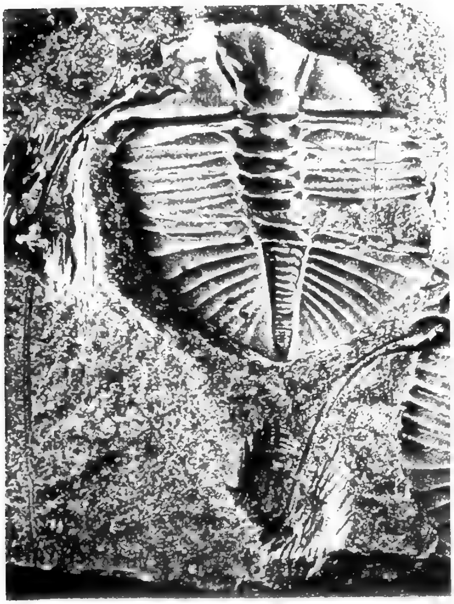
FIG. 2. Cephalic doublure with genal spine, showing median notch (n) an inner margin. g—indicates the position of the genal angle. It. 2692. × 3. (See also Whittington, 1959: 476, text-fig. 8c, pl. 32, figs. 2, 3.)

Llandeilo, above right bank of stream 200 yards east of Pen-cerig Lodge. G.R. SO.047538.

FIG. 4. External mould showing granular ornament on cranidium. BU. 365. × 10.

?Llandeilo, " Builth ", exact locality unknown.

FIG. 5. Internal mould of large individual showing bases of genal spines, genal ridge, and muscle scars on pygidial axis. GSM. 35388. × 1·5.



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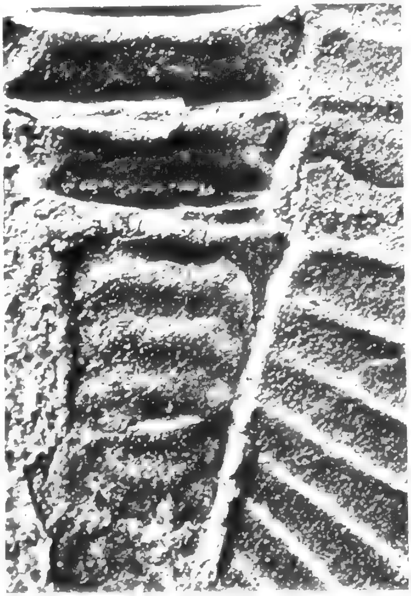

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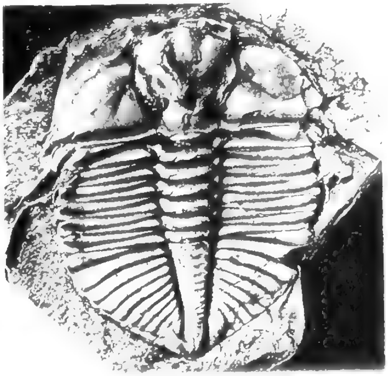

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PLATE 4

Cnemidopyge nuda (Murchison) **granulata** Whittard p. 69

?Llandeilo, Holywell Burn, 30 yards W 22° N of The Mount,
near Rorrington, Shropshire.

FIG. 1. Holotype. External mould showing ornament on part of cranidium. GSM. 92950. × 10.

Horizon as for Fig. 1, but 12 yards W 25° N of The Mount.

FIG. 3. Paratype. External mould of thorax and part of pygidium. GSM. 92951. × 2.

Llandeilo, stream section 400 yards north-east of Gorse.
G.R. SO.072617.

FIG. 2. External mould of hypostoma. It. 2704. × 6.

FIG. 4. Internal mould showing general features of dorsal exoskeleton. It. 2702. × 2.

FIG. 5. External mould showing surface ornament. It. 2705. × 3.

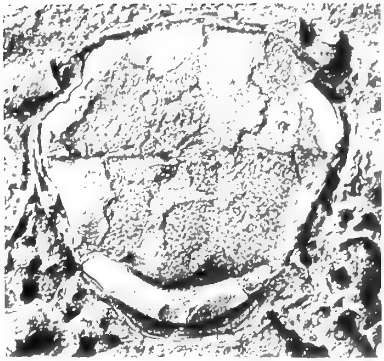
FIG. 6. Internal mould of meraspis ?degree 3. It. 2703. × 15.

Cnemidopyge parva sp. nov. p. 71

Llandeilo, left bank of stream section east of Bach-y-graig,
40 yards east of the point where the footpath enters the wood
at the western end of the section. G.R. SO.071610.

FIG. 7. Paratype. Internal mould of cranidium showing frontal glabellar spine. It. 2697. × 3.

1



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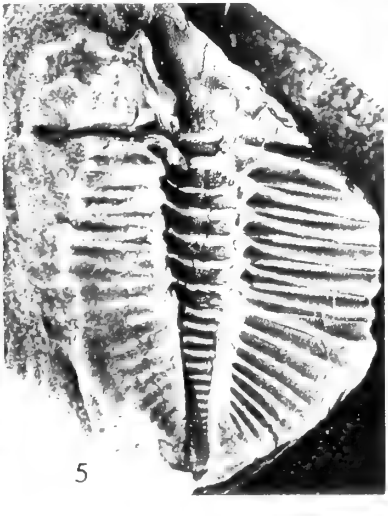

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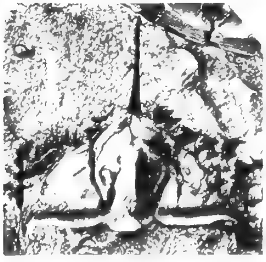

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PLATE 5

Cnemidopyge nuda (Murchison) ***granulata*** Whittard p. 69

Llandeilo, stream section 400 yards north-east of Gorse.
G.R. SO.072617.

FIG. 1. External mould showing granular ornament on the glabella. It. 2705. ×10.

?Llandeilo, Holywell Burn, 300 yards W 22° N of The Mount,
near Rorrington, Shropshire.

FIG. 5. Holotype. Internal moulds of cranidium. GSM. 92950. ×3.

Cnemidopyge parva sp. nov. p. 71

Llandeilo, left bank of stream section east of Bach-y-graig, 40 yards
east of the point where the footpath enters the wood at the western
end of the section. G.R. SO.071610.

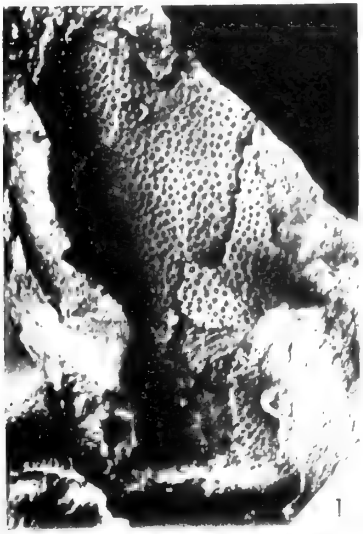
FIG. 2. Internal mould of librigena and spine. It. 2699. ×2·5.

FIG. 3. Internal mould of meraspis ?degree 2. It. 2700. ×10.

FIGS. 4, 8. Paratype. External mould of incomplete cranidium showing ornament. It. 2695. Fig. 4. ×3; Fig. 8. ×10.

FIG. 6. External mould of meraspis transitory pygidium of unknown degree. It. 2701. ×10.

FIG. 7. Paratype. Internal mould of pygidium with five ribs. It. 2698. ×3.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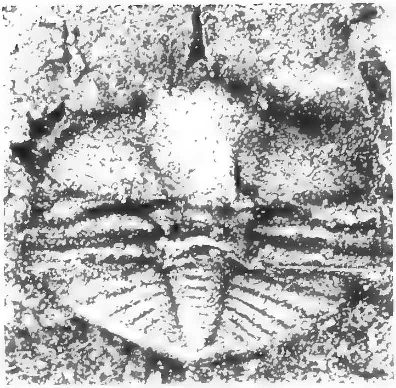
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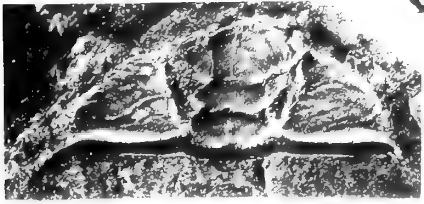
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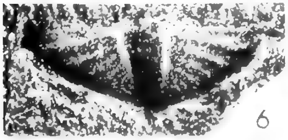
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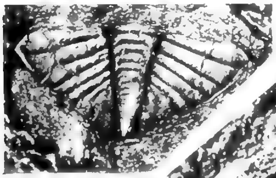
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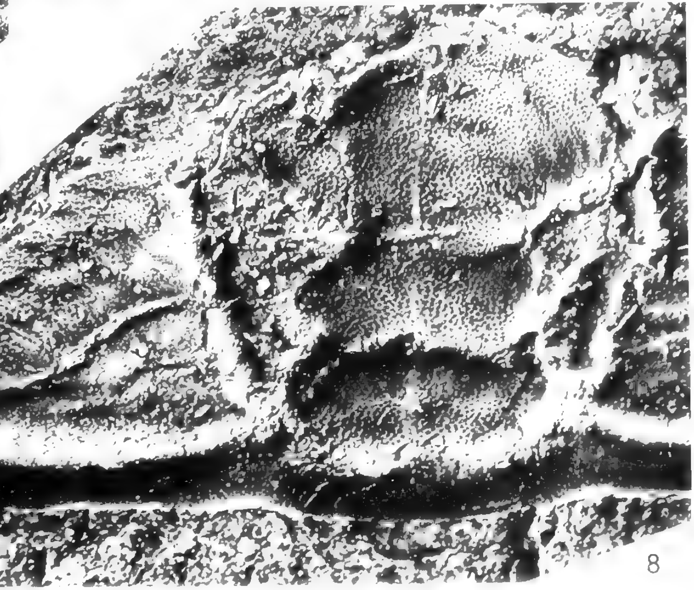
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PLATE 6

Cnemidopyge parva sp. nov. p. 71

Llandeilo, left bank of stream section east of Bach-y-graig,
40 yards east of the point where the footpath enters the wood
at the western end of the section. G.R. SO.071610.

FIG. 1. Holotype. Internal mould of nearly complete specimen. It. 2694. × 4.

Cnemidopyge bisecta (Elles) p. 74

Basal Caradoc, middle quarry, Llanfawr, Llandrindod.
G.R. SO.066617.

FIG. 2. Internal mould of nearly complete specimen showing irregularities of the pygidial ribs. It. 2710. × 3.

FIG. 4. Paratype. Internal mould of large cranidium. SM. A.10,074. × 2.

FIG. 5. External mould of pygidium showing granular surface and irregular rib development. It. 2708. × 3.

FIG. 6. Internal mould of pygidium showing two pairs of muscle scars on each axial ring. It. 2711. × 3.

FIG. 8. Internal mould of thorax and pygidium showing irregularities in rib development. It. 2716. × 3.

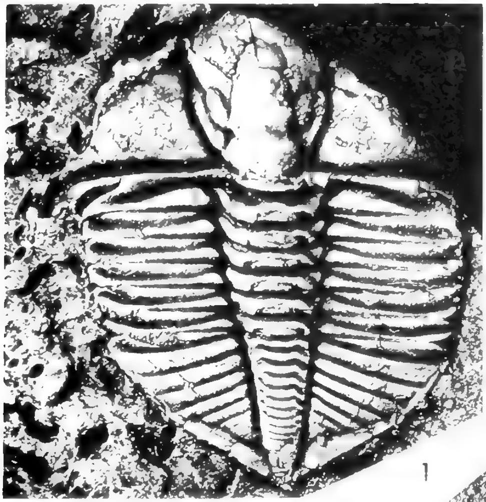
FIG. 9. External mould of part of anterior thoracic segment showing surface granulation. It. 2707. × 10.

?Basal Caradoc, locality uncertain but possibly as for Fig. 2.

FIG. 3. External mould showing long genal spine. I. 4289. × 1·5.

Basal Caradoc, quarry at Gwern-yfed-fâch, half a mile south-
east of Builth Road station. G.R. SO.030526.

FIG. 7. Internal mould of small ?meraspis cranidium. It. 2713. × 10.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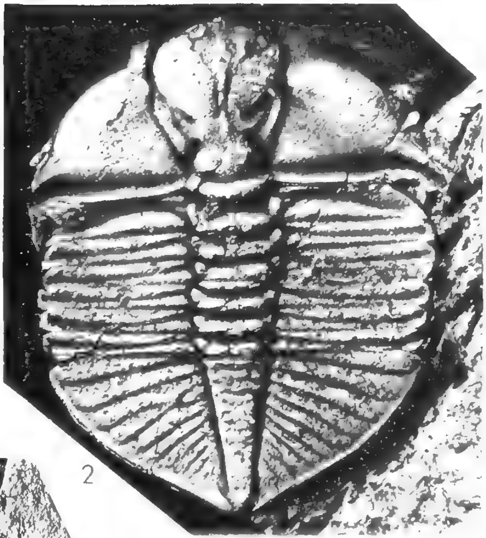
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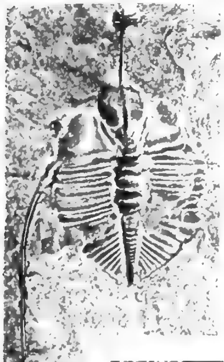
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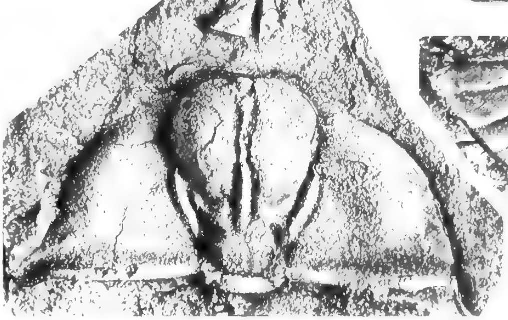
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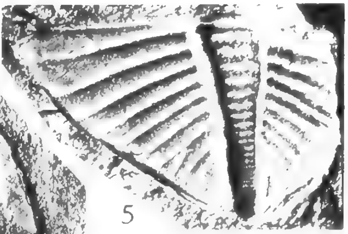
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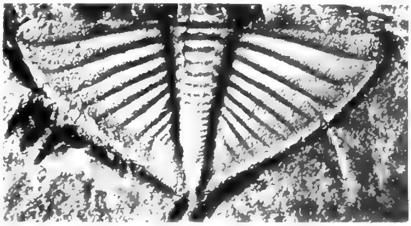
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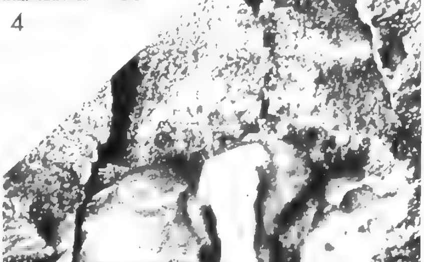
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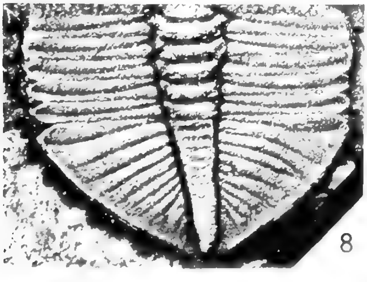
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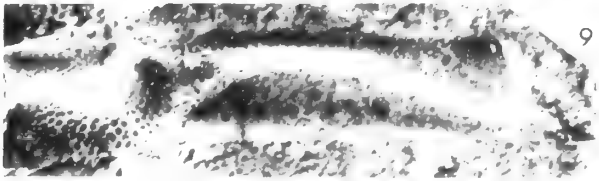
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PLATE 7

Cnemidopyge bisecta (Elles) p. 74

Basal Caradoc, middle quarry, Llanfawr, Llandrindod.
G.R. SO.066617.

FIG. 1. Internal mould of pygidium showing slight irregularities in rib development. It. 2712. ×3.

FIG. 2. Internal mould of pygidium showing pathological irregularity of ribs. It. 2717. ×3. (Specimen donated by Shropshire County Museum, Ludlow).

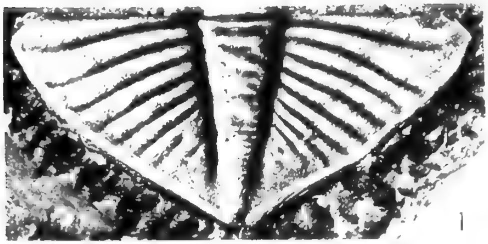
FIG. 3. External mould of part of pygidium showing surface ornament. It. 2714. ×10.

FIG. 5. External mould of part of cranidium showing surface ornament. It. 2715. ×10.

Cnemidopyge parva sp. nov. p. 71

Llandeilo, left bank of stream section east of Bach-y-graig,
40 yards east of the point where the footpath enters the wood
at the western end of the section. G.R. SO.071610.

FIG. 4. Paratype. External mould of nearly complete specimen. It. 2696. ×4.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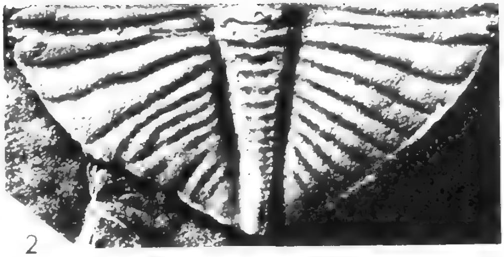
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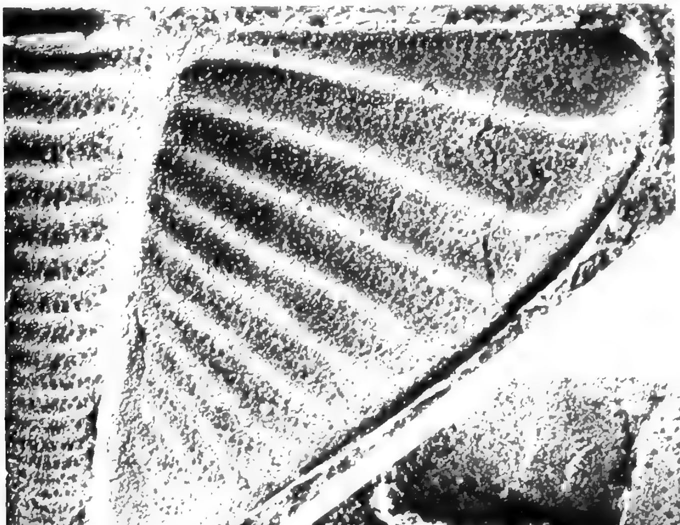
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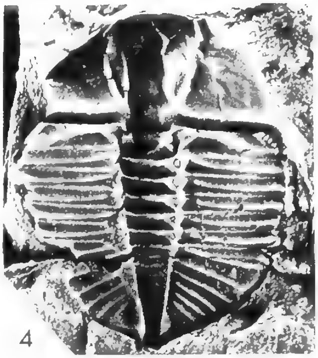
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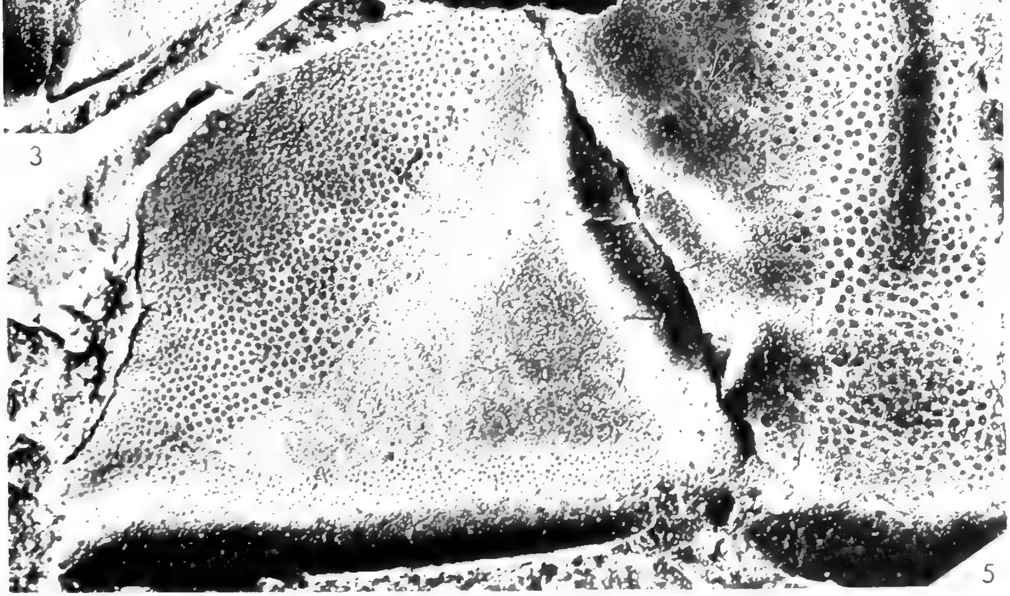
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PLATE 8

Raphiophorid sp. indet. p. 77

Lower Llanvirn, Camnant Brook, exact locality unknown.

FIGS. 1, 2. External mould and latex cast of cranidium and part of thorax. It. 2718. ×3·5. (Specimen donated by Shropshire County Museum, Ludlow.)

Cnemidopyge bisecta (Elles) p. 74

Basal Caradoc, middle quarry, Llanfawr, Llandrindod.
G.R. SO.066617.

FIG. 3. Holotype. Internal mould of nearly complete specimen. SM. A.10,073. ×2·5.

Placoparina sedgwickii (M'Coy) p. 79

Llandeilo, " 2 miles north of Builth ", exact locality unknown.

FIGS. 4, 5. Holotype. External and internal moulds of nearly complete specimen. SM. A.15,616b, a. ×1·25.

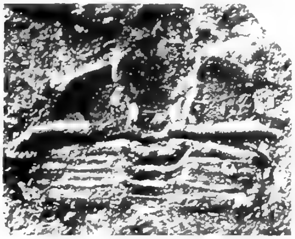
Llandeilo, about 80 yards west of the junction of the Cefnllys
road and the lane to Gorse. G.R. SO.072614.

FIG. 6. Internal mould of incomplete cranidium. BU. 367. ×2·5.

Flexicalymene aurora sp. nov. p. 81

Lower Llanvirn, track 100 yards east of Bwlch-llŵyn.
G.R. SO.115595.

FIG. 7. Paratype. Internal mould of incomplete cranidium. It. 2975. ×5.



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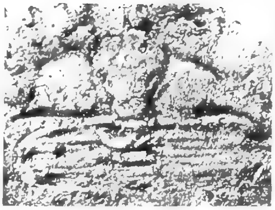

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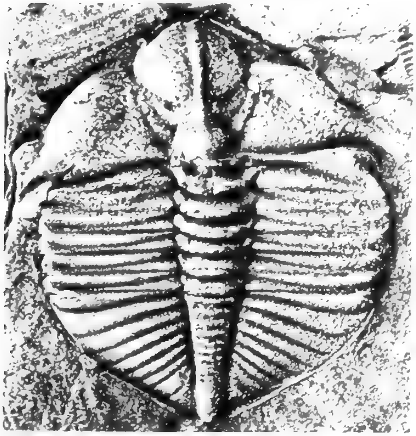

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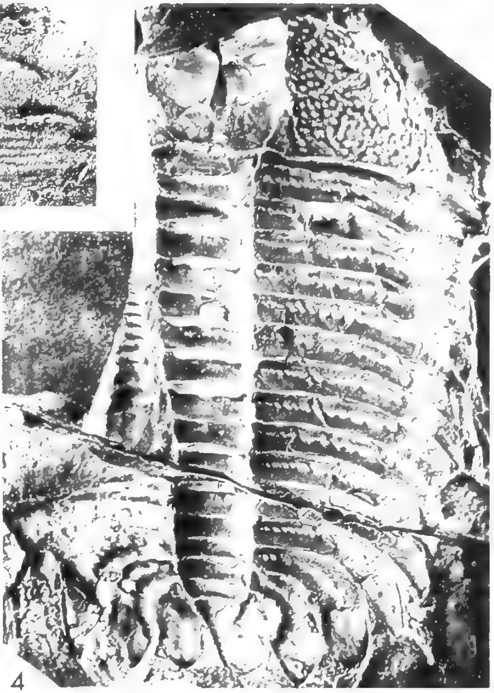

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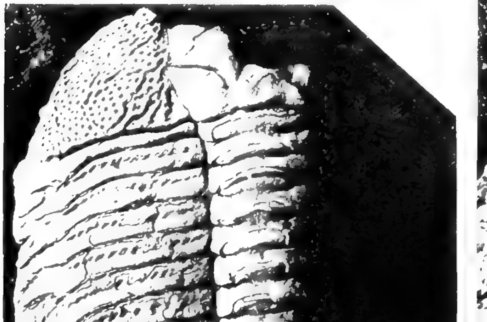

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PLATE 9

Flexicalymene aurora sp. nov. p. 81

Lower Llanvirn, track 100 yards east of Bwlch-llŵyn.
G.R. SO.115595.

FIGS. 1, 2. Internal and external moulds of left librigena. It. 2976. ×5.

FIG. 4. Holotype. Internal mould of cephalon and part of thorax, showing rostral plate and buttresses. It. 2974. ×5.

FIG. 7. Paratype. Internal mould of pygidium. It. 2977. ×5.

Lower Llanvirn, cliff section on left bank of Howey Brook half a
mile east-south-east of Carregwiber. G.R. SO.089582.

FIG. 8. Paratype. External mould of pygidium showing surface ornament. It. 2978. ×6.

Placoparina sedgwickii (M'Coy) p. 79

Llandeilo, " 2 miles north of Builth ", exact locality unknown.

FIG. 3. Holotype. Part of pygidium of external mould of nearly complete specimen (see Pl. 8, fig. 4) showing surface ornament. SM. A.15,616b. ×10.

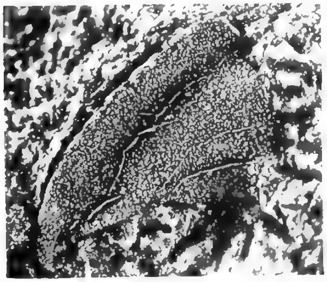
Platycalymene duplicata (Murchison) p. 84

Basal Caradoc, middle quarry, Llanfawr, Llandrindod.
G.R. SO.066617.

FIG. 5. Internal mould of thorax and pygidium of small individual with only eight pygidial ribs. It. 3009. ×3·5.

Caradoc, " Wilmington near Marton Pool ", Shropshire.

FIG. 6. Holotype. Internal mould of pygidium. GSM. 6847. ×3.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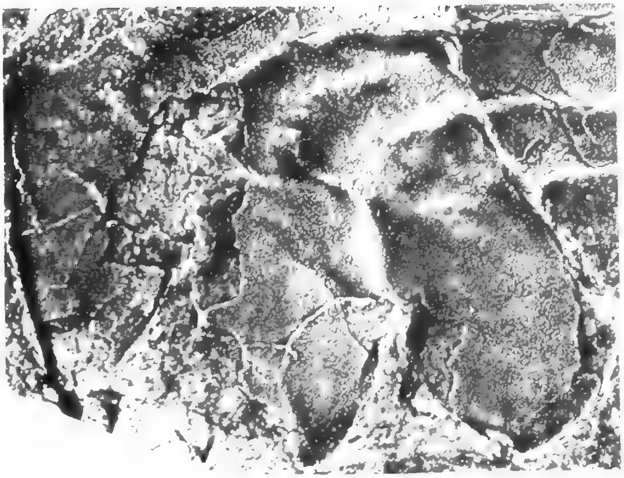
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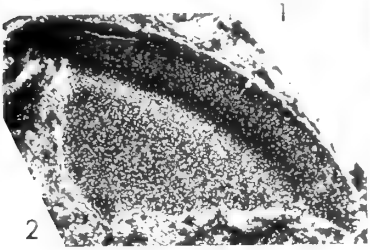
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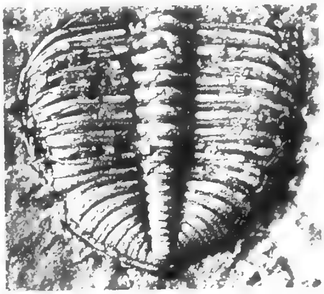
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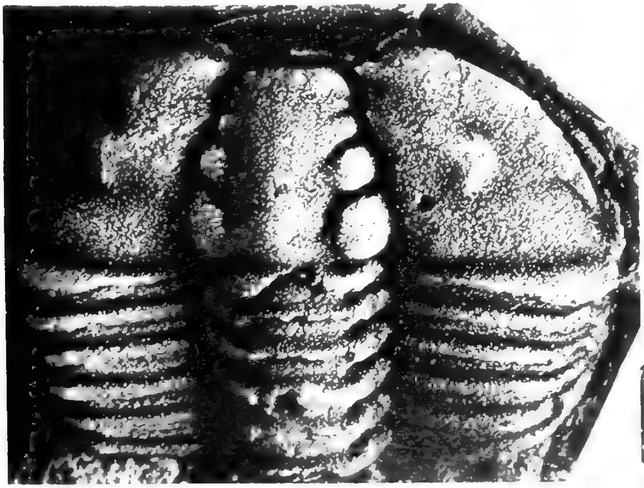
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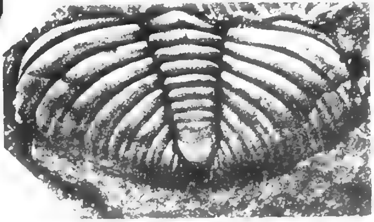
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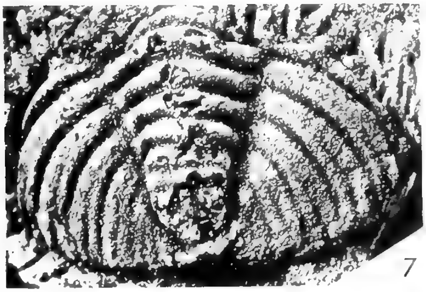
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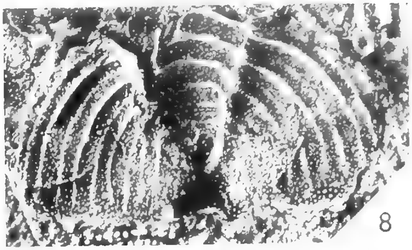
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PLATE 10

Platycalymene duplicata (Murchison) p. 84

Basal Caradoc, middle quarry, Llanfawr, Llandrindod.
G.R. SO.066617.

FIG. 1. Latex cast showing surface ornament of thorax. It. 3003. ×3.

FIG. 2. Internal mould of pygidium showing traces of furrows along the entire rib. It. 3002. ×2.

FIG. 3. Internal mould of right librigena. It. 3000. ×3.

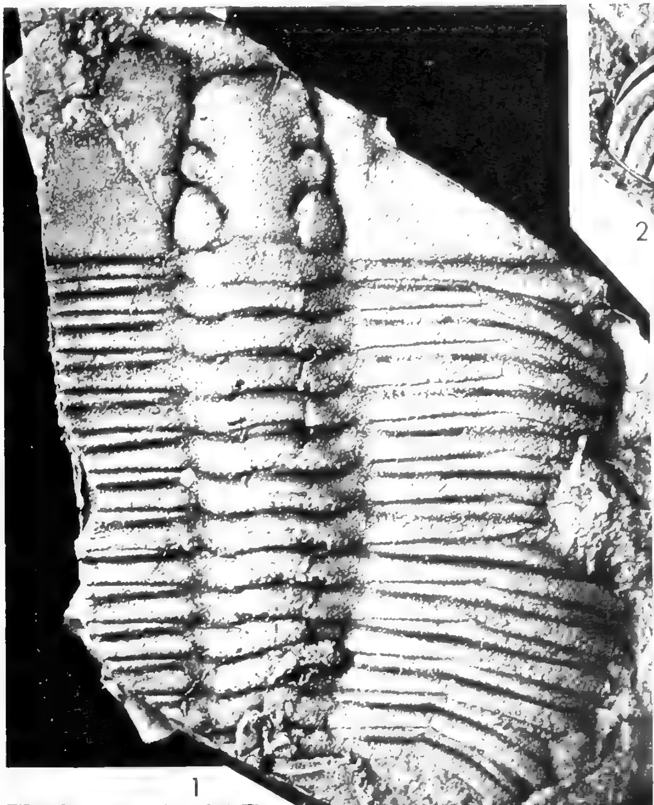
FIG. 4. Latex cast of right librigena showing surface ornament. It. 2988. ×3.

FIG. 5. Internal mould of nearly complete specimen showing general form of dorsal exoskeleton. Wattison Collection. H 13. ×1·25.

FIG. 6. Internal mould of small incomplete specimen. It. 3008. ×3.

FIG. 7. Internal mould of hypostoma. It. 2989. ×5.

FIG. 8. External mould of hypostoma showing invagination in posterior margin and surface ornament. It. 2983. ×5.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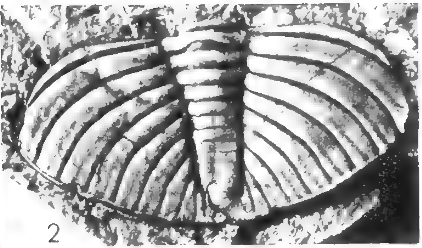
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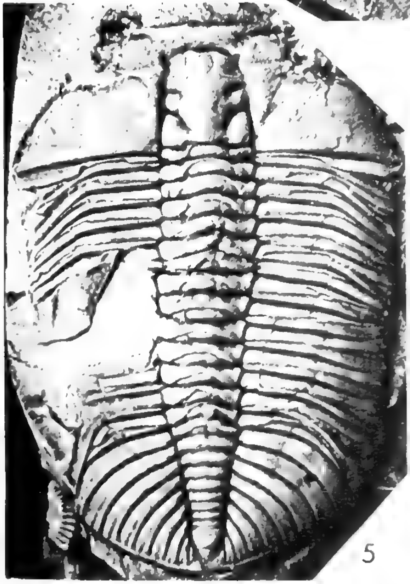
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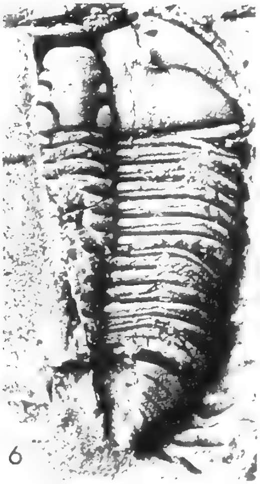
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PLATE 11

Platycalymene duplicata (Murchison) p. 84

Basal Caradoc, middle quarry, Llanfawr, Llandrindod.
G.R. SO.066617.

FIG. 1. Latex cast showing surface ornament with smooth areas in the lateral glabellar furrows. It. 3007. ×14.

FIG. 2. Internal mould of incomplete pygidium showing injury damage to left pleural field. It. 3001. ×2·5.

FIG. 3. Internal mould of incomplete ?meraspis cranidium. It. 3006. ×10. (Specimen donated by Radnorshire County Museum, Llandrindod Wells.)

FIG. 4. Internal mould of incomplete cranidium showing occipital node. It. 2995. ×3·5.

FIG. 5. Latex cast of pygidium showing ornament. It. 2984. ×7.

FIG. 6. Internal mould of cranidium showing only two pairs of lateral glabellar furrows. It. 2990. ×5.

FIG. 7. Internal mould of thoracic segment. It. 2985. ×2.

FIG. 8. Internal mould of pygidium showing only seven well-developed ribs. It. 2991. ×5.

FIG. 9. Internal mould of incomplete cranidium showing *4p* furrows developed and two pairs of apodemal pits. It. 2982. ×3.


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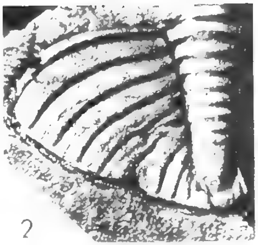
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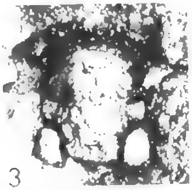
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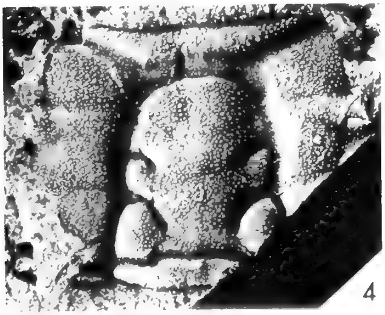
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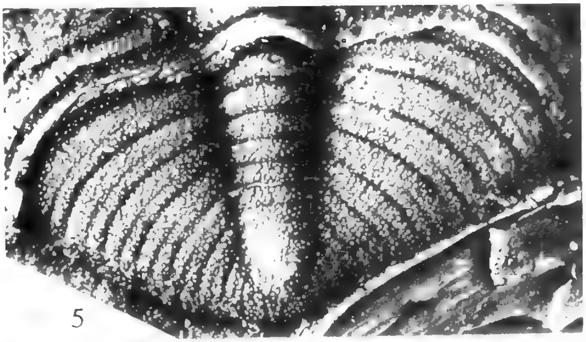
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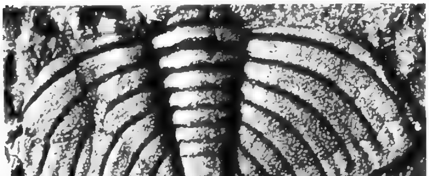
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PLATE 12

Platycalymene duplicata (Murchison) p. 84

Basal Caradoc, middle quarry, Llanfawr, Llandrindod.
G.R. SO.066617.

FIG. 1. Internal mould of incomplete cranidium showing small projection in the anterior wall of the apodemal pits. It. 2994. ×2.

FIG. 4. Latex cast of incomplete cranidium showing eye ridges and surface ornament (for enlargement see Pl. 11, fig. 1). It. 3007. ×3.

FIG. 5. Internal mould of cranidium with two pairs of apodemal pits. It. 2986. ×3.

Platycalymene cf. ***duplicata*** (Murchison) p. 92

Uppermost Llandeilo, small quarry at south-western end of
Pen-cerig Lake. G.R. SO.043541.

FIG. 2. Internal mould of pygidium. It. 3012. ×6.

FIG. 7. Internal mould of cranidium. It. 3011. ×6.

Platycalymene tasgarensis Shirley ***simulata*** subsp. nov. p. 93

Llandeilo, 160 yards south-east of Tre coed on
left bank of stream. G.R. SO.054552.

FIG. 3. Paratype. External mould of cranidium showing eye ridges and surface ornament. It. 3014. ×6.

Llandeilo, stream section 15 yards south-west of the
old quarry 350 yards west of Maesgwynne.
G.R. SO.059566.

FIG. 6. Internal mould of librigena. It. 3019. ×6.

FIGS. 8, 9. Paratype. Internal and external moulds of pygidium. It. 3016. ×4.

Llandeilo, 120 yards south-east of Tre coed on
left bank of stream. G.R. SO.054552.

FIG. 10. Paratype. Internal mould of cranidium showing eye ridges and small buttresses. It. 3015. ×6.


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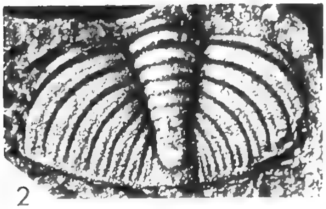
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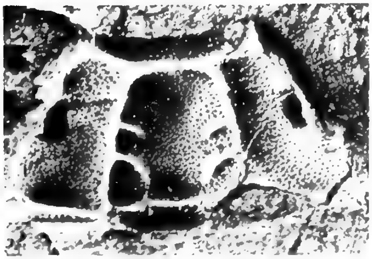
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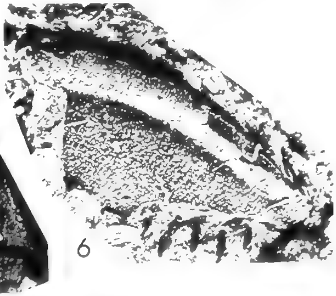
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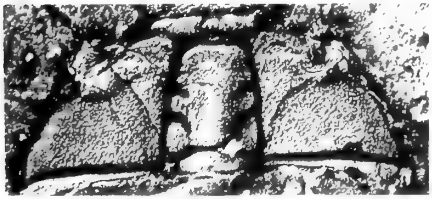
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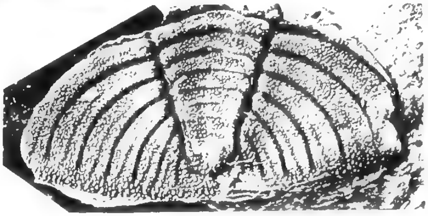
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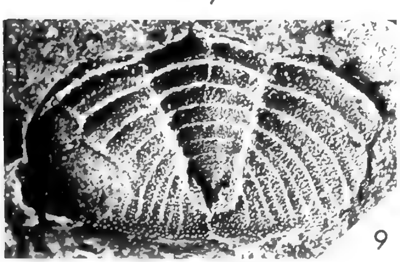
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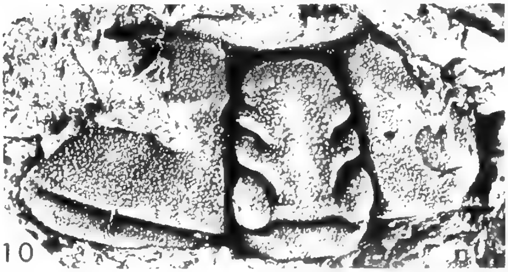
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PLATE 13

Platycalymene tasgarensis Shirley **simulata** subsp. nov. p. 93

Llandeilo, stream section 15 yards south-west
of the old quarry 350 yards west of Maesgwynne.
G.R. SO.059566.

FIG. 1. Paratype. Internal mould of pygidium. It. 3017. × 5.

Llandeilo, 120 yards south-east of Tre coed on
left bank of stream. G.R. SO.054552.

FIG. 2. Paratype. External mould of incomplete cranidium showing the smooth lateral glabellar furrows. It. 3015. × 6.

Llandeilo, left bank of Dulas Brook, 150 yards south-west
of the old quarry 350 yards west of Maesgwynne.
G.R. SO.058564.

FIG. 3. Holotype. Internal mould of cranidium. It. 3013. × 5.

Plaesiacomia sp. p. 95

Lower Llanvirn, right bank of upper reaches of
Camnant Brook, 230 yards S 13° W of the fence crossing
near the stream source. G.R. SO.088575.

FIGS. 4, 5. Left lateral and dorsal views of internal mould of pygidium. It. 3026. × 8.

FIG. 6. Internal mould of pygidium showing axial segmentation. It. 3027. × 10.

FIGS. 7, 8. Dorsal and oblique views of internal mould of incomplete cranidium. It. 3024. × 8.

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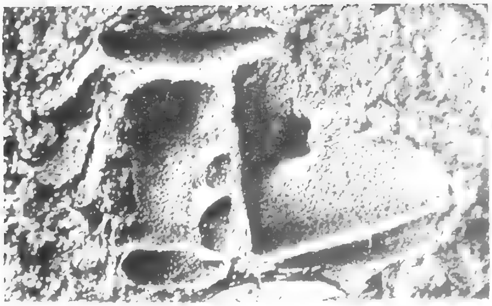

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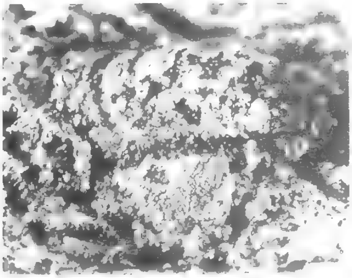

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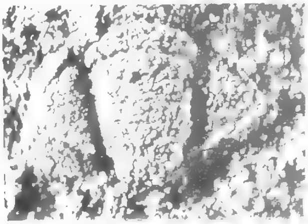

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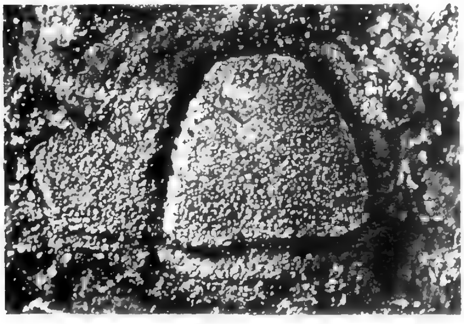

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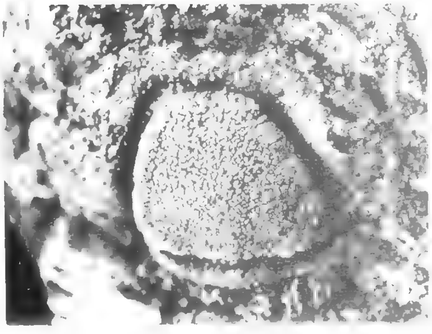

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PLATE 14

Plaesiacomia sp. p. 95

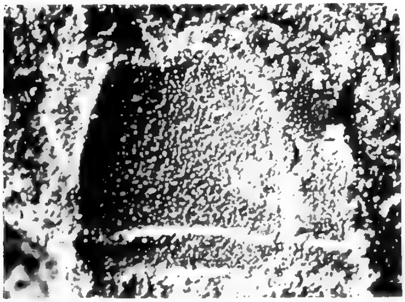
Lower Llanvirn, right bank of upper reaches of
Camnant Brook, 230 yards S 13° W of the fence crossing
near the stream source. G.R. SO.088575.

FIG. 1. External mould of incomplete cranidium. It. 3025. ×8.
FIG. 2. Internal mould of incomplete cranidium. It. 3023. ×6.

Platycoryphe vulcani (Murchison) p. 97

Horizon and locality as for Fig. 1.

FIGS. 3, 6. External and internal moulds of incomplete cranidium. It. 2832. ×3.
FIG. 4. External mould of pygidium. It. 2836. ×4.
FIG. 5. Internal mould of librigena. It. 2835. ×5.
FIG. 7. Internal mould of pygidium. It. 2833. ×3.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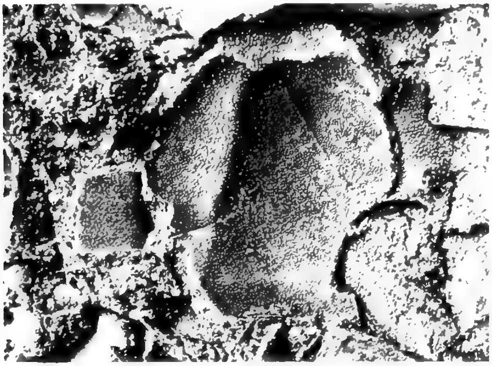
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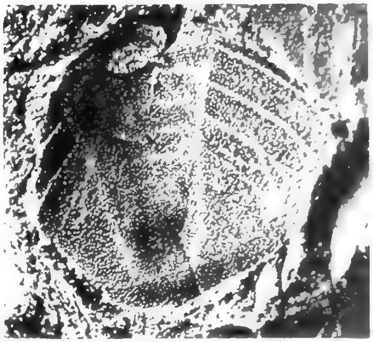
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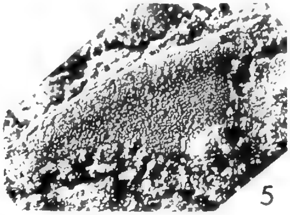
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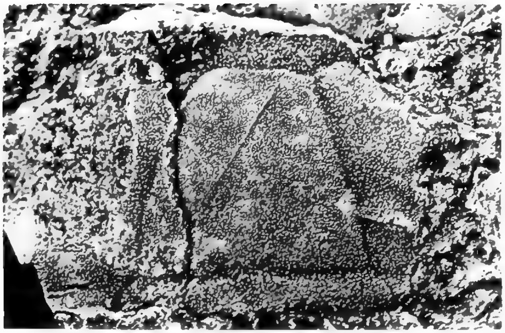
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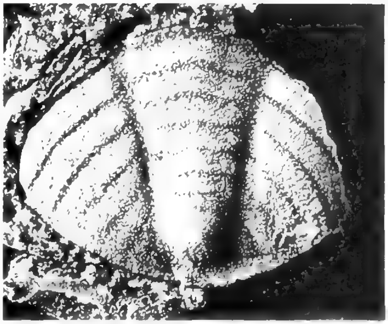
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EIFELIAN BRACHIOPODS FROM PADAUKPIN, NORTHERN SHAN STATES, BURMA

M. M. ANDERSON, A. J. BOUCOT

and

J. G. JOHNSON

BULLETIN OF
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GEOLOGY Vol. 18 No. 4
LONDON : 1969

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Pp. 105–163; 10 *Plates* 10; *Text-figures*

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EIFELIAN BRACHIOPODS FROM PADAUKPIN, NORTHERN SHAN STATES, BURMA

By M. M. ANDERSON, A. J. BOUCOT & J. G. JOHNSON

CONTENTS

SYNOPSIS

The articulate brachiopods from the Padaukpin area include thirty-two species assigned to thirty-one genera. *Cimicinoides struvei* is proposed as a new genus and species of terebratulid brachiopods. The fauna has marked affinity with the Eifelian brachiopod fauna of western Europe and is concluded to be of Eifelian age. From a provincial point of view it is noteworthy that the Padaukpin brachiopods have stronger affinity with European Eifelian brachiopods than those of regions to the north in the U.S.S.R.

Padaukpin conodonts and foraminifera, previously undescribed, are also referred to in the discussion on the age of the brachiopod fauna.

I. INTRODUCTION

A LARGE collection of fossils was made between 1959 and 1961 from fossiliferous beds close to Padaukpin, some ten miles east-north-east of the administrative centre of Maymyo (Text-fig. 1a), in the Northern Shan States of Burma while one of us (M.M.A.) was Colombo Plan Visiting Professor of Geology at the University of Mandalay. This site is an historic one as the fossils have long been used locally as charms and about the middle of the last century King Mindoon Min had pits dug in the area because it was thought that the fossils indicated hidden treasure. The first geologist to visit Padaukpin was La Touche of the Geological Survey of India who several years later published a Memoir on the Geology of the Northern Shan States (1913) which is still the only authoritative work on the region, as little has been published on any aspect of the geology of this part of Burma, apart from mineral deposits of economic interest, since that date. La Touche collected a great variety of fossils which were described by Cowper Reed (1908).

Padaukpin (lat. 22° 5′ 48″, long. 96° 37′ 30″)[1] is a small village lying about a mile east-south-east of Wetwin railway station on the Mandalay Lashio railway which here

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[1] La Touche (1913), Cowper Reed (1908 on information supplied by La Touche), and later writers quoting these works give the position of Padaukpin as lat. 22° 6′ 30″, long. 96° 44′, but more accurate surveying since that time shows that the lines of latitude and longitude on the maps which accompany La Touche's Memoir are slightly incorrect.

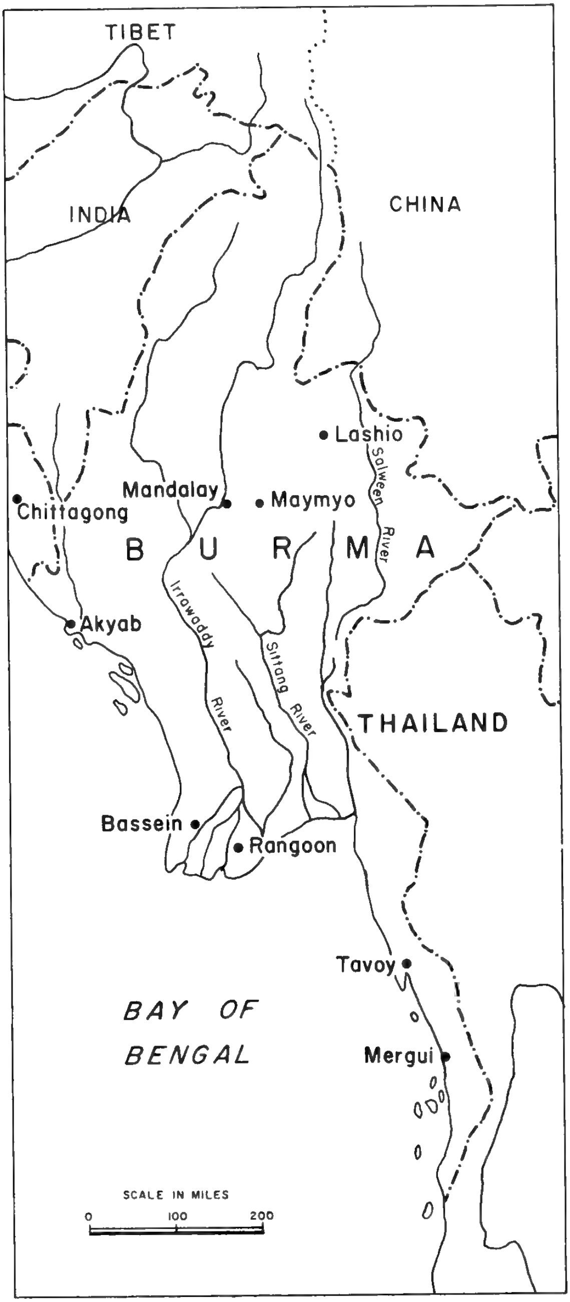

FIG. 1a. Outline map of Burma showing the position of Maymyo.

runs more or less parallel to the main road from Maymyo to Lashio (see Text-fig. 1b). Just before the road reaches the railway station it is joined by a motorable track which runs almost east and then south-east to a power station on the Ge-raung chaung[1] (chaung = stream). This track passes to the west and south of Padaukpin and it is along the bullock-cart tracks that lead from it to the western side of the village that the exposures described by La Touche (1913) occur. The exposures are present, however, only over a short distance of about 20 yards before the entrance to the village where the bullock-cart tracks lead up over a gentle rise marking the position of the limestone beds; laterally the beds can be traced for about a hundred yards. Even over this small area only a few low rounded outcrops of small size appear through the overlying clay soil which is covered with bushes and trees between the tracks, so that exposures are practically confined to the places where the wheels of the bullock-carts have cut through the clay and exposed bedrock. The beds dip gently to the east and probably only about ten feet of limestone beds are present. Fossils were difficult to extract from the hard limestone but large

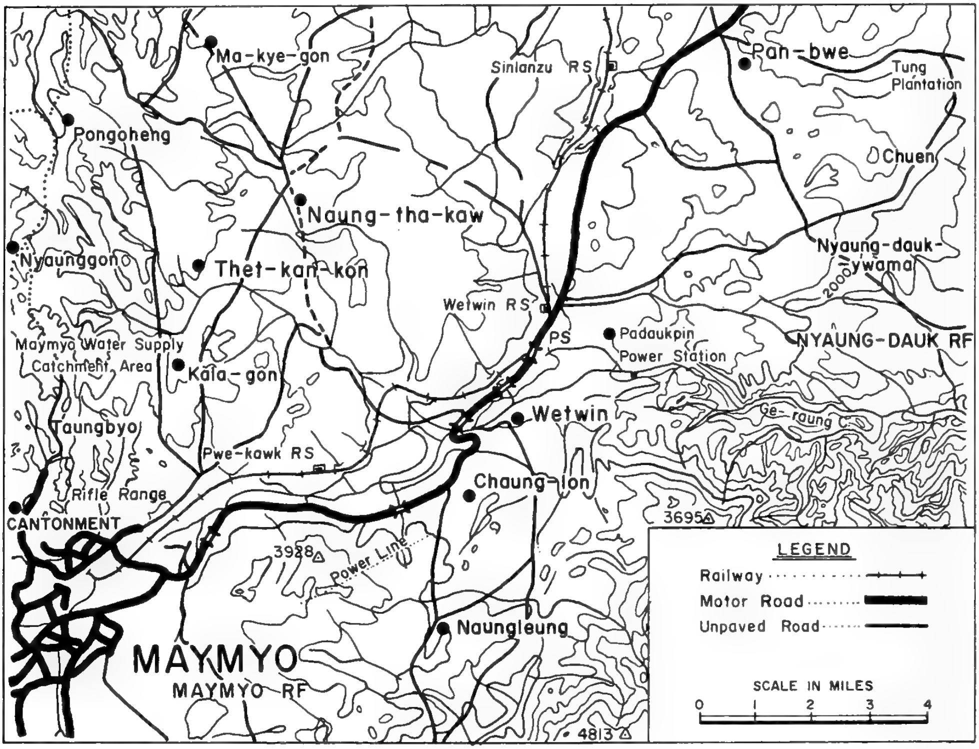

FIG. 1b. Wetwin area, east of Maymyo, with Padaukpin village lying about one mile east-south-east of Wetwin railway station.

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[1] Spelt Ke-laung on map accompanying La Touche's Memoir (1913).

numbers were collected from the overlying clay which has resulted from the *in situ* weathering of the limestone.

A second, previously unknown, fossil locality at the same horizon was found to occur along the strike of the limestone beds on another gentle bush and tree covered slope south of Padaukpin. A footpath runs south from the village to join the motorable track to the power station, and the locality occurs just east of the path about a quarter of a mile from the village (see Text fig.-1c). The limestone beds are again poorly exposed but their presence is indicated by the large number of fossils which have weathered out. These were collected over an area similar in extent to the first locality. Here, however, the overlying clay is much thinner and large colonies of tabulate corals and stromatoporoids were lying on the surface or close to it, apparently undisturbed, in their original positions of growth.

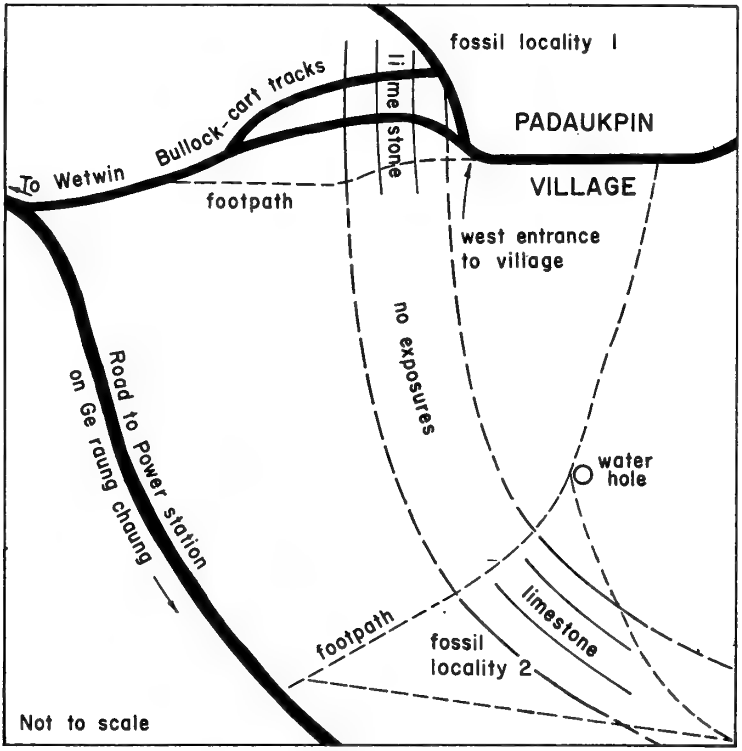

FIG. 1c. Fossil localities at Padaukpin.

The collection of fossils from Padaukpin described by Cowper Reed (1908) included species belonging to the following invertebrate groups: corals (tetracorals and tabulates), stromatoporoids, brachiopods, crinoids, bryozoa, lamellibranchs, gastropods, cephalopods, trilobites, and annelids. In addition to these groups the new collection from the two Padaukpin localities contains conodonts, foraminifera, ostracodes, sponges, tentaculites, blastoids, and echinoids; the conodonts were isolated by Dr. Gilbert Klapper of Pan American Petroleum Corporation, Tulsa, Oklahoma, from a relatively small sample of the limestone, and his report is given below. Dr. D. F. Toomey, also of the Pan American Petroleum Corporation, has provided information on the foraminifera extracted from the same sample (see page 117 and Toomey 1968). The Padaukpin fauna thus includes not only benthonic forms but also the remains of some of the pelagic and planktonic micro-organisms which were living in the overlying waters at the same time.

Conodonts, ostracodes, sponges, tentaculites, blastoids, and echinoids have not previously been recorded from the Devonian of Burma. Unfortunately no complete sponges or echinoids were discovered; the presence of the former is indicated by abundant loose spicules while the latter are represented by spines, which are fairly common, and, more rarely, by individual interambulacral plates. La Touche did not find any foraminifera at Padaukpin but he mentioned the presence of numerous minute foraminifera, including species of *Endothyra*, *Textularia* and possibly *Trochammina*, in an oölitic dolomite near Mongyaw (1913 : 191) which is also considered to be Devonian in age.

La Touche (1913) described the Padaukpin limestones as a coral reef. There is, however, no development of a reeflike structure at either locality and although corals represent an important part of the fauna they are probably matched in abundance by stromatoporoids, brachiopods, crinoids and possibly even by bryozoa so that a special emphasis on corals is misleading. The limestones were laid down as distinct beds and since they consist largely of the remains of organisms and are almost entirely of biochemical origin they can be referred to as biostromes (Cummings 1932). An account of the palaeoecology of the fossil communities within the Padaukpin biostromes will be published elsewhere.

The area between the two localities, which is partly cultivated and partly covered with thick vegetation, was carefully searched for exposures of limestone, but none were found; attempts to find the bed elsewhere in the district were equally unsuccessful. This was not for lack of outcrops in the vicinity as the bedrock is well exposed, and even though some of the outcrops are only a few yards away from the Padaukpin limestone beds, in all cases it is found to be dolomite. It seems likely, therefore, that, as was first suggested by La Touche (Cowper Reed 1908, from notes supplied by La Touche), the limestones are interbedded with the dolomite. They also appear to pass laterally into dolomite as shown by the fact that along the strike of the Padaukpin beds, a short distance south of the second locality, dolomite is present in which the outlines of fossils can be recognized, and brachiopods in particular are represented by cavities with a drusy lining of dolomite. Such cavities are rarely seen elsewhere in the dolomite beds which have a wide distribution in the Northern Shan States and generally appear to be unfossiliferous. However, these dolomites do occasionally show traces of fossils, generally indeterminate but sometimes the outlines of corals, crinoid ossicles, brachiopods, and foraminifera can be made out.

Thin sections of the fossiliferous dolomite of the Padaukpin area, and of the dolomites from elsewhere that show traces of fossils, reveal that the original shell or skeletal material has been completely replaced by dolomite and the structure of the fossils totally destroyed. The former presence of fossils is indicated by ghost structures, by dust particles outlining the original shapes, and by differences of grain size between areas formerly occupied by fossils and the surrounding matrix. In the last case the large, but variable, size of the dolomite grains of the matrix contrasts with the small and uniform size of the grains which have replaced the fossil structures: this difference is probably attributable to selective replacement. The outlines of fossil fragments are, in general, only discernible and not readily recognizable but occasionally they can be identified; La Touche (1913 : 192) drew attention to the fact that foraminifera are the only organisms within the dolomite to have escaped replacement. He also described oölitic dolomite (1913 : 191) in which some of the oöids still show a concentric structure of alternate minutely crystalline and " dirty " bands while others are represented only by circular or oval outlines within which there is a partial or complete filling of large euhedral crystals of dolomite.

The presence of oöids, recognizable fossils and discernable but unidentifiable fossils in the dolomite beds (the positive and negative relicts of Teodorovich 1958) is proof of the replacement origin of the dolomite. The dolomite beds in the Northern Shan States, with which the Padaukpin limestones are associated, have thus originated by replacement of calcium carbonate during diagenesis, and the Padaukpin limestones therefore represent a part of the sequence which escaped dolomitization. Although this dolomitization was regional in extent it must have operated selectively as apart from the Padaukpin limestones, other " patches " of limestone are known within the succession which have escaped replacement or suffered only partial dolomitization.

The limestones and dolomites of the Padaukpin area belong to the Plateau Limestone. La Touche (1913 : 182) gave this name to the " limestones " because they underlie the greater part of the plateau country of the Shan States and their weathering is responsible for the distinctive scenery of these upland areas; he considered them to range from Devonian to Permian in age. The systematic survey of the geology of the Northern Shan States by La Touche and his colleagues of the Indian Geological Survey, which culminated in his Memoir (1913), was carried out during field seasons from 1899 to 1912, and it seems likely that this name was adopted before they realized that the Plateau Limestone is, in fact, almost entirely a dolomite formation. True limestones, which overlie the dolomite beds and yield a different fauna, represent only the upper part of the formation which is very much thinner than the lower part of this carbonate sequence. Therefore, when La Touche came to write his Memoir he divided the formation on a lithological and a faunal basis into a lower section to contain the dolomite beds with a Devonian fauna and an upper or Anthracolithic section for the limestones with a Permo-Carboniferous fauna.

The name Plateau Limestone is clearly inappropriate for either the formation as a whole, or for one or other of its subdivisions, because the lower is dominantly dolomitic with only subordinate limestones while the upper is not restricted to plateau country, and the true limestones are, in any case, less widespread in the Northern Shan States than the beds of dolomite. For the time being no nomenclatorial revision is attempted.

The two divisions of the Plateau Limestone were not mapped separately by La Touche (1913) because he believed that the lower passed without any stratigraphic break into the upper thus giving a Carboniferous to Permian age range for the true limestones. However, no diagnostic Carboniferous fossils have yet been found in these limestones and, in spite of its apparent conformity, Holland *et al.* (1956) and the authors regard the upper section of the Plateau Limestone as a separate formation, Permian in age.

The lower, Devonian, division of the Plateau Limestone is of considerable thickness; La Touche (1913 : 186) estimated that in the valley of the Nám Tu river north of Hsipaw it was about 6,600 feet. Even this figure represents an underestimate because the top of the formation in this area was eroded before the deposition of the overlying Jurassic strata, and the lowermost beds, here resting on Silurian or Lower Devonian sandstones, are probably not the actual basal beds as there is a progressive overlap of older beds by younger beds within this formation. However, the general scarcity of fossils within the dolomite beds makes it impossible at present to determine which part of the Devonian is represented by a particular locality in the Northern Shan States with the exception of the beds in the immediate vicinity of the fossiliferous localities of Padaukpin, Wetwin, and one small area in the valley of the Kelaung chaung (= Ge-raung chaung). Although these three localities are all within a few miles of one another (see Text-fig. 1b) they appear to represent three different horizons within the Devonian. Unfortunately it has not been found possible to trace these beds laterally so that their field relationships are unknown.

The Padaukpin limestones are considered by the authors to be Eifelian, thus confirming the work of Cowper Reed (1908). The locality in the valley of the Kelaung chaung is also in limestones, lithologically similar to those of Padaukpin, but the small fauna of corals, brachiopods, and a single species of annelid is a different assemblage. Cowper Reed (1929) regarded the fauna as a whole as indicative of the Givetian. At Wetwin the fossiliferous beds are yellow clay shales, and associated with this change in facies the shales are dominated by lamellibranchs and gastropods but include bryozoa and mud-dwelling brachiopods. The Wetwin Shales represent a local intercalation within the Devonian dolomitic sequence. Cowper Reed (1908 : 183) stated that in " view of the absence of stratigraphical and more definite palaeontological indications we may provisionally refer the Wetwin beds to the upper Middle Devonian on the strength of the American affinities ". He suggested that these beds overlie the Padaukpin limestones.

In the Zebyngi area La Touche (1913 : 166) stated that the Zebyngi beds, then regarded as uppermost Silurian, are succeeded without any apparent stratigraphical break by the basal beds of the overlying dolomite sequence. This seeming paradox is explained by the fact that the Zebyngi beds carry Lower Devonian graptolites. According to Professor W. B. N. Berry, University of California, Berkeley (oral communication, 1967) graptolites from the Zebyngi beds and now in the Sedgwick Museum seem closest to the Bohemian Lower Emsian species *Monograptus atopus*. These are specimens that were labelled *M. dubius* in the Sedgwick collections. Other specimens labelled *M.* cf. *M. riccartonensis* were determined by Berry as *Monograptus* sp. of the *hercynicus* type.

This paper deals only with the Brachiopoda from the Padaukpin limestones. It is mainly concerned with a revision of the genera and species present in the fauna based on the specimens in La Touche's original collection from the fossiliferous exposure immediately west of Padaukpin village as well as on the specimens in the new collection obtained from this locality and from the previously unknown locality south of the village. The beds at these two places belong to the same horizon and contain an identical fauna so that no distinction is made here between the specimens obtained from one or other of the localities. In addition to describing the species present and considering their systematic position, the age, correlation, and palaeogeography of the brachiopod fauna are also discussed.

La Touche's collection was described by Cowper Reed (1908) who identified forty-five species (excluding three unnamed species of uncertain genus) which he grouped within twenty genera. Of the forty-five species, four were named as new species and four as new varieties by Cowper Reed, and the rest he considered to be species already known from Europe, North America, or China. The authors recognize thirty-two species, including one new species, in the brachiopod fauna from Padaukpin, and as only two of these belong to the same genus thirty-one genera are represented.

The new collection from the Padaukpin limestones is housed in the British Museum (Natural History) and the specimens figured from this collection are catalogued under the code number BB, but there are a few specimens illustrated which came from the La Touche collection in the Sedgwick Museum, and these have a code number beginning with A.

II. ACKNOWLEDGEMENTS

Preparation of this paper was done at the California Institute of Technology and supported by a National Science Foundation grant, number GP-3743. The government of the Union of Burma (Ministry of National Planning) financed Anderson's field work in the northern Shan States. Mr. A. G. Brighton, Curator, Sedgwick Museum, Cambridge, made available a collection made by La Touche. The writers thank Dr. Gilbert Klapper and Dr. D. F. Toomey of the Pan American Petroleum Corporation, Tulsa, Oklahoma for their contributions dealing with conodonts and foraminifera from Padaukpin.

III. AGE AND CORRELATION

Reed (1908 : 142–146) discussed the age of the fossiliferous beds at Padaukpin that yielded the large fauna he described. He concluded (1908 : 143) that the fauna was of late Eifelian age. The correlation is well based because of the relatively high percentage of forms that are either conspecific or closely comparable to those in the Middle Devonian of the Eifel. The brachiopods can certainly be so characterized and the strong representation of the Eifelian coral *Calceola* points to a similar age assignment. Indeed, these broad conclusions based on the overall aspect of the fauna leave little doubt of Middle Devonian age of the containing beds. A significant number of the Padukpin species are not known to occur below the Middle Devonian in the Eifel, but there is always the presumption that a favourable facies in beds of perhaps late Emsian age would support a fauna of strong Eifelian aspect. However, turning to stocks that are known to cross the Emsian-Eifelian boundary, such as *Reticulariopsis* and *Devonaria,* the strictly post-Lower Devonian position of *R. eifliensis* and *D. minuta* in Europe allows some confidence in a similar age for the beds at Padaukpin.

With regard to the proper assignment of the fauna to the Eifelian or to the Givetian, it must be noted that many of the brachiopods that can be described in the west European nomenclature are species that are known in both the Eifelian and Givetian; notable exceptions are *Devonaria minuta* and *Plectospira ferita.* Neither of these species is known to range above the top of the Eifelian in Europe. However, the strongest indications from the brachiopods of an early Middle Devonian age are afforded by the ribbed spiriferids, *Indospirifer* and *Alatiformia.* So far as the writers are able to discover, both of these have a range of upper Emsian to Eifelian. The external similarity of the new genus and species *Cimicinoides struvei* to the middle Eifelian form called *Cimicinella simulatrix* by Struve (1964) suggests the possibility of an age correspondence based on these forms, especially since *Cimicinoides* has a distinctly different loop structure from the late Emsian-early Eifelian *Cimicinella cimex.*

Part of the Burma sample, weighing 5·4 kg., was processed for conodonts by Dr. G. Klapper of the Pan American Petroleum Corporation, Tulsa, Oklahoma. The following conodonts are listed from the sample:

Polygnathus linguiformis linguiformis Hinde, 1879—(9 specimens)
Polygnathus sp. (cf. *Polygnathus xylus sensu* Bischoff & Ziegler 1957)—(14 specimens)
indeterminate fragments of *Polygnathus* Hinde, 1879—(12 specimens)
Angulodus sp. indet. (1 specimen)
Hibbardella sp. indet. (1 specimen)
Hindeodella sp. indet. (1 specimen)
Synprioniodina sp. indet. (1 specimen)
indeterminate fragments of compound conodonts (28)
Belodella triangularis (Stauffer 1940)—(11 specimens)

According to Klapper (written communications, 3rd July, 1966, and 26th May, 1968), the nominate subspecies of *Polygnathus linguiformis* occurs in the Eifelian, Givetian, and in the lowermost part of the *Manticoceras*-Stufe. At least one specimen of the nominate subspecies is also known from the Emsian (Zorgensis-Kalk, Ziegler 1956, pl. 7, figs. 17, 18), although *Polygnathus foveolatus* Philip & Jackson 1967, is the common polygnathid in upper Emsian strata (Schönauer Kalk, Murrindal Limestone, and Taemas Formation). The form listed as *Polygnathus* sp. seems to be closely comparable to specimens assigned to *Polygnathus xylus* in the sense of Bischoff & Ziegler (1957, pl. 5, figs. 11–17). Twelve of the Burma specimens in this category are most like that of Bischoff & Ziegler (1957, pl. 5, fig. 11) from the Kalkige Zwischenschichten (upper Eifelian), whereas the remaining two Burma specimens under this designation are more comparable to that of Bischoff & Ziegler (1957, pl. 5, fig. 13) from the Günteröder Kalk (upper Eifelian). *Polygnathus xylus sensu* Bischoff & Ziegler is reported by them to range from the upper Eifelian into the lower part of the Givetian (Odershäuser Kalk) and, in the slightly different sense of Bultynck (1966, p. B 199–200, pl. 2, figs. 1–3), is reported to range from the upper Couvinian (Co2d) into the base of the Givetian in Belgium. The remaining conodonts listed do not as yet bear on long-range correlation. Thus the evidence derived from study of the specimens of *Polygnathus*, although admittedly inadequate, would suggest a correlation of the Burma sample with upper Eifelian through lower Givetian strata in central Europe.

It is of interest to note that conodonts have been recorded recently from relatively nearby areas. Conodonts were described from the northern part of west Pakistan (Barnett, Kohut, Rust, & Sweet, 1966). This fauna indicates a Pridoli (i.e. latest Silurian) or Gedinnian (i.e. early Early Devonian) age. The presence of Middle or possibly Upper Devonian conodonts has been noted from near Lutherwan in Kashmir by Gupta, Rhodes, & Austin (1967). These conodont occurrences appear to be older and younger respectively than the Padaukpin occurrence noted here.

IV. PADUKPIN FORAMINIFERA

From acid etching of a sample of Padaukpin " limestone " weighing 5·4 kg. a residue of 56·5 gm. was obtained (fraction retained on a 115 microns screen). The residue was " picked clean " over a period of 28 hours, and yielded approximately 1122 identifiable specimens of smaller foraminifers. A few gastropod and smooth-shelled ostracode steinkerns, and a few scolecodont specimens were also obtained. The following foraminifers compose the Padaukpin assemblage:

A. Agglutinated Form—
  1. *Minammodytes* sp. (582 specimens = 51·8%)
  2. *Hyperammina*?-like forms (7 specimens = 0·6%)
  3. *Hemisphaerammina* sp. cf. *H. bradyi* Loeblich & Tappan 1957, (452 specimens = 40·3%)
  4. *Metamorphina* sp. cf. *M. tholsus* (Moreman), (27 specimens = 2·4%)
  5. *Thurammina*?-like forms (34 specimens = 3·0%)

B. Calcareous Form (pyritized steinkerns)—
  6. *Nanicella* sp. (8 specimens = 0·7%)

C. Calcareous/or Agglutinated Form (pyritized steinkerns)—
  7. *Semitextularia* sp. cf. *S. thomasi* Miller & Carmer 1933, (12 specimens = 1·0%).

Paleoecologically, the foraminiferal assemblage is unique in that it is a dominantly encrusting microfauna (over 97%), suggesting that the foraminifers must have lived on some sort of perishable support, i.e., marine grasses. The foraminiferal assemblage is primarily agglutinated, but this is undoubtedly prejudiced by the type of sample preparation (acid residues). Two large (2 inch × 3 inch) thin-sections were prepared from the limited sample available and searched for calcareous foraminifers, but none were observed. However, the presence in the acid residues of a limited number of pyritized steinkerns of originally calcareous forms such as *Nanicella* and possibly *Semitextularia* indicates that originally both agglutinated and calcareous foraminifers composed the microfauna.

Stratigraphically, the foram assemblage appears to be of little help in age-dating the Padaukpin Beds of Burma. This is primarily due to the lack of study of pre-Upper Devonian foraminiferal microfaunas.

It is to be noted that comparable species of agglutinated foraminifers representing the genera *Minammodytes*, *Hyperammina*, *Hemisphaerammina*, *Metamorphina*, and *Thurammina*, are relatively common in rocks as old as Upper Silurian (Wenlockian).

Two foraminiferal species from the Padaukpin Beds which may have potential age significance are the foraminifers *Nanicella sp.* and *Semitextularia* sp. cf. *S. thomasi* Miller & Carmer 1933.

The genus *Nanicella*, up until recently, had been considered as an Upper Devonian form. Mouravieff & Bultynck (1967) however, reported and described pyritized steinkerns, similar to the Padaukpin specimens, from the Couvinian Co2c interval (= Eifelian) of Belgium, in beds which may be roughly of the same age as the Padaukpin Beds of Burma. These two occurrences of *Nanicella* mark the oldest reported occurrences to date of this genus. Mouravieff & Bultynck (1967) also have illustrated similar pyritized steinkerns from the Frasnian (Upper Devonian) of Belgium. In North America, *Nanicella* has only been reported from Upper Devonian rocks.

The foraminifer *Semitextularia thomasi* Miller & Carmer 1933, has been reported (Sobat 1966) from the Middle Devonian (Eifelian) Wissenbacher Schiefer of the Rheinisches Schiefergebirge of West Germany. More recently (Mouravieff & Bultynck 1967) described and illustrated pyritized steinkerns of *Semitextularia* sp., similar to the specimens from the Padaukpin Beds of Burma, from the Couvinian Colb interval (= Eifelian) of Belgium. Both of these occurrences of *Semitextularia*, in Burma and Belgium, mark the oldest occurrence of this form to date. In North America, the oldest occurrence of *S. thomasi* Miller & Carmer 1933, is from the upper Middle Devonian (Givetian) rocks (Wanakah Shale, Hamilton Group) of New York State (Copeland & Kesling 1955). Frasnian pyritized steinkerns of *Semitextularia* have also been illustrated by Mouravieff & Bultynck (1967).

V. PALAEOGEOGRAPHICAL DISTRIBUTION

The brachiopod fauna described in this paper, which may be annotated as the *padaukpinensis* fauna, is recognizable at several localities in southern China or its occurrence is suggested by citation of a few of the diagnostic forms described here.

A faunal occurrence has been noted (China, board of editors and others 1958 : 69) from thick beds of dolomitic limestone interbedded with shale and thin bedded limestone in western Yunnan. The reported assemblage consists of *Leptaena* " *rhomboidalis* ", " *Camaroforia* " *lummatoniensis*, *Reticulariopsis curvatus*, *R. aviceps*, *Sieberella brevirostris*, " *Atrypa reticularis* ", *Spinatrypa aspera sinensis*, *Indospirifer padaukpinensis*, *Aulacella eifeliensis*, *Productella baitelensis*, and *Schizophoria striatula*. Insofar as comparisons can be made from faunal lists, the western Yunnan occurrence appears to closely duplicate in part the fauna from Padaukpin and may realistically indicate to some extent the paleogeographic distribution of that fauna.

In the French edition of the Chinese Stratigraphic Lexicon (Roger 1965) *Indospirifer padaukpinensis* is noted in association with *Stringocephalus* sp., but the accompanying brachiopods, including *Spinatrypina bodini* (Mansuy), indicate little relation to the *padaukpinensis* fauna as described here. The cited occurrence is in the Kutaoling Limestone or eastern Kansu Province (Roger 1965 : 462–463).

Also in Roger (1965 : 653) *Indospirifer padaukpinensis* is listed in association with *Spinatrypina bodini*, *Atrypa pechiensis*, and species of *Productella*, *Emanuella*, *Schizophoria*, *Leptostrophia maccarthyi* Grabau, and others. This assemblage, from central Hunan, does not include *Stringocephalus*, but appears to be related to the locality discussed immediately above and not to the *padaukpinensis* fauna. The presence of *Stringocephalus* in the latter association supports a Givetian age and certainly Givetian age sedimentary rocks are widespread in China and are represented by *Stringocephalus* at many localities as noted by Boucot, Johnson & Struve (1966).

In Turkestan, Middle Devonian brachiopod assemblages have long been known that in part resemble the *padaukpinensis* fauna. Nalivkin (1930, pl. 6, fig. 1) illustrated the rhynchonellid " *Hypothyris* " *pentagona* that closely resembles the Burmese specimens. Closest comparisons can be made with the outcrop number 697 in the thick series of silicious and argillaceous shales and limestones composing the Liaglian series in south Ferghana (Nalivkin 1930 : 200, 201). Listed brachiopods of locality 697 include " *Stropheodonta* " *subtetragona*, " *Schuchertella* " *umbraculum*, " *Chonetes* " *minuta*, and " *Hypothyris*" *subsignata*. Also listed are typical Eifelian species such as " *Stropheodonta* " *lepis* and *Kayseria lens*; also the tetracoral *Calceola sandalina*. Associated with the typical Eifelian elements (including those that compare closely with the Burmese fauna) are Bohemian-Uralian elements such as *Carinatina arimaspus*, *Janius irbitensis*, " *Theodossia* " *superbus*, and others. Nalivkin (1930 : 218–221) recognized the provincial mixture of brachiopods that compose the Liaglian fauna and reached essentially the same conclusions about provincial relations of the Eifelian faunas as are noted here.

VI. EMSIAN FAUNA IN SOUTHEAST ASIA

Amongst brachiopod faunas in close proximity to the area of distribution of the *padaukpinensis* fauna is the so-called *Acrospirifer tonkinensis* fauna of northern Indo-China and adjacent regions in the south of China. Principal elements of the *tonkinensis* fauna, including the nominate species, were first described by Mansuy (1908) with additions in a later paper (Mansuy 1916). An additional valuable study of the *tonkinensis* fauna was made by Patte (1926). The characteristic brachiopods of the *tonkinensis* fauna include *Acrospirifer tonkinensis*, *Hipparionyx*? *lantenoisi*, *Dicoelostrophia annimitica*, *Ancylostrophia* sp. (= *Stropheodonta* nov. sp. aff. *S. lepis* Patte, 1926, pl. 3, figs. 9–13), *Machaeraria* sp., (= *Camarotoechia prolifica* Patte, pl. 4, figs. 7–11), and *Parachonetes*, including *P. yenlacensis* and probably " *Chonetes* " *zeili* (cf. Johnson, 1966 : 366). This association appears to be Emsian because of the presence of *Acrospirifer tonkinensis*, which most closely resembles the lower Emsian guide *A. hercyniae*. *Parachonetes* is probably restricted to pre-Eifelian rocks and *Ancylostrophia*, elsewhere is only known from the Upper Emsian Kondel

Group. Forms like the so-called *Hipparionyx lantenoisi* occur in the Lower Devonian of southeastern Australia.

In southern China the *tonkinensis* fauna has its best representation in the Yükiang Formation (Wang 1955, 1956) of Kwangsi Province. Wang (1955) recorded *Dicoelostrophia* as a characteristic element of the Yükiang Formation fauna and in his subsequent paper (1956) he illustrated a probable *Parachonetes* (*Chonetes kwangsiensis* Wang 1956, pl. 1, fig. D) and a probable *Nadiastrophia* or *Phragmostrophia* (Wang 1956, pl. 3, figs. B, C). *Acrospirifer tonkinensis* is cited from both Lower and Middle Devonian beds (China, Board of Editors and others 1958 : 74, 98, 100, 122), but the listed associated brachiopods are not significant to confirm the identification of the *tonkinensis* fauna. Similar occurrences are listed by Roger (1965 : 426, 562, 564, 612). These are all equivocal faunules, but according to Roger *Acrospirifer tonkinensis*, *Dicoelostrophia annimitica*, and a few other brachiopods characterize the Tchanyi beds assigned to the Lower Devonian in central and southern Kweichou Province (Roger 1965 : 640).

A number of important elements of the *tonkinensis* fauna are reported in the Pochiao Shale of eastern Yunnan (Yin 1938) and include *Acrospirifer tonkinensis*, a probable representative of *Ancylostrophia* (*Stropheodonta inaequistriata* var. *pattei* Yin, pl. 2, fig. 3D) and *Dicoelostrophia annimitica*. Yin described a dalmanellid from the Pochiao fauna as *Thiemella*? *communis*, and this is probably the source of citations of the genus *Thiemella* in several of the occurrences of the *tonkinensis* fauna cited above. The form is a peculiar one not easily diagnosed from the published figures, but appears to have some features in common with the dalmanellid genus *Reeftonia* from the Lower Devonian of New Zealand and southeastern Australia.

VII. FAUNAL PROVINCE

The provincial relations of both the *padaukpinensis* and *tonkinensis* faunas appear to be about the same; they consist primarily of genera and species that are characteristic of the Rhenish Community and are particularly lacking in elements that are ordinarily diagnostic of the Bohemian and Uralian subprovinces as defined by Boucot, Johnson, & Talent (1967). In the case of the older *tonkinensis* fauna, one peculiar endemic form, *Dicoelostrophia*, marks the fauna as provincially distinct, but the Eifelian *padaukpinensis* fauna resembles Rhenish Eifelian faunas without any generic exceptions and this points up a certain lessening in provinciality of the Middle Devonian brachiopod faunas compared to those of the Lower Devonian.

Both of the faunas discussed above appear to be restricted geographically and have their principal development between about 15 and 25 degrees north latitude in the southeast Asian peninsula. The Turkestan occurrence is much further north and west, but conveniently located geographically in accordance with its mixed or transitional fauna. The Uralian Lower and Middle Devonian brachiopod faunas are all well to the north even of the transitional Turkestan locality. Rhenish type faunas appear to have undergone a latitudinal shift of some 30 (by comparison with present-day latitudinal positions) degrees in the span of the Eurasian landmass.

VIII. SYSTEMATIC DESCRIPTIONS

Phylum Brachiopoda

Class *ARTICULATA*

Order ORTHIDA

Suborder ORTHOIDEA

Superfamily **DALMANELLACEA** Schuchert 1913

Family **RHIPIDOMELLIDAE** Schuchert 1913

Subfamily **RHIPIDOMELLINAE** Schuchert 1913

Genus ***AULACELLA*** Schuchert & Cooper 1931

Type species. *Orthis eifeliensis* Schnur 1853 : 213, pl. 37, fig. 6, *pro* Verneuil 1850 : 161 (*nom. nud.*).

Aulacella eifeliensis (Schnur 1853)

(Pl. 1, figs. 1–12)

1853 *Orthis eifliensis* Schnur : 213, pl. 37, figs. 6a-c.
1908 *Orthis* (*Rhipidomella*) *eifeliensis* Reed : 81, pl. 13, figs. 25–26a.
1931 *Aulacella eifelensis* Schuchert & Cooper : 246.
1932 *Aulacella eifelensis* Schuchert & Cooper : 122, pl. 19, figs. 7, 8, 10, 11, 13.
1959 *Aulacella eifeliensis* Biernat : 26, pl. 1, figs. 10–15; pl. 2; pl. 3, figs. 9–10; pl. 12, figs. 1–2.
1965 *Aulacella eifeliensis* Wright : H333, fig. 212, 1.

Material. Fifty specimens.

Figured specimens. BB 55500-BB 55507.

Description. *Exterior.* The valves are subequally biconvex in lateral profile, generally having the pedicle valve strongest posteriorly, and only very slightly convex in its anterior portions. The brachial valve is more evenly curved from front to back. In outline the shells are suboval to subquadrate with a short hinge line and maximum width anterior to midlength. The pedicle valve is more or less flat across its anterior extremities and the brachial valve commonly bears a shallow sulcus that begins at about the dorsal umbo.

The ventral interarea is narrow, less than half the maximum width of the valves, and is nearly flat and triangular and is steeply apsacline to catacline. It is cleft by a triangular open delthyrium. The interarea of the brachial valve is very narrow, flat, triangular, and orthocline.

The external ornament consists of fine radial costellae crossed at irregular intervals by well marked growth lines. The growth lines are uncommon in shells less than 1 cm. in length, but are prominent anteriorly.

Interior of pedicle valve. The specimens available for description are small and on these the hinge teeth are triangular in their outline parallel to the plane of commissure, but are plate-like on their extremities which are directed toward the anterior portion of the brachial valve. Dental lamellae are not present, but the teeth are supported basally by thickenings of the shell that join the teeth to the wall of the valve. The apex of the delthyrial cavity bears a triangular concave pedicle callist.

The muscle scars are impressed posteriorly and bordered by low bounding ridges around their anterolateral portions. The diductor impressions widen posteriorly, then have subparallel or converging anterolateral edges, and may be faintly flabellate anterolaterally. The adductor scars are not impressed. Generally the anterior half of the diductor impressions is separated by a rounded myophragm.

Interior of brachial valve. The brachiophores in small specimens are triangular and somewhat plate-like, but curved so that the convex surfaces of the plates face dorsomedially. The outer edges of the brachiophores bound the sockets medially and the inner edge of the interarea bounds the sockets posterolaterally. The sockets are developed on the base of the valve which may be slightly thickened and elevated, but no fulcral plates are present. In small specimens the cardinal process arises from the floor of the triangular notothyrial cavity as a rod or prism of suboval cross-section. In larger specimens the cardinal process becomes elongated and erect and wider on its anterior edge, narrowing to a knife-like wedge toward the apex. Larger specimens develop a ponderous myophragm and shell material posteriorly that wholly fills up the notothyrial cavity and increases the size of the brachiophores with pad-like additions of shell material on their medial sides. The myophragm posteriorly is relatively narrow, thick, high, and rounded. It broadens but becomes lower anteriorly. The anterior and posterior adductors are only poorly differentiated by deeper impression of the anterior pair. Muscle bounding ridges are not developed. The posterior adductors are more or less triangular and deeply impressed, especially posteriorly, while the anterior pair is more widely set-apart due to the broad myophragm and each is more or less trapezoidal in outline. The adductor impressions merge almost imperceptibly with the interior of the shell anteriorly.

Internal crenulations. In small pedicle valves the internal crenulations developed around the periphery are grouped commonly in two, three, or four with interspaces of various widths separating the individual rod-like elements of the crenulations one from another, and the groups are separated by interspaces that are a little wider than those separating the individuals. In the brachial valve the crenulations also are grouped, but the rods in the several groups are not so well developed, and each group has somewhat flat and grooved appearance rather than a group of rods.

Superfamily **ENTELETACEA** Waagen 1884

Family **SCHIZOPHORIIDAE** Schuchert & LeVene 1929

Subfamily **SCHIZOPHORIINAE** Schuchert & LeVene 1929

Genus ***SCHIZOPHORIA*** King 1850

TYPE SPECIES. *Conchyliolithus Anomites resupinatus* Martin 1809, pl. 49, figs. 13, 14.

Schizophoria schnuri Struve 1965

(Pl. 1, figs. 13–17)

1908 *Orthis* (*Schizophoria*) *striatula* Reed : 79, pl. 13, figs. 19–24.
1965 *Schizophoria schnuri* Struve : 202, pl. 19, fig. 4, pl. 20–21.

MATERIAL. Thirty-five specimens.

FIGURED SPECIMENS. BB 55508–BB 55510.

DESCRIPTION. *Exterior.* The valves are biconvex; in small specimens where the maximum dimension is about a centimeter the valves are evenly biconvex. In larger specimens the relative convexity of the brachial valve becomes greater, becoming very deep and strongly curved throughout its length. Pedicle valves, as they get larger, tend to flatten out anteriorly, so that the place of maximum curvature is well to the posterior, near the umbo. Small specimens are transversely oval in outline, but with short hinge line and maximum width near mid-length. Larger specimens tend to broaden out anteriorly, making the outline subpentagonal with the maximum width anterior to mid-length. Large specimens commonly develop a broad, shallow sulcus in the pedicle valve, but the complementary fold in the brachial valve is only faintly developed.

The exterior bears numerous fine rounded costellae separated by rather narrow interspaces. The costellae increase in number anteriorly both by bifurcation and by implantation. In a few cases newly formed costellae also disappear anteriorly and generally the size of the costellae increases very slightly in width toward the anterior. The costellae are hollow and commonly display small suboval openings at irregular intervals. The costellae are crossed by a few concentric growth lines posteriorly, but the growth lines may become numerous anteriorly on large specimens.

Interior of pedicle valve. The teeth are not well preserved on the available specimens, but appear to be supported basally by shell thickening in the umbonal cavities. Small specimens apparently had dental lamellae that bounded the muscle bounding ridges posterolaterally. Diductor impressions are elongate subpyriform with a variably developed myophragm dividing the impressions medially. Commonly there is some slight flabellation to the anterior edge of the diductor impression which reaches to midlength in larger specimens. The ventral adductor impressions are not discernible. The internal margin is crenulated by the costellae.

Interior of brachial valve. The brachiophores are widely divergent and supported by brachiophore supporting plates that define the sockets on their medial sides. Fulcral plates define the sockets basally. Thickening in and around the brachiophore plates in large specimens causes them to loose their plate-like character. In the notothyrial cavity there is a trilobate cardinal process with a relatively thin triangular plate medially and two smaller rod-like lobes on either side. The adductor muscle scars are poorly impressed forming a nearly subcircular pattern bisected anteriorly by a low myophragm which however is thick and slopes off only gradually laterally. Two pairs of vascular tracks subparallel to the midline emanate from the medial region and continue anteriorly. The internal margin is crenulated by the costellae.

The interarea of the pedicle valve is narrow, commonly less than half the maximum width of the valve and is apsacline, low, triangular, and nearly flat except for the beak which is incurved. The interarea of the brachial valve is well developed, flat, and triangular and is orthocline to hypercline.

Family **MYSTROPHORIDAE** Schuchert & Cooper 1931

DISCUSSION. In the most recent study of the mystrophorids (Cooper 1955), *Kayserella* and *Mystrophora* are contained together in the family Mystrophoridae. Both genera are characterized by relatively well developed elevated dorsal adductor platforms. More recently Wright (1965 : H337–339) in his synopsis of the dalmanellid brachiopods has proposed two new families for small septate dalmanellids with dorsal adductor platforms. The writers see no justification for distinguishing *Kayserella* from *Mystrophora* at the family level. Very little evidence has been suggested to date to indicate the phylogeny of the small septate dalmanellids which Wright includes in his family Kayserellidae, and therefore the true family associations of the assigned genera are still in doubt. The writers therefore regard Wright's family Kayserellidae as a straight synonym of Schuchert & Cooper's family Mystrophoridae. The subfamily Prokopiinae, which Wright assigns to his family, improperly includes the schizophoriid genus *Monelasmina* (Cooper 1955 : 53; Johnson & Talent 1967). Furthermore we see no reason why *Prokopia* or *Phragmophora* should be closely associated with *Kayserella*.

Genus ***MYSTROPHORA*** Kayser 1871

TYPE SPECIES. *Orthis areola* Quenstedt 1871 : 589.

Mystrophora areola (Quenstedt 1871)
(Pl. 1, figs. 18–22)

1871 *Orthis areola* Quenstedt : 589, pl. 57, fig. 27.
1871 *Mystrophora areola* Kayser : 612, pl. 13, fig. 5.
1908 *Scenidium areola* Reed : 82, pl. 13, figs. 28–30.
1955 *Mystrophora areola* Cooper : 48, pl. 11, figs. 39–50.

MATERIAL. Three specimens.

FIGURED SPECIMEN. BB 55511.

DESCRIPTION. *Exterior.* The pedicle valves are broadly subpyriform in outline and brachial valves are transversely shield-shaped to suboval. In lateral profile the valves are unequally biconvex with a deep pedicle valve, three or four times as convex as the brachial valve. The convexity of the brachial valve is modified by the presence of a relatively deep sulcus. The ventral beak is prominent and considerably extended posteriorly. The portions of the valve anterior to the umbo are broadly flattened without a median fold, the hinge line is relatively long and straight and equal to slightly more than two-thirds the maximum width which commonly is anterior to midlength. Cardinal angles are obtuse and strongly rounded. The ventral interarea is relatively high and triangular, slightly incurved, and apsacline, although not steeply so. The dorsal interarea is moderately well developed, flat to very slightly incurved, and is anacline. The delthyrium is open and triangular, encompassing an angle of about 30 degrees. There is a small plug of shell material in its apex.

The exterior is covered by numerous low subangular costellae that increase in number anteriorly by intercalation and by bifurcation. Growth lines are not well developed.

Genus ***KAYSERELLA*** Hall & Clarke 1892

TYPE SPECIES. *Orthis lepida* Schnur 1853 : 218, pl. 45, fig. 9.

Kayserella cf. ***lepida*** (Schnur 1853)
(Pl. 2, figs. 1–3)

1853 *Orthis lepida* Schnur : 218, pl. 45, fig. 9.
?1908 *Kayserella lepida* Reed : 77, pl. 13, fig. 15.
1955 *Kayserella lepida* Cooper : 48, pl. 11, figs. 12–23.
1959 *Kayserella lepida* Biernat : 36, pl. 3, figs. 1–8.

MATERIAL. Fourteen specimens.

FIGURED SPECIMENS. BB 55512, BB 55513.

DESCRIPTION. *Exterior.* The shells are transversely shield-shaped in outline and unequally biconvex in lateral profile with the pedicle valve the deepest. The cardinal angles are slightly obtuse and maximum width is commonly near midlength. The ventral interarea is relatively well developed, flat, and triangular and is catacline in its inclination. The dorsal interarea is broad, flat, and also catacline.

The exterior is covered by numerous, fine, subangular to rounded, radial costellae. Concentric ornament is not developed.

Interior structures. No pedicle valve interiors are available. In the brachial valve the cardinal process is triangular and bilobed, crenulated posteriorly. The sockets are set against the posterior valve margin and defined on their inner edges by relatively stout brachiophores. Fulcral plates are not developed, but the shell material may be considerably thickened beneath the bases of the brachiophores and the sockets. There commonly is a more or less well developed notothyrial platform in the apex. A pair of elevated triangular plates originates just above the bases of the brachiophores and projects free anteriorly except along the midline where it joins a blade-like median septum that reaches approximately to the anterior margin of the valve. The median septum also is present dividing the scoop-shaped ventral surface of the adductor platform. Valves are crenulated along the margins by simple, elevated, rounded ridges.

Shell structure. The shell substance is endopunctate.

Order PENTAMERIDA
Suborder PENTAMEROIDEA
Superfamily **PENTAMERACEA** M'Coy 1844
Family **GYPIDULIDAE** Schuchert & LeVene 1929
Subfamily **GYPIDULINAE** Schuchert & LeVene 1929
Genus ***SIEBERELLA*** Oehlert 1887

TYPE SPECIES. *Pentamerus sieberi* von Buch *in* Barrande 1847 : 103, pl. 21, figs. 1, 2.

***Sieberella* cf. *brevirostris* (Phillips 1841)**

(Pl. 2, figs. 4–12)

1841 *Stringocephalus brevirostris* Phillips : 80, pl. 32, fig. 143.
1864–65 *Pentamerus brevirostris* Davidson : 72, pl. 15, figs. 1–14.
1908 *Pentamerus* (*Gypidula*) *brevirostris* Reed : 83, pl. 14, figs. 1–7.

MATERIAL. Fourteen specimens.

FIGURED SPECIMENS. BB 55514, BB 55515.

DESCRIPTION. *Exterior.* The valves are strongly biconvex with the pedicle valve very deep. The beaks of both valves are strongly incurved with the ventral beak short and directed approximately toward the dorsal umbo. The pedicle valves are roughly pentagonal in outline with width and length approximately equal Brachial valves are transversely subpentagonal. The hinge line is narrow and curved and the cardinal angles are rounded with maximum width at about midlength in medium sized pedicle valves and commonly posterior to midlength in the opposed brachial valves. The pedicle valve bears a broad, low, flat fold that becomes differentiated about half an inch anterior to the ventral beak and the brachial valve bears a broad, shallow sulcus. Shells are plicated anteriorly with the plications beginning about at the point of differentiation of the fold or very slightly posterior in the mid-regions which commonly have three or four plications. The flanks are also plicated, but the plications are of slightly lesser strength and affect the areas adjacent to the fold and sulcus, but not the lateral portions of the flanks.

Interior of pedicle valve. Hinge teeth are not preserved on the available specimens, but beneath the level of the interarea there is a rhomboidal spondylium of deep U-shaped cross-section that is supported by a median septum that continues anteriorly a short distance beyond the edge of the spondylium, sloping off gradually. The umbonal regions on medium and large sized shells are moderately thickened with shell material. The floor of the spondylium is longitudinally grooved by numerous fine striae. Anteriorly, the surface is corrugated by the impress of the plications.

Interior of brachial valve. The inner brachial plates and sockets are not exposed on the available specimens, but the outer plates are very long and closely set together, converging basally to meet where they are supported on a very low ridge-like median septum most of their length. In the prepared internal mould of the brachial valve (pl. 2, figs. 4–7) most of the thickness of the external shell material showed a single plate-like structure but when all the shell material was removed a pair of tracks remained. This apparently is due to deposition of a small amount of shell material over the whole of the interior. The structure must have been closely comparable with that of *Sieberella brevirostris* as figured by Davidson (1864, 65, pl. 15, fig. 13).

DISCUSSION. The species *brevirostris*, as originally figured by Phillips, is not a recognizable species and the writers interpret it as illustrated by Davidson as noted in the synonomy above. There are some differences to be noted between the Burmese shells and those illustrated by Davidson. The latter are generally more elongate and have the plications even more poorly developed and on most specimens confined to the fold and sulcus. Burmese shells have fairly well developed plications that are also present on the flanks anteriorly. In shape of the valves and size of the plications the specimens from Burma more closely resemble a subspecies *Sieberella costata lata* LeMaitre (1952, pl. 16, figs. 22–36), but that species has the plications developed more strongly posteriorly.

Order STROPHOMENIDA
Suborder STROPHOMENOIDEA
Superfamily **STROPHOMENACEA** King 1846
Family **LEPTAENIDAE** Hall & Clarke 1895
Genus ***LEPTAENA*** Dalman 1828

Type species. *Leptaena rugosa* Dalman 1828 : 106, pl. 1, fig. 1.

Leptaena sp.

(Pl. 2, figs. 13, 14)

1908 *Leptaena rhomboidalis* Reed : 74, pl. 13, fig. 1.

Material. Six specimens.

Figured specimens. BB 55516, BB 55517.

Description. *Exterior.* The valves are subsemicircular to subquadrate in outline and planoconvex in lateral profile. Large specimens are dorsally geniculate around the anterior and lateral margins. The hinge line is long and straight and may be the place of maximum width. Some specimens have slightly auriculate cardinal angles. In large specimens there may be a slight widening anteriorly so that the place of maximum width is anterior to midlength. The ventral interarea is long, low, flat, and triangular; its inclination is low apsacline. There is a circular open foramen apically. The triangular delthyrium is mostly closed by an externally convex pseudodeltidium. The interarea of the brachial valve is long, flat, and ribbon-like. Its inclination is low, anacline. There is a well developed, medially cleft, externally convex chilidium closing the notothyrium.

The external ornament consists of concentric rugae crossed by fine rounded radial costellae that are continuous across the crests and troughs of the concentric rugae.

Interior of pedicle valve. The available material does not show the ventral interior to good advantage, however, one exfoliated specimen shows a cordate diductor impression.

Interior of brachial valve. The cardinalia consist of a pair of closely set triangular process lobes that face posteriorly and slightly ventrally, and diverge anterolaterally. The sockets are incised into the shell substance lateral to the cardinal process lobes and are bounded posteriorly by the edge of the interarea. Medially they are bounded by inner socket ridges that are anteriorly continuous with muscle bounding ridges that surround the dorsal adductors. The posterior adductors are broadly spaced and are subtriangular or fan-shaped. They are separated medially by the anterior adductors which are smaller and subpyriform. Both adductor pairs are separated posteriorly by a low rounded myophragm that narrows anteriorly from the broad base of the cardinal process lobes. At the end of the myophragm and adjoining the anteromedial edges of the anterior adductors, there is a broad, shallow central pit. Anterior to the central pit there is a low triangular breviseptum that is considerably thickened laterally near its highest point. A pair of short brachial ridges is present lateral to the breviseptum and well anterior to the area of adductor muscle attachment. The interior is not crenulated by the external corrugations, but the interior is smooth or is pustulose beyond the areas of muscle attachment. The adductor muscle sites are roughened, evidently formed of different textured shell material than the remainder of the valve.

Shell structure. The shell material is pseudopunctate.

Superfamily **DAVIDSONIACEA** King 1850 (*pro* ORTHOTETACEA)

Family UNCERTAIN

Genus ***XYSTOSTROPHIA*** Havlíček 1965

TYPE SPECIES. *Terebratulites umbraculum* Schlotheim 1820.

Xystostrophia umbraculum (Schlotheim 1820)

(Pl. 2, figs. 15–20)

1820 *Terebratulites umbraculum* Schlotheim : 256.
1853 *Orthis umbraculum* Schnur : 216, pl. 38, fig. 2; pl. 44, fig. 4.
1864,–65 *Terebratulites umbraculum* Davidson : 76, pl. 16, fig. 6; pl. 18, figs. 1–5.
1908 *Orthotetes umbraculum* Reed : 75, pl. 13, figs. 2–14.
1966 *Schellweinella* (*Schellweinella*) *umbraculum* Biernat : 59, pls. 9, 10.
1967 *Xystostrophia umbraculum* Havlíček : 197, pl. 40, figs. 3, 4, 7, 10, 11.

MATERIAL. Eighty-seven specimens.

FIGURED SPECIMENS. BB 55518–BB 55520; Sedgwick Mus. A 2760, A 2762.

DESCRIPTION. *Exterior.* The valves are sub-semicircular in outline and convexo-concave (resupinate) in lateral profile. The hinge line is long and straight and may be the place of maximum width. Small shells are decidedly transverse in outline, but larger shells gain in relative length with lateral margins commonly at right angles to the hinge line. In these the maximum width may be anywhere between the hinge line and a point in the anterior half of the length of the valves. The anterior commissure is rectimarginate.

The interarea of the pedicle valve is flat, apsacline, and triangular. It bears a broad, triangular delthyrium almost completely covered by the slightly convex pseudodeltidium whose base is arcuate with a concave side facing dorsally.

The interarea is divided into inner and outer parts on either side of the midline. The inner triangular area (secondary area of Thomas 1910) has transverse growth lines that are continuous with those across the pseudodeltidium, and finer grooves perpendicular to the hinge line. Lateral to this, the outer part of the interarea, appears to be unstriated. The interarea of the brachial valve is long and ribbonlike, very low and steeply anacline. The posterior base of the dorsal cardinalia is covered by a low, almost ribbon-like chilidium that is slightly higher medially on large specimens.

The external ornament consists of numerous radial costellae somewhat elevated and rounded on their crests and separated by broad, U-shaped interspaces. Costellae increase in number anteriorly on both valves by intercalation and individual costellae become slightly wider as they extend anteriorly. The costellae are crossed by a few irregularly and widely spaced growth lines and by very numerous concentric filae that are pominent across the costellae and less well marked in the interspaces. The number of costellae measured in the mid-region of a brachial valve commonly is about 9 in a space of 5 mm., 10 mm. anterior to the beak.

Interior of pedicle valve. The teeth are stubby and triangular and project posteriorly. They are supported basally by long but low dental lamellae that diverge at a high angle, commonly over 100 degrees. The dental lamellae continue as muscle bounding ridges adjacent to transversely oval flabellate diductor impressions posterolaterally. A myophragm is only uncommonly developed crossing from the anterior edge of the adductor impressions to the anterior edge of the diductor impressions. The adductor scars are faintly impressed elongate-suboval. The interior, on most specimens—even the larger ones, is crenulated over most of their surface by the costellae.

Interior of brachial valve. The cardinalia consist of socket ridges that diverge anterolaterally commonly at about 90 degrees to one another. They are connected posteriorly by a flat plate-like structure that serves as the base of a bilobate cardinal process that faces posteriorly. In larger specimens the distal ends of the socket ridges flare laterally in much wider angles, and the anterior edge of the plate bears a short longitudinal ridge medially. The myophore faces on the separate lobes are quadrilobate and approximately parallel to the plane of the ventral interarea. They commonly are visible in the small opening above the pseudodeltidium. The interior is crenulated over most of its area by the impress of the costellae.

Shell structure. The shell material appears to be impunctate and without pseudopunctae.

Family **STROPHEODONTIDAE** Caster 1939

Subfamily **LEPTOSTROPHIINAE** Caster 1939

Genus ***LEPTOSTROPHIA*** Hall & Clarke 1892

TYPE SPECIES. *Stropheodonta magnifica* Hall 1857 : 54.

Leptostrophia sp.

(Pl. 2, fig. 21; Pl. 3, figs. 1–6)

1908 *Stropheodonta* (*Leptostrophia*) *palma* Reed : 70, pl. 12, fig. 1.

MATERIAL. Three specimens.

FIGURED SPECIMENS. BB 55521–BB 55523.

DESCRIPTION. *Exterior.* The valves are planate with the brachial valve flat and the pedicle valve having a very faint curvature. The body cavity is very thin. The single articulated specimen is broken so that the outline is uncertain, however, a few poorly developed growth lines indicate that maximum width probably was slightly anterior to the long straight hinge line and was relatively elongate-subcircular with about equal width and length. The interarea of the pedicle valve is long, flat, and apsacline, more ribbon-like than triangular and it is denticulate the whole of its length. The delthyrium is mostly closed by a convex or subangular pseudodeltidium with a low, open V-shaped space near its base. The interarea of the brachial valve is long, linear, and slightly hypercline.

The external ornament is finely parvicostellate with very closely set costellae.

Interior of pedicle valve. A single fragment of pedicle valve, exposed as an internal mould, reveals a triangular muscle field defined posterolaterally by muscle bounding ridges. It is divided medially by a prominent, narrow myophragm (Pl. 3, fig. 5) For another illustration the reader is referred to the specimen illustrated by Reed (1908, pl. 12, fig. 1) which probably is conspecific.

Interior of brachial valve. The cardinal process lobes are blunt and directed posteroventrally. They are joined on their sides by short socket plates subparallel to the midline that are attached to the cardinal process lobes, but that are considerably shorter. The anterior bases of the socket plates connect with long, strongly divergent ridges that persist about half way to the lateral margins of the valve and diverge slightly from the hinge line. The base of the cardinal process is continuous with a stout, but short, myophragm that narrows and disappears in a short distance anteriorly between the adductor impressions. The adductor scars are not deeply impressed, but are strongly accentuated by the presence of high triangular bounding ridges that adjoin them posterolaterally. Anteriorly they fade imperceptibly into the interior of the shell. The areas lateral to the adductor impressions are pustulose.

Subfamily **LEPTODONTELLINAE** Williams 1965

Discussion. Williams (1965 : H403) included *Leptodontella*, *Leptodonta*, and *Parastrophonella* in his subfamily. The writers agree that *Leptodontella* and *Parastrophonella* belong in close association, but *Leptodonta* (and the related *Altaestrophia*) have cardinal process lobes unlike those of *Leptodontella* or any leptostrophiid, from which the subfamily must have been derived. *Leptodonta* Khalfin (Williams 1965 : H402, fig. 1a) and *Altaestrophia* Bublitschenko (Khalfin 1948 : 255, fig. 33) also lack socket plates like those that characterize *Leptodontella* and *Parastrophonella*. Thus we disagree that *Altaestrophia* Bublitschenko is a junior synonym of *Leptodontella* Khalfin as it was recorded by Williams (1965 : H403). In our conception the subfamily Leptodontellinae comprises *Leptodontella*, *Parastrophonella*, *Zophostrophia*, and *Rotundostrophia*. All are essentially planate shells, geniculate dorsally or ventrally at a late growth stage. All have leptostrophiid cardinalia with their peculiarly close-set socket plates and all have a relatively similar adductor muscle arrangement and brachial ridge arrangement in the brachial valve.

Genus ***LEPTODONTELLA*** Khalfin 1948

Type species. *Leptaena caudata* Schnur 1853 : 224, pl. 42, figs. 4a–c.

Leptodontella caudata (Schnur 1853)

(Pl. 3, figs. 7–11)

1853 *Leptaena caudata* Schnur : 224, pl. 42, figs. 4a–c.
1908 *Strophonella caudata* Reed : 71, pl. 12, figs. 2–12.
1953 *Glossostrophia caudata* Williams : 43, pl. 11, figs. 1–4.
1966 *Leptodontella caudata* Biernat : 50, pl. 7; pl. 8, fig. 17.
1967 *Leptodontella caudata* Havlíček : 165, pl. 46, figs. 9, 12.

MATERIAL. Sixteen specimens.

FIGURED SPECIMENS. BB 55524–BB 55526, Sedgwick Mus. A 2654.

DESCRIPTION. *Exterior.* In outline the valves are subsemicircular, commonly with acute or even mucronate cardinal angles, giving the outline a transverse shield-shaped aspect. The hinge line is the place of maximum width. In lateral profile the valves are subplanate and the major part of the anterolateral margins on larger specimens are geniculate ventrally. In addition, there is an irregular development of a median U-shaped sulcus in the anterior geniculation where it is reversed and bent toward the brachial valve. The external ornament is not preserved on the available specimens although on those illustrated by Reed there appears to be a faint development of a parvicostellate pattern anteriorly. The interarea of the pedicle valve is long, flat, and low triangular, apsacline in inclination. The apical half of the delthyrium is closed by chevron-like layers of shell forming the pseudodeltidium. The remainder of the delthyrial opening is filled by the cardinal process lobes and socket plates which are covered by a large band-like chilidium. The dorsal interarea is long, ribbon-like, flat, and anacline. Both interareas are denticulate the whole of their length.

Interior of pedicle valve. The ventral process, evident in the material illustrated by Reed, is not well shown on the available material. However, the ventral musculature consists of a very large triangular field moderately impressed and without true bounding ridges. It reaches considerably further anterior than midlength, and generally in large specimens may be semi-flabellate in that its lobes may be divided by short radial ridges near the anterior termination of the scar. The ventral adductor scars are impressed in the posterior part of the muscle field and separated by a broad, rounded myophragm. The diductor scars are smooth, but the remainder of the interior of the pedicle valve is pustulose.

Interior of brachial valve. The cardinal process lobes are set on thickened shell material posteriorly. They diverge strongly near their bases, then persist subparallel, separated by a relatively broad groove, and face posteriorly. The cardinal process lobes are adjoined laterally by heavy ridge-like socket plates that diverge anteriorly at small angles from the midline. In large specimens the adductor muscle field is relatively broad and the bounding ridges are decidedly elevated and ridge-like. The posterior adductors are widely set kidney-shaped impressions that postero-laterally enclose the closely-set suboval anterior adductors. There is also a well developed set of brachial ridges that emanate from the anterolateral extremities of the posterior adductors and are strongly convex laterally. The area within the brachial ridges may be greatly elevated above the pustulose floor of the valve anterolaterally, and generally there is a short median ridge continuing anteriorly from the edge of the adductor field. No central pit was noted. Beyond the anterior terminus of the brachial ridges on the one large specimen illustrated there is a broad rounded ridge that continues to the anterior margin of the valve from the raised area enclosed by the brachial ridges. Judging from the specimens of *Leptodontella* that have been seen by the writers the latter is a gerontic feature not seen on most specimens, even of considerable size.

Subfamily **DOUVILLININAE** Caster 1939

Genus ***MESODOUVILLINA*** Williams 1950

TYPE SPECIES. *Stropheodonta* (*Brachyprion*) *subinterstrialis* var. *seretensis* Kozlowski 1929 : 96, 97, figs. 28, 29; pl. 4, figs. 1–7.

Mesodouvillina birmanica (Reed 1908)

(Pl. 3, figs. 12–17; Pl. 4, figs. 1–4)

1908 *Stropheodonta interstrialis* (Phillips) var. *birmanica* Reed : 66, pl. 10, figs. 11–13; pl. 11, figs. 1–6.

MATERIAL. Fifty specimens.

FIGURED SPECIMENS. BB 55527–BB 55531, Sedgwick Mus. A 2738, A 2745.

DESCRIPTION. *Exterior*. The shells attain medium to large size for the genus and are moderately to strongly concavo-convex. The valves are commonly shield-shaped with the maximum width attained at the hinge line. Well preserved specimens commonly show some development of auricular projections at the cardinal extremities, tending to make the anterolateral margins concave. The convexity of the pedicle valves is modified across the posterior which is nearly flat near the hinge line; but curvature is more even across the transverse dimension anteriorly. From back to front the rate of curvature does not change appreciably so that no real anterior geniculation is developed.

The interarea of the pedicle valve is long, flat, and orthocline, attaining a little greater height near the midline. The interarea of the brachial valve is long, straight, extremely low, and hypercline. The ornament consists of a parvicostellate radial development that coarsens anteriorly due to prominence of the primary costellae. Some specimens have a few well developed concentric growth lines anteriorly.

Interior of pedicle valve. The inner margin of the palintrope is denticulate, commonly along its middle half. The ventral process is a low triangular structure, made prominent by the development of two diverging ridges that make up its lateral edges. Anteriorly it blends with a poorly impressed suboval pair of adductor scars. The diductors are cordate, moderately impressed, but well defined by high, thick, muscle bounding ridges that are nearly straight to gently curved, convex laterally and diverging slightly anteriorly. They are quite widely set apart at their posterior ends. Anteriorly the diductor impressions end abruptly, but without bounding ridges and may be divided medially in their anterior portion by a short but moderately elevated myophragm. The remainder of the interior posteriorly is more or less pustulose, due to the pseudopunctae.

Interior of brachial valve. The posterior margin of the valve is denticulate inside the edge of the interarea. The cardinal process lobes are strongly disjunct, diverging posteriorly with only very slight ventral inclination. The posterior face of each lobe is medially grooved. The socket plates are widely set apart lateral to the cardinal process lobes and are set close to the hinge line, diverging strongly laterally. The adductor impressions are broadly subtrigonal, rounded laterally, and more or less straight, and diverging anteriorly along their medial edges. The lateral portions are bounded by poorly developed, mound-like muscle bounding ridges that diverge anterolaterally. The brace plates originate medially between the adductor impressions and diverge slightly anterolaterally as long, low, pustulose ridges.

Subfamily **PHOLIDOSTROPHIINAE** Stainbrook 1943

Genus ***TELAEOSHALERIA*** Williams 1950

TYPE SPECIES. *Orthis subtetragona* Roemer 1844 (= *Shaleria* (*Telaeoshaleria*) *sulcata* Williams 1950).

Telaeoshaleria padaukpinensis (Reed 1908)

(Pl. 4, figs. 5–12)

1908 *Stropheodonta subtetragona* (F. Roemer) var. nov. *padaukpinensis* Reed : 69, pl. 11, figs. 7–12.

DIAGNOSIS. Posteriorly flat, shield-shaped, sulcate *Telaeoshaleria* with well marked parvicostellate ornament on the pedicle valve.

MATERIAL. Thirty-eight specimens.

FIGURED SPECIMENS. BB 55532–BB 55536.

DESCRIPTION. *Exterior.* The shells are small to medium sized for the genus. They are subquadrate shield-shaped in outline and plano- to concavo-convex in lateral profile. The hinge line is long and straight and is the place of maximum width. The ventral interarea is well marked; on some specimens faintly triangular near the midline, but for the most part nearly ribbon-like. It is orthocline to gently apsacline and denticulate along the mid two-thirds of its length. The delthyrium is narrow and triangular, enclosing an angle of about 30 degrees. It is completely covered by a flat to very gently convex pseudodeltidium except at its base where a small semi-circular opening is present. There appears to be a complete chilidium. The dorsal interarea is long, linear, and hypercline. The cardinal angles are acute because of the development of small auricular projections. The lateral margins are straight and curve into an anterior margin that is parallel to the hinge line but gently indented. On larger specimens there is a well developed geniculation at about two-thirds of the length and the angle of geniculation is something less than 90 degrees. The geniculate portion of the shell is broadly sulcate medially and the brachial valve is subquadrate and either flat or gently concave.

The exterior bears a well developed parvicostellate ornament with stronger, widely spaced, primary costellae that divide sectors commonly bearing six to twelve very fine radial costellae. The spaces between the primary costellae are flat and may be corrugated on the posterior portion of the valve, but commonly become concave anteriorly.

Interior of pedicle valve. The diductor tracks are long, narrow, deeply impressed furrows with bounding ridges defining them on their inner and outer sides. There is a V-shaped depression separating them anteriorly. The visceral disc is transversely suboval, well defined, and bounded laterally and anteriorly on larger specimens by a peripheral ridge.

Interior of brachial valve. The cardinal process lobes are medially cleft, but join basally along the midline. Each lobe is strongly furrowed forming a pair of lobes, one facing posteriorly and one laterally. Socket plates are small and ridge-like, situated lateral to the extremities of the cardinal process lobes well to the posterior and strongly divergent anterolaterally. The adductor muscle field is small and transversely subquadrate in outline, defined laterally by strongly elevated, almost plate-like bounding ridges, that are subparallel but converge very slightly anteriorly. The posterior adductors are subtriangular and may be deeply impressed, lying posterolateral in the adductor muscle field. The anterior adductors are also triangular, but are elevated and lie anteromedially within the muscle field. The anterior adductors are joined anteriorly by strong plate-like inner brachial ridges that are faintly arcuate, convex laterally. They are separated at their posterior ends by a faint elliptical central pit. The inner brachial ridge is defined by a more or less elongate-suboval depressed area divided in its anterior portion by a breviseptum of triangular outline and relatively short length. Posterolateral portions of the inner surface are strongly pustulose corresponding to the inner terminations of the pseudopunctae.

COMPARISON. Reed (1908 : 69) described the Burma specimens as a variety of Kayser's species *subtetragona*, which they very closely resemble. Specimens of *T. subtetragona* at hand from the Nohner Schichten and the Freilinger Schichten are commonly of larger size, but also are more rounded in the contour of the pedicle valve and appear not to develop concave spaces between the primary costellae.

Genus ***RADIOMENA*** Havlíček 1962

TYPE SPECIES. *Orthis irregularis* Roemer 1844 : 75, pl. 4, figs. 1a–c.

Radiomena cf. ***irregularis*** (Roemer 1844)

(Pl. 4, figs. 13–17)

1844 *Orthis irregularis* Roemer : 75, pl. 4, figs. 1a–c.
1853 *Leptaena irregularis* Schnur : 224, pl. 41, fig. 3.
1962 *Radiomena irregularis* Havlíček : 471.
1966 *Radiomena irregularis* Biernat : 58, pl. 8, figs. 14–16.
1967 *Radiomena irregularis* Harper, Johnson, & Boucot : 431, pl. 9, figs. 6, 7; pl. 10, figs. 1–6.
1967 *Radiomena irregularis* Havlíček : 131, pl. 25, figs. 1–10.

MATERIAL. Three specimens.

FIGURED SPECIMENS. BB 55537–BB 55539.

DESCRIPTION. *Exterior.* The pedicle valve is moderately convex, both from the beak to the anterior margin and from side to side. The outline is roughly subquadrate and shield-shaped. The long straight hinge line is slightly less than the maximum width. A few poorly marked growth lines indicate that the cardinal angles are faintly mucronate, with a broadening of the shell anteriorly so that the maximum width is anterior to midlength. No fine ornament is preserved. Shell substance is pseudopunctate.

Interior of brachial valve. There are two fragments of brachial valve in the collections at hand. One is sufficient for description of the cardinalia. The cardinal process lobes are widely set apart ponderous plates with roughly triangular posterior faces. The long axes of the two plates diverge strongly anterolaterally. Their medial faces are concave inward, forming a cup-shaped depression open anteriorly. The second fragment includes what are apparently dendritic dorsal adductor impressions, a low breviseptum raised anteriorly into a mound-like prominence, and a pair of kidney-shaped structures slightly raised around the edges and irregularly depressed toward their centres.

Suborder CHONETOIDEA

Superfamily **CHONETACEA** Bronn 1862

Family **CHONETIDAE** Bronn 1862

Genus ***DEVONARIA*** Biernat 1966

(synonym *Plicodevonaria* Boucot & Harper, 1968, p. 162)

TYPE SPECIES. *Chonetes zeuschneri* Sobolev 1909.

Devonaria minuta (von Buch 1836)

(Pl. 5, figs. 1–12)

1836 *Orthis minuta* Von Buch : 68, ex Goldfuss ms.
1871 *Chonetes minuta* Kayser : 633 (with a synonymy).
1908 *Chonetes minuta* Reed : 78, pl. 13, figs. 16, 17.
1962 *Retichonetes minutus* Muir-Wood : 63, pl. 4, figs. 8–11.
1968 *Plicodevonaria minuta* Boucot & Harper : 162, pl. 28, figs. 2–10.

MATERIAL. Twenty-two specimens.

FIGURED SPECIMENS. BB 55540–BB 55544.

DESCRIPTION. *Exterior.* The valves are roughly shield-shaped in outline with a very prominent ventral umbo. Either length or width may be the maximum dimension. In lateral profile the valves are deeply concavo-convex with a very strongly incurved ventral beak. The ventral interarea is anacline, flat, and ribbon-like or slightly incurved near the midline. The delthyrium is low, triangular, and is closed apically by an externally convex crescentic pseudodeltidium. The remainder of the delthyrium is filled by the cardinal process. The interarea of the brachial valve is well defined and flat with a height equal to about one-third to one-half of that of the pedicle valve and with equal length. The dorsal interarea is hypercline.

The exterior is covered by strong, rounded, radial costae separated by well defined U-shaped interspaces that are commonly slightly narrower than adjoining costae.

A few plications bifurcate anteriorly on the pedicle valve and new plications are generally added on the brachial valve by intercalation. On the brachial valves where it is easier to observe the origin of costae only a few are observed that continue from the dorsal beak. Progressively lateral costae originate along the hinge line and the lateralmost costae originate anterior to the hinge line, but so disposed that their posterior projection would intersect the hinge line. Reed's figures (1908, pl. 13) well illustrate a fine concentric ornament of filae across the crests of the costae. The preservation of our material is too poor to well display the fine ornament, but faint vestiges of the concentric filae were observed on one specimen.

Interior of pedicle valve. Hinge teeth were not observed on the available specimens. The hinge line is denticulate, most of its length. The musculature is poorly impressed and is divided posteriorly by a blade-like median septum.

Interior of brachial valve. The cardinal process is a triangular block with four lobes on its posterior face. Internally it is bilobate and consists of an elongate mound-like region with a faint medial groove. Long, prominent inner socket ridges diverge anterolaterally from the lateral bases of the cardinal process. There is a pair of short divergent anderidia lateral to a long subparallel pair of accessory septa and a breviseptum. The latter structures originate at about midlength of the anderidia adjoining them. In the largest and thickest shelled specimens the anterior ends of the accessory septa are thickened and join laterally with slightly raised, concentrically disposed brachial ridges. The posterior points or origin of the brachial ridges, however, are too faintly developed to ascertain with any certainty. The interior is not crenulated by the impress of the costae.

Suborder PRODUCTOIDEA

Superfamily **PRODUCTACEA** Gray 1840

Family **PRODUCTELLIDAE** Schuchert and LeVene 1929

Genus ***PRODUCTELLA*** Hall 1867

TYPE SPECIES. *Productus subaculeatus* Murchison 1840 : 255.

Productella? sp.

(Pl. 5, figs. 13–17)

MATERIAL. Two specimens.

FIGURED SPECIMEN. BB 55545.

DESCRIPTION. *Exterior.* The valves are of about equal width and length with the anterior rounded and the posterior modified by the rounded ventral beak protruding posteriorly past a short straight hingeline. In lateral profile the valves are deeply concavo-convex. The ventral beak is short, strongly incurved, and blunt posteriorly. The delthyrium is low and trapezoidal. The ventral interarea is flat and hypercline and equal to just a little more than half the width. The dorsal interarea is linear; no chilidium was noted. The cardinal angles are blunt and rounded without any indication of auriculation, but the deeply convex ventral umbo is distinct from the posterolateral flanks that flatten out. The areas adjacent to the umbo may be concave; the remainder of the valve anteriorly is strongly convex. The brachial valve is generally concave except for the posterolateral margins that are flatter. The exterior is sparsely covered with irregularly distributed knob-like spine bases that are not set on radial ridges. The anterior portion of one pedicle valve shows the spines preserved. They are long and tube-like and lie flat against the valve in a radial fashion. The concentric ornament consists of very fine irregular lirae.

Interior structures. The available specimens do not expose the interior, but the posterior face of the cardinal process is visible through the open delthyrium. A pair of lobes, diverging ventrally, are exhibited. On the outside of the brachial valve there is a small knob-like " umbo " like that typically developed on specimens that bear an internal alveolus at the anterior edge of the cardinal process. A medial line in the shell material of the brachial valve indicates the presence of a breviseptum.

Order RHYNCHONELLIDA

Suborder RHYNCHONELLOIDEA

Superfamily **RHYNCHONELLACEA** Gray 1848

Family **UNCINULIDAE** Rzhonsnitskaya 1956

Genus ***UNCINULUS*** Bayle 1878

TYPE SPECIES. *Hemithyris subwilsoni* d'Orbigny 1850 : 92.

Uncinulus subsignata (Reed 1908)

(Pl. 5, figs. 18–31; Text-figs. 2, 3)

1908 *Rhynchonella* (*Camarotoechia?*) *subsignata* Reed : 93, pl. 14, figs. 19–22; pl. 15, figs. 1–4.
1930 *Hypothyris subsignata* Nalivkin : 79, pl. 4, figs. 14, 15.

MATERIAL. Seventy-nine specimens.

FIGURED SPECIMENS. BB 55546–BB 55549, BB 55589A & B.

DESCRIPTION. *Exterior.* The valves are subtrigonal in outline with long straight posterolateral margins diverging from a beak angle of about 100 degrees or slightly more. The valves are unequally biconvex in lateral profile; the pedicle valve is less convex. It is gently convex posteriorly and flattens out toward mid-length. The brachial valve is strongly convex with the convexity emphasized by the anterior development of a median fold. The pedicle valve has a median sulcus with a long geniculate tongue that is accommodated by the dorsal fold. The anterolateral flanks of the pedicle valve commonly are slightly reflexed. The hinge line is short and curved. The ventral beak is small, pointed, and only moderately incurved. The dorsal beak is strongly incurved and is not visible on the exterior.

The external ornament consists of low, rounded, simple costae which originate anterior to the umbones of both valves. There are commonly 3 to 5 costae in the ventral sulcus and 6 or 7 costae on each flank. Costae flatten out at the commissure and adjoining them the interspaces become knife-like grooves. The junctions of

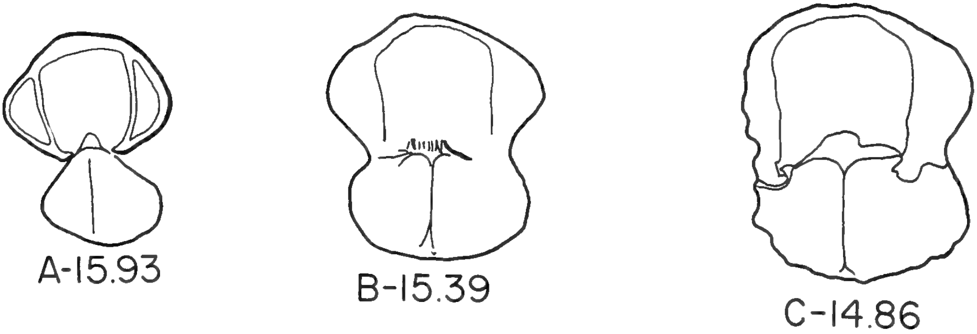

Fig 2. *Uncinulus subsignata*, serial sections of BB 55589A × 5·5. Numbers indicate distance in millimeters from the anterior. Original length was 16·18 mm.

adjacent plications project as flaps or platelets that interlock by internal insertion beneath the flattened costae of the opposite valve.

Interior of pedicle valve. Extremely short, thin, dental plates are present. The delthyrial cavity is straight-sided, diverging anterolaterally. The adductor scars are impressed moderately posteriorly and are divided by a thin plate-like myophragm. The ventral diductors are not impressed. All ventral musculature is extremely poorly impressed considering what is known to develop in other species of *Uncinulus*. The shell material is thin and the interior is crenulated by the impress of the costae.

Interior of brachial valve. The brachial valve bears a long blade-like median septum that reaches to about mid-length. It supports a shallow V-shaped septalium

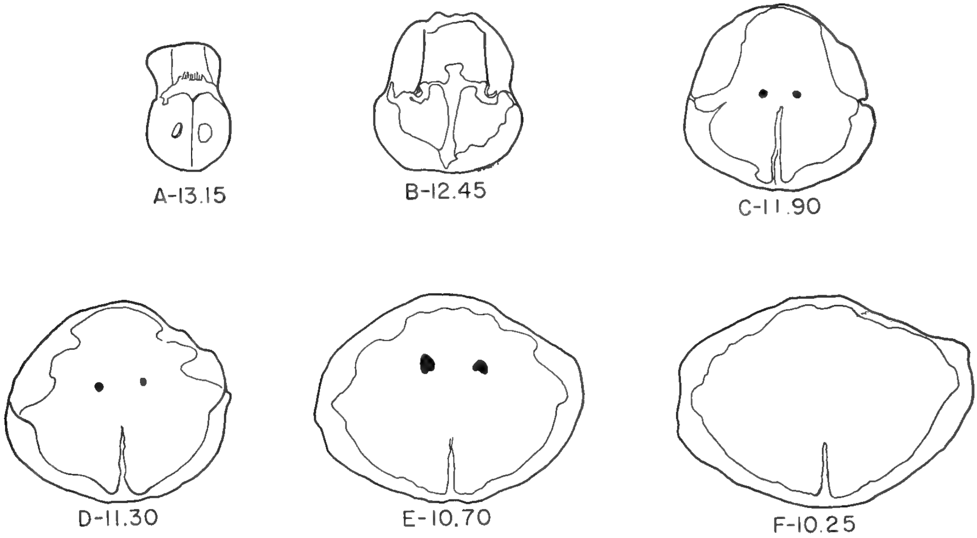

Fig. 3. *Uncinulus subsignata*, serial sections of BB 55589B × 3. Numbers indicate distance in millimeters from the anterior. Original length was 13·80 mm.

that is covered by a plate of shell material that is longitudinally striate medially forming a comb-like site of diductor attachment. The interior is crenulated anteriorly by the impress of the costae.

Genus ***MARKITOECHIA*** Havlíček 1959

TYPE SPECIES. *Uncinulus marki* Havlíček 1956 : 568, pl. 9, figs. 5–10, 12.

Markitoechia? cf. ***pentagona*** (Kayser 1871)

(Pl. 6, figs. 1–4; Text-fig. 4)

1871 *Rhynchonella parallelpipeda* var. *pentagona* Kayser : 508, pl. 9, fig. 4.
1908 *Rhynchonella* (*Hypothyris*) *pentagona* Reed : 91, pl. 14, fig. 15.
1930 *Hypothyris pentagona* Nalivkin : 79, pl. 6, fig. 1.
1961 *Uncinulus pentagonus pentagonus* Havlíček : 147, pl. 27, fig. 8.
1966 *Uncinulus pentagonus pentagonus* Biernat : 91, pl. 21, figs. 3–15.

MATERIAL. Nine specimens.

FIGURED SPECIMEN. BB 55550, BB 55589C.

DESCRIPTION. *Exterior.* The valves are small, pentagonal in outline, and subequally biconvex subcuboidal in lateral profile. The ventral beak is short, stubby, slightly incurved, and bears an apical foramen. The beak of the brachial valve is relatively prominent and closely adjoins the ventral palintrope at the edge of the ventral foramen. There is a broad faint sulcus in the pedicle valve anteriorly. The anterior commissure is bowed slightly toward the brachial valve medially, and there is a hump-like fold anteriorly on the brachial valve. There are 7 or 8 low rounded costae on each flank of the pedicle valve and 5 to 7 costae in the sulcus of the pedicle valve. The costae on the flanks are disposed radially, but the lateral costae in the sulcus are added anterior to the umbo and subparallel to the midline of the valves.

At the commissure the costae flatten out and become wider at the expense of the bounding interspaces which become very narrow and groove-like. The points of

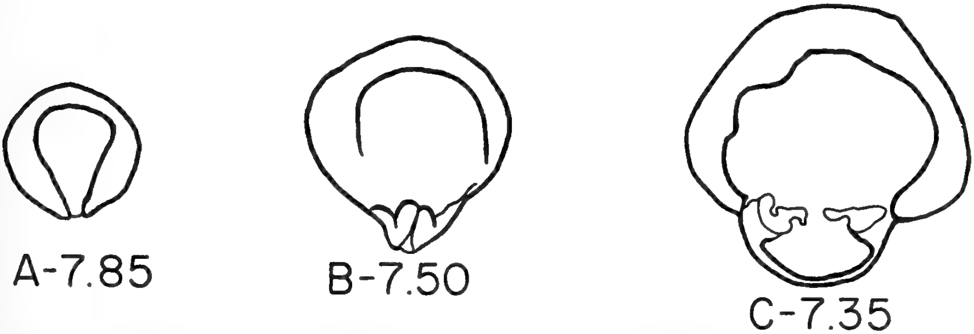

FIG. 4. *Markitoechia*? cf. *pentagona*, serial sections of BB 55589C × 10 (section A) and × 12 (sections B, C). Numbers indicate distance in millimeters from the anterior. Original length was 8·25 mm.

juncture of adjoining costae extend as spines accommodated by the flat dorsal costae. This is seen in partially exfoliated specimens as elevated dorsal costae that terminate a slight distance dorsal to the valve margin along the anterior geniculate portion of the valves.

Internal structures. An internal mould of one specimen reveals very short, thin dental lamellae in the pedicle valve and a long thin median septum in the brachial valve. The dorsal cardinalia were not seen.

Family **YUNNANELLIDAE** Rzhonsnitskaya 1959

Genus ***SCHNURELLA*** Schmidt 1964

TYPE SPECIES. *Terebratula schnurii* deVerneuil 1840 : 261.

Schnurella cf. ***schnuri*** (deVerneuil 1840)

(Pl. 6, figs. 5, 6)

1840 *Terebratula schnurii* de Verneuil : 261, pl. 3, fig. 2.
1853 *Terebratula schnurii* Schnur : 179, pl. 23, fig. 8.
1908 *Rhynchonella* (*Hypothyris*) *schnuri* Reed : 91, pl. 14, figs. 16–18.
1965 *Schnurella schnuri* Schmidt : 17, fig. 22.

MATERIAL. The single specimen illustrated was the only one available for study.

FIGURED SPECIMEN. Sedgwick Mus. A 2779.

DESCRIPTION. *Exterior.* The specimen is subtrigonal in outline with a poorly developed ventral sulcus and dorsal fold. The exterior is covered with numerous low radial lirae that do not bifurcate anteriorly, but which increase in width toward the anterior of the valves. The anterior and anterolateral margins of the shell are plicate.

Family **CAMAROTOECHIIDAE** Schuchert & LeVene 1929

Subfamily **SEPTALARIINAE** Havlíček 1960

Genus ***SEPTALARIA*** Leidhold 1928

TYPE SPECIES. *Terebratula ascendens* Steininger 1853 : 61.

Septalaria? sp.

(Pl. 6, figs. 7–11)

1908 *Camarophoria* cf. *ascendens* Reed : 87, pl. 14, fig. 12.

MATERIAL. The single illustrated specimen was the only one available for study.

FIGURED SPECIMEN. BB 55551.

DESCRIPTION. *Exterior.* The specimen is transversely subrhomboidal in outline and strongly unequally biconvex in lateral profile. The pedicle valve is flattened anteriorly and develops a broad, sulcus that projects dorsally as an extremely long geniculate tongue that is accommodated by a great elevation of the brachial valve anteriorly.

Most of the valve surface is smooth, but the anterolateral margins bear low rounded costae. The ventral tongue also bears costae near the point of geniculation, but at the extremities of the tongue the costae become flattened and grooved medially while the adjoining inner spaces become narrow and groove-like. It appears that the ventral tongue fits inside the extremities of the dorsal costae.

Order SPIRIFERIDA

Suborder ATHYRIDOIDEA

Superfamily **ATHYRIDACEA** M'Coy 1844

Family **ATHYRIDIDAE** M'Coy 1844

Subfamily **ATHYRIDINAE** M'Coy 1844

Genus ***ATHYRIS*** M'Coy 1844

TYPE SPECIES. *Terebratula concentrica* von Buch 1834 : 123.

Athyris sp.

(Pl. 7, figs. 1–5; Text-fig. 5)

1908 *Athyris concentrica* Reed : 110, pl. 16, figs. 18, 19.

MATERIAL. Twenty specimens.

FIGURED SPECIMENS. BB 55559, BB 55589D.

DESCRIPTION. *Exterior.* In outline the shells are rhomboidal and in lateral profile they are subequally biconvex. The pedicle valve bears a prominent pointed incurved ventral beak and a short, curved hinge line equal to about half the maximum width which is met near midlength. Width and length commonly are approximately equal. The ventral beak is pierced by a large circular foramen joining a broad, low, triangular delthyrium anteriorly. Most of the delthyrium is filled with the beak of the brachial valve.

The pedicle valve bears a broad, shallow sulcus and the brachial valve bears a faintly developed fold which manifests itself in some shells as a faintly subcarinate form. The exterior is covered by numerous lamellose concentric growth lines.

FIG. 5. *Athyris* sp., serial sections of BB 55589D × 5 (sections A, B) and × 6 (section C). Numbers indicate distance in millimeters from the anterior. Original length was 14·70 mm.

Interior structures. The pedicle valve bears short dental lamellae set close to the lateral margins of the interior. The brachial valve bears a flat cardinal plate with a longitudinal median crest on its dorsal face. There is a dorsal myophragm, but no median septum.

Discussion. There is some resemblance of the indeterminate species at hand to *Athyris concentrica*, but only a few poorly preserved specimens are available. For this reason and because the named species of *Athyris* show a trend for rather marked variability in form, the Burmese specimens are left specifically indeterminate.

Family **MERISTELLIDAE** Waagen 1883

Subfamily **MERISTINAE** Hall and Clarke 1895

Genus ***MERISTA*** Davidson 1851

Type species. *Terebratula herculea* Barrande 1847 : 382.

Merista subdidyma (Reed 1908)

(Pl. 6, figs. 12, 13; Text-fig. 6)

1908 *Meristella? subdidyma* Reed : 116, pl. 16, figs. 25–27.

Material. Eleven specimens.

Figured specimens. BB 55552, BB 55589E.

Description. *Exterior.* The valves are subrhomboidal in outline with the posterior pointed and the anterior margin rounded. In lateral profile the valves are subequally biconvex, but generally the pedicle valve is slightly deeper. The ventral beak is moderately incurved with an apical foramen. The lateral palintropes are somewhat flattened. There is a triangular delthyrium closed medially by a deltidial plate. The dorsal umbo is prominent and knob-like. The pedicle valve bears a very shallow medial sulcus that may be slightly accentuated at the anterior commissure which is deflected toward the brachial valve. External ornament is lacking.

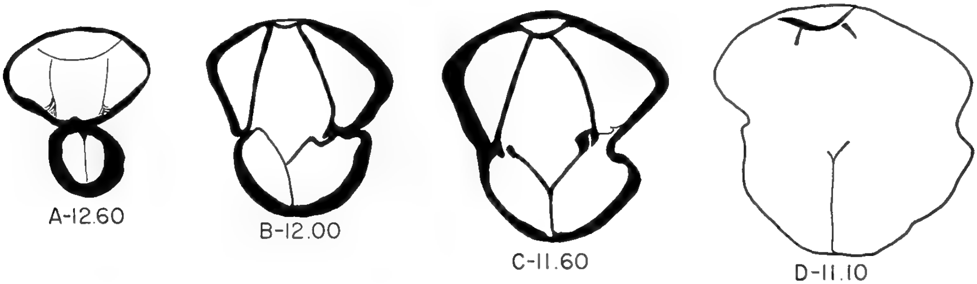

Fig. 6. *Merista subdidyma*, serial sections of BB 55589E × 5. Numbers indicate distance in millimeters from the anterior. Original length was 13·34 mm.

Interior of pedicle valve. The dental lamellae are long, slender, and plate-like. Their ventral edges rest on the flanks of a long shoe-lifter process that continues anteriorly slightly further than the distal ventral edges of the dental lamellae.

Interior of brachial valve. The dorsal cardinalia consist of a deep V-shaped septalium supported by a long, thin, blade-like median septum.

Family **NUCLEOSPIRIDAE** Davidson 1881

Genus ***NUCLEOSPIRA*** Hall 1859

TYPE SPECIES. *Spirifer ventricosus* Hall 1859 : 24.

Nucleospira sp.

(Pl. 6, figs. 14–18)

1908 *Nucleospira lens* Reed : 111, pl. 16, figs. 21, 21A, 21B; not Schnur 1853.

MATERIAL. Fifty-two specimens.

FIGURED SPECIMEN. BB 55553.

DESCRIPTION. *Exterior.* The outline varies from sub-circular to sub-oval with either the transverse or longitudinal dimensions being slightly greater. The ventral beak is short, stubby, and strongly incurved over a narrow flat, triangular interarea with length less than half the maximum width of the valves. The interarea is cleft medially by a very broad triangular open delthyrium. The inclination of the ventral interarea is apsacline. The dorsal interarea is not exposed, but apparently is also apsacline. Neither fold nor sulcus are developed.

The exterior is covered with a fine mat of radially arranged thread-like spinules. In the posterior region of the brachial valve the spinules are directed posterolaterally from the dorsal umbo toward the hinge line.

Interior structures. No free specimens are present in the collection, but preparation of an internal mould of one specimen reveals that each valve has a long, low, plate-like median septum extending from the posterior all the way to the anterior margin.

DISCUSSION. The figures of *Nucleospira lens* given by Schnur (1853, pl. 36, figs. 6A–D) are of a subquadrate species, but none of more than a score of specimens from Burma have a subquadrate outline.

Suborder RETZIOIDEA

Superfamily **RETZIACEA** Waagen 1883

Family **RETZIIDAE** Waagen 1883

Genus ***PLECTOSPIRA*** Cooper 1942

TYPE SPECIES. *Terebratula ferita* von Buch 1834 : 96.

Plectospira ferita (von Buch 1834)

(Pl. 6, figs. 19–27)

1834 *Terebratula ferita* von Buch : 76, pl. 2, fig. 37.
1853 *Terebratula ferita* Schnur : 184, pl. 25, figs. 4a–g.
1960 *Plectospira ferita* Rzhonsnitskaya : 285, pl. 67, fig. 7.
1966 *Plectospira ferita* Biernat : 146, pl. 28, fig. 1.

MATERIAL. Thirty-two specimens.

FIGURED SPECIMENS. BB 55554–BB 55556.

DESCRIPTION. *Exterior.* The outline varies from elongate subpyriform to sub-oval. In lateral profile the valves are subequally biconvex. The ventral beak is straight and pointed and may be short or of moderate length; it bears an apical foramen. The delthyrium is completely closed with a flat deltidium. The hinge line is very short and rounded and lacks an interarea.

The shells are plicate; each flank of the pedicle valve bears two or three high rounded plications separated by very deep V-shaped to rounded interspaces. Pedicle valves bear a pair of medial plications that tend to bound a sulcus anteriorly. The brachial valve bears a prominent elevated median plication. In the typical form the plications become strongly accentuated anteriorly so that the commissure is sharply deflected into a number of zig-zags. In these specimens generally there is a median rib anteriorly between the pair of median plications on the pedicle valve.

Shell substance. The endopunctate condition is evident under the microscope on almost all of the available specimens.

Discussion. Reed (1908 : 112) assigned the two specimens that he had available to Kayser's species *longirostris* and illustrated an elongate subpyriform shell with only moderately developed plications. However, most of the specimens composing the larger group available to the present writers have the typical deep flaring plications of *Plectospira ferita.* Three of our specimens are, however, in close agreement with Kayser's proposed species and are described below as *Plectospira longirostris.*

Plectospira longirostris (Kayser 1871)

(Pl. 6, figs. 28–32)

1871 *Retzia longirostris* Kayser : 558, pl. 10, fig. 5.
1908 *Ptychospira longirostris* Reed : 112, pl. 16, fig. 22.

MATERIAL. Three specimens.

FIGURED SPECIMENS. BB 55557, BB 55558.

DESCRIPTION. *Exterior.* The outline is long-pyriform and the lateral profile is subequally biconvex. The valves are very narrow at the posterior end and this is accentuated by the presence of a relatively long and prominent ventral beak. It bears an apical foramen and a flat, complete deltidium, giving the ventral beak the shape of a truncated cone. The apical angle of the pedicle valve is small and equals about 45 degrees or slightly more. The hinge line is very short and sharply rounded. The anterior margins are evenly curved in a semicircular manner.

The ornament consists of strongly elevated, narrow, radial plications with deep narrow U-shaped interspaces. Pedicle valves commonly have eight plications spaced about equally from one another without the suggestion of a median sulcus. The anterior part of the shell is crossed by relatively prominent concentric growth lamellae that give an imbricate surface to the valves. The anterior commissure is strongly serrate, but lacks the exaggerated zig-zag development of *Plectospira ferita.*

DISCUSSION. This species is distinguished from the more common *P. ferita* in the Burmese collection by the more numerous and narrower plications and by the anteriorly prominent concentric growth lamellae. Furthermore, the ventral beak is relatively longer and more pointed and the hinge line is decidedly narrower in conjunction with a smaller apical angle. Schnur's figures (1853, pl. 25, fig. 4) of

P. ferita show growth lines, but they are not as prominent as those of *Plectospira longirostris* from the Burmese collection. The accompanying specimens of *P. ferita* in the latter collection do not appear to have any development of imbricating growth lamellae. The writers considered the possibility that *P. longirostris* might be a variety or a subspecies of *P. ferita*, but there seems to be no intergrade between the two forms that are so easily distinguished in the Burmese collection. Therefore we continue to regard them as distinct species.

Suborder ATRYPOIDEA

Superfamily **ATRYPACEA** Gill 1871

Family **ATRYPIDAE** Gill 1871

Subfamily **ATRYPINAE** Gill 1871

Genus ***ATRYPA*** Dalman 1828

TYPE SPECIES. *Anomia reticularis* Linnaeus 1758 : 702.

***Atrypa* " *reticularis* "** (Linnaeus 1758)

(Pl. 7, figs. 6–19)

1908 *Atrypa reticularis* Reed : 96, pl. 15, figs. 5–7.

MATERIAL. Over 200 specimens.

FIGURED SPECIMENS. BB 55560–BB 55563.

DESCRIPTION. *Exterior.* Small specimens are lenticular or they may be unequally biconvex with the pedicle valve the deeper. Most small specimens are decidedly elongate suboval with a very short hingeline and maximum width slightly posterior to mid-length. Larger specimens attain a slightly greater relative width with a longer hinge line that modifies the outline to rounded subtrigonal, but with maximum width slightly further posterior and with the length still greater than the width. Medium size specimens with a width of 10 to 15 mm. generally are unequally biconvex with the brachial valves deeper. In large specimens having a width commonly of 25 to 30 mm. or more the brachial valve is deeply convex and the pedicle valve slightly convex to subplanar anteriorly. Outline proportions are roughly the same as for medium size specimens. Beak features for specimens in all size ranges are the same with a very small pointed ventral beak and an apical foramen strongly incurved over the dorsal umbo. No interareas are exposed and no deltidial plates are developed in the pedicle valve. Large specimens commonly develop an anterior geniculate tongue-like sulcus in the pedicle valve with a corresponding strong deflection in the anterior commissure of the brachial valve.

The ornament consists of rounded radial costellae and shallow rounded interspaces or approximately the same width. The density of ribs measured in the mid-region of pedicle valves at a distance of 15 mm. anterior to the beak varies slightly, from three to four ribs in a distance of 2 mm. The concentric costae are crossed by imbricating concentric growth lines distributed over the whole of the valves. Frilly growth lamellae are not generally developed except anteriorly on large specimens.

Interior of pedicle valve. Hinge teeth are stubby and elliptical in cross-section, attached directly to the inner wall of the valve and delineated from the posterolateral valve margin by a denticular groove. Short, broadly divergent dental lamellae are present on smaller specimens, but are wholly obsolescent on large ones. The ventral muscle field is large and flabellate, reaching considerably past midlength and commonly is relatively deeply radially striated and raised along its anterolateral edges by a strongly pitted ridge-like thickening of shell material.

Interior of brachial valve. The sockets are broad and shallow with a low corrugated median ridge. Socket plates are discrete, strongly curved posteroventrally, and divergent anteriorly. The notothyrial cavity commonly is built up by a thickening of secondary shell material forming a notothyrial platform. Dorsal musculature is not impressed.

COMPARISON. This form, as developed in the Burmese collections, is closely comparable to the Polish Middle Devonian species *Atrypa subtrigonalis* Biernat (1964, pl. 2).

Genus ***SPINATRYPA*** Stainbrook 1951
Subgenus ***INVERTRYPA*** Struve 1961

TYPE SPECIES. *Spinatrypa kelusiana* Struve 1956 : 385.

S. (Invertrypa) cf. ***asperoides*** (Biernat 1964)
(Pl. 7, figs. 20–28)

1964 *Spinatrypa asperoides* Biernat : 313, pl. 6, figs. 1–5, 12; pl. 7, figs. 7, 8.

MATERIAL. Fifty-one specimens.

FIGURED SPECIMENS. BB 55564–BB 55566.

DESCRIPTION. *Exterior.* The specimens are small to medium size; commonly the larger specimens attain a maximum width of about 15 mm. In lateral profile the valves are subequally biconvex. Maximum width of most specimens is posterior to midlength. The hinge line is short and rounded, with width and length approximately equal. Most pedicle valves have a slight carination that emphasizes the convexity, but the ventral flanks are also convex. On some of the larger specimens the anterior commissure is slightly bowed toward the brachial valve. The beaks are short, small, and pointed and are incurved over the umbo of the brachial valve. There is a small ventral foramen apically, but no deltidial plates, the area being covered by the posterior edge of the brachial valve.

The ornament consists of rounded radial costae and U-shaped interspaces of the same width, or which may be of slightly less width than the adjoining costae. The latter increase in number anteriorly by bifurcation and by intercalation. At the anterior commissure of specimens between 12 and 15 mm. there are commonly 5 or 6 costae in a space of 5 mm. The radial costae are crossed by evenly spaced frilly growth lamellae, prominent over the whole of both valves.

Interior structures. Interiors are not exposed on the specimens at hand, but one internal mould prepared by removal of the shell shows that dental lamellae are lacking. The ventral diductors appear to be flabellate, but poorly impressed. The costae may be strongly impressed on the internal mould or there may be internal corrugations corresponding to only every 2 or 3 external costae. In the brachial valve the hinge plates are discrete and widely divergent anterolaterally. Dorsal adductor muscle scars are not impressed.

Genus ***DESQUAMATIA*** Alekseeva 1959

TYPE SPECIES. *D. khavae* Alekseeva 1959 : 421–424.

Desquamatia cf. ***microzonata*** Struve 1966

(Pl. 8, figs. 1–6)

1908 *Atrypa reticularis* var. *desquamatà* Reed : 98, pl. 15, figs. 8, 9.
1966 *Desquamatia* (*Synatrypa*) *microzonata* Struve : 151, pl. 16, fig. 12.

MATERIAL. Thirty-three specimens.

FIGURED SPECIMENS. Sedgwick Mus. A 2791, A 2793, A 2794.

DESCRIPTION. *Exterior.* In outline brachial valves are subcircular with slight variations in width and length so that either may be greater in a group of specimens. The pedicle valve has the aspect of a doubly-truncated circle with the two flat sides diverging posteriorly from a very large apical angle. In lateral profile the shells are more or less lenticular with the pedicle valve commonly slightly deeper in small specimens, but with the brachial valve becoming the deepest in larger ones. The hingeline is short and curved. The ventral beak is short, straight, and pointed exposing an apical foramen posterior to conjunct deltidial plates. The beak of the brachial valve is not prominent and is strongly incurved. Most specimens show a slight carination of the pedicle valve in its posterior portion. The brachial valve is evenly rounded. The anterior commissure is rectimarginate.

The external ornament consists of fine, rounded, radial costae separated by U-shaped interspaces about the same amplitude as the joining costae. Costae increase in number anteriorly by splitting, principally on the pedicle valve, and by intercalation, principally on the brachial valve, though exceptions are noted in both cases. Costae are crossed by widely spaced and generally ill-defined concentric growth lines over most of the shell, but which may become slightly lamellose anteriorly on large specimens.

DISCUSSION. The Burmese specimens described above appear to differ slightly from the German Eifelian species (Struve 1966, pl. 16) in having slightly coarser radial costae and slightly better developed concentric growth lamellae at distant intervals. The same comparison may be made with specimens from the Givetian in the Holy Cross Mountains illustrated as *Desquamatia prisca* by Biernat (1964 pl. 10, figs. 1, 2).

Suborder SPIRIFEROIDEA

Superfamily **DELTHYRIDACEA** Phillips 1841

Family **DELTHYRIDIDAE** Phillips 1841

Subfamily **FIMBRISPIRIFERINAE** Pitrat 1965

[*nom. transl.* herein (*ex* Fimbrispiriferidae Pitrat 1965)]

Genus ***INDOSPIRIFER*** Grabau 1931

TYPE SPECIES. *Spirifer padaukpinensis* Reed 1908 : 101, pl. 15, figs. 12–15.

Diagnosis. Biconvex, multiplicate spiriferids, fold and sulcus plicate, fine ornament of radial lirae originating at many points on the valve. Dental lamellae well developed. Excessive shell material lacking posteriorly. Small subdelthyrial plate present. Dorsal cardinalia with crural plates.

Discussion. This genus somewhat resembles a number of Lower Devonian or Eifelian fully ribbed spirifers such as *Costispirifer*, *Fimbrispirifer*, and *Multispirifer*, and a combination of characters serves to distinguish *Indospirifer* from the others. *Indospirifer* commonly is easy to distinguish from *Costispirifer* because of the long outline of the latter, but *Costispirifer* has low plications with narrow interspaces and without a distinctly developed fold and sulcus in most specimens. The fine ornament of *Costispirifer* consists of exceedingly fine thread-like radial lirae, very different from the diverging sets of radial lirae of *Indospirifer*. *Multispirifer* has coarse angular plications and a well developed subdelthyrial plate in the pedicle valve.

Indospirifer and *Fimbrispirifer* appear to be closest. They each have a rib pattern in which the sulcus is defined by a pair of primary plications that run all the way from the beak. Lateral plications also emanate from the beak or increase by bifurcation. However, the medial plications in both genera are characterized by a pattern with a median plication and adjoining plications that are subparallel to it (Pl. 8, figs. 9, 14) rather than radial, and which originate along the inner edges of the primary pair that bound the sulcus. Both genera have well developed dental lamellae, although the muscle field in the specimens of *Fimbrispirifer* studied by the writers is considerably broader than the narrow, elongate muscle field of *Indospirifer*. In addition, *Fimbrispirifer* has well developed, finely lamellose, concentric growth lines with concentric rows of fine spines, whereas the fine ornament of *Indospirifer* is dominated by the subradial pattern with the concentric portion less strongly developed.

Nalivkin (1960 : 383, pl. 89, fig. 5) named a species *Indospirifer maritimus* from the Eifelian of Novaya Zemlya. The genus may be widely represented by the so-called *Fimbrispirifer scheii* of the Canadian Arctic (Meyer 1913, pl. 6; McLaren in Fortier *et al.* 1963 : 327).

Indospirifer padaukpinensis (Reed 1908)

(Pl. 8, figs. 7–15)

1908 *Spirifer padaukpinensis* Reed : 101, pl. 15, figs. 12–15.

Material. Seventeen specimens.

Figured specimens. BB 55567–BB 55570.

Description. *Exterior*. The outline of the pedicle valve is rhomboidal and transversely extended. The outline of the brachial valve is subtrigonal to subsemicircular. In lateral profile the valves are strongly biconvex with the pedicle valve the deeper. The ventral beak commonly is prominent and strongly incurved over a well developed moderately long palintrope. Maximum width is at the hinge line or very slightly anterior to it depending on the degree of rounding of the cardinal angles. They may be acute or obtuse, but specimens with mucronate cardinal angles were not observed. The interarea of the pedicle valve is relatively long and only gently curved except near the beak where it is commonly strongly curved.

Its inclination is apsacline, but low, commonly near to the orthocline position. Most of the interarea is deeply striated normal to the hinge line. The material at hand is not sufficient to allow an accurate description of the dorsal interarea. The delthyrium is triangular and open enclosing a relatively broad angle that on large specimens is only a little less than 90 degrees. Flanks and medial regions are both plicate. The flanks bear well developed rounded and elevated plications that commonly are simple, but which may increase in number by branching. The innermost two plications on each flank of the pedicle valve may be a little more greatly elevated than adjoining lateral plications and define the margins of the ventral sulcus. The sulcus is plicate, but the plications commonly are smaller than the adjoining plications on the lateral slopes. The pattern develops around a relatively small median plication on moderate sized specimens. There commonly are two more plications on either side of the median one, but within the sulcus. These additional plications are parallel or nearly parallel to the median plication and they originate from the inner edges of the bounding plications rather than emanating from the ventral beak. On the available specimen that best illustrates the median plications, the fine ornament consists of numerous thread-like raised lirae that may originate from any point on the shell. The lirae diverge out of the interspaces anteriorly and converge over the crests of the plications on the flanks. In the mid-regions they very closely parallel the axes of the median plications.

Interior of pedicle valve. Hinge teeth are plate-like with semicircular dorsal tips whose long axes parallel the interareas. Ventral faces of the hinge teeth are within the delthyrium. The dental lamellae are long, divergent, plate-like, and generally lie just outside the pair of plications bounding the sulcus. The sites of ventral muscle attachment are not impressed although on one specimen there is a short myophragm posteriorly. The apex of the valve is partly closed by a pair of ridges of shell material that are attached to the inner faces of the dental lamellae and which coalesce apically to close a small part of the delthyrium.

Interior of brachial valve. The sockets are poorly preserved on the material available.

Short crural plates are present, and on small specimens project subparallel to the median line, but on larger specimens they converge medially and anteriorly. Generally the area between the crural plates is partly filled with shell material forming a more or less well developed notothyrial platform from which a knob-like site of diductor attachment may arise apically. The site of diductor attachment is deeply striated longitudinally in a comb-like fashion. The dorsal adductors are not impressed, but commonly there is a long thin myophragm. The interior is crenulated by the impress of the plications, but is otherwise smooth.

Subfamily **SPINOCYRTIINAE** Ivanova 1959

Genus ***ALATIFORMIA*** Struve 1963

TYPE SPECIES. *Spirifer alatiformis* Drevermann 1907 : 126; Kayser 1889, pl. 1, figs. 7, 8.

Alatiformia? sp.

(Pl. 8, figs. 16–26)

1908 *Cyrtina heteroclita* var. *multiplicata* Reed : 108, pl. 16, figs. 11–16, *non* Davidson.

MATERIAL. Three specimens.

FIGURED SPECIMENS. BB 55571–BB 55573.

DESCRIPTION. *Exterior.* The outline is subtrigonal and strongly transverse with a long straight hinge line being the place of maximum width. In lateral profile the valves are unequally biconvex with a strong subpyramidal pedicle valve and a very gently convex brachial valve. The pedicle valve bears a well developed U-shaped sulcus equal in width to approximately two and a half of the adjoining plications. The brachial valve develops a low, somewhat flat-topped fold that rises above the adjoining plications and is equal in width to approximately two of the adjoining plications. The ventral interarea is high, flat, and nearly catacline. It is cleft medially by a high triangular open delthyrium enclosing an angle of about 30 degrees. Deltidial plates take the form of rod-like flanges along the inner edge of the delthyrium, but are not plate-like or projecting. The interarea of the brachial valve is not exposed, but evidently is nearly linear and very poorly developed.

The flanks of both valves are radially plicated and each flank of the pedicle valve bears about eight plications emanating from near the beak. There may be three or four more plications that originate away from the beak along the beak ridges. The fine ornament consists of numerous rod-like spine bases arranged more or less in a radial fashion, but not aligned in concentric rows over most of the shell. However, anteriorly where a few poorly developed growth lines occur, there is some differentiation of concentric rows. On the flanks the rods are more or less aligned on radial ridges that diverge out of the interspaces and converge over the tops of the plications. The fold and sulcus lack plications.

Interior of pedicle valve. The hinge teeth are not exposed in the available specimens, but an internal mould of one specimen reveals short, broadly divergent plate-like dental lamellae in the positions of the first interspaces lateral to the ventral sulcus. Medially there is a well defined prominent myophragm, but the ventral musculature is not impressed and is not discernible. The umbonal cavities are wholly free of infilling shell material. Beneath the level of the interarea and in approximately the apical third of the delthyrium, there is a transverse subdelthyrial plate; it is nearly flat and very thin, and may have an internal medial ridge near its dorsal extremity. The ridge is extended dorsally as a medial crest-like projection in the otherwise concave dorsal edge of the plate.

Interior of brachial valve. The available material is not preserved in the region of the cardinalia. The one internal mould available shows the development of a very fine myophragm, but the sites of muscle attachment are not impressed. The interior of both valves is strongly corrugated by the impress of the plications.

Family **RETICULARIIDAE** Waagen 1883

Genus ***RETICULARIOPSIS*** Frederiks 1916

TYPE SPECIES. *Spirifer* (*Reticularia*) *dereimsi* Oehlert 1901 : 236, pl. 6, figs. 2–16.

Reticulariopsis eifliensis (Scupin 1900)

(Pl. 9, figs. 6–20)

1900 *Spirifer robustus* var. *eifliensis* Scupin : 56, pl. 5, figs. 5a–d.
1908 *Spirifer* (*Reticularia*) *aviceps* Reed : 105, pl. 16, figs. 1–3, *non* Kayser.
1908 *Spirifer* (*Reticularia*) *curvatus* Reed : 104, pl. 15, fig. 17, *non* Schlotheim.
1962 "*Spirifer*" *robustus* var. *eifliensis* Boucot : 416, pl. 51, figs. 12, 13.
1966 *Eoreticularia eifliensis* Biernat : 126, pl. 30, figs. 13–19.

MATERIAL. Twenty-three specimens.

FIGURED SPECIMENS. BB 55575–BB 55580.

DESCRIPTION. *Exterior.* Brachial valves are pentagonal in outline and pedicle valves commonly are rhomboidal. Width is characteristically greater than the length on the brachial valves, but the pedicle valves are more nearly equidimensional. The valves are unequally biconvex in lateral profile with the pedicle valve three or four times as deep as the brachial valve. The pedicle valve bears a well defined U-shaped sulcus medially and on some specimens it is accentuated by the development of bordering plications. The brachial valve bears a complimentary fold and on some specimens very faintly developed bounding furrows. The interarea of the pedicle valve is high, triangular, and curved apsacline. The interarea commonly occupies a small portion of the palintrope so that it is considerably less wide than the hinge line and is commonly about half the maximum width of the valves. Beak ridges are well marked, even though they do not coincide with a break in slope of the shell posteriorly.

The delthyrium encompasses an angle of approximately 60 degrees and is bounded laterally by a prominent pair of deltidial plates that meet apically, but which do not close the delthyrium because they are set at angles more nearly normal to the plane of the interarea than parallel to it. The interarea of the brachial valve is narrow, nearly linear, and hypercline. Maximum width is found in the posterior half of the brachial valve and generally near midlength in pedicle valves. The external ornament consists of numerous, evenly spaced, concentric growth lines, each bearing a set of fine radial striae.

Interior of pedicle valve. The teeth are not exposed in the available specimens. Dental lamellae are long, thin plates that diverge anterolaterally at a moderate angle and are set relatively far apart. The sites of diductor muscle attachment are not impressed, but evidently are situated between the dental lamellae and are divided medially by a low rounded myophragm coincident with the internal expression of the ventral sulcus. On some specimens there is a very short, blade-like myophragm 2 or 3 mm. long in the apex on large specimens.

Interior of brachial valve. The sockets are shallow and diverge laterally at wide angles and only slightly away from the hinge line. The median sides of the socket plates are joined by short crural plates that converge basally, but which may either converge or diverge anteriorly. In most specimens a notothyrial platform is developed with a median ridge-like elevation forming the site of diductor attachment. The dorsal adductor impressions are long and narrow and may be bounded laterally by a pair of low bounding ridges.

Discussion. The genus *Reticulariopsis* is now recognized as a senior subjective synonym of *Tingella* following Pitrat (1965 : H719).

It appears that there are three recognizable species groups most common in beds of Eifelian age in western and central Europe. The first group, characterized by *R. eifliensis* and *R. remesi* (Havlíček 1951 : 15, pl. 3, figs. 1, 3), in which the brachial valve is subtrigonal and the pedicle valve is deeply convex with a long palintrope. The second group comprises *R. reticularioides* (Grabau), *R. dereimsi* (Oehlert 1901; Vandercammen 1958, pl. 2, figs. 9–14), and *R. bicollina* (Struve 1961 : 332, pl. 1, figs. 1, 2). These last three species are biconvex and transversely suboval in outline with the pedicle valve not so deep and a little more strongly curved in the ventral interarea than the first group. The third group includess species generally assigned to "*Spirifer*" *curvatus* Schlotheim (Scupin 1900, pl. 26; see also LeMaitre 1952, pl. 14, figs. 16, 17) which has an extravagant development of ventral sulcus and dorsal fold.

Family **AMBOCOELIIDAE** George 1931

Genus ***EMANUELLA*** Grabau 1923

Type species. *Nucleospira takwanensis* Kayser 1883 : 86.

Emanuella inflata (Schnur 1853)

(Pl. 9, figs. 1–5; Text-fig. 7)

1853 *Spirifer inflatus* Schnur : 211, pl. 37, figs. 2A–D.
1908 *Spirifer* (*Martinia*) *inflatus* Reed : 106, pl. 16, figs. 5, 5A.
1965 *Martinia inflata* Jux & Strauch : 58, pls, 1, 2.
1966 *Crurithyris inflata* Biernat : 122, pl. 29, figs. 1–9.

Material. Forty-four specimens.

Figured specimens. BB 55574, BB 55589F.

Description. *Exterior.* The shells are small and unequally biconvex with the pedicle valves larger. Shape is variable; some specimens being transversely subtrigonal to rhomboidal, others are longer than wide and the changes are due to a variable width of the interareas and of the degree of curvature of the ventral beak. The hinge line in all of the specimens is less than the maximum width which commonly is attained posterior to midlength. Cardinal angles are bluntly rounded. The ventral interarea is equal to about one-half to two-thirds the maximum width of the valves; it is triangular and incurved to a variable degree although all inclinations may be described as apsacline. In general, smaller specimens are more steeply apsacline and larger ones may be considerably incurved approaching the orthocline position. Neither fold nor sulcus are developed, although on several specimens a flattening may be seen at the ventral midline anteriorly, suggesting the incipient development of a sulcus there.

The fine exterior ornament revealed, in spite of imperfect preservation, consists of very numerous thread-like radial spinules that may or may not be situated in concentric rows on the growth lines. There appears to be a somewhat greater tendency to develop a set of spinules along radial lines rather than having each concentric row of spines separately defined as shown in some specimens studied by Veevers (1959 : 904). The delthyrium is triangular and open, encompassing an

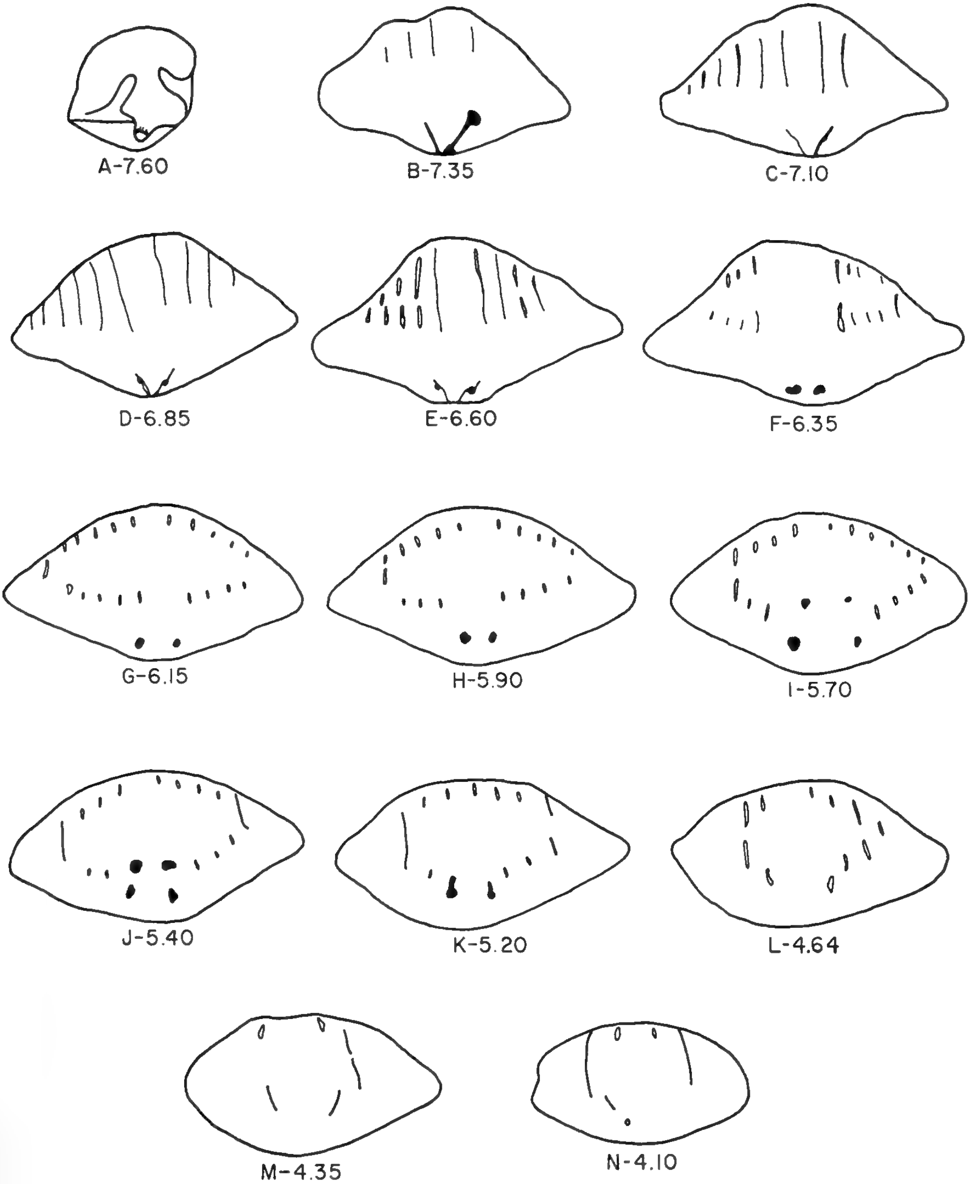

FIG. 7. *Emanuella inflata*, serial sections of BB 55589F × 5. Numbers indicate distance in millimeters from the anterior. Original length was 8·60 mm.

angle of a little less than 30 degrees. The dorsal interarea is short, flat, and triangular and is anacline.

Interior of pedicle valve. The apex bears a rod-like thickening disposed longitudinally and partly protruding into the apex of the open delthyrium. Hinge teeth develop thick tracks, but are unsupported by dental lamellae.

Interior of brachial valve. The site of diductor attachment in the notothyrial cavity develops comb-like longitudinal striations on a small thickening of shell material apically. Crural plates are present projecting anteriorly and very slightly laterally and converging towards one another at the base of the valve, but the crural plates are not united to form a cruralium supported by a median septum. The crural bases are thick and rod-like in cross section, somewhat more prominent than the thin cural lamellae. They are joined on their ventral edges by a pair of ribbon-like outer hinge plates that continue for some distance anteriorly. The crura continue anteriorly in a subparallel position near the base of the brachial valve and evidently recurve somewhere near the anteromedial portion of the valve to join the primary volutions of the spiralia which consist of 5 or 6 volutions with their apices directed laterally.

Superfamily **CYRTINACEA** Frederiks 1912

[*nom. transl.* Johnson 1966 (*ex* Cyrtininae Frederiks 1912)]

Family **CYRTINIDAE** Frederiks 1912

Genus ***CYRTINA*** Davidson 1858

Type species. *Calceola heteroclita* Defrance 1828 : 306; by subsequent designation of Miller (1889 : 342).

Cyrtina heteroclita (Defrance 1828)

(Pl. 10, figs. 1–11; Text-fig. 8)

Material. Sixty-nine specimens.

Figured specimens. BB 55581–BB 55585, BB 55589G.

Description. *Exterior.* The valves are strongly unequally biconvex with a deep subpyramidal pedicle valve and a flat gently convex brachial valve. The ventral interarea is high, triangular, and catacline, commonly flat; but in some specimens the beak may be strongly incurved or incurved and slightly twisted to one side. In outline the valves are subtriangular with a long straight line that is the place of maximum width. The interarea of the brachial valve is relatively long, flat, and orthocline. Most of the specimens are wider than long, with the greatest relative width being about twice that of the length. The ventral beak is pointed and slopes off precipitously toward the anterior and the lateral flanks.

Medially there is a shallow rounded or subangular sulcus without plications. The brachial valve bears a corresponding rounded fold whose elevation appears to be considerably variable. The flanks on both valves are plicate and the number of plications on the flank of a pedicle valve is subject to considerable variability from as few as two, even on large specimens, to as many as seven small plications on other specimens. The delthyrium is high, triangular, and narrow, commonly encompassing between 10 and 20 degrees. The fine ornament consists of numerous very fine, stubby, rod-like projections aligned on poorly defined radial lirae that diverge anteriorly out of the interspaces and converge over the crests of the plications.

Interior of pedicle valve. The hinge teeth were not observed. There is a pair of long thin dental lamellae paralleling the inner edges of the delthyrium. Dental lamellae converge to meet in the apex of the valve where they join to form a very short median septum. As the dental plates progress anteriorly they join the median septum at continually greater distances above the apex of the pedicle valve and form a spondylium. In the trough between them there is a flatly oval tube-like tichorhinum that is split into a pair of chambers by a blade-like longitudinal process. The median septum continues anteriorly some distance beyond the anterior edges of the convergent dental lamellae. The spiral brachidium consists of a pair of rounded cones. In the specimen sectioned there were five complete volutions in each of the two spiralia and their apices point ventrolaterally at about 45 degrees inclination to the plane of the commissure.

Interior of brachial valve. The sockets are suboval or even subcircular shallow depressions within the interarea. The inner edges of the plates that define the sockets are connected medially by a block of shell material supported by a short pillar-like septum and divided posteriorly into two more or less well differentiated lobes that are longitudinally striate forming a comb-like diductor attachment surface. Outer socket ridges may develop in large specimens. The crura are not preserved. There is a deep depression medially internal to the dorsal fold and the posterior

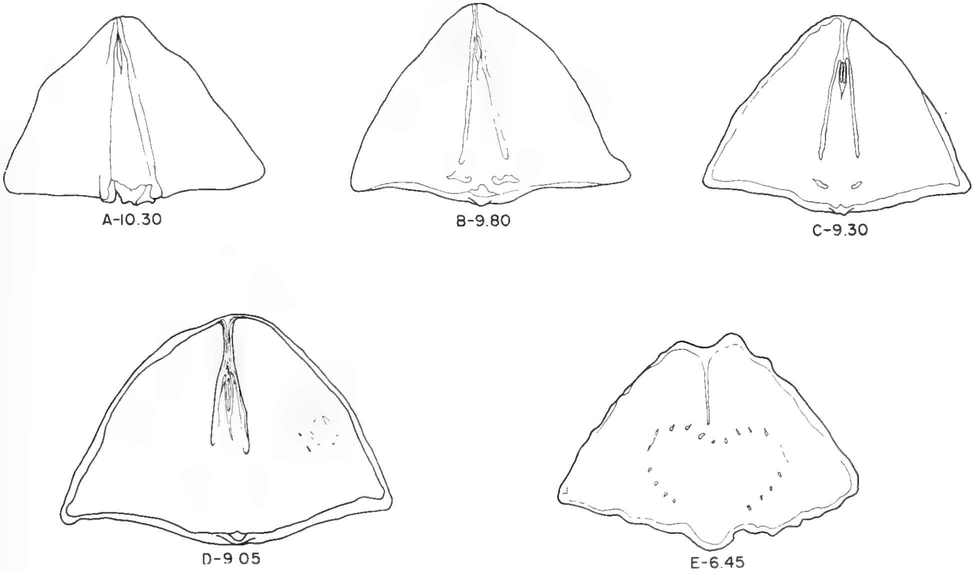

FIG. 8. *Cyrtina heteroclita*, serial sections of BB 55589G × 2·5 (sections A, B, C) and × 3 (sections D, E). Numbers indicate distance in millimeters from the anterior. Original length was 10·70 mm.

portion of the shell in this area may bear a slender myophragm, but the adductor muscle impressions are not clearly differentiated.

Shell structure. The shell material is endopunctate. Punctae are densely crowded together without any appreciable pattern.

DISCUSSION. Pitrat in Moore (1965 : H678) discarded the subsequent designation of Dall (1877 : 24) as invalid and instead selected the subsequent designation of Hall and Clarke (1893 : 44). The latter designation was, however, preceded by Miller's noted above.

Order TEREBRATULIDA

Suborder CENTRONELLOIDEA

Superfamily **STRINGOCEPHALACEA** King 1850

Family **MUTATIONELLIDAE** Cloud 1942

Subfamily **CIMICINELLINAE** Stehli 1965

Genus ***CIMICINOIDES*** gen. nov.

TYPE SPECIES. *Cimicinoides struvei* sp. nov.

DIAGNOSIS. Externally like *Cimicinella*, but with the loop connected by a horizontal anterior plate which bears a ventrally directed plate-like median septum.

DISCUSSION. This small smooth terebratuloid is a homeomorph of *Cimicinella*. The external configuration is particularly marked in the structure of the ventral beak which bears a delthyrium closed by deltidial plates that are pierced by a hypothyrid foramen. In the presence of short dental lamellae and in the configuration of the cardinalia the two genera are also apparently identical although Stehli (1965 : H752) noted that crural plates are present in *Cimicinella*. *Cimicinoides* lacks crural plates and Stehli's indication of their presence in *Cimicinella* evidently refers to the so-called " inneren Troges " shown in Schmidt's reconstruction (1946 : 69, fig. 6B, C). The latter is something of an enigmatic structure, unlike anything that the writers are familiar with in Lower and Middle Devonian terebratuloids, but in any event the two individuals of *Cimicinoides struvei* that were sectioned do not show a similar structure.

Cimicinoides struvei sp. nov.

(Pl. 10, figs. 12–22; text-figs. 9, 10)

?1908 *Glassia whidbornei* Reed : 100, pl. 15, fig. 11; not Davidson.

MATERIAL. Thirty specimens.

FIGURED SPECIMENS. BB 55586 (holotype), BB 55587, BB 55588, BB 55589H & I (paratypes).

DESCRIPTION. *Exterior.* The shells are elongate, subelliptical in outline, and unequally biconvex in lateral profile. Pedicle valves of the larger specimens are

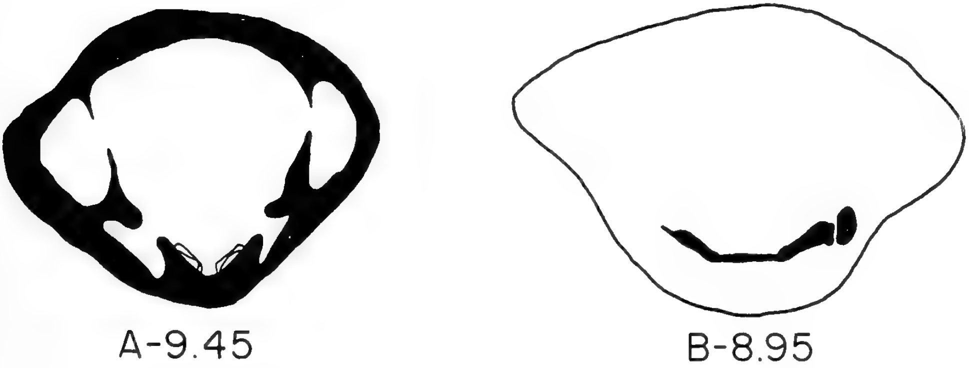

FIG. 9. *Cimicinoides struvei*, serial sections of BB 55589H × 12. Numbers indicate distance in millimeters from the anterior. Original length was 10·80 mm.

commonly about twice as deep as the brachial valves. The shape is relatively constant with the beak angle about 90 degrees or slightly less, with the posterolateral margins continuing almost straight or they are slightly curved, convex outward. The anterior margin may be evenly rounded from the midline or it may be slightly flattened. The ventral beak is relatively prominent, narrow, and incurved to the suberect position. The ventral palintropes are somewhat flattened and prominent. There is a triangular delthyrium pierced by a hypothyrid foramen. The hinge line is short and rounded. Maximum width is near midlength and the anterior commissure is rectimarginate. The surface of the valves is smooth.

Interior structures. There is a pair of very short thin widely spaced subparallel dental lamellae in the pedicle valve. In the brachial valve the hinge plates are divided posteriorly with their inner surfaces relatively flat and parallel to the surface of the valve. There is a pair of thin layers of shell material forming a faint bilobed notothyrial platform at the apex. Anterior to the sockets the hinge plates join to form a medially flattened cardinal plate. Crural plates are not present. The initial ribbons of the loop are subparallel to the median plane, but twist slightly as they diverge anteriorly so that they are more nearly parallel to the inner surface of the brachial valve. The bands converge again anteriorly a short distance past midlength where they join a small, saddle-shaped median plate that bears a ventrally and posteriorly projecting blade-like median septum. The median plate and median septum bear fine spines of circular cross-section that project anteriorly.

DISCUSSION. *Cimincinoides struvei* very closely resembles *Cimicinella simulatrix* Struve (1964, pl. 42) although that species includes slightly larger shells. Struve (1964 : 448) described the foramen of *C. simulatrix* as submesothyrid, a slightly different position than the foramen of *C. struvei*. Even so these two forms rather closely resemble one another. Further comparison may prove worthwhile when the loop of *C. simulatrix* is illustrated.

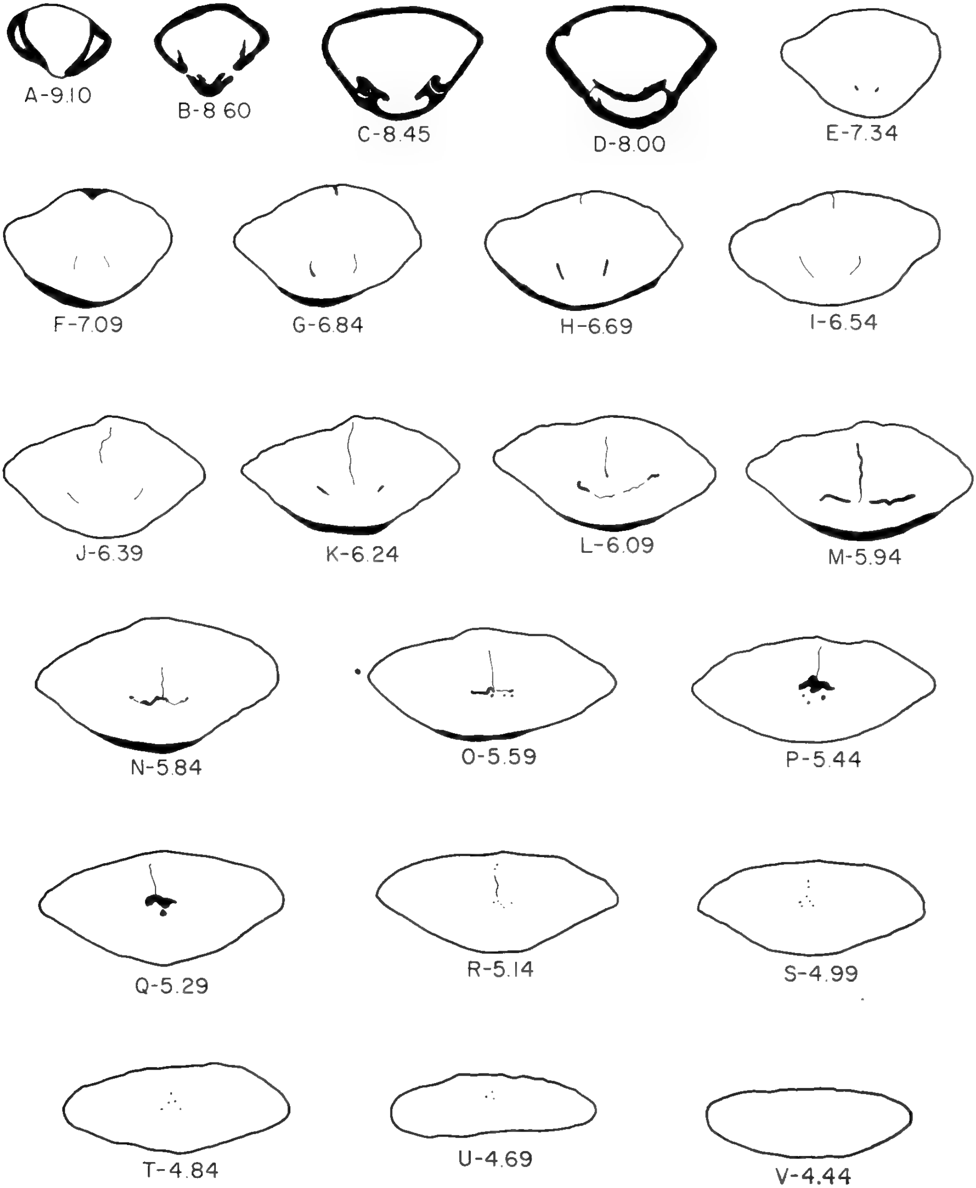

FIG. 10. *Cimicinoides struvei*, serial sections of BB 55589I × 5. Numbers indicate distance in millimeters from the anterior. Original length was 9·45 mm.

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PLATE 1

Aulacella eifeliensis (Schnur 1853)

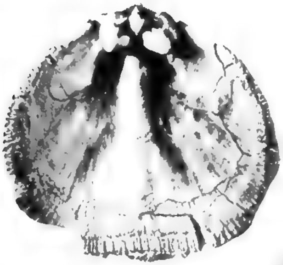
FIG. 1. Interior of brachial valve × 2 BB 55500.
FIG. 2. Internal mould of pedicle valve × 2 BB 55501.
FIGS. 3, 4. Ventral and dorsal views of a crushed specimen × 2, BB 55502.
FIG. 5. Interior of pedicle valve × 2, BB 55503.
FIGS. 6, 7. Dorsal and anterior views of interior of brachial valve × 6, BB 55504.
FIGS. 8, 9. Dorsal and anterior views of interior of brachial valve × 5, BB 55505.
FIG. 10. Interior of fragment of brachial valve × 3, BB 55506.
FIGS. 11, 12. Ventral and dorsal views × 2, BB 55507.

Schizophoria schnuri (Struve 1965)

FIGS. 13, 14. Dorsal and ventral views × 1, BB 55508.
FIG. 15. Postero-dorsal view of internal mould of brachial valve × 1·25, BB 55509.
FIGS. 16, 17. Ventral and posterior views of internal mould × 1·5, BB 55510.

Mystrophora areola (Quenstedt 1871)

FIGS. 18, 22. Anterior, posterior, side, dorsal, and ventral views × 4, BB 55511.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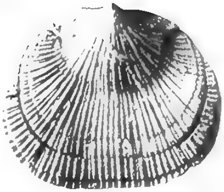
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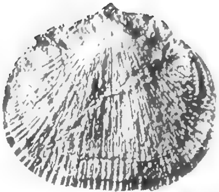
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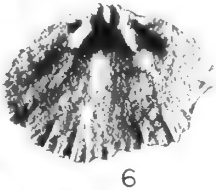
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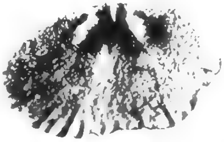
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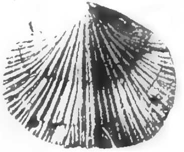
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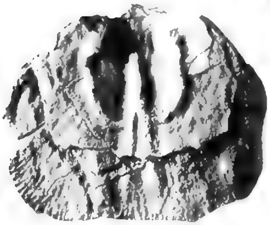
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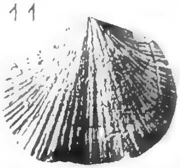
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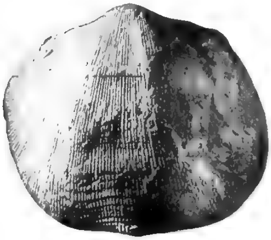
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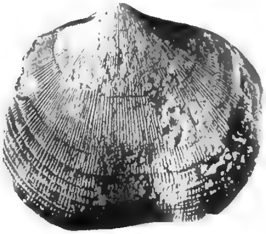
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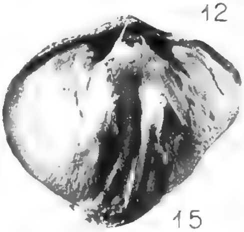
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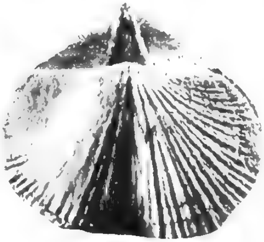
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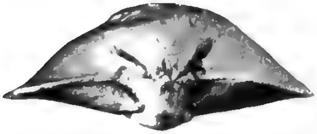
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PLATE 2

Kayserella cf. ***lepida*** (Schnur 1853)

FIG. 1. Interior of brachial valve × 10, BB 55512.
FIGS. 2, 3. Ventral and dorsal views × 10, BB 55513.

Sieberella cf. ***brevirostris*** (Phillips 1841)

FIGS. 4–7. Anterior, posterior, side, and dorsal views of internal mould × 1·5, BB 55514.
FIGS. 8–12. Anterior, posterior, ventral, dorsal, and side views × 1·5, BB 55515.

Leptaena sp.

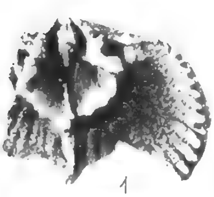
FIG. 13. Interior of fragment of brachial valve × 2, BB 55516.
FIG. 14. Ventral view × 1, BB 55517.

Xystrostrophia umbraculum (Schlotheim 1820)

FIG. 15. Ventral view of internal mould of pedicle valve × 1, BB 55518.
FIG. 16. Ventral view of internal mould of pedicle valve × 1·25, BB 55519.
FIGS. 17, 18. Side and ventral views × 1, Sedgwick Museum, A2760.
FIG. 19. Dorsal view × 1, Sedgwick Museum A2762.
FIG. 20. Dorsal view of internal mould of brachial valve × 1·5, BB 55520.

Leptostrophia sp.

FIG. 21. Dorsal view of posterior part of internal mould of brachial valve × 3, BB 55521. See also Pl. 3, figs. 1–6.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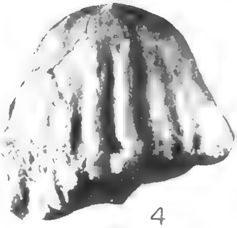
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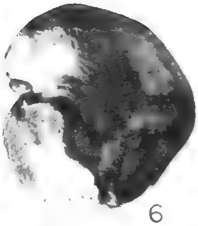
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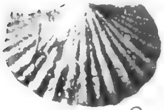
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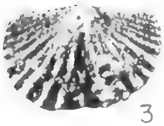
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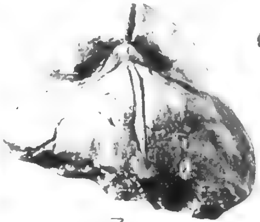
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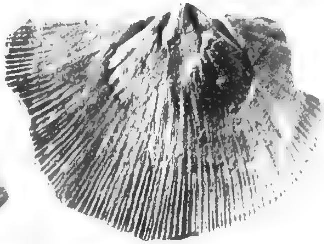
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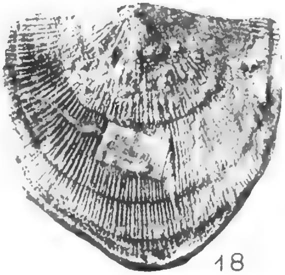
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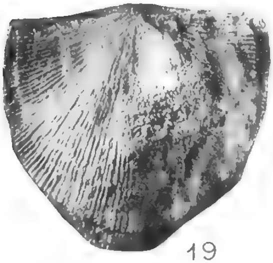
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PLATE 3

Leptostrophia sp.

FIG. 1. Dorsal view of internal mould of brachial valve × 1·5; internal mould of specimen in figures 2–4.

FIGS. 2–4. Posterior, dorsal, and ventral views × 1·5, BB 55521.

FIG. 5. Internal mould of fragment of pedicle valve × 2, BB 55522.

FIG. 6. Interior of brachial valve × 5, BB 55523.

Leptodontella caudata (Schnur 1853)

FIG. 7. Interior of pedicle valve × 1, BB 55524.

FIGS. 8, 9. Posterior and anterior views × 1·5, BB 55525.

FIG. 10. Interior of brachial valve × 1·5, BB 55526.

FIG. 11. Interior of brachial valve × 1·25, Sedgwick Museum, A2654.

Mesodouvillina birmanica (Reed 1908)

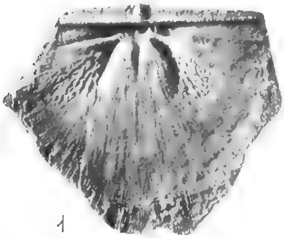
FIG. 12. Internal mould of brachial valve × 2, BB 55527.

FIG. 13. Interior of brachial valve × 2, BB 55528.

FIGS. 14, 15. Side and posterior views × 1·25, BB 55529.

FIG. 16. Internal mould of pedicle valve × 1·5, BB 55530.

FIG. 17. Internal mould of pedicle valve × 1·25, BB 55531. See also Pl. 4, figs. 1–4.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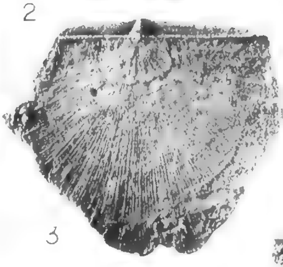
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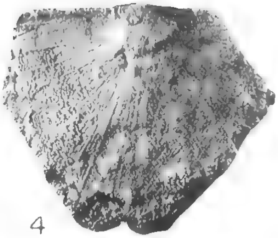
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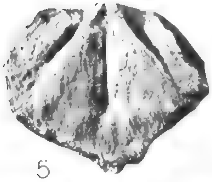
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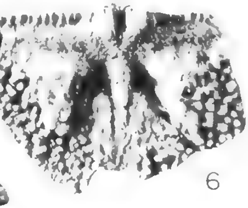
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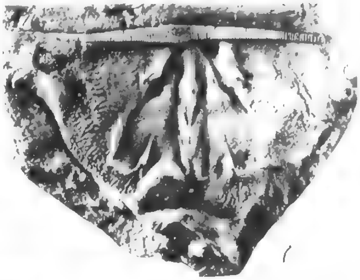
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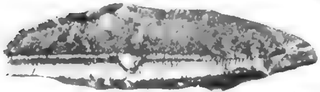
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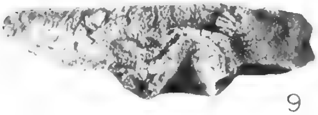
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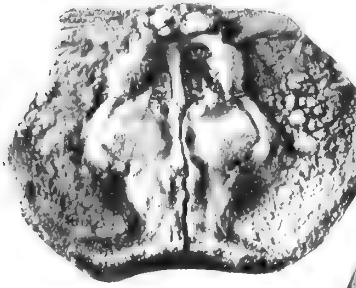
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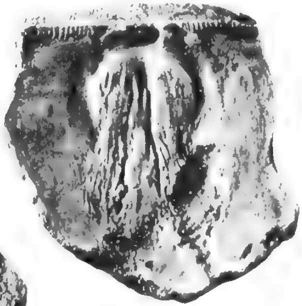
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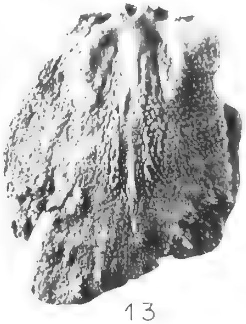
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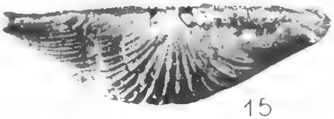
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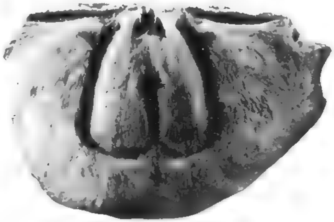
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PLATE 4

Mesodouvillina birmanica (Reed 1908)

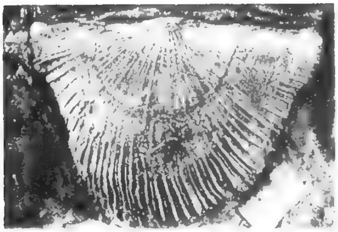
FIG. 1. Ventral view × 1, Sedgwick Museum, A2745.
FIG. 2. Interior of brachial valve × 2, Sedgwick Museum, A2738.
FIGS. 3, 4. Antero-ventral and ventral views × 1·25, BB 55529. See also Pl. 3, figs. 14, 15.

Telaeoshaleria padaukpinensis (Reed 1908)

FIGS. 5–8. Side, anterior, posterior, and ventral views × 4, BB 55532.
FIG. 9. Interior of brachial valve × 6, BB 55533.
FIG. 10. Ventral view of internal mould of pedicle valve × 3, BB 55534.
FIG. 11. Interior of fragment of brachial valve × 10, BB 55535.
FIG. 12. Ventral view × 4, BB 55536.

Radiomena* cf. *irregularis (Roemer 1844)

FIG. 13. Ventral view × 1, BB 55537.
FIGS. 14–16. Anterior, dorsal, and posterior views of cardinalia × 3, BB 55538.
FIG. 17. Dorsal view of fragment of brachial valve interior × 3, BB 55539.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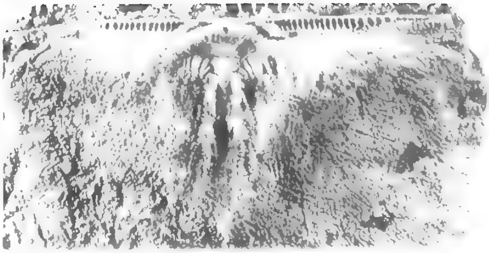
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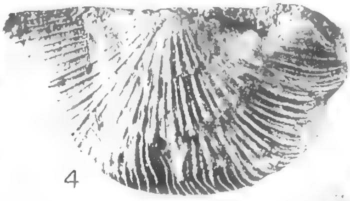
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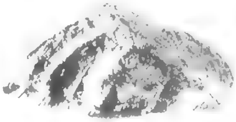
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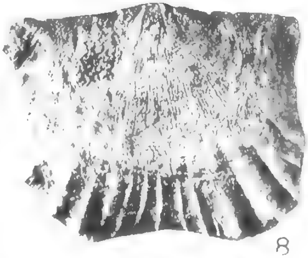
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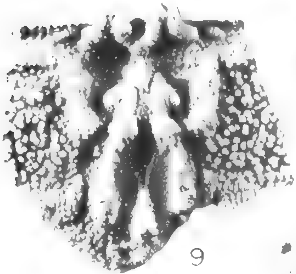
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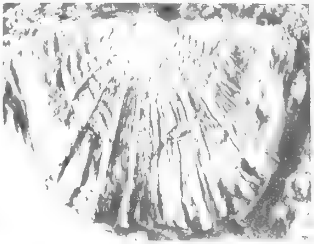
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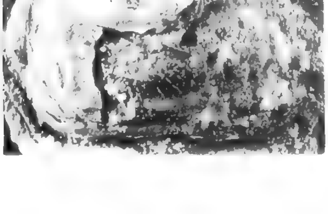
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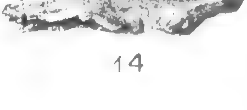
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PLATE 5

Devonaria minuta (von Buch 1836)

FIGS. 1–5. Anterior, posterior, side, ventral, and dorsal views × 2, BB 55540.

FIG. 6. Dorsal view of specimen in figures 1–5, × 4.

FIG. 7. Internal mould of brachial valve × 3, BB 55541.

FIG. 8. Internal mould of brachial valve × 3, BB 55542.

FIGS. 9, 10. Ventral and posterior views of internal mould of pedicle valve × 2, BB 55543.

FIGS. 11, 12. Dorsal and ventral views × 3, BB 55544.

Productella? sp.

FIGS. 13–17. Ventral, dorsal, anterior, side, and posterior views × 3, BB 55545.

Uncinulus subsignata (Reed 1908)

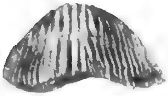
FIGS. 18, 19. Dorsal and ventral views × 3, BB 55546.

FIGS. 20, 21. Dorsal and ventral views × 3, BB 55547.

FIGS. 22–26. Side, posterior, anterior, dorsal, and antero-ventral views of internal mould × 1·5, BB 55548.

FIGS. 27–31. Side, ventral, anterior, dorsal, and posterior views × 1·5, BB 55549.

PLATE 5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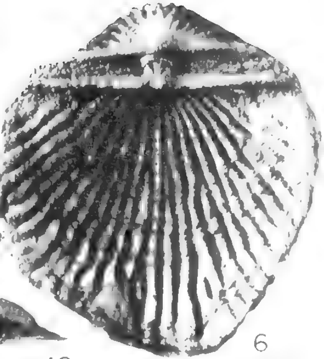
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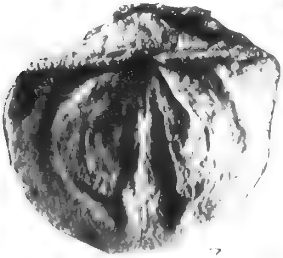
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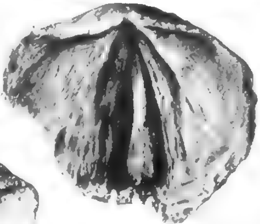
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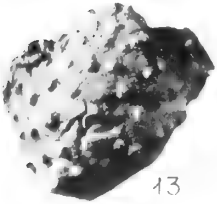
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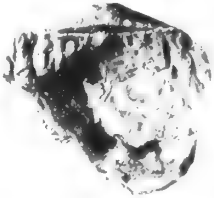
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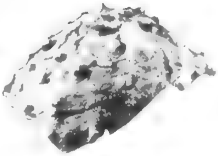
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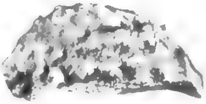
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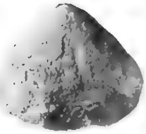
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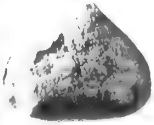
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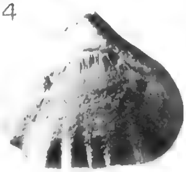
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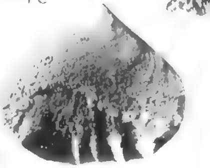
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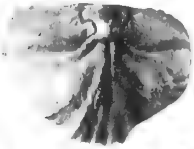
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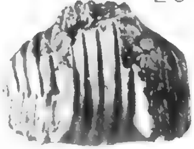
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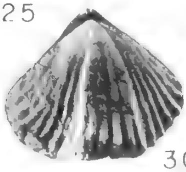
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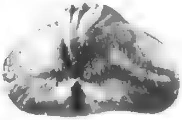
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PLATE 6

Markitoechia?* cf. *pentagona (Kayser 1871)

FIGS. 1–4. Dorsal, side, posterior, and anterior views × 4, BB 55550.

Schnurella* cf. *schnuri (Verneuil 1840)

FIGS. 5, 6. Ventral and dorsal views × 1·5, Sedgwick Museum, A2779.

***Septalaria?* sp.**

FIGS. 7–11. Antero-ventral, ventral, dorsal, side, and anterior views × 1·5, BB 55551.

Merista subdidyma (Reed 1908)

FIGS. 12, 13. Ventral and dorsal views × 4, BB 55552.

***Nucleospira* sp.**

FIGS. 14–18. Dorsal, ventral, side, anterior, and posterior views × 3, BB 55553.

Plectospira ferita (von Buch 1834)

FIGS. 19–23. Anterior, dorsal, ventral, posterior, and side views × 5, BB 55554.
FIGS. 24, 25. Dorsal and ventral views × 5, BB 55555.
FIGS. 26, 27. Dorsal and ventral views × 5, BB 55556.

Plectospira longirostris (Kayser 1871)

FIGS. 28, 29. Ventral and dorsal views × 4, BB 55557.
FIGS. 30–32. Side, ventral, and dorsal views × 4, BB 55558.


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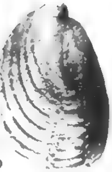
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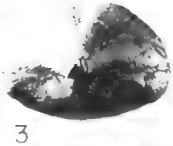
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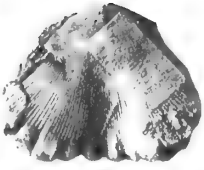
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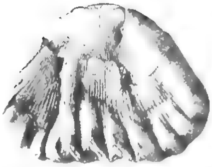
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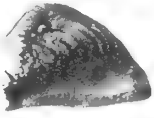
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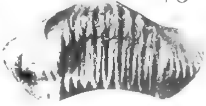
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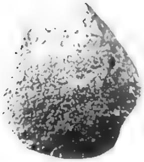
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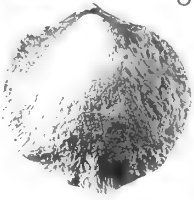
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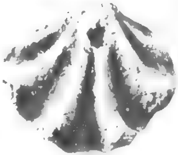
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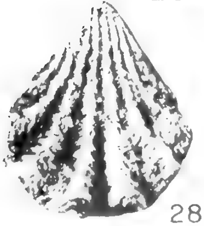
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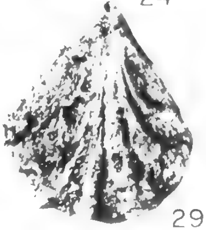
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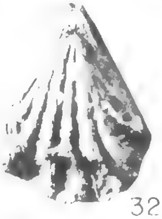
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PLATE 7

Athyris sp.

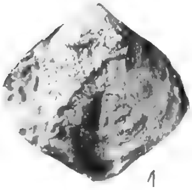
FIGS. 1–5. Ventral, dorsal, side, anterior, and posterior views × 2, BB 55559.

***Atrypa* " *reticularis* "** (Linnaeus 1758)

FIGS. 6–10. Side, anterior, posterior, ventral, and dorsal views × 1·25, BB 55560.
FIGS. 11, 12. Ventral and dorsal views × 1·25, BB 55561.
FIGS. 13, 14. Dorsal and ventral views × 2, BB 55562.
FIGS. 15–19. Ventral, anterior, posterior, side, and dorsal views of internal mould × 2, BB 55563.

Spinatrypa* (*Invertrypa*)** cf. ***asperoides (Biernat 1964)

FIGS. 20–24. Ventral, dorsal, side, anterior, and posterior views × 2, BB 55564.
FIGS. 25, 26. Ventral and dorsal views × 2, BB 55565.
FIGS. 27, 28. Ventral and dorsal views × 2, BB 55566.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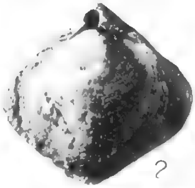
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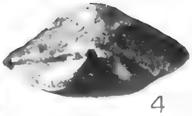
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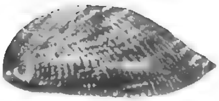
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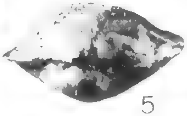
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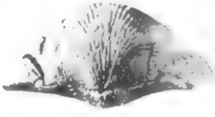
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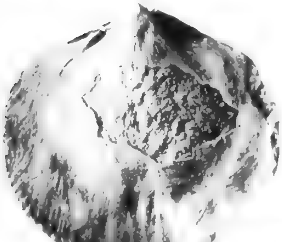
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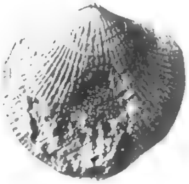
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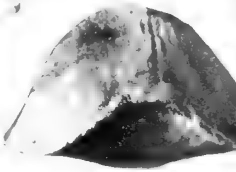
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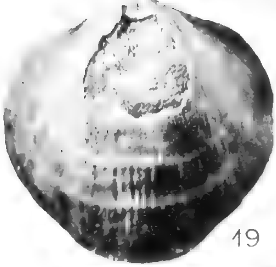
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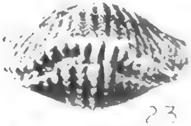
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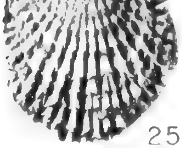
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PLATE 8

***Desquamatia* cf. *microzonata* Struve 1966**

FIGS. 1, 6. Ventral and side views × 2, Sedgwick Museum, A2791.

FIG. 2. Dorsal view × 2, Sedgwick Museum, A2793.

FIGS. 3–5. Posterior, ventral, and side views × 2, Sedgwick Museum, A2794.

***Indospirifer padaukpinensis* (Reed 1908)**

FIG. 7. Interior of pedicle valve × 2, BB 55567.

FIGS. 8, 9, 14. Anterior, posterior, and ventral views × 2, BB 55568.

FIG. 10. Enlargement of the medial region of pedicle valve of specimen in figure 14 × 5.

FIGS. 11–13. Posterior, dorsal, and ventral views of internal mould × 2, BB 55569.

FIG. 15. Posterior view of internal mould of brachial valve × 5, BB 55570.

***Alatiformia?* sp.**

FIGS. 16–18. Dorsal, ventral, and posterior views × 2, BB 55571.

FIGS. 19–23. Side, dorsal, ventral, anterior, and posterior views of internal mould × 2, BB 55572.

FIGS. 24–26. Posterior, anterior, and ventral views × 2, BB 55573.


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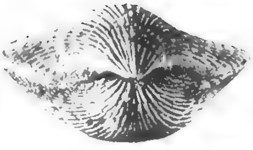
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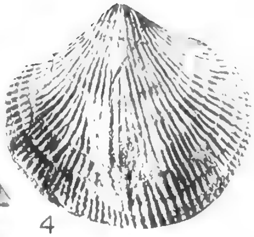
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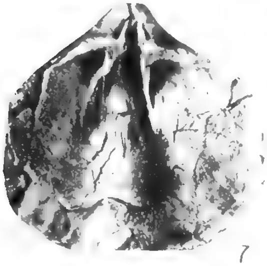
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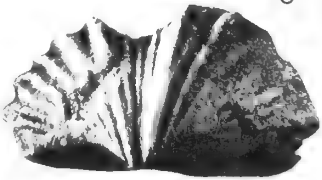
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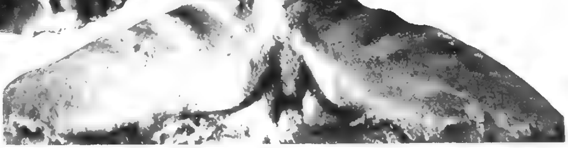
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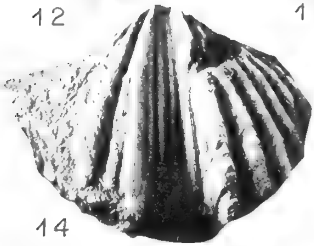
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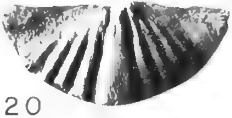
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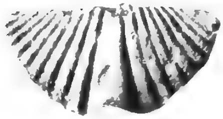
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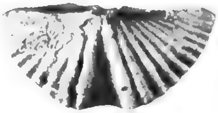
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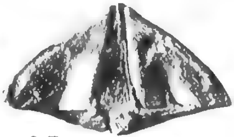
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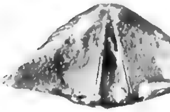
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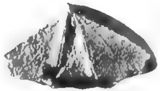
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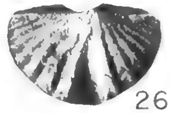
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PLATE 9

Emanuella inflata (Schnur 1853)

FIGS. 1–5. Posterior, dorsal, ventral, side, and anterior views × 4, BB 55574.

Reticulariopsis eifliensis (Scupin 1900)

FIGS. 6–10. Side, dorsal, anterior, posterior, and ventral views of internal mould × 2, BB 55575.

FIGS. 11–13. Posterior, side, and ventral views × 4, BB 55576.

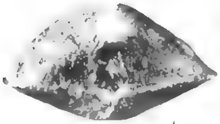
FIGS. 14, 15. Side and posterior views × 2, BB 55577.

FIGS. 16, 17. Ventral and dorsal views × 2, BB 55578.

FIG. 18. Fine ornament on right flank of pedicle valve of specimen in figure 16, × 5.

FIG. 19. Posterior view of medial portion of internal mould × 5, BB 55579.

FIG. 20. Posterior view of medial portion of internal mould × 5, BB 55580; note prominent myophragm in apex of pedicle valve.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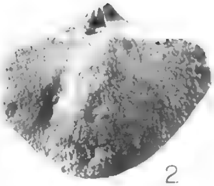
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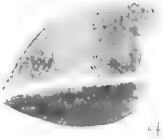
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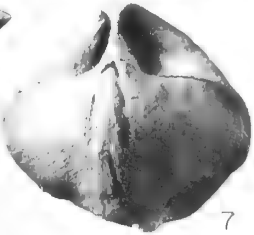
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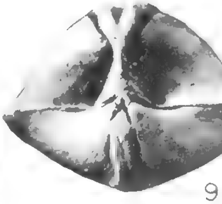
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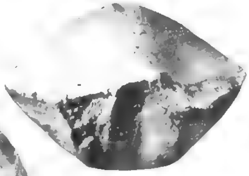
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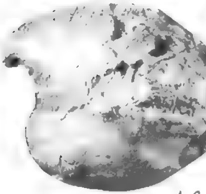
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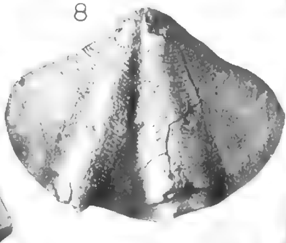
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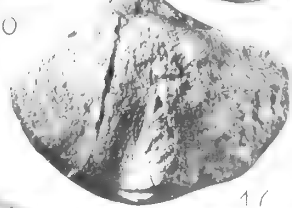
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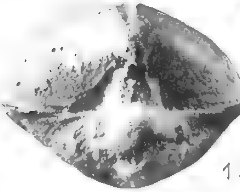
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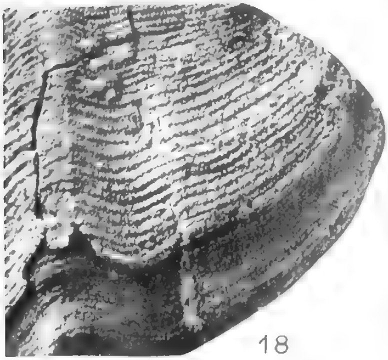
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PLATE 10

Cyrtina heteroclita (Defrance 1828)

FIGS. 1–5, 9, 10. Postero-dorsal, posterior, anterior, antero-ventral, side, dorsal, and ventral views × 2, BB 55581.

FIG. 6. Fine ornament on left flank of brachial valve × 10, BB 55582.

FIG. 7. Interior of brachial valve × 10, BB 55583.

FIG. 8. Interior of brachial valve × 5, BB 55584.

FIG. 11. Interior of brachial valve × 3, BB 55585.

Cimicinoides struvei gen. nov. et sp. nov.

FIGS. 12–16. Dorsal, ventral, side, posterior, and anterior views of the holotype × 4, BB 55586.

FIGS. 17–21. Ventral, dorsal, side, anterior, and posterior views of a paratype × 4, BB 55587.

FIG. 22. Dorsal view of a paratype × 10, BB 55588; note deltidial plates.


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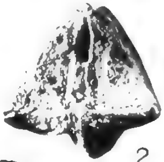
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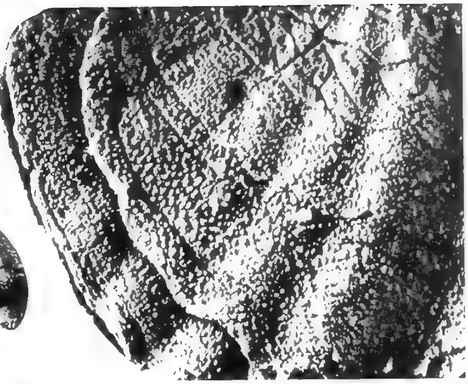
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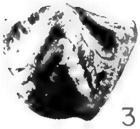
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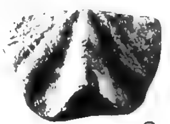
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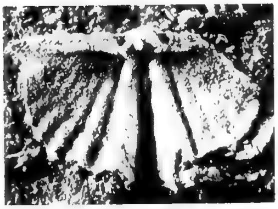
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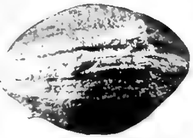
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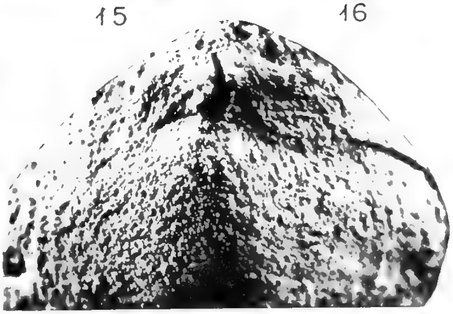
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C. B. COX

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BY

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Pp. 165–196; 1 *Plate,* 13 *Text-figures*

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THE PROBLEMATIC PERMIAN REPTILE *EUNOTOSAURUS*

By CHRISTOPHER BARRY COX

CONTENTS

SYNOPSIS

Eunotosaurus, which has been suggested as a possible ancestral chelonian, is re-investigated and described. Little of the skull is preserved. The vertebrae are amphicoelous and notochordal, with small neural spines and horizontal zygapophyses. There are small intercentra. Ten dorsal vertebrae are known. The outer surfaces of the dorsal ribs are greatly expanded antero-posteriorly. There is a single sacral attachment. There is no trace of dermal ossifications, and it seems likely that the expanded ribs themselves had a protective function and were covered by horny scales. The body is short and not very flexible. The humerus is rather slender, with the ends expanded and at an angle of *c*. 50° to one another; there are entepicondylar and ectepicondylar foramina.

The structure of its vertebrae indicates that *Eunotosaurus* is a cotylosaur, but it shows no close similarities to any other member of that group and is therefore best regarded as constituting a separate family of the sub-order Captorhinomorpha. The absence of separate ribs on the last dorsal vertebra may preclude *Eunotosaurus* from being ancestral to the Chelonia. Its carapace-like form, shortened body and elongate dorsal vertebrae appear to be merely convergent with the chelonian structure, and there are no other features suggesting relationship between the groups.

I. INTRODUCTION

The first specimen of *Eunotosaurus africanus* was described and named by Seeley in 1892, who noted also that the slender elongate vertebrae, which lack transverse processes, were reminiscent of those of the Chelonia, and that the expanded ribs " simulate the ribs and costal plates of chelonians " (1892, p. 585). These suggestions were later expanded by Watson (1914) who deduced, from the characters and trends of later chelonians, the structure of an ancestral " Archichelone ". After studying the four specimens of *Eunotosaurus* in the British Museum (Natural History) and finding structures which he identified as dermal ossifications, Watson compared *Eunotosaurus* with his hypothetical " Archichelone ". He concluded that " it is by no means improbable that it is an actual ancestor of the Chelonia " (1914, p. 1020).

Thenceforward, *Eunotosaurus* was often placed in a separate sub-group of the Chelonia (e.g. Nopcsa 1923; Romer 1966). Apart from passing references by Broom (1941) and Gregory (1946), no further study was made of *Eunotosaurus* for nearly fifty years. The next re-appraisal was that of Parsons & Williams (1961), who concluded that the expanded ribs and possible dermal ossifications were basically quite unlike the chelonian carapace and are " primarily interesting as *another* method by which a similar result may be achieved " (1961, p. 98).

This denial of its affinities with the Chelonia left the taxonomic position of *Eunotosaurus* completely uncertain, since no other relationship for the genus had ever been suggested. Together with the greater potentialities of the newer chemical and mechanical techniques of preparation, this made it seem worthwhile to attempt a re-study of the genus. Thanks to the extremely generous co-operation of the authorities of the British Museum (Natural History), the U.S. National Museum in Washington, the Bernard Price Institute for Palaeontological Research in Johannesburg, and the South African Museum, Cape Town, all the eleven known specimens of *Eunotosaurus* were made available for study and preparation.

II. SYSTEMATIC DESCRIPTION

MATERIAL AND METHODS. For convenience, each specimen has been allocated a letter by which reference will be made to it in the remainder of this paper. The skeletal elements identified from each specimen are as follows.[1]

Specimen A BM(NH) No. R1968 (Holotype). Figured by Seeley, 1892, figs. 1, 2. Seven articulated vertebrae and their ribs; damaged right pubis (?) and ilium; right femur, proximal ends of right tibia and fibula.

Specimen B BM(NH) No. R4054. Figured by Watson 1914, pl. VII, figs. 3, 4. Eight articulated vertebrae and their ribs, plus a single more anterior rib; impressions of small parts of the right scapula and ilium.

Specimen C BM(NH) No. R4949. Ten articulated vertebrae and their ribs; eroded coracoid region; isolated podial elements.

Specimen D BM(NH) No. 49423. Figured by Watson 1914, pl. VII, figs. 1, 2. Eroded remains of five articulated vertebrae and of their ribs; damaged right half of pectoral girdle, and interclavicle; remnants of both humeri.

Specimen E BM(NH) No. 49424. Reconstruction of skull figured by Watson 1914, text-fig. 1. Eroded snout and lower jaw; seven articulated vertebrae and their ribs; remnants of right scapula and of both humeri; both pubes (?).

Specimen F SAM No. K1132. Eight articulated vertebrae and their ribs, plus three isolated vertebrae; ventral portion of pectoral girdle, proximal part of left humerus.

Specimen G SAM No. K1133. Nine articulated vertebrae and their ribs; traces of left scapula and of right humerus.

Specimen H SAM No. 4328. Natural mould of nine articulated vertebrae and their ribs, of right half of pelvic girdle, and of parts of left femur.

Specimen I BPI No. 3514. Five articulated vertebrae and their ribs, plus other disarticulated, poorly preserved elements including an interclavicle.

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[1] Abbreviations:

BM(NH)—British Museum (Natural History), London
SAM—South African Museum, Cape Town
BPI—Bernard Price Institute for Palaeontological Research, Johannesburg
USNM—United States National Museum, Washington D.C.

Specimen J BPI No. 3515. Five articulated vertebrae and their ribs, plus five other displaced vertebrae (including one cervical and one caudal) and a rib; proximal end of left humerus, and two podial elements.

Specimen K USNM No. 23099. Series of three vertebrae and five pairs of ribs, plus four other displaced vertebrae; right humerus, right ilium, damaged left pelvis and right (?) scapula.

As far as is known, all the specimens are derived from the Middle Permian Tapinocephalus Zone of the Beaufort Series of South Africa. The locality data of specimens C, E, G and H are unknown, except that specimen H was acquired from the museum of the boys' school at the town of Fraserburg Road, in the Cape Province of South Africa. The remaining seven specimens were all found within a radius of 40 miles of that town. Specimens A and D were found on the farm Weltevreden, and specimen B on the farm Rietfontein; these two farms lie in the Prince Albert District, about 15 miles south-west of Fraserburg Road. Specimen F was found on the farm Boesmansrivier, in the Beaufort West District, about 25 miles north-east of Fraserburg Road. Specimens I, J and K were collected about half a mile east of the Waikraal River on the farm De Bad, which lies in the Beaufort West District about 40 miles north-west of Fraserburg Road. These three specimens were collected in 1961 by Dr. N. Hotton III of the U.S. National Museum, Washington and Mr. James Kitching, Field Officer of the Bernard Price Institute for Palaeontological Research, Johannesburg, who kindly provided all the above locality data.

The specimens are preserved in a non-calcareous, olive-grey, silty mudstone (subgreywacke), which shows traces of haematite staining. Most specimens appear to have been fossilized lying on their dorsal or ventral surfaces, so that compression has caused the ribs to lie more or less in the horizontal plane. Specimens B and G, however, appear to have been lying on their side when fossilized; as a result, the ribs have come to lie more in the vertical plane, with the distal ends of the right and left ribs nearly touching. These two specimens therefore look very like bivalve molluscs in shape (see Watson 1914, pl. VII, figs. 3, 4).

Specimens A, C, D, E, I, J and K were prepared with acetic acid until any identifiable and well-preserved skeletal elements were free of matrix. The shapes of any superficial impressions of bones were conserved by filling them with a hard-setting plastic before starting to prepare the specimen. Specimens B, F and G were not prepared as their matrix did not soften in acetic acid. Specimen H, a natural mould, was studied from rubber latex casts.

Some specimens contain articulated series of ribs and vertebrae. Comparison of these series has made it possible to homologize them; the resulting combined series includes ten presacral vertebrae (numbered 1–10), one sacral vertebra and two caudal vertebrae. Dorsal vertebrae and ribs belonging to such articulated series have therefore been referred to in the text by a letter identifying the specimen, followed by the appropriate number indicating its position in the dorsal series. Disarticulated elements are preserved in specimens F, I, J and K; these have been numbered 21–40 in each specimen, so as to avoid confusion with elements from the articulated series. Thus " vertebra K5 " indicates the articulated fifth dorsal of specimen K, while " vertebra F27 " indicates a disarticulated element from specimen F.

All paired postcranial bones have been drawn as though they were those of the left side. Where necessary, bones of the right side have therefore been drawn as mirror images of themselves.

OSTEOLOGY. SKULL. The only fragment of the skull, 2 cm. long and up to 1·5 cm. across, is that found in specimen E. Unfortunately it is even less complete than Watson (1914) believed, and includes only the middle region of the snout and lower jaw, lacking both the anterior tip and everything posterior to the level of the transverse processes of the pterygoids. The skull has also been eroded or broken horizontally at the level of the palatal bones, so that all the roofing bones are missing, and the palate is visible dorsally in horizontal section.

Lateral view (Fig. 1A, B; Pl. 1A). Apart from the incomplete and damaged tooth rows and portions of the tooth-bearing bones, very little can be seen. The teeth are simple and rather blunt. The right and left tooth-bearing bones do not meet anteriorly, and those of the left side were slightly dislocated outwards from the palatal bones. On the left side, the portion of bone which bears the three most anterior upper teeth appears to be part of the premaxilla; this suggestion is supported by several features. It is separated, by a very narrow band of matrix, from the more posterior bone, the anterior end of which is smooth, unbroken and toothless, suggesting that this is the anterior end of the maxilla, overlapped by the posterior end of the premaxilla. The fragment of premaxilla is also somewhat inclined antero-ventrally, though this may be a post-mortem occurrence.

Behind the fragment of premaxilla, nine teeth are visible on the preserved portion of the left maxilla. On the right side there is no trace of the premaxilla, and all twelve teeth visible in the upper jaw belong to the maxilla. The more posterior of these teeth are represented only by small fragments and by curved depressions in the underlying matrix.

Most of the lower teeth are obscured by matrix or by the upper teeth. One or two of their tips are visible and bear slight longitudinal grooves and ridges. The lower jaw itself is fairly deep, though thin in cross-section. On the right side, the anterior end of the angular can be seen overlapping the dentary. More posteriorly, the angular forms the ventral margin of the lower jaw, which is here rather wider and flattened. Medially there is a large splenial.

Dorsal view (Fig. 1C; Pl. 1B). The dorsal surface of the palatal bones has been lost, and the bones have also been broken and dislocated. Despite these difficulties, some of the elements can be identified, though sutures are extremely difficult to distinguish. What little of the sutural pattern that can be discerned is not identical on the two sides, but this may be because the palatal bones have not been broken at the same level on each side.

The most easily identified elements are the paired pterygoids, the posterior regions of which extend slightly inwards towards the mid-line. The roots of small palatal teeth can be seen on the medial portion of the pterygoids. The ventral side of the right pterygoid was exposed by preparation, and the palatal teeth were found to be blunt and about 0·4 mm. in diameter.

The ectopterygoids also are clearly visible, lying postero-laterally to the pterygoids and forming the transverse flanges of the palate. Further forwards there is a large

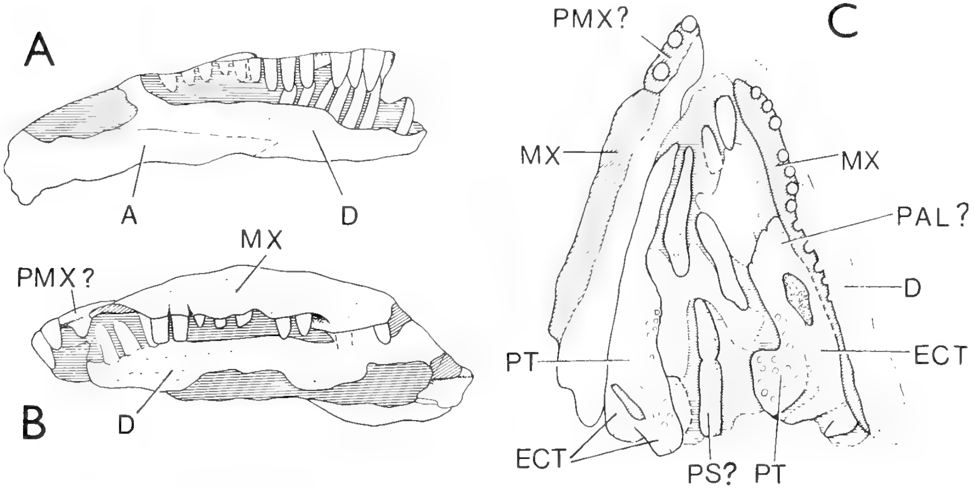

FIG. 1. *Eunotosaurus africanus.* BM(NH) no. 49424 (specimen E). Skull fragment × 3 (approx.). A, right lateral view. B, left lateral view. C, view of eroded dorsal surface of palate. Abbreviations: A, angular; D, dentary; ECT, ectopterygoid; MX, maxilla; PAL?, palatine?; PMX?, premaxilla?; PS?, parasphenoid?; PT, pterygoid. Horizontal lines indicate matrix; diagonal lines indicate broken surfaces.

foramen on the right side. Apparently bounded by the pterygoid, ectopterygoid and palatine, this is presumably the posterior palatal (or suborbital) foramen. It cannot be seen on the left side, but the bones of this region appear to have been folded, so that the area is covered by bone which originally lay more laterally.

An elongate fragment of bone lying in the midline between the pterygoids is probably part of the parasphenoid. Other pieces of bone lie more anteriorly, but these are too fragmentary and too disorderly in arrangement to provide any anatomical information.

VERTEBRAL COLUMN. Portions of the vertebral column are preserved in all eleven specimens. These portions vary in extent, from a series of ten articulated vertebrae to a few damaged fragments.

Size of specimens. Vertebrae and ribs are the only elements preserved in every specimen; since the ribs are often badly eroded, measurements of the vertebrae provide the only evidence of the relative sizes of the different specimens. Where possible, these measurements are of the lengths of individual centra. In some cases only the neural arches, and not the centra, of the articulated vertebrae are exposed. In these cases (specimens B, E and G) an approximate measurement of the total length of the series of articulated neural arches is given, since this should not be very different from the sum of the lengths of the centra themselves. These measurements are given in Table 1.

The vertebrae of specimen C are the best preserved, and this specimen has therefore been used as the standard for comparison in the following attempt to establish the relative sizes of the remaining specimens.

TABLE 1

Lengths of vertebrae, in centimetres
(I indicates that the vertebra is preserved but incomplete)

Specimen	C (centra)	A (centra)	H (centra)	B (neural arches)	G (neural arches)	E (neural arches)
Dorsal 1	I				I	
2	0·8			I	c. 5·1	
3	1·0	I		c. 5·4		
4	1·1	0·95	I			c. 4·2
5	1·2	1·0	I			
6	1·2	1·0	I			
7	1·3	I	1·2			
8	1·15	I	1·0		I	
9	1·05	I	0·9	I		
10	I	I	0·8			
Sacral 1			0·75			
Caudal 1			0·7			
2			I			

The only vertebral measurement available in specimen F is the length of the fourth dorsal vertebra, from the anterior end of its prezygapophysis to the posterior end of the neural spine. This is 1·25 cm., indicating that the specimen is slightly larger than specimen C in which this distance is 1·1 cm. The neural arches of vertebrae 3 and 4 of specimen J are slightly (0·05 cm.) longer than those of specimen C. The centrum of the fifth preserved vertebra of specimen K is 1·4 cm. long, appreciably longer than any of the centra of specimen C. The vertebrae of specimen I are badly damaged, but direct comparisons show that they are slightly smaller than those of specimen C, but slightly larger than those of specimen H. Specimen D is too badly preserved for any measurements to be possible.

Specimens K and F therefore appear to be the largest. They are followed by specimens J, C, I, H and A in that order, all of which are of comparable size. These are followed by the noticeably smaller specimens B, G and E in that order.

Morphology of the vertebrae. As can be seen from Table 1, specimens C and H together provide a series of ten dorsal, one sacral and two caudal vertebrae. Many of these are also represented in other specimens, while cervicals and more posterior caudals are known from specimens J and K.

Specimen C contains the longest series of well preserved vertebrae (Fig. 2). As in all the other specimens, weathering has removed the neural spines of all those vertebrae which are preserved in their natural position. Fortunately, vertebra C8 had been displaced to a more ventral position, and its neural spine is perfectly preserved (Fig. 3). The anterior border of the neural spine slopes upwards rather gradually, but its posterior border is steeper. The spine is quite low but wide in proportion. The top of the neural spine lies posterior to a point halfway along the vertebra. There is no trace of a suture between the neural arch and the centrum.

The centra are notochordal and their ends are deeply concave. As can be seen from Table 1, their lengths steadily increase to a maximum at C7 and then diminish.

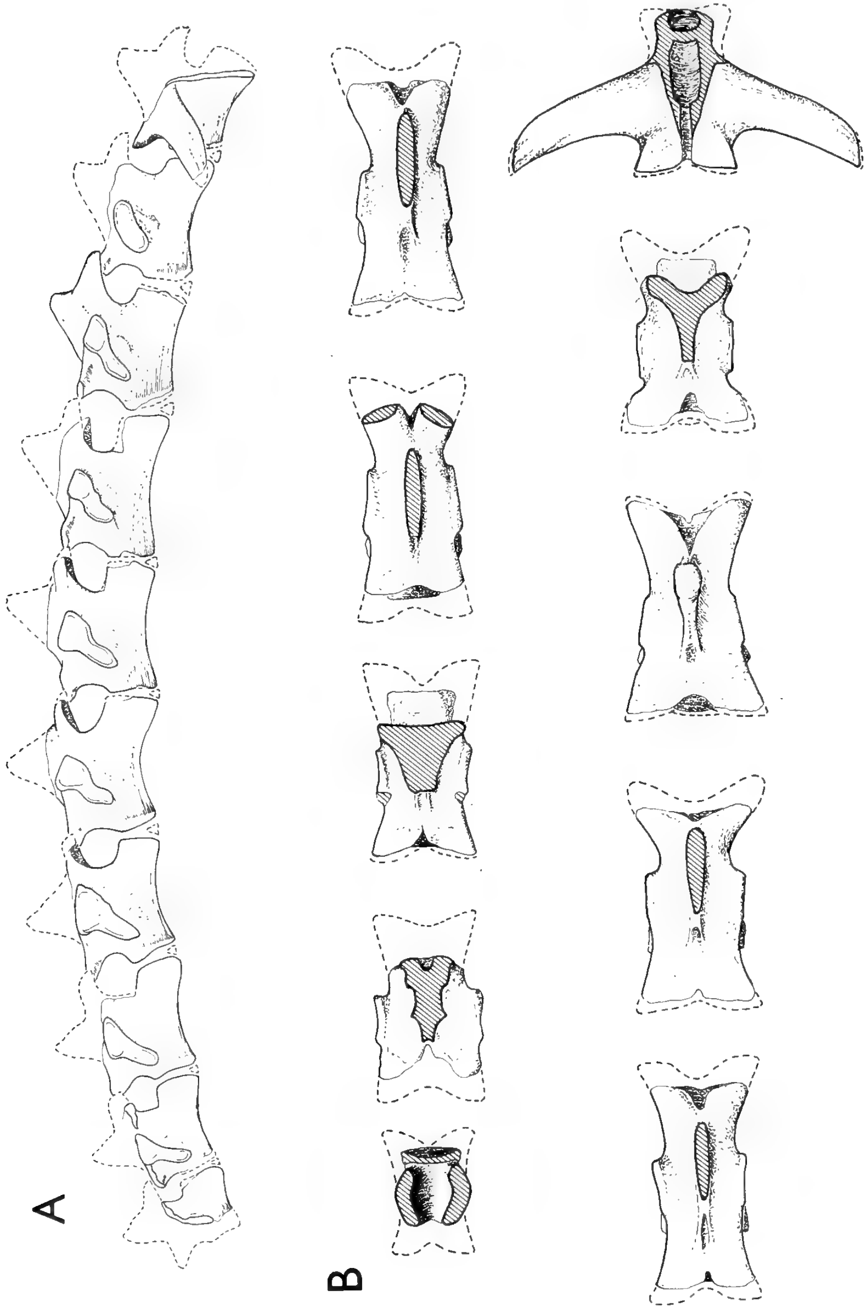

FIG. 2. *Eunotosaurus africanus.* BM(NH) no. R4949 (specimen C). Associated dorsal vertebrae 1–10. A, lateral view × 1·5. B, dorsal views, × 2.

The sides of the centra are slightly hollowed, so that the centra are rather hour-glass shaped in ventral view.

Tiny intercentra are visible in the ventral midline of specimen H (the natural mould), between the centra of the eighth, ninth and tenth dorsal vertebrae, and between those of the sacral and the first caudal. These areas are not exposed in the more anterior region of this specimen, but it seems reasonable to assume that they were present throughout the vertebral series. They were not detected during development of the other specimens, doubtless because of their small size and fragile nature.

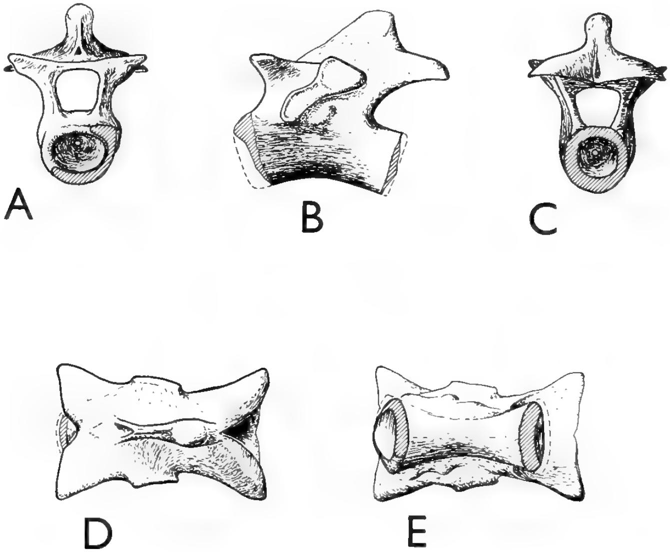

Fig. 3. *Eunotosaurus africanus*. BM(NH) no. R4949 (specimen C). Eighth dorsal vertebra, × 2. A, anterior view; B, lateral view; C, posterior view; D, dorsal view; E, ventral view

Cervical vertebrae. No cervical vertebrae are preserved as part of an associated vertebral column, but specimen K38 appears to be a cervical vertebra (Fig. 4A–D). This is indicated by its shortness compared with the elongated dorsal vertebrae, and by the fact that the rib facet is borne on a short transverse process. The neural spine is rather wide in anterior and posterior views, but pointed in lateral view. Vertebra I24, preserved under the anterior end of the series of dorsal vertebrae of specimen I. is closely similar to specimen K38.

Dorsal vertebrae. The zygapophyses are quite wide, and the post-zygapophyses are strengthened by being slightly swollen. The zygapophysial facets are horizontal, or nearly so, in all the vertebrae of specimen C. Though those of some individual vertebrae from other specimens (e.g. K40, Fig. 4E–H) are placed at a smaller angle to one another, it seems clear that the pose of the zygapophyses of specimen C is natural rather than the result of dorso-ventral compression. This follows from the fact that this horizontal pose is found even in the displaced vertebra C8. Since this was lying

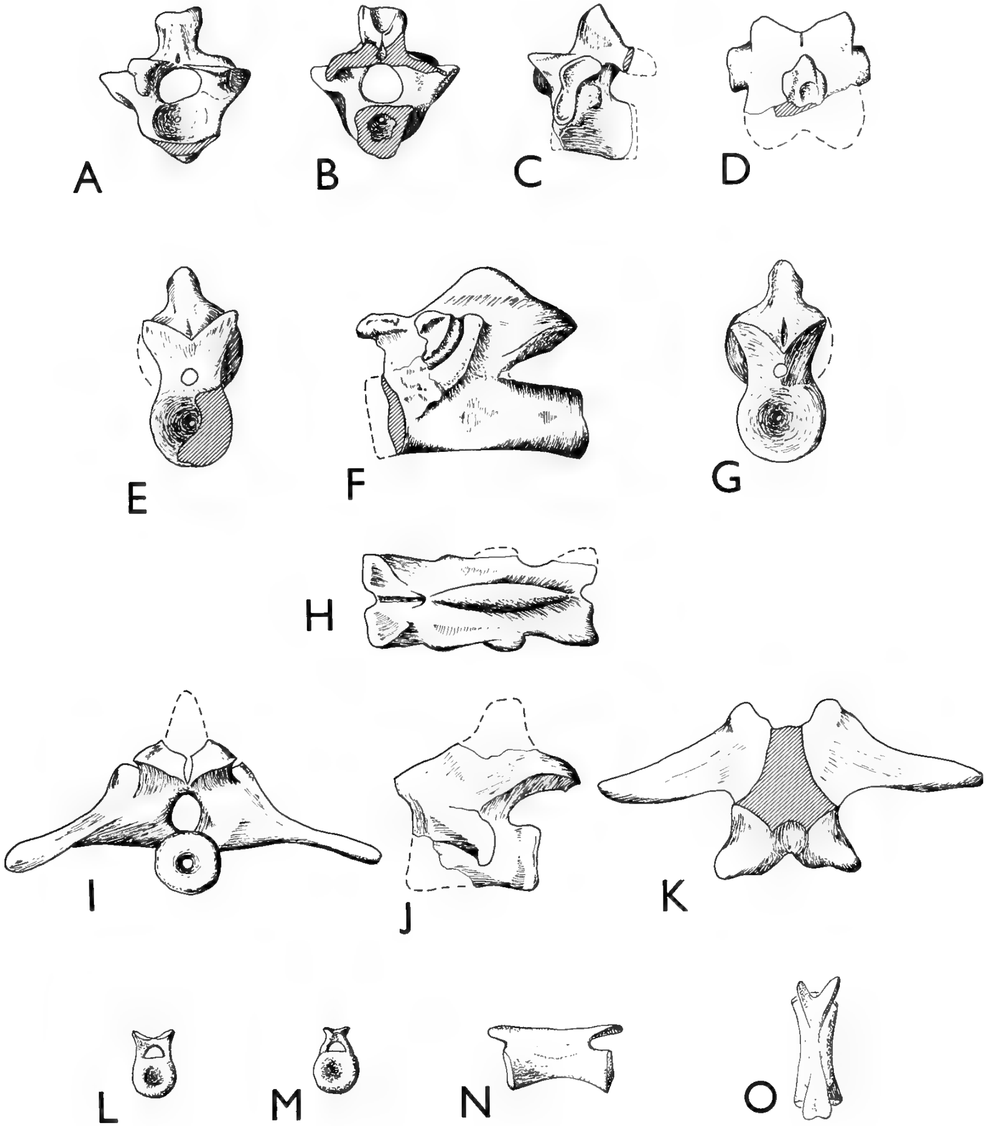

Fig. 4. *Eunotosaurus africanus*. USNM no. 23099 (specimen K) and BPI no. 3514 (specimen I). Vertebrae, × 2. A–D, specimen K38, cervical vertebra. E–H, specimen K40, dorsal vertebra. I–K, specimen K31, presumed anterior caudal vertebra. L–O, specimen I24, posterior caudal vertebra. A, E, L, anterior views; B, G, I, M, posterior views; C, F, J, N, lateral views; D, H, K, O, dorsal views.

on its side, any dorso-ventral compression of the specimen as a whole would have resulted in lateral compression of the zygapophyses of this vertebra.

There are no transverse processes on dorsal vertebrae 1–9, the ribs attaching directly to the neural arches. The facet for the rib lies on the anterior half of the side of the neural arch, sloping downwards and forwards; it hardly rises above the level of the zygapophysis. There is a low tubercle on the side of the centrum just posterior to the rib facet.

Three examples of the tenth dorsal vertebra are known: C10 (Fig. 2), H10 (Fig. 6) and K37 (Fig. 5). Unlike the other dorsal vertebrae, the tenth bears a large lateral process on either side; this arises from the side of the neural arch and curves ventro-laterally, tapering to a blunt distal end. That of specimens C10 and H10 curves slightly forwards, but that of K37 curves slightly backwards (Fig. 5). The dorsal surface of this process bears a pattern of longitudinal grooves similar to that found on the ribs of the more anterior dorsal vertebrae (Fig. 8). There is no trace of a suture between the neural arch and this process, which may therefore be either a transverse process or a co-ossified rib. The zygapophyses of this tenth dorsal vertebra are rather wide.

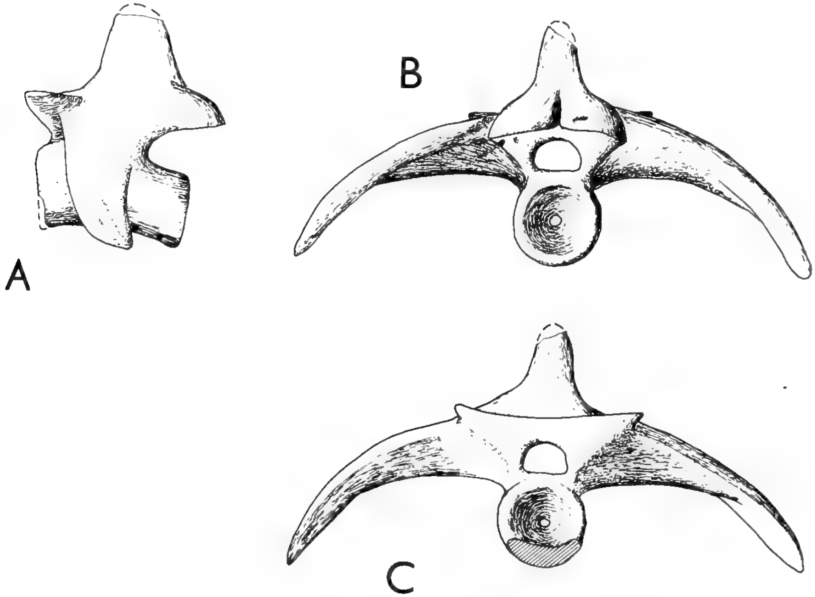

FIG. 5. *Eunotosaurus africanus*. USNM no. 23099 (specimen K). Specimen K37, last dorsal vertebra, × 2. A, lateral view; B, posterior view; C, anterior view.

Sacral vertebra (Fig. 6). Specimen H (the natural mould) contains the only example of a sacral vertebra, which is preserved as part of an articulated series of vertebrae extending as far posteriorly as the second caudal. Only the ventral regions of this vertebra are preserved in the mould, but this includes the whole of the sacral facet. The facet covers the whole of the internal surface of the associated ilium, and it is therefore clear that there was only a single sacral vertebra. As in the case of the preceding tenth dorsal vertebra, there is no sign of a suture between the neural arch and the sacral process. It is possible, therefore, that the ilium attached directly to the transverse process, but it is perhaps more likely that the sacral rib had become completely co-ossified with the neural arch.

The sacral rib (or transverse process) curves ventro-laterally and anteriorly. Its distal end does not reach as far laterally as does that of the preceding tenth dorsal vertebra. The expanded distal end is approximately diamond-shaped in outline (Fig. 6B) and bears a pattern of grooves similar to those found on the medial surface of the ilium.

Caudal vertebrae. The ventral regions of the first caudal vertebra, and of part of the second, are preserved as a natural mould in specimen H (Fig. 6). The transverse process of the first caudal is fairly powerful; it extends laterally and slightly anteriorly, curving ventrally to a distal end which is slightly expanded antero-posteriorly. The transverse process of the second caudal vertebra is more slender and is directed laterally, but also curves slightly ventrally.

Specimen K31 (Fig. 4, I–K) is probably a more posterior caudal vertebra. The transverse processes extend laterally and taper distally. The centrum is rather small compared with the size of the neural arch.

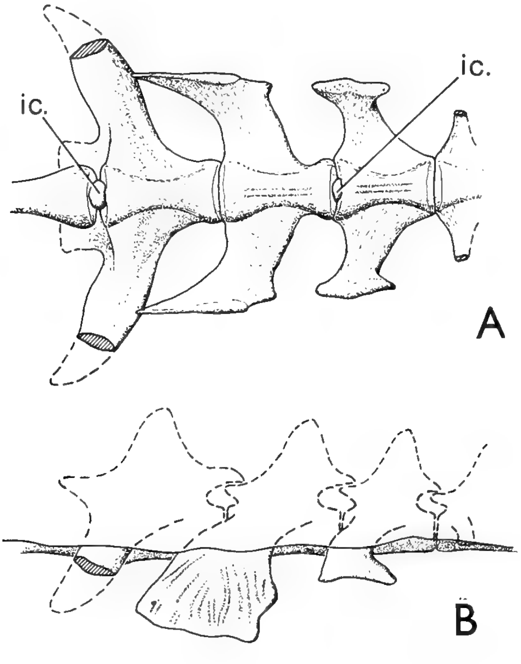

FIG. 6. *Eunotosaurus africanus*. SAM no. 4328 (specimen H). Cast of natural mould of sacral region, including ventral regions of last dorsal vertebra, sacral vertebra and first two caudal vertebrae, × 2. A, ventral view; B, lateral view. Abbreviation: IC, intercentrum.

Specimen I24 (Fig. 4, L–O) is an even more posterior caudal vertebra. It is an elongate centrally constricted cylinder, lacking any trace of a neural spine, with close-set zygapophyses.

RIBS (Figs. 7, 8).

TABLE 2

Specimen	A	B	C	D	E	F	G	H	J
Rib 1		√	√				√		
2	√	√	√			√	√		
3	√	√	√	√	√	√	√		√
4	√	√	√	√	√	√	√	√	√
5	√	√	√	√	√	√	√	√	√
6	√	√	√	√	√	√	√	√	√
7	√	√	√	√	√	√	√	√	√
8	√	√	√		√	√	√	√	√
9	√	√	√		√	√	√	√	

Reconstruction. Ribs are preserved in all eleven specimens, though in many cases they are too incomplete to provide any useful information. Table 2 shows the number of ribs preserved in each specimen, except for specimens I and K. In each of these two specimens only five ribs are preserved, and those are so incomplete that it is impossible to determine where they belong in the dorsal series.

It was possible to remove completely from the matrix all the ribs of specimens A (eight pairs) and C (nine pairs). The following account is based on these specimens, unless otherwise stated.

In specimen C, the vertebrae (including the rib facets) and the proximal parts of the ribs (including the rib heads) are all well preserved and these elements could all be re-assembled. The more distal parts of the ribs are missing in this specimen, but are well preserved and almost undistorted in specimen A, in which the rib heads are missing. The shape of the rib cage had to be reconstructed using the information from both these specimens, since none of the eleven specimens included a complete series of undamaged ribs. Though there are obviously possible sources of error in this method, the resulting restoration (Fig. 7) provides a simple shape for the rib cage as a whole despite the complex shape of the individual ribs, and it seems likely that it is approximately correct.

The true edges of ribs shown in Fig. 7 are present in specimen A; the outlines of the more proximal regions of the ribs are restored from specimen F, in which these regions are well preserved. The ribs are more powerfully developed in specimen F (the largest specimen) than in specimens A and C, and the gaps between their expanded portions are smaller than those shown in Fig. 7. The vertebral column shown in Fig. 7A is that of specimen C, slightly reduced in size to approximate to that of the remains of the vertebral column of specimen A, and with the missing neural spines and parts of the neural arches restored (*cf.* Fig. 2B).

Morphology. The head of the first rib shows a slight trace of division into capitulum and tuberculum, but the remaining ribs are single-headed. This head slopes strongly downwards and forwards (Fig. 7E). The proximal part of the rib also curves strongly upwards from the rib head (Fig. 7F).

As noted by both Seeley (1892) and Watson (1914), the most remarkable feature of *Eunotosaurus* is the way in which the outer surfaces of the dorsal ribs are expanded antero-posteriorly. These expansions together enclose the dorsal and dorso-lateral regions of the body almost completely. The remaining part of the rib is not expanded and runs like a rounded keel down the inner surface of the expanded area to its extreme distal end. Sections through the ribs show that this keel is hollow.

In all specimens where they are visible, the first and second ribs run backwards at a more acute angle than the remaining ribs. This is probably related to the presence of the shoulder girdle in this region (see below, p. 181).

The expansion of the first two ribs is confined to their proximal regions, that of the second rib being slightly larger than that of the first. The more distal part of the first rib is slender and rod-like, while that of the second is stouter and ends in a slightly concave oval facet.

The expansion of the first rib rises dorsally and only slightly posteriorly from its shaft. This fact is shown both by examination of the first ribs of specimen C, prepared free of the matrix, and also by the posture of the undisturbed first left rib of specimen G. Similarly, these specimens show that the expansion of the second rib lies considerably closer to the horizontal plane.

The degree of expansion of the more posterior ribs increases progressively to reach a maximum at rib 5, and then decreases progressively. The proximal parts of these expansions lie approximately in the horizontal plane, though those of the last two or three ribs may be inclined so that their surfaces face slightly postero-dorsally. As the more distal parts of the ribs curve round ventrally, the posterior border tends to flare outwards a little. This region may slightly overlap the front edge of the next rib, and it is worth noting that in all cases where the specimens show any overlap (e.g. specimen F) it is the anterior rib which overlaps the posterior.

The expansion of the third rib does not extend to its distal end; the distal portion of this rib is rod-like, ending in a concave facet like that of the second rib. The distal ends of the remaining ribs, 4–9, taper to a fairly sharp point. In ribs 4 and 5, in which the expansion is most fully developed, the posterior border curves rapidly forwards from the point of maximum expansion. The remaining ribs taper more gradually. Though the pointed ends of ribs 4–8 are slightly eroded in specimen A, casts of the natural mould (specimen H) confirm that these ribs lack the rod-like continuation and distal facet of ribs 2 and 3. The left ninth rib of specimen A is slightly larger than that of the right side.

Surface markings. A pattern of longitudinal ridges and grooves (Fig. 8) covers parts of ribs 2–9 (Fig. 7A, B). In general, these striations cover the distal parts of the expanded areas, but they are absent from the extreme distal regions of ribs 7 and 8.

PECTORAL GIRDLE (Fig. 9). No single specimen includes a complete pectoral girdle. The ventral, coracoid, region is present in specimens C, D and F; specimen D also includes a clavicle, a partial scapula and traces of the interclavicle. Part of the interclavicle is also preserved in specimen I.

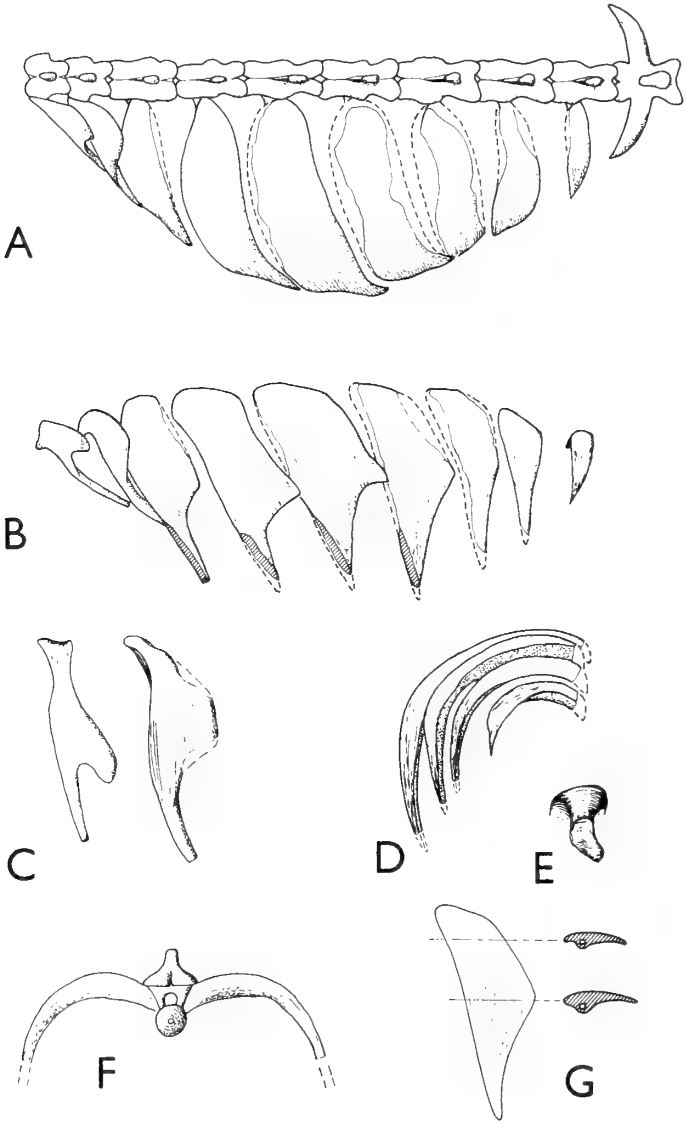

FIG. 7. *Eunotosaurus africanus.* Holotype, BM(NH) no. R1968 (specimen A), BM(NH.) no. R4949 (specimen C) and SAM no. K1132 (specimen F). Morphology of the ribs. A, B, rib cage reconstructed from specimens A, C and F (approx. natural size). A, dorsal view (including vertebral column); B, lateral view. C, ribs C1 and C2 in antero-dorsal view, natural size. D, posterior view of ribs A6–A9, natural size. E, medial view of head of left rib C5, natural size. F, specimen C, eighth dorsal vertebra and ribs in posterior view, natural size. G, rib C6, lateral view with cross-sections, natural size.

The dorsal, scapular, portion of the girdle lay in front of the first greatly expanded rib (the third) and lateral to the smaller first and second ribs. This position is shown clearly in specimens C and F, and also by faint traces of the scapulae in specimens B and G. The base of the scapula is preserved in specimens C, D and F, but the blade is present only on the right side of specimen D, and even this is damaged. The preserved part of the blade is 1·8 cm. high, but its dorsal and anterior borders are missing; it is set at an angle to the midline of the body, the anterior edge being directed antero-medially (Fig. 13A). It has a thickened posterior border and becomes thinner anteriorly. There is no supraglenoid buttress or foramen, nor a suprascapular fossa. A groove on the inner side of the scapula leads ventro-medially into the dorsal opening of the coracoid foramen.

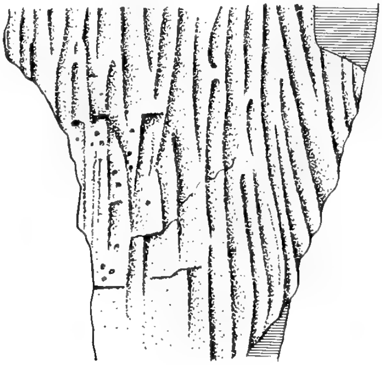

FIG. 8. *Eunotosaurus africanus*. Holotype, BM(NH) no. R1968 (specimen A). Part of ornament of dorsal surface of distal region of rib A4, × 5.

The ventral surface of the coracoid region is eroded in all the specimens. Its dorsal surface is well preserved in specimen C (Fig. 9A), but the different elements are so fused together that it is extremely difficult to distinguish any sutures. The " grain " of the bone seems to indicate that the line of meeting between the scapula and the coracoid region ran through the coracoid foramen towards the glenoid. It is not possible to be sure whether there was a coracoid alone or whether there was also a precoracoid. A very well developed process for the head of the triceps muscle rises dorsally from the edge of the coracoid plate, just behind the rear edge of the glenoid.

The glenoid fossa is rather elongate. The anterior region, on the scapula, faces laterally and somewhat posteriorly. The middle region, where the fossa is highest dorso-ventrally, faces laterally. The posterior region curves round on to the base of the triceps process to face laterally and slightly anteriorly.

A slender bone, 1·6 cm. long, lay near the midline of specimen D, just in front of the coracoids; one end of the bone is set at a slight angle to the remainder (Fig. 9D). In view of its length and curvature, this bone is most easily interpreted as the left clavicle, the angled end meeting the acromion region of the scapula while the remainder of the bone ran along the front edge of the coracoid. A small fragment of bone which lies under the front edge of the right scapula may represent part of the cleithrum.

The median shaft of the interclavicle is preserved as specimen I28; it is narrow and flattened (Fig. 9B). This region is also preserved, though badly eroded, in specimen D, where it reaches to the level of the posterior end of the coracoids. An impression of the anterior end of the shaft in specimen D shows that it became wider anteriorly, but the transverse region which met the clavicles is missing.

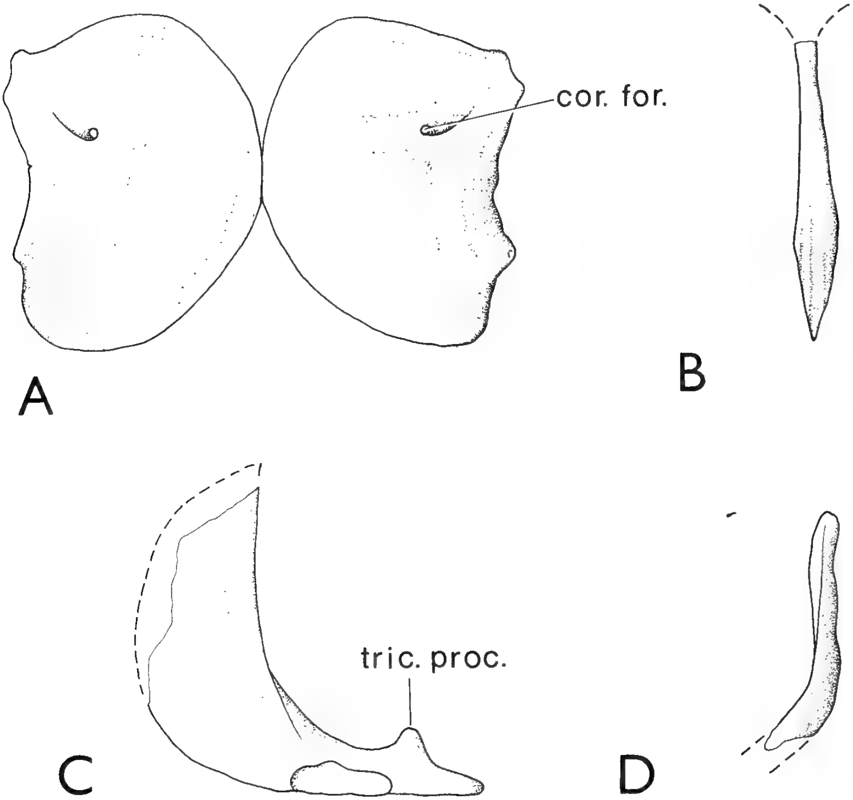

Fig. 9. *Eunotosaurus africanus.* BM(NH) no. R4949 (specimen C), BPI no. 3514 (specimen I), and BM(NH) no. 49423 (specimen D). Pectoral girdle, × 2. A, dorsal view of flattened ventral region of scapulo-coracoids of specimen C. B, ventral view of interclavicle, specimen I28. C, lateral view of scapulo-coracoid of specimen D. D, anterior view of clavicle of specimen D. Abbreviations: cor. for., coracoid foramen; tric. proc., process for head of triceps muscle.

Humerus (Fig. 10). Though several fragmentary proximal ends are preserved in specimens E, F and J, the only complete humerus is specimen K42, which is that of the right side.

The humerus, 3·5 cm. long, is rather slender in general appearance, the two expanded ends meeting at a narrow shaft region. The planes of the two ends of the bone are at an angle of about 50° to one another. Although the exact pose of the humerus is uncertain, it will be described upon the assumption that the distal surface, which bears the capitellum, faced ventrally.

The head of the humerus is not very well developed. It does not project on to the posterior surface of the proximal part of the humerus as a swollen area, but the anterior surface of this part of the humerus is slightly damaged.

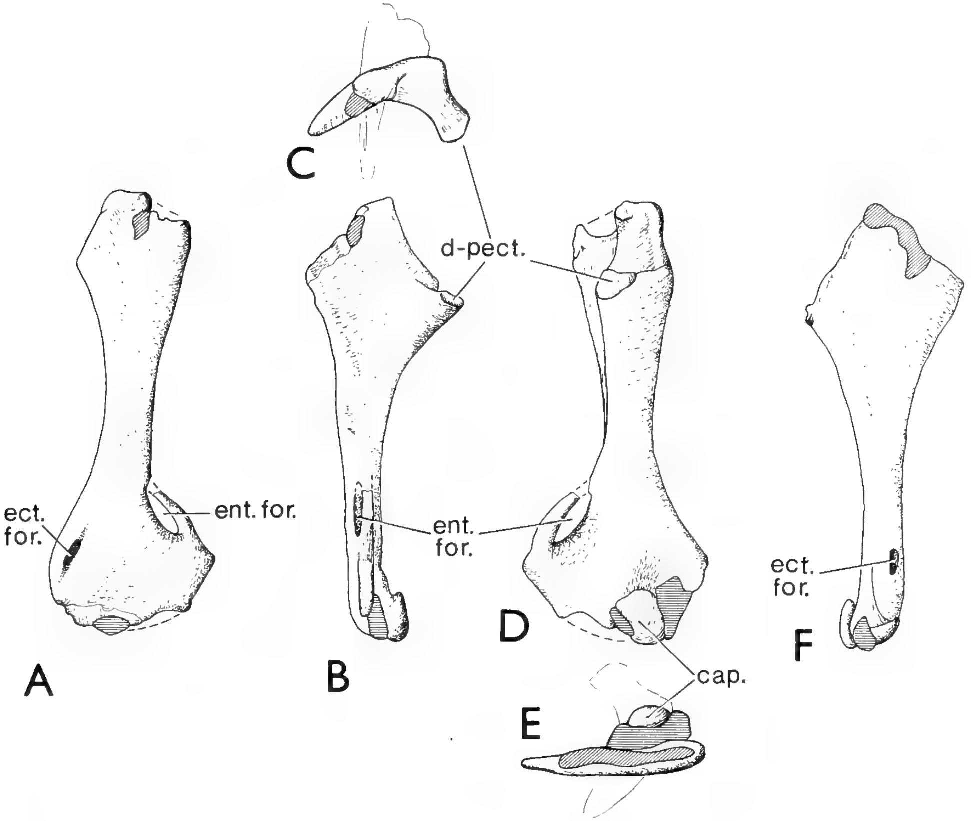

FIG. 10. *Eunotosaurus africanus*. USNM no. 23099 (specimen K). Left humerus, specimen K42, ×2. A, dorsal view; B, posterior view; C, proximal view; D, ventral view; E, distal view; F, anterior view. Abbreviations: cap, capitellum; d-pect., delto-pectoral crest; ect.for., ectepicondylar foramen; ent.for., entepicondylar foramen.

The proximal half of the humerus consists of a rather flat, anteriorly-facing surface and a concave posteriorly-facing surface. The latter is bordered ventrally by the prominent, powerful delto-pectoral crest, which is directed postero-ventrally.

The distal end of the humerus is rather thin. Two openings can be seen on the almost flat dorsal surface. A fairly large entepicondylar foramen pierces the bone close to its posterior margin; it runs distally and ventrally to open into a large concave area on its ventral surface. A much smaller ectepicondylar foramen pierces the bone close to its anterior margin; it runs distally and only slightly ventrally to open ventrally near the antero-distal corner of the humerus. In addition to these foramina, the ventral view of the bone shows the well developed capitellum for articulation with the radius. The region where the trochlear facet for the ulna would have been is unfortunately damaged.

No remains of the radius or ulna are preserved. A few isolated and damaged podial elements are visible in specimen C.

PELVIC GIRDLE (Fig. 11). The general morphology of the pelvic girdle is best shown by a cast of the natural mould of the almost complete right half of the pelvic girdle of specimen H.

The acetabulum is bounded anteriorly by a thick ridge on the ilium, but has no well defined posterior margin; it is therefore directed laterally and somewhat posteriorly. The ilium is quite narrow above the acetabulum. The blade is directed dorsally and slightly posteriorly; its distal end is only slightly expanded antero-posteriorly, being no wider than the single sacral facet. Both the lateral and the medial surfaces of the distal end of the blade both bear a pattern of ridges.

The edges and ventral surfaces of the pubis and ischium are damaged. These bones meet the ilium at an angle of *c.* 105°. The pubis and ischium also meet each other at a slight angle, so that the ventral surface of the ischio-pubic plate is slightly concave, The front edge of the pubis is quite thin; its edge below the acetabulum is damaged. There may have been a little post-mortem movement between the ischio-pubic plate

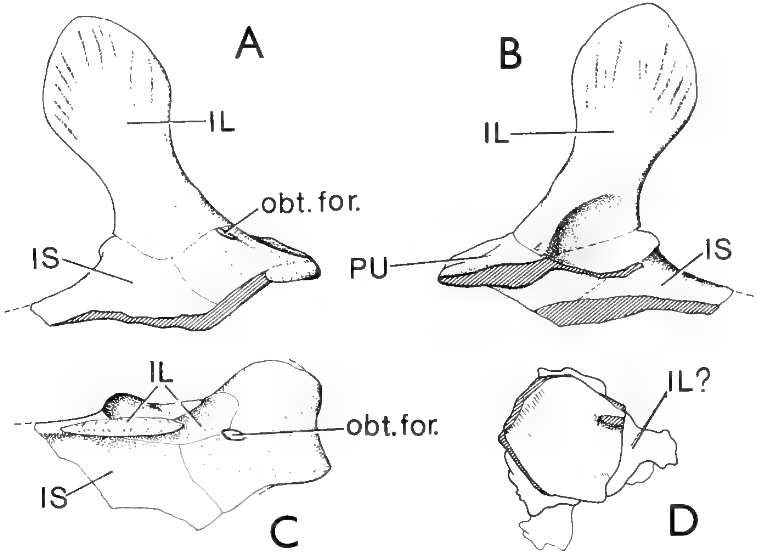

FIG. 11. *Eunotosaurus africanus*. SAM no. 4328 (specimen H). Pelvic girdle, left side, ×2. A–C, cast of natural mould of pelvis. A, medial view; B, lateral view; C, dorsal view. D, pubis (?) of holotype, BM(NH) no. R1968 (specimen A), ×2. Abbreviations: IL, ilium; IS, ischium; obt.for., obturator foramen; PU, pubis.

and the ilium, since there is a slight notch between these two elements posterior to the acetabulum, and the ischium projects slightly into the acetabulum.

The obturator canal is well preserved in specimen K36, a left acetabular region, and runs dorso-ventrally. Though the position of the dorsal opening is not obvious at the corresponding position in specimen H, closer examination shows that there is a slight indication of its presence in the existence of a shallow elongate depression in the back edge of the pubis just medial to the level of the blade of the ilium. The foramen appears, therefore, to have been slightly occluded in specimen H, perhaps by the movement (mentioned above) between the ilium and the ischio-pubic plate. The ventral opening of the obturator canal lies immediately below its dorsal opening, within the pubis.

There is no trace of a thyroid fenestra in the preserved parts of the pubis and ischium. If the pelvis is placed against the sacral rib (which belongs to the same side of this same specimen), the preserved parts of the ischium extend to about one millimetre from the midline. The missing median regions of the pubis and ischium must therefore have been so small that it is impossible that they enclosed thyroid fenestrae.

A polygonal, notched element in the pelvic region of the holotype (Fig. 11D) was identified as a pubis by Seeley (1892). The pubis of specimen H is so incomplete that it is impossible to confirm this, but it remains a likely possibility. A pair of similar bones was found under the skull fragment of specimen E.

FEMUR (Fig. 12A–F). The only femur known is that from the right side of specimen A. The shaft is 2·0 cm. long and bears a number of ridges. Unfortunately, the relationships between these ridges and the features of the articular ends of the femur cannot be established, as the articular regions of this femur are lacking. This appears to be due, not to damage, but to immaturity, for the ends of the bone have the appearance characteristic of surfaces covered by cartilage: they are slightly concave and surrounded by a slightly projecting collar of periosteal bone. Even after making allowance for the absence of the articular portions, the femur seems surprisingly short compared to the humerus, which is 3·5 cm. long.

A strong ridge runs up the postero-dorsal corner of the proximal part of the bone. As a result of this ridge, there is an extensive posteriorly-facing surface on the femur. A lower ridge along the antero-ventral corner of the proximal part of the bone presumably led up to the internal trochanter. A depression which runs down the middle of the ventral surface of the distal part of the bone presumably continued into the popliteal space.

TIBIA AND FIBULA (Fig. 12G–K). The proximal ends of these two bones were preserved in specimen A, in articulation with the femur, but show no features worth description.

"DERMAL OSSIFICATIONS". Watson (1914) believed that traces of bone substance could be distinguished in specimen D, in two areas lying at a level above the ribs and neural arches, and believed that these were the remains of dermal ossifications. His figure (1914; plate VII, fig. 1) shows clearly the position of these two areas. They were closely examined before preparation of this specimen, and proved merely to be areas of discolouration, resulting from the detachment of fragments of matrix.

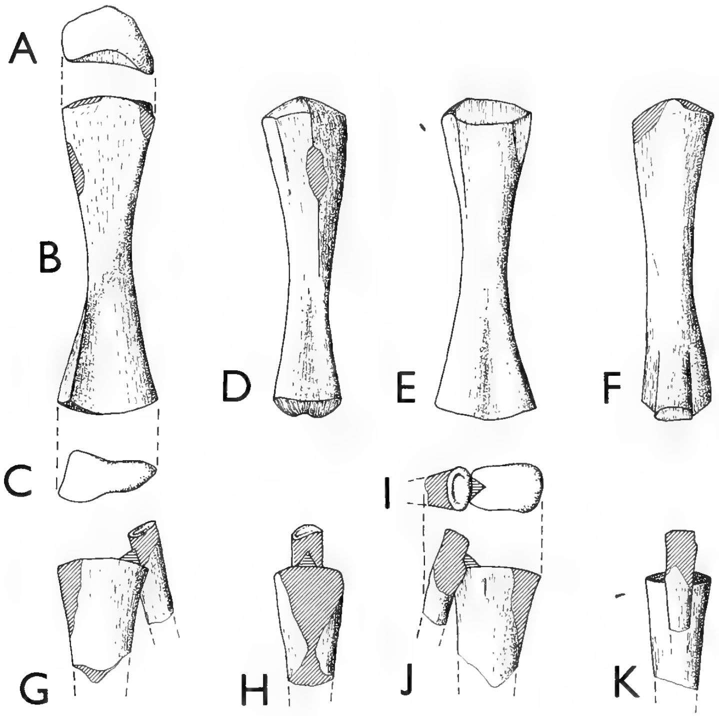

FIG. 12. *Eunotosaurus africanus*. Holotype, BM(NH) no. R1968 (specimen A). A–F, left femur, × 2. G–K, proximal regions of left tibia and fibula, × 2. A, I, proximal views; B, G, dorsal views; C, distal view; D, H, anterior views; E, J, ventral views; F, K, posterior views.

Despite careful observation, no sign of any bony elements was found during preparation of this specimen, nor in any of the other ten specimens.

III. RECONSTRUCTION AND FUNCTIONAL MORPHOLOGY

The vertebral column, ribs, girdles and humerus described above have been assembled together in Fig. 13. Most of these elements are derived from specimens A, C and H. These three specimens are all, as already noted, of the same order of size, and the error involved in assembling them together is therefore acceptably small. The humerus and the cervical and second caudal vertebrae shown belong to specimen K and are specimens K42, K38 and K31 respectively. From a comparison of the lengths of their last dorsal centra, it seems that specimen K is about 15% longer than specimen H, and these bones have accordingly been reduced by 15% from the original. The last vertebra shown in Fig. 13 is the isolated caudal I24.

The shortness, width and depth of the trunk region are very noticeable in Fig. 13. The carapace-like form which results from the expansion of the ribs could be

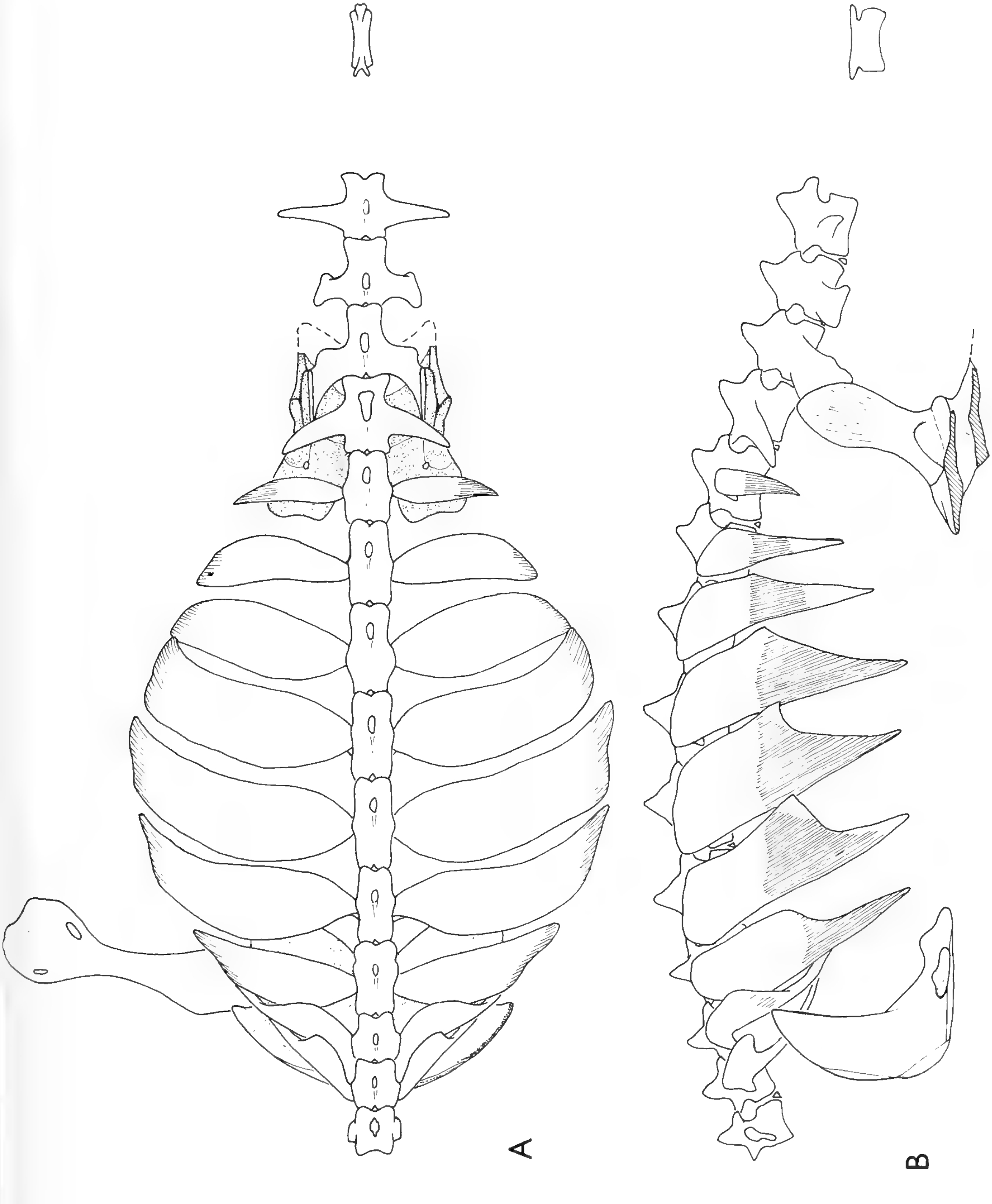

FIG. 13. *Eunotosaurus africanus*. Reconstruction of post-cranial skeleton, × *c*. 1·4. A, dorsal view; B, lateral view.

interpreted either as a modification to carry dermal armour or as protective in its own right. In the first case, the degree of development of the ribs would imply the presence of a heavy and elaborate system of bony plates (*cf. Peltobatrachus*; Panchen, 1959). No traces of such an armour were found in any of the eleven specimens, even in specimens I, J and K, in which a number of dissociated bones were found lying under the rib cage. Furthermore, it would seem likely that the neural spines of the trunk vertebrae would have been enlarged distally to bear the median parts of such an armour (*cf. Stagonolepis*; Walker 1961) but they are not.

Since, then, it seems unlikely that the ribs were expanded to support a bony armour, their expansion presumably served in itself to protect the body. The presence of striations on the lateral parts of the ribs suggests that these areas must have been very close to the skin, and it is quite possible that they lay immediately underneath epidermal horny scales—the presence of such horny scales in all the living reptiles suggests that they originated early in reptile evolution.

If the striation of the lateral parts of the ribs implies that these areas were close to the skin, the lack of striation on their more dorso-medial parts similarly implies that there was here a greater thickness of other tissues, presumably muscular, between the ribs and the skin. This dorso-medial region of the ribs corresponds to the area which is normally occupied by the epaxial portion of the trunk musculature—the iliocostalis, longissimus dorsi and transverso-spinalis muscles. Other features of the ribs and vertebrae support the view that the trunk region still possessed at least a limited degree of flexibility and therefore retained the corresponding musculature. If there were no such flexibility, it would be expected that there would be some fusion between the expanded blades of the ribs, between the rib-heads and the vertebral centra, and between the vertebrae themselves. In fact, all these elements are distinct from one another, and there are well-developed zygapophyses between the vertebrae. These zygapophyses are horizontal, implying that the vertebral column was probably flexible only in the lateral plane. Some slight lateral flexure would have been permitted by two features. Firstly, each of the ribs slightly overlaps its posterior neighbour. Secondly, the simple nature of the single rib-head, and the orientation of this head on the vertebra, would have allowed the ribs on the contracted side to fold slightly inwards and postero-ventrally.

The vertebrae would have had to become elongate as the ribs widened, since the total length of the trunk centra must clearly be similar to the combined widths of the ribs. Such elongation of the vertebrae would in turn have resulted in an elongation of the body itself unless the number of trunk vertebrae had been reduced. This factor alone may have been responsible for the reduction in the number of trunk vertebrae, but its effects may have been aided by other factors. In most reptiles the length of the stride is increased by sigmoid flexure of the body, which in turn is facilitated by the presence of a large number of vertebrae, so that a few degrees of flexure at each intervertebral articulation will produce the sigmoid curve of the body. Once this flexibility had been greatly reduced by the expansion of the ribs, so that flexure of the body could no longer be used to increase the stride, the adaptive reason for retaining a large number of dorsal vertebrae would have disappeared. If the function of the expansion of the ribs was to provide protection for the body, it would then be both possible and advantageous that the number of junctions between these ribs (effectively, chinks in the armour) should be reduced to a minimum.

It is interesting to note that a similar widening of the ribs is found in the living two-toed South American anteater *Cyclopes*. However, nothing appears to be known about the functional significance of this feature.

The base of the tail of *Eunotosaurus*, as restored, appears rather powerful, but it should not be forgotten that the only anterior caudal vertebrae known are the first two (from specimen H) and one other isolated caudal (K31); it is therefore not possible to restore the rate of diminution of the tail with any degree of accuracy. The long, tubular shape of the more posterior caudal vertebra (I24) suggests that the distal part of the tail was long and thin.

IV. THE RELATIONSHIPS OF *EUNOTOSAURUS*

Though very little of the skull remains, the presence of transverse flanges on the pterygoid bones is sufficient to answer the most fundamental question, as to whether *Eunotosaurus* is a reptile or an amphibian. The presence of these flanges and of dorsal intercentra are reptilian features, absent in the microsaurs which in many ways parallel the early reptiles (Carroll & Baird 1968).

Since *Eunotosaurus* is found in the Middle Permian Tapinocephalus Zone, its possible earlier relatives must be sought among the Upper Carboniferous and Lower Permian reptiles. These are known primarily from North America, with a few known also from European Russia.

In the absence of most of the skull, the relationships of *Eunotosaurus* must be deduced from the characteristics of its post-cranial skeleton. The clearest indications of its probable position are provided by the structure of its vertebral column: relatively small, amphicoelous, notochordal centra; relatively large neural arches; more or less horizontal zygapophyses; small, low neural spines; persistent, though small, intercentra. This type of vertebra, lightly built and providing little space for muscle insertion, is widespread in the small cotylosaurs—the captorhinomorphs and procolophonids. Not surprisingly, the larger early reptiles such as the pareiasaurs and pelycosaurs have more strongly built vertebrae, with larger neural spines. The absence in *Eunotosaurus* of the elaborate pareiasaur dentition also makes relationship to that group unlikely. It is more difficult to exclude any possibility of relationship to the synapsids, because the modifications accompanying their large size would in any case mask any similarities to little *Eunotosaurus*. However, this difference in size may in itself be a significant feature. Even the smallest synapsid is four or five times the size of *Eunotosaurus*, and the synapsids are in general quite large reptiles, forming the fish-, flesh- and plant-eating elements of the Texas Lower Permian fauna. They, therefore, contrast greatly with the lizard-like captorhinomorphs which formed the invertebrate-eating element of this fauna (Olson 1966). Little *Eunotosaurus* seems, then, more likely to be a specialized captorhinomorph than a survivor of an otherwise unknown, primitive type of synapsid.

Only a few of the small cotylosaurs, with which *Eunotosaurus* must now be closely compared, are sufficiently well known for a detailed comparison to be possible. These are: *Hylonomus* (Carroll 1964) from the Lower Pennsylvanian Joggins Formation of Nova Scotia; *Captorhinus* (Fox & Beerbower 1966) and *Araeoscelis* (Vaughn 1955), both from the Lower Permian Red Beds of Texas; and the early procolophonid *Nycteroleter* (Efremov 1940) from the Middle Permian Zone II of Archangel Province, U.S.S.R. (*Araeoscelis* has been considered as a possible theropsid on the basis of its middle ear (Vaughn 1955) and as possibly allied to the ichthyosaurs and plesiosaurs on the basis of its temporal opening (Romer 1967). However, the features of its post-cranial skeleton are almost identical with those of other small captorhinomorphs, and it seems best to regard it as merely a captorhinomorph which had developed a small temporal opening in the skull.)

In addition to the vertebral characteristics already mentioned, the following features are found in *Eunotosaurus* and in all the cotylosaurs mentioned above: the interclavicle has a long stem, there is a coracoid foramen in the pectoral girdle, an entepicondylar foramen in the humerus, and an obturator foramen in the pelvis. Furthermore, in all except *Nycteroleter* there is a prominent knob behind the glenoid for the origin of the coracoid head of the triceps muscle, and the blade of the ilium is rather narrow, not greatly expanded antero-posteriorly. However, these features are all characteristic of primitive reptiles in general. Their presence in *Eunotosaurus* merely confirms that it is basically a primitive reptile, and that its closest relatives are therefore likely to be the cotylosaurs.

As might be expected from its early date, *Hylonomus* is structurally a possible ancestor for *Eunotosaurus*, as it is for all the other later cotylosaurs (for example, like *Eunotosaurus*, it has only a single sacral rib). *Eunotosaurus* is therefore no less (and no more) closely related to it than are the other cotylosaurs.

None of the earlier cotylosaurs, of course, shows any positive signs of direct relationship to *Eunotosaurus* in having indications of reduction of the number of dorsal vertebrae or widening of the ribs. It is possible to find individual characteristics in which *Eunotosaurus* is similar to one or other of these cotylosaurs, but in each case there are also other features in which the earlier form is more specialized than *Eunotosaurus* and therefore cannot be ancestral to it. For example, the incomplete premaxilla of *Eunotosaurus* is slightly downturned upon the maxilla; this may be a post-mortem feature, but it is significant that the premaxilla of the captorhinids and of *Romeria* is downturned in just this way. On the other hand, *Captorhinus* and its relatives in the family Captorhinidae (Seltin 1959) are specialized in the multiplication of the tooth rows in the middle and posterior parts of the jaws; there is no sign of this condition in *Eunotosaurus*. *Araeoscelis* is the only other cotylosaur which possesses an ectepicondylar foramen in the humerus, but in its elongate lizard-like body it is quite unlike short-bodied *Eunotosaurus*. In its lack of a supraglenoid buttress and foramen *Nycteroleter* is similar to *Eunotosaurus*; on the other hand, *Nycteroleter* is approximately contemporary with *Eunotosaurus* but already has three sacral ribs.

In conclusion it is clear that, on the one hand, *Eunotosaurus* is a cotylosaur and that, on the other hand, it is an extremely specialized genus, not closely related to any of the other known Permian forms. Its position is best expressed taxonomically by transferring the family Eunotosauridae Nopcsa 1923 to the suborder Captorhinomorpha of the order Cotylosauria.

Eunotosaurus and the Chelonia. The similarity between *Eunotosaurus* and the

Chelonia was noted by Seeley in his original description (1892), while Watson (1914), accepting and expanding this view, concluded that *Eunotosaurus* was possibly an actual ancestor of the Chelonia. As will be seen, the supposed features which led Watson to this opinion have now been found either incorrect or unreliable. It may therefore be as well to state at the outset of this discussion that there are no detailed similarities between *Eunotosaurus* and the Chelonia which would unequivocally and convincingly demonstrate a phyletic relationship between them. Therefore, if there were any relationship between the two, its possibility could be demonstrated only by showing that the features of *Eunotosaurus* were consistent with such a relationship, and by showing that the features of the Chelonia were comprehensible only if the group had passed through a *Eunotosaurus*-like stage in its history. These two aspects of the problem will be dealt with in turn.

As already mentioned, the skull fragment of *Eunotosaurus* shows few significant features. It now lacks the whole of the anterior end of the snout. However, Watson (1914, p. 1017) states " When I first saw the specimen the whole of the extreme anterior end of the skull was covered by matrix, which I removed with a needle under a Zeiss binocular dissecting microscope. Whilst doing so I found no trace whatever of any internarial processes of the premaxillae, and believe them to have been certainly absent; the anterior nares are consequently confluent and look directly forward ". As Parsons & Williams (1961) have pointed out, the external nares are not confluent in the earliest known indisputable chelonian, *Proganochelys* (= *Triassochelys*) from the Upper Triassic of Germany (Jaekel 1916). If Watson's interpretation were correct, *Eunotosaurus*, though earlier in time, would already be further advanced in this feature than *Proganochelys*. However, there seem to be some grounds for doubting Watson's interpretation. He stated that there were about eight maxillary teeth and three premaxillary teeth. In the present investigation, traces of nine left and twelve right maxillary teeth have been found, and Watson's identification of three premaxillary teeth has been provisionally supported. These facts indicate that all of the skull as described by Watson is still present, i.e. none of the snout has been lost during the intervening period. The orientation of this region, as seen in Fig. 1, certainly does not suggest that it includes the most anterior, median, portions of the complete premaxillae. It therefore seems likely that this part of the snout was lost before Watson prepared the specimen, that his dissection of the anterior region merely penetrated between the remaining fragments of the premaxillae, and that the morphology of the external nares is quite unknown.

Marginal teeth and tiny palatal teeth are present in *Eunotosaurus*, but these would be expected in any early ancestor of the Chelonia.

Watson (1914) also suggested that *Eunotosaurus* might have resembled the Chelonia in having a long, flexible neck. However, since his sole evidence for this was the fact that the only skull known was found lying under the body, his suggestion must remain completely hypothetical.

The main resemblances of *Eunotosaurus* to the Chelonia lie, of course, in the structure of the vertebrae and ribs of the trunk region. Watson believed that its vertebrae were Chelonia-like in that the rib attachments and neural arches lay very far forwards on the centra. However, the positions of the rib-facets and neural arches of *Eunotosaurus* do not in fact appear to be at all unusual. Since, as discussed above, *Eunotosaurus* also lacks the dermal ossifications which Watson believed he had detected, its chelonian features are restricted to those first noted by Seeley (1892): the trunk vertebrae are individually very elongate, but are reduced in number; they lack transverse processes, so that the single-headed ribs attach directly to the sides of the centra; and the expanded ribs resemble the chelonian carapace.

As has already been noted, the elongation of the vertebrae of *Eunotosaurus* is a result of the widening of the ribs. Whether or not this similarity to the vertebrae of the Chelonia, and the resemblance of the expanded ribs to a carapace, indicate affinity must depend on one's view of the history of the chelonian carapace, and will be discussed below.

One very striking coincidence is the fact that in both *Eunotosaurus* and the Chelonia the number of trunk vertebrae has been greatly reduced, only ten or eleven remaining. The similarities and differences between the trunk and sacral regions of the two are best shown in the form of a table (Table 3), comparing those regions in *Eunotosaurus* and *Proganochelys*. The ten dorsal vertebrae known in *Eunotosaurus* are compared to dorsals 2–11 (i.e., the last ten) of *Proganochelys*.

TABLE 3

Proganochelys		*Eunotosaurus*
Dorsal 1	Rib short and free	Not preserved
2	Rib joined to carapace for only part of its length	Rib slightly expanded
3	Rib incorporated into carapace	Rib slightly more expanded
4–10	Ribs incorporated into carapace	Ribs greatly expanded
11	Rib incorporated into carapace	Vertebra bears long, fairly wide fused process which may represent transverse process and/or rib
Sacral 1	Separate sacral rib	Sacral rib absent or fused to vertebra
2?	Rib unknown	1st caudal, but some expansion of distal end of rib/transverse process

There are, as can be seen, differences between the two forms. Firstly, though only ten associated presacrals are known in *Eunotosaurus*, it is unknown whether any of the more anterior vertebrae were also dorsals. If not, the trunk region of *Eunotosaurus* comprised only ten vertebrae, even fewer than in that of *Proganochelys*. Secondly, the ribs of the last presacral and of the sacral in *Eunotosaurus* are not free but are either absent or (more likely) fused to their vertebrae. Finally, there is only a single sacral vertebra in *Eunotosaurus*. However, though there are two sacral ribs in some living Chelonia, there is no evidence of attachment of a second sacral rib to the ilium in *Proganochelys*. The fact that the rear face of the first sacral vertebra of *Proganochelys* is roughened suggested to Jaekel (1916) that the succeeding vertebra might have been suturally united with it, and the distal end of the first sacral rib bears a slight posterior facet to which a second sacral rib might have been attached. Jaekel's view remains, however, a possibility rather than an established fact.

The lack of transverse processes on the dorsal vertebrae of both *Eunotosaurus* and the Chelonia, noted by Seeley, may merely reflect the facts that the flexibility of the column had been reduced or lost, and that the bony processes giving attachment to muscles producing this movement were correspondingly reduced and lost altogether. This similarity could, then, be due either to phyletic relationship or to convergence.

Turning now to the differences between the trunk vertebrae of *Eunotosaurus* and those of the Chelonia there is the fact, already noted, that the neural arches and ribs of *Eunotosaurus* are in their normal positions, above and lateral to the centra respectively. In chelonians, on the other hand, the neural arches lie intercentrally. This is probably due to their association with the neural plates of the carapace—it is clearly advantageous that these plates should cover the more vulnerable junctions between the centra rather than lie above the centra themselves. There seems, on the other hand, to be no obvious explanation of the intercentral position of the rib heads in chelonians.

Parsons & Williams (1961) believe that the width of the ribs of *Eunotosaurus* is a feature which rules it out as a possible relative of the Chelonia. They point out (p. 96) that " in several lines of marine turtles, the dermal component of the carapace is strongly reduced and the ribs appear as separate, narrow, well-spaced elements ". However, since these chelonians have strongly reduced the dermal component of the carapace, it would be surprising if they had retained broad heavy ribs, even if this were their original, primitive condition. Furthermore, though the ribs of these forms are not as expanded as those of *Eunotosaurus*, they are nevertheless slightly expanded and leaf-shaped rather than parallel-sided (*cf. Dermochelys* and *Protosphargis*, Zangerl 1939, figs. 1, 9).

There are many differences between the pectoral girdle of *Eunotosaurus* and that of chelonians, but these all result from the great specialization of this region in the Chelonia. In the absence of an external carapace, the pectoral girdle of *Eunotosaurus* remains lateral to the ribs, the coracoid is large, the glenoid is directed postero-laterally rather than antero-laterally, and the humerus is not strongly bowed. Similarly, in the absence of a plastron, the clavicles and interclavicle remain as small elements associated with the scapulo-coracoid. These differences are therefore to be expected.

Like the pectoral girdle, the pelvic girdle of *Eunotosaurus* is merely more primitive than that of the Chelonia. There is no evidence in *Eunotosaurus* of the large thyroid fenestra of living chelonians, but this is normally absent in primitive reptiles.

From the above discussion, it can be seen that nearly all the differences between *Eunotosaurus* and the Chelonia are due simply to the more primitive condition of *Eunotosaurus*. The absence of a free rib on the last presacral vertebra of *Eunotosaurus* may debar it from direct ancestry of the Chelonia.

As already mentioned, the significance of the similarities between the Chelonia and *Eunotosaurus* in the reduction of the number of trunk vertebrae, in the elongation of the vertebrae, and in the common possession of a protective development in the trunk region, must depend on one's view of the history of the chelonian carapace. Unfortunately, there is no palaeontological evidence on this question. *Proganochelys* of the Upper Triassic possessed a carapace which was already fully chelonian, differing from the living forms in three points only. The first dorsal vertebra of *Proganochelys* has become an additional, last, cervical in the later Chelonia; the ribs of the second dorsal vertebra of *Proganochelys* are joined to the carapace (though for only the middle part of their length), whereas the corresponding ribs in later chelonians are greatly reduced and do not touch the carapace; finally, the last presacral rib is incorporated into the carapace in *Proganochelys* but is small and free in later chelonians. These points merely indicate what is in any case clear on other grounds, that the number of body segments involved in the trunk and carapace has been progressively reduced in the Chelonia.

It is possible to reconstruct a theoretical history of the chelonian carapace, beginning with a *Eunotosaurus*-like stage in which the ribs are enlarged and covered by horny epidermal plates. If the dermis below these plates were to produce bony plates, as it does in many reptiles, these might eventually cohere to form a carapace, the contribution of the ribs to this structure being concurrently reduced. However, since a protective bony armour was already in existence, there seems to be no obvious reason why the main rôle in the formation of this armour should be thus transferred to a new and more superficial level. Furthermore, if the expanded ribs of *Eunotosaurus* represent a fairly advanced stage in the development of the carapace, it is somewhat surprising to find no sign of any corresponding advance towards the development of a plastron.

An alternative theory, excluding any *Eunotosaurus*-like stage, would be that the dermal armour arose first, as a series of segmental plates similar to those of the Triassic stagonolepidids (Walker 1961). As suggested above in the discussion of *Eunotosaurus* itself, the development of an armour limiting the flexibility of the body would probably be accompanied by a reduction in the number of trunk segments. (Indeed, this process seems to have occurred also in the Triassic placodonts, in which unarmoured *Helveticosaurus* had *c.* 31 trunk vertebrae, while only fourteen remain in the most heavily armoured form, *Henodus*.) The armour would originally have been separated from the ribs and vertebrae by the dorsal musculature of the body, but this would have been progressively reduced and lost as the flexibility of the trunk region was diminished. The armour would at this final stage come into contact with the vertebrae and ribs. As Ruckes (1929) has shown, the ribs are drawn into a superficial position, dorsal and lateral to the girdles, because they become incorporated into the developing carapace. This is readily explicable if, as suggested here, the carapace was from the beginning general and superficial, and therefore itself lay lateral to the girdles.

Though by its nature inconclusive, one further line of reasoning seems to be worth discussing. It is surprising, if *Eunotosaurus* is ancestral to the Chelonia, that no chelonian remains have been found in faunas of ages intermediate between the Mid-Permian Tapinocephalus Zone (which contains *Eunotosaurus*) and the Upper Triassic Stubensandstein and Knollenmergel of Germany (which contain the earliest indisputable chelonian, *Proganochelys*). This lack cannot be ascribed to a poverty of vertebrate faunas of this period, or to a poverty of vertebrate faunas of any particular ecological nature. The vertebrates of the period of time between *Eunotosaurus* and *Proganochelys* are preserved in the abundant terrestrial faunas of the Endothiodon, Kistecephalus and Cynognathus Zones and the equally abundant semi-aquatic fauna of the Lystrosaurus Zone, all of South Africa, followed in Europe by the fresh-water Bunter fauna and the marine Muschelkalk fauna, in East Africa by the terrestrial Manda fauna, and in South America by the terrestrial Chañares, Santa Maria and Ischigualasto faunas. Equally, the lack of chelonian remains throughout this period cannot be ascribed to any inherent properties of these remains; they are not particularly difficult to identify, nor particularly fragile. Indeed, quite the reverse, for not only are the elements of the axial and appendicular skeleton highly recognizable, but the stout bony elements of the carapace and plastron provide additional and highly characteristic evidence of the presence of the group. These points make it seem somewhat unlikely that the chelonians had been in existence for very long before they are first found in the Upper Triassic, and therefore unlikely that they are descended from Mid-Permian *Eunotosaurus*.

It can be seen from the above discussions that neither the comparative morphology of *Eunotosaurus* and the Chelonia, nor the probable history of the chelonian carapace, nor the evidence of the fossil record, supports the view that *Eunotosaurus* was ancestral to the Chelonia.

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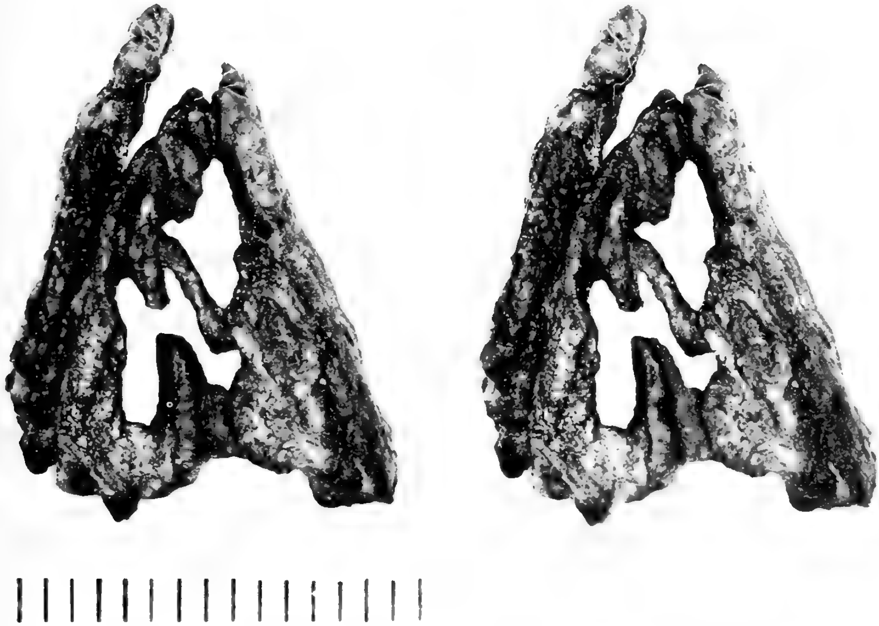
PLATE 1

Eunotosaurus africanus. BM(NH) no. 49424 (specimen E). Stereo-photographs of skull-fragment (one division of scale = 1 mm.). A, left lateral view (above) and right lateral view (below). B, view of eroded dorsal surface of palate.

A



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BY

JOHN TEMPEST TEMPLE

(Birkbeck College, University of London)

Pp. 197–230; 6 *Plates,* 4 *Text-figures*

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LOWER LLANDOVERY (SILURIAN) TRILOBITES FROM KEISLEY, WESTMORLAND

By J. T. TEMPLE

CONTENTS

SYNOPSIS

A trilobite fauna of Lower Llandovery (Silurian) age is described from Keisley, Westmorland (northern England). The fauna contains probably eight species, the uncertainty being due to the difficulty of drawing interspecific boundaries among Proetidae. Young stages of *Diacanthaspis sladensis* (Reed) and *Lichas laciniatus* (Wahlenberg) are described, the latter suggesting a revised interpretation of the origin of the lateral glabellar lobes in that species. The fauna has little in common with that of the underlying Keisley Limestone.

I. INTRODUCTION

In this paper are described the trilobites from the Lower Llandovery limestone at Keisley, Westmorland (grid reference NY 7136 2377), of which the brachiopods were described recently (Temple 1968). The stratigraphical position of the limestone appears to be conformably between the underlying Keisley Limestone and overlying shales of the *Monograptus atavus* zone, i.e., probably lowest Silurian.

The trilobites, which are all disarticulated and preserved as moulds in the weathered limestone, are far less abundant than the brachiopods and, although well preserved, have suffered distortion more commonly than the brachiopods which are rarely distorted. Many specimens are incomplete, apparently as a result of breakage : this is true particularly of the large *Lichas laciniatus* (large, that is, by the standards of the other trilobites in the fauna, but small in comparison with Swedish material of the species), and of the proetids, in which the occipital ring is rarely preserved intact.

The terminology used is largely that of the *Treatise on Invertebrate Paleontology, Part O*, although the term *glabella* is used to include the occipital ring. The notation for the glabellar lobes (L) and furrows (S) numbered from back to front is that of Jaanusson (1956). The *lateral glabellar lobes* of *Lichas* are so called as their ontogeny (see p. 213) does not suggest that they are of composite origin. Shaw & Ormiston's (1964) term *eye socle* is used for the rim of free cheek immediately beneath the visual surface.

Registration numbers of specimens prefixed by A are those of the Sedgwick Museum, Cambridge, those prefixed by It of the British Museum (Natural History), London, that prefixed by ar. of the Palaeontological Institute, Uppsala, that prefixed by G of the National Museum of Ireland, Dublin.

II. TAXONOMIC PROCEDURE

The taxonomic treatment is similar to that adopted for the brachiopods (Temple 1968 : 3). It is considered that measurements should form the basis of the description and comparison of samples of fossil species ; and that only those species based on quantitatively described topotype samples of adequate size can be considered to be well established. The arbitrary criterion of sample sufficiency adopted is not less than ten specimens of (in trilobites) whichever part of the integument includes the holotype and on each of which all of four or more variates can be measured.

The greater complexity of trilobite than brachiopod skeletons leads to an embarrassingly greater choice of measurable variates. The procedure adopted here may in some cases err on the side of too extensive measurement: this seems, however, to be inevitable until experience has shown how many (and which) variates are needed to distinguish between, for instance, allied species of *Diacanthaspis* or *Flexicalymene.*

The ultimately subjective basis of the recognition of specific limits in a fossil sample (Temple 1968) constitutes a practical difficulty in the present fauna only in the case of the Proetidae, and to a lesser extent *Otarion.* The Keisley proetids (like the enteletaceans among the brachiopods) appear to show considerable shape variation, and there seems to be no way of deciding if this is inter- or intra-specific, especially as the numbers of specimens are too few for discontinuity of shape variation to be demonstrated. The other trilobites fall into six species, of which four are compared with earlier established species—*Diacanthaspis sladensis* (Reed), *Lichas laciniatus* (Wahlenberg), *Otarion megalops* (M'Coy) and *Dalmanitina mucronata brevispina* Temple. The original material of these species has been examined and measurements are given here, but in all cases the topotype samples are small and do not fulfil the criterion of sample sufficiency, so that the names of these species can be used at present only informally. The Keisley samples are also small, only that of *Diacanthaspis sladensis* consisting of more than ten adequately preserved specimens. Quantitative comparisons of the Keisley material are therefore hampered on both sides by small numbers.

Semi-quantitative comparisons of Keisley material with topotype specimens of *Diacanthaspis sladensis* and *Otarion megalops* have been made by plotting individual specimens on the shape eigenvectors (Temple 1968 : 6) of the variance-covariance matrices of the Keisley specimens (Text-figs. 1 and 4). In this way multivariate shape variation can be reduced to two dimensions, and the mutual relations of two samples and the continuity or discontinuity of their shape variation can be assessed visually. The direction of maximum shape difference between two samples can be calculated (Burnaby 1966 : 99) as the projection of the line joining their means on to the " plane " orthogonal to the size eigenvector of the Keisley sample (see pp. 210, 223).

III. MEASUREMENTS

Shaw, in a forward-looking article (1957), has discussed the problem of measuring trilobites and has suggested a standardised set of symbols for measurements. The attempted application of Shaw's symbols, however, raises immediately the problem of projection. Shaw projected on to the plane defined by the palpebral lobes, but in many cases (e.g. *Flexicalymene* and *Diacanthaspis* here) the palpebral lobes are too small, even if adequately preserved, to define a plane accurately—and of course in several trilobite families they are absent. An alternative is to project on to a " horizontal " plane at right angles to that passing through the posterior margin of the occipital ring (Whittington & Evitt 1954 : 11). In this case also there is considerable uncertainty about the exact orientation of the plane so defined, because the posterior margin of the occipital ring rarely lies exactly on a plane. The course adopted in most instances in the present work is to project on to the symmetrical plane defined by the " normal " projection of the sagittal cranidial length, i.e. at right angles to the straight line joining the midpoint of the anterior margin of the cranidium to the midpoint of the posterior margin of the occipital ring. Any departure from projection on to this plane is explicitly noted in the measurements given, as for instance in *Diacanthaspis* where measurements of the distances between paired glabellar spines are given as normal projections of themselves so as to be mutually comparable. For pygidia, projection is on to the plane defined by the lateral and posterior pygidial margins (as Shaw), or, if this plane is not definable, on to the plane defined by normal projection of the sagittal pygidial length. Shaw's symbols have not been quoted, in spite of the advantages of standardisation, so as to avoid confusion with his differently projected measurements.

Where possible, measurements have been made on external moulds, both in order to provide measurements that can be compared with those made on testiferous material, and because the furrows that define many measurements are usually sharper and thinner externally than internally. When, because of scarcity of external moulds, measurements have to be made on internal moulds, overall lengths and widths include the thickness of the integument, unless explicitly stated otherwise. Furrows are measured at the deepest points of their cross-sections. Measurements are quoted in mm. Doubled half-values of nominally symmetrical structures are printed in parentheses. Measurements of holotypes or lectotypes are printed in bold type. Specimens which have suffered distortion are indicated by an asterisk at the beginning of the line of measurements. In obliquely distorted specimens sagittal and exsagittal measurements have been made parallel to the distorted axial line and not at right angles to transverse measurements.

IV. FREQUENCIES OF SPECIES

The numbers in Table 1 are based on the specimens collected during the first and second counts of the brachiopods (1968 : 9, Table 1). They are less accurate than the brachiopod figures as they record only retained material and exclude the poorly preserved specimens transitorily exposed during preparation. Except for this slight downward bias the figures are comparable with the " combined count " brachiopod figures, so that for instance the frequencies of combined cranidia and pygidia can be compared with the frequencies of combined pedicle and brachial valves of brachiopods (*op. cit.*, Table 1, column 7). *Diacanthaspis sladensis*, the most common trilobite, is seen to be about as abundant in the whole Keisley fauna as *Salopina* sp. nov., the fourteenth most common brachiopod species.

TABLE I.

Frequencies of species

	Cranidia	Free cheeks	Hypostomes	Pygidia	Protaspides
Diacanthaspis sladensis	18	2	3	3	0
Lichas laciniatus	8	2	2	1	0
Proetidae	8	5	1	9	0
Otarion megalops	4	0	0	1	0
Flexicalymene sp.	4	2	2	4	0
Dalmanitina mucronata brevispina	1	1	0	2	1

Note. No specimens of *Aulacopleura* sp. were found during the counts on which the figures in the table are based.

V. DISCUSSION OF FAUNA

The Keisley Lower Llandovery trilobite fauna is small, consisting probably of eight species, although, as trilobites are rare in the Keisley Lower Llandovery as a whole, the proportion of species undiscovered by collecting may be relatively high. Certainly the list of families which occur in both Ordovician and Silurian strata but which have not been found in the present fauna is impressive—illaenids, harpids, raphiophorids, cheirurids, thysanopeltids, encrinurids, homalonotids, and phacopids ; and of these missing families the first four are known from the underlying Keisley Limestone (Reed 1896 : 408). On the other hand the Keisley Lower Llandovery trilobite fauna is somewhat richer than that of the presumably slightly earlier *Hirnantia* fauna which, at its richest in Bohemia, has only three species (Havlíček & Vanek 1966 : 61).

The known affinities of the trilobites are mostly with forms of closely similar or slightly earlier age: *Diacanthaspis sladensis* occurs in the St. Martin's Cemetery Beds of South Wales, the published fauna of which (Reed 1907 : 537) suggests that it is coeval with the Keisley fauna; *Lichas laciniatus* is from the Dalmanitina Beds of Västergötland, also probably close in age; *Dalmanitina mucronata brevispina* occurs in basal Silurian strata in Yorkshire (Temple 1952; 14); *Otarion trigoda* is from the presumably slightly earlier (Upper Ordovician) Boda Limestone of Dalarne. Only *Otarion megalops* suggests comparison with younger strata, M'Coy's species coming from rocks of probably Upper Llandovery age in Galway (Whittington & Campbell 1967 : 461).

It is interesting that there is little affinity between the Keisley Lower Llandovery trilobites and those of the underlying Keisley Limestone, only *Lichas laciniatus* being common to the two faunas (Warburg 1925 : 300). Reed's record (1896 : 411) of '*Calymene blumenbachi* var. *caractaci*' from the Keisley Limestone might suggest comparison with *Flexicalymene* sp. here, but the cranidium in question (A 11781) appears to be referable to *Diacalymene*, while the pygidium (A 11782 a, b) is very poorly preserved.

VI. ACKNOWLEDGMENTS

I am indebted to several persons for assistance, which is gratefully acknowledged: Sir James Stubblefield, F.R.S., and Mr. R. P. Tripp have read and commented on the manuscript; Mr. A. G. Brighton, Dr. W. T. Dean, Mr. C. E. O'Riordan and Dr. Anders Martinsson have made specimens available for study; the calculations have been facilitated by programs written by Mr. M. R. Farmer and Mr. E. G. Dee; the photographs are the work of Mr. M. S. Hobbs; technical assistance has been given by Mr. K. R. Coventry; the material was collected with the help of a grant from the Central Research Fund of London University.

VII. SYSTEMATIC DESCRIPTIONS

Family **ODONTOPLEURIDAE** Burmeister 1843

Genus ***DIACANTHASPIS*** Whittington 1941

TYPE SPECIES. *Diacanthaspis cooperi* Whittington 1941 by original designation of Whittington (1941 : 501).

Diacanthaspis sladensis (Reed 1905)

(Pl. 1, figs. 1–22)

1905 *Acidaspis sladensis* Reed : 100, pl. 4, figs. 8–12

LECTOTYPE (here selected). Internal and external moulds of cranidium, A 4646 a, b figured by Reed, 1905a, pl. 4, fig. 8 (Pl. 1, figs. 17–18 here), from St. Martin's Cemetery Beds, Haverfordwest, Pembrokeshire, Wales.

DESCRIPTION (of Keisley material). *Cranidium*: Longitudinal convexity strong. Axial furrows distinct opposite glabellar lobes, indistinct opposite glabellar furrows. Glabella narrowing rapidly forwards from posterior margin to end of occipital furrow, then widening slightly around L_1 and S_1, narrowing again to the end of S_2

and then approximately parallel-sided. L_1 and L_2 stand only slightly above level of cheeks but central lobe of glabella has strong independent transverse and longitudinal convexity and becomes nearly vertical in front; central lobe narrows opposite L_1 and L_2, its outlining longitudinal furrows deepest opposite L_1; S_1 and S_2 oblique, S_1 deepened to a pit at its inner end, S_2 deepened along its length, both apparently apodemous; S_3 and small oblique L_3 rarely distinguishable. Occipital furrow broad and transverse behind central lobe, deepened and apodemous behind L_1 where it turns obliquely forwards; occipital ring wide (sag. & exsag.) behind central lobe, declining and narrowing rapidly distally as posterior margin strikes obliquely forwards to axial furrow; faintly cut-off occipital lobes; in large specimens a furrow curves around from inner ends of occipital lobes sub-parallel to margin of occipital ring, separating a narrow posterior strip which bears paired marginal spines and a small axial spine.

Fixed cheek highest opposite L_1, sloping very steeply backwards to posterior border furrow and less steeply forwards; palpebral lobe elevated, opposite highest point of cheek. Eye-ridge extends in slight outwardly convex curve to anterior end of axial furrow; eye-ridge bounded internally by parallel furrow ending in slight depression at axial furrow; cheek within furrow semicrescentic in front of palpebral lobe and with independent convexity. Anterior branch of facial suture diverges from eye-ridge progressively forwards across deep wide concave intervening strip on to anterior border; posterior branch of facial suture runs in sinuous curve to just within genal angle; both branches apparently run along sutural ridges. Anterior border sub-horizontally disposed relative to plane tangent to posterior part of glabella, narrowest axially. Posterior margin of cheek beyond axial furrow slopes obliquely back in slightly outwardly convex curve; posterior border furrow broad; posterior border roll-like and widening outwards.

Surface of cranidium (except for the various furrows including that beyond the eye-ridge) with spines of different sizes, regularly arranged in places, the most conspicuous being distributed as follows: occipital ring with strong posterodorsally directed paired marginal spines and small axial spine on posterior strip, strong axial and smaller paired flanking spines dorsally directed on anterior part; single row on eye-ridge; semi-crescentic cheek within eye-ridge bearing three rows posteriorly in large forms; strong paired glabellar spines which are conspicuous early in development (see below) are usually in large forms not easily distinguishable from subsequently developed glabellar spines which cover central lobe in more or less symmetrical pattern.

Free cheek: Eye elevated on vertical stalk; lenses visible on internal but not external moulds. Cheek slopes strongly down from base of stalk to broad border furrow beyond which border has strong independent convexity; border widening posteriorly. Librigenal spine deflected outwards from margin of cheek and curved convexly outwards, about as long as extreme oblique length of cheek. Margin of cheek with radially directed or sub-parallel spines wider and longer posteriorly; 11, 12, 13, 14 spines counted in 4 doubtfully complete cheeks; last spine (? more than one) on librigenal spine. On border a row of dorsally directed spines fewer than (8 counted on each of the same 4 cheeks) and not corresponding to marginal spines, and on large forms an internal row of smaller spines. Within border furrow scattered spines with smaller spines intercalated in large forms.

Hypostome: Outline sub-rectangular, ratio of minimum width to sagittal length averaging about 1·2 : 1; anterior margin convex; posterior margin shallowly indented axially; lateral margins indented. Middle body strongly outlined laterally and posteriorly, with paired furrows running obliquely back from just within anterior corners where they are wide and deep, dying out before mid-line; furrows define elongated posterior lobes confluent axially. Anterior border flat, narrowing out axially; posterior border wide, inclined gently upwards (ventrally); middle portions of lateral borders inclined more steeply upwards. Anterior lateral wings flat proximally, slightly declined (dorsally) distally; posterior lateral wings flattened relative to adjacent parts of borders. Surface bearing short spines. Doublure poorly known; dorsal surface apparently smooth.

Thoracic segments: The number of thoracic segments is unknown. Two types of isolated segment are known.

TYPE 1 (presumably anterior): Axial ring not known in detail but apparently with two (?) pairs of dorsally or dorsoposteriorly directed strong spines. Pleura horizontally disposed. Anterior pleural band narrow (exsag.), with 5 small hollow dorsally directed spines. Pleural furrow transverse; at its distal end is developed a hollow anterior pleural spine directed nearly straight downwards and curving slightly backwards. Posterior pleural band about as wide (exsag.) as combined anterior band and pleural furrow, raised, bearing two strong dorsally directed hollow spines, continued distally into horizontal transversely directed hollow posterior pleural spine from base of which arise a dorsolaterally directed spine and proximal to this a smaller spine more dorsally directed. Behind posterior band a narrow (exsag.) horizontal flange.

TYPE 2 (presumably posterior): Differs in the anterior pleural spine being directed nearly horizontally (only slightly backwards and downwards), and in the posterior pleural spine being directed postero-dorsoad-axially (so that in the single known specimen its broken tip lies behind and above the axial furrow) and without two spines at its base.

Pygidium: Outline roundedly sub-triangular, strongly elongated transversely, ratio of maximum width (at anterior margin) to sagittal length (both excluding spines) averaging about 3·6 : 1; ratio of width of axis to width of pygidium along anterior margin averaging about 0·3 : 1. Pleural lobes flat; axis defined by independent convexity but axial furrows not clearly marked except posteriorly. Articulating half-ring narrow; articulating furrow and ring furrow steepest anteriorly. Axis with two rings; first axial ring approximately parallel-sided, the central transverse strip independently raised; second ring narrower (tr.) but longer (sag. & exsag.), slightly indented axially behind, its posterolateral portions with slight independent convexity and forming in large specimens a bilobed terminal piece. Posterior margin with 7, 8, 9 spines on each side in 2, 6, 1 specimens; spines directed slightly dorsally initially but curving gently downwards, approximately radial to margin, equally spaced and of equal size except for most anterior one which is closer and smaller and squeezed in just within anterolateral corner of pygidium; third spine outwards from mid-line connected to first axial ring by faint pleural rib. Pleural rib sharply geniculated a short distance away from axial furrow; behind geniculation pleural rib runs sub-parallel to axial line or slightly postero-adaxially in outwardly slightly concave curve. Dorsal spines distributed as follows: on first ring and on anterior part of second ring a strong pair and up to 2 (in largest specimen) flanking pairs in transverse line; sagittal spines (in largest specimens) at fronts of first and second rings and immediately in front of furrow behind second ring (between lobes of "terminal piece"); on each pleural lobe one strong spine near geniculation of pleural rib, 2 others (3 in largest specimen) diminishing in size in approximately transverse line outwards, 3 small spines in front near anterior margin and (in largest specimen) 2 small spines behind; one each at bases of proximal marginal spines (up to sixth outwards in largest pygidium). Doublure directed obliquely down and inwards from margin.

Outer surface of cephalon and pygidium: Finely granular between spines.

MEASUREMENTS.
Cranidium (all lengths except no. 6 measured as normal projections)
1 = sagittal length of glabella (exclusive of axial occipital spine)
2 = sagittal length of occipital ring (exclusive of axial spine)
3 = sagittal length of preoccipital glabella
4 = mid-point of S_1 to midpoint of lateral part of occipital furrow (exsag.)
5 = mid-point of S_2 to midpoint of S_1 (exsag.)
6 = mid-point of occipital furrow to midpoint of palpebral lobe (exsag.) (projected normal to plane tangent to glabella on either side of occipital furrow)
7 = width of glabella (maximum) across L_1
8 = width of glabella at midlength of L_2
9 = width of frontal lobe of glabella
10 = minimum width of central lobe of glabella (opposite L_1)
11 = transverse separation of midpoints of outer edges of palpebral lobes
12 = base of paired occipital spine to base of spine 2a (exsag.)
13 = base of spine 2a to base of spine 2 (exsag.)
14 = base of spine 2 to base of spine 3 (exsag.)
15 = base of spine 3 to base of spine 4 (exsag.)
16 = base of spine 4 to base of spine 5 (exsag.)
17 = transverse separation of bases of paired occipital spines
18 = transverse separation of bases of spines 2a
19 = transverse separation of bases of spines 2
20 = transverse separation of bases of spines 3
21 = transverse separation of bases of spines 4
22 = transverse separation of bases of spines 5

N.B. The tops of the palpebral lobes are often missing, in which case 6 and 11 are estimates. Bevelling of the corners of the central lobe of the glabella makes 10 difficult to measure consistently.

Variates		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Individual		0·44	0·10	0·34	—	—	—	—	—	0·21	0·12	—	—	—	0·08	0·12	—	—	—	0·07	—	0·06	—
specimens		0·58	0·15	0·46	0·15	0·15	0·27	0·39	0·39	0·36	0·24	0·85	0·17	0·11	0·16	—	—	0·21	0·10	0·12	0·13	—	—
		0·80	0·16	0·64	0·19	0·17	—	0·48	0·46	0·39	0·28	—	—	0·15	0·17	0·19	—	—	—	0·16	—	0·16	—
		—	0·19	—	0·22	0·16	0·18	0·40	0·39	—	0·23	0·87	0·22	0·15	0·17	0·22	—	—	0·11	0·15	0·15	0·15	—
	*	0·92	0·22	0·73	0·22	0·21	—	—	0·59	0·51	0·30	—	0·29	0·13	0·18	0·22	0·10	0·29	0·23	0·17	0·19	0·19	—
	*	—	0·32	0·70	0·22	0·19	—	0·53	0·48	—	0·29	—	0·30	0·16	0·19	0·22	—	0·32	0·18	0·18	0·19	0·18	—
		0·95	0·27	0·73	0·22	0·22	0·19	0·63	0·58	—	0·32	1·14	0·27	0·16	0·19	0·19	0·15	0·34	0·13	0·15	0·16	0·18	0·24
		0·95	0·22	0·75	0·19	0·21	—	0·48	0·46	0·48	0·27	—	0·27	0·15	0·18	0·21	0·10	0·24	0·12	0·17	0·17	0·21	0·22
		1·02	0·22	0·80	0·24	0·24	0·24	0·81	0·78	0·69	0·44	1·65	0·24	0·21	0·24	0·27	0·13	0·30	0·19	0·22	0·23	0·29	—
		1·04	0·22	0·82	0·34	0·17	0·19	0·61	0·53	0·52	0·32	1·21	—	0·18	0·18	0·27	0·15	0·36	0·12	0·16	0·16	0·17	0·24
	*	1·08	0·32	0·87	0·29	0·22	—	0·56	0·51	0·44	0·27	—	0·34	0·24	0·21	0·21	0·12	0·33	0·15	0·17	0·21	0·19	0·24
		1·16	0·29	0·90	0·27	0·24	0·36	0·89	0·79	—	0·51	(1·85)	0·34	0·18	0·19	0·34	0·15	0·44	0·22	—	0·19	0·22	0·32
	*	1·21	0·27	0·97	0·27	0·32	—	0·85	0·78	0·68	0·44	—	0·27	0·22	0·22	0·33	0·16	0·44	—	0·19	0·22	0·22	0·24
		1·21	0·29	0·97	0·29	0·29	0·25	0·90	0·85	0·68	0·51	1·94	0·30	0·23	0·27	0·28	0·12	0·48	—	0·27	0·28	0·30	0·25
		1·26	0·29	0·99	0·34	0·32	0·35	0·87	0·75	0·61	0·48	1·60	—	—	—	—	—	0·41	—	—	—	0·27	0·23
		1·31	0·32	1·02	0·30	0·30	0·27	—	—	0·63	0·48	1·75	0·36	0·22	0·29	0·29	0·16	0·41	0·28	0·21	0·19	0·22	0·30
		1·33	0·34	1·09	0·36	0·32	0·25	1·09	1·02	0·97	0·61	2·30	—	0·29	0·27	0·32	0·17	0·56	0·22	0·29	0·34	0·36	0·36
		1·33	0·36	1·01	0·39	0·33	0·25	0·99	0·95	0·78	0·52	1·85	0·41	0·22	0·32	0·24	—	0·56	0·17	0·32	0·40	0·36	—
		—	—	1·21	—	0·34	—	—	0·87	0·78	—	—	—	0·25	0·33	0·36	0·21	—	0·18	0·27	0·29	0·32	0·35
		—	—	1·21	0·42	0·39	0·40	1·19	1·09	0·97	0·61	—	0·39	0·30	0·30	0·36	0·19	—	0·39	0·32	0·24	0·34	0·41
		1·58	0·41	1·31	0·42	0·39	0·25	1·02	0·90	0·82	0·56	1·90	0·48	0·27	0·33	0·34	0·21	0·56	0·29	0·29	0·29	0·30	0·34
		—	—	1·31	0·53	0·36	0·25	1·21	1·07	0·92	0·63	—	0·53	0·30	0·27	0·39	0·21	—	0·15	0·30	0·30	0·36	0·40
	*	—	0·44	—	0·41	0·39	—	1·14	1·02	0·90	0·55	—	0·51	0·29	0·32	0·34?	—	0·61	0·19	0·29	0·24	0·29	—
	*	—	0·51	—	0·58	0·56	—	1·55	1·38	—	0·85	—	0·73	0·42	0·44	0·44	—	0·87	0·32	0·44	0·40	0·36	—
		1·96	0·36	1·58	0·48	0·44	—	(1·21)	(1·12)	—	(0·68)	—	0·48	0·33	0·33	0·45	0·27	—	0·27	0·29	0·32	0·34?	0·35
		2·40	0·58	1·84	0·61	0·45	0·45	1·55	1·33	1·15	0·91	3·10	0·61	0·41	0·44	0·51	0·27	—	0·42	0·48	0·46	0·46	0·47
	*	—	0·58	1·99	0·68	0·61	0·60	2·23	1·89	1·58	1·31	4·35	0·61	0·48	0·55	0·61	0·34	—	—	—	—	0·58	0·65
	*	3·00	0·73	2·50	0·87	0·78	0·50	2·01	1·82	—	1·09	3·95	0·97	0·56	0·56	0·80	—	—	0·41	0·51	0·55	—	—
		3·55	0·75	2·90	1·00	0·95	—	2·75	2·40	1·90	1·30	—	—	0·50	0·75	—	—	—	0·55	—	0·80	—	—
sladensis	*	—	—	2·15	1·05	0·65	—	2·20	2·00	—	0·80	(4·2)	0·70	0·45	0·70	—	—	0·80	0·40	0·60	0·65	—	—
topotypes	*	**2·50**	**0·75**	**1·90**	—	**0·65**	**0·35**	**2·00**	**1·80**	**1·45**	**0·85**	**3·7**	**0·75**	**0·50**	**0·50**	—	—	**0·85**	**0·25**	**0·50**	**0·60**	—	—

Hypostome (all lengths projected as 23)
23 = sagittal length (normal projection)
24 = overall length (exsag.)
25 = sagittal length of middle body
26 = maximum width (at anterior wings)
27 = width at posterior wings
28 = minimum width

Variates	23	24	25	26	27	28
Individual specimens	0·8	—	0·7	1·25	—	1·05?
	1·05	1·1	0·85	—	1·4	1·25
	1·2	—	0·95	1·9?	1·75?	1·55
	1·25?	—	0·95	1·55	—	1·2
	1·25	—	1·05	—	1·9	1·75
	* 1·3	1·35	—	—	—	1·65
sladensis topotype	1·2	1·25	1·0	1·55?	1·45	1·3

Pygidium (all lengths projected on to plane of margin)
29 = sagittal length (exclusive of half-ring and posterior spines)
30 = overall length of axis (exclusive of half-ring) (sag. or exsag.)
31 = length (sag.) of first axial ring
32 = maximum width (exclusive of spines)
33 = width of axis at anterior margin
34 = transverse separation of bases of paired spines on first axial ring
35 = transverse separation of bases of paired spines on second axial ring
36 = transverse separation of bases of paired spines at geniculations of pleural ribs
37 = base of paired spine on first axial ring to base of paired spine on second axial ring (exsag.)
38 = transverse separation of bases of third (from axial line) marginal spines

Variates	29	30	31	32	33	34	35	36	37	38
Individual specimens	0·6	0·55	0·25	—	0·65	0·25	0·15	0·8	0·25	0·8
	0·6	0·55	0·25	—	0·7	0·25	0·15	0·9	0·25	0·85
	0·65?	0·5	0·2	2·7?	—	—	0·2	1·05	0·2	1·0
	0·65	0·6	0·25	2·6?	0·9	0·25	0·25	1·15	0·25	1·05
	0·7	0·55	0·25	2·3	0·8	0·25	0·25	1·0	0·25	0·95
	0·8	0·65	0·3	*(3·15)*	0·9	0·3	0·25	1·2	0·3	1·2
	0·8	0·7	0·3	2·25?	0·75	0·25	0·2	1·05	0·35	1·1
	—	0·7	0·35	—	1·0?	0·3	0·3	1·3	0·35	1·3
	1·05	0·9	0·4	3·85	1·25	0·45	0·3	1·65	0·4	1·7
sladensis topotype	0·85?	0·65	0·3	3·55	0·9	—	0·3	1·4	—	1·4

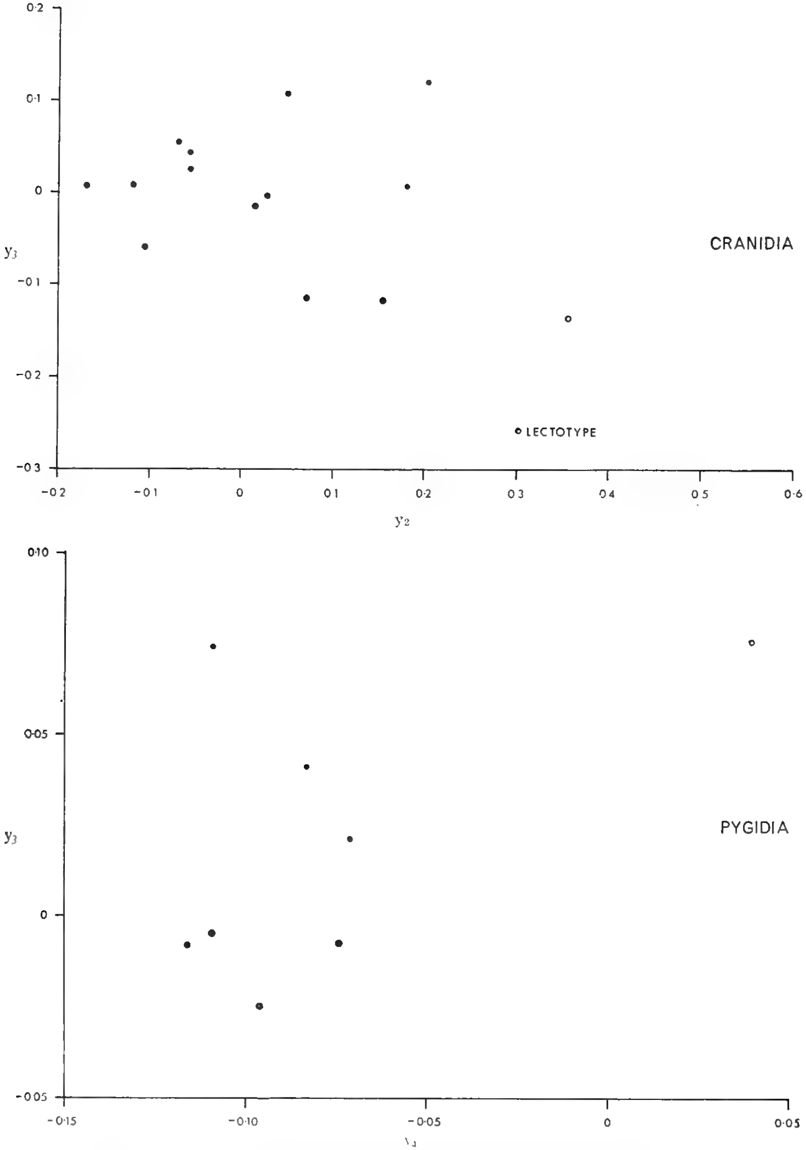

FIG. 1. Cranidia (above) and pygidia (below) of *Diacanthaspis sladensis* from Wales (open circles) and Keisley (closed circles) plotted on respectively the second and third (y_2 and y_3) and third and fourth (y_3 and y_4) eigenvectors of the variance-covariance matrices of the Keisley specimens. Transformed scale units correspond to original measurements in mm.

The scatters show the disposition of the Welsh and Keisley specimens relative to two of the axes of shape variation of the Keisley samples, the effects of size differences having been removed by, as it were, viewing the scatters down the first eigenvectors. See text for further details.

ONTOGENY. A cranidium of glabellar length 0·58 mm. shows spines on the occipital ring as described above except for lack of the pair of smaller flanking spines on the anterior part; on the central lobe of the glabella there are paired spines (notation after Whittington 1956: text-fig. 1) just in front of the occipital furrow (2a), opposite the inner ends of S_1 (2), and behind S_2 (3), pair 2 being closer to 2a than to 3, and further forwards an axial spine (beyond this the anterior part of the central lobe is poorly preserved), one spine on L_1, none on L_2, three strong spines proximally on fixed cheek (A_1, A_2, A_3) as well as more distal ones and a row of spines along posterior border. A cranidium of glabellar length 0·80 mm. (Pl. 1, fig. 12) is better preserved anteriorly and shows on the anterior part of the central lobe in front of the axial spine a pair of spines (4) and then a row of three spines (5); it has a full complement of occipital spines and there is an incipient axial spine opposite the posterior end of L_2 which has itself acquired a small spine. By a glabellar length of 0·95 mm. some spines have appeared laterally on the central lobe, and at a length of 1·02 mm. a row of three spines has appeared on the central lobe opposite L_1 which now has two spines.

In the smallest assigned hypostome (0·8 mm. long) the paired furrows are very deep anteriorly.

Of the two flanking pairs of tubercles on the pygidial axial rings the proximal pairs appear first, and of those pairs that on the second ring appears before that on the first.

REMARKS. The original type material of *D. sladensis* (refigured here on Pl. 1, figs. 17–21) consists of two cranidia and a pygidium, together with some associated material not described by Reed. Among the latter are a hypostome, a free cheek and two pleural fragments, all on the same block as the lectotype cranidium. The lectotype shows better-developed S_3 and L_3 than any of the Keisley specimens, but the pygidium (with 8 pairs of marginal spines) appears to be very similar to those from Keisley. The associated Welsh hypostome, free cheek (which has 13 visible marginal spines and another on the librigenal spine) and pleural fragments are also very similar to their Keisley equivalents. The Welsh material is too scanty for a detailed quantitative comparison, but informal comparisons of the cranidia and pygidia can be based on shape variation (Text-fig. 1). For cranidia the plot is of the scores of 13 Keisley specimens and two *sladensis* syntypes (one being the lectotype) on the second and third eigenvectors of the variance-covariance matrix of the Keisley specimens based on variates 3, 5, 7, 8, 10, 12, 13, 14, 18, 19, 20 (the choice of variates is dictated by missing observations in the measured sample). It will be seen that for both y_2 and y_3 the scores of the two Welsh syntypes lie beyond the range of variation of the Keisley sample. The direction cosines of the maximum shape difference between the samples are (−0·48, −0·02, 0·44, 0·44, −0·45, −0·19, −0·05, 0·19, −0·20, 0·10, 0·24): Welsh glabellas are relatively shorter, wider across L_1 and L_2, and with a narrower central lobe. The principal component analysis of pygidia, which is based on variates 29, 30, 31, 33, 35, 36 and 38, shows that the single available Welsh specimen is not separable from Keisley specimens on y_2 but has scores beyond the Keisley range for y_3 and y_4. The direction cosines of the maximum shape difference are (−0·11, −0·52, −0·16, −0·63, 0·22, 0·37, 0·33): the Welsh pygidium has a narrower and shorter axis but more widely separated pleural ribs and third marginal spines.

Despite these detailed differences the overall resemblances of the Keisley and Welsh specimens are sufficient to justify reference of the former to *sladensis*. Reed's species is referred for convenience to *Diacanthaspis* pending clarification of the relations within the Odontopleurinae, because of the relative complexity of the occipital ring, the spininess of the dorsal surface, and the absence of major pygidial spines. Kielan (1960 : 106) has remarked on the difficulty of distinguishing *Diacanthaspis* from *Primaspis*, and to this may be added the difficulty of distinguishing *Diacanthaspis* from *Xanionurus* Whittington & Campbell (1967 : 478) and also from *Odontopleura* itself, of which the holotype of the type species has recently been redescribed (Bruton 1967 : 216). The genera of Odontopleurinae have been narrowly interpreted since R. & E. Richter's (1917) revision, but objective generic distinctions (if any such exist in the subfamily) have not yet emerged.

Family **LICHIDAE** Hawle & Corda 1847

Genus ***LICHAS*** Dalman 1827

Type species. *Entomostracites laciniatus* Wahlenberg, 1818, by original designation of Dalman (1827 : 71).

Lichas laciniatus (Wahlenberg, 1818)

(Pl. 2, figs. 1–14; Pl. 3, figs. 1–10)

1818 *Entomostracites laciniatus* Wahlenberg : 34, pl. 2, fig. 2*.
1925 *Lichas laciniatus* (Wahlenberg); Warburg : 295, pl. 8, figs. 14–18, 20, ?19, text-fig. 20.
1939 *Lichas laciniatus* (Wahlenberg); Warburg : 15, pl. 9, figs. 1–8.

Holotype. Pygidium, ar. 1, figured by Wahlenberg, 1818, pl. 2, fig. 2* (Pl. 3, fig. 5 here), from the Dalmanitina Beds, Bestorp, Mösseberg, Västergötland, Sweden.

Description (of Keisley material). Detailed description is given only of the free cheek and hypostome. The pygidium is apparently identical with Warburg's description, and the slight differences in the cranidium are discussed below.

Free cheek: Visual surface reniform, its long axis inclined anteriorly inwards, convex laterally but almost vertical overall so that lowest parts are slightly overhung; lenses visible on both internal and external moulds. Eye socle beneath eye vertical, bounded outside by furrow. Free cheek beyond furrow sloping, outwardly convex. Lateral border furrow represented by change in slope within lateral border. Lateral border almost flat, nearly horizontal, widening posteriorly but becoming indistinguishable before reaching posterior border. Lateral margin well-defined and angular in section. Posterior border furrow broad, curving backwards and directed centrally down librigenal spine so that posterior border narrows at its distal end. Librigenal spine strong, tapering rapidly, its outer margin continuing line of cheek margin. Posterior border with slight independent convexity. Lateral doublure steeply inclined at margin, rapidly becoming nearly flat and slightly outward-sloping proximally, reaching about to lateral border furrow, widening posteriorly and with terraced lines curving inwards at posterior margin (6 & 9 terraced lines observed opposite end of posterior border furrow on two specimens). Anterior facial suture running in outwardly convex curve to become almost tangential to margin in approximately exsagittal line with anteroproximal extremity of eye. Posterior facial suture directed almost transversely away from eye and then in an oblique outwardly convex curve. Free cheek (except furrow beyond eye socle) with low tubercles of different sizes affecting both surfaces of test, smaller on eye socle and becoming smaller and sparse towards lateral margin.

Hypostome: Outline evenly rounded anteriorly, axially indented posteriorly. Transverse convexity greatest across anterior lobe of middle body. Middle furrow directed back at about 45° to axial line, branching shortly inwards; anterior branch dying out before axial line but connected by a depression across middle body; posterior branch nearly parallel to adjacent part of lateral furrow, dying out shortly; intervening lobe with slight independent convexity. Lateral furrow deepest at end of middle furrow, swinging out and shallowing around posterior lobe, commonly branching obscurely before dying out before axial line. Border narrowing out rapidly around front of middle body, widening posteriorly; border continuous posteriorly with middle body. Opposite anterior lobe of middle body the distal edge of border is downturned (dorsally) to form small anterior wing; near end of middle furrow the downturned part becomes completely overturned to form behind this region the doublure of posterolateral border. Posterior doublure nearly flat, with (at head of embayment) a strong axial boss sharply delimited in front by a deep furrow separating it from anteriorly extended inner axial part of doublure which slopes steeply up (ventrally) to near surface of hypostome. Ventral surface of hypostome and dorsal surface of doublure smooth except for terraced lines on border and anterior wing near anterior lobe of middle body.

Thoracic segment: The pleural furrow is steep-sided anteriorly; beyond the fulcrum it becomes shallower and is directed down the middle of the pleural spine.

Pygidium: The pygidial doublure lies close and parallel to the dorsal surface; it widens slightly backwards and has 9 terraced lines posteriorly on a pygidium about 5·0 mm. long.

MEASUREMENTS.

Cranidium

1 = sagittal length (normal projection)
2 = preoccipital sagittal glabellar length (normal projection)
3 = minimum width (tr.) of central lobe of glabella, measured if necessary midway between turning points of left and right lateral furrows
4 = width (tr.) of left lateral lobe measured along continuation of line of 3
5 = width (tr.) of right lateral lobe measured along continuation of line of 3
6 = maximum width of glabella (across lateral lobes)
7 = width of glabella across widest part of frontal lobe
8 = mid-point of occipital furrow to anterior end of lateral lobe (exsag.) (projected as 2)

Variates		1	2	3	4	5	6	7	8
Individual		1·1?	0·85	0·19	0·07	0·09	0·36	0·41	0·27
specimens	*	1·75	1·3	0·35	0·2	0·2	0·85	0·85	0·7
	*	3·15?	2·55	0·65	0·65	—	—	2·15	1·5
	*	—	—	0·7	—	0·6	—	—	—
		—	2·8	0·75	0·75	0·75	2·65	2·5	1·6
	*	—	2·4?	1·0	0·85	1·0	3·3	—	1·4
	*	—	—	1·1	—	1·05	—	—	—
		—	—	1·1	0·9	0·75	—	—	—
		—	—	1·4	1·2	—	—	—	—
		5·25	4·15	1·4	1·35	1·4	5·0	4·7	2·55
		—	5·8	1·25	1·15	—	4·15	3·85	3·8
		—	6·5	1·75	—	1·5	—	—	4·5

Hypostome (all lengths projected as 9)

9 = sagittal length (normal projection)
10 = overall length (exsag.)
11 = mid-point of anterior margin to inner end of anterior branch of middle furrow (exsag.)
12 = maximum width
13 = minimum width
14 = maximum width of anterior lobe of middle body
15 = maximum width of posterior lobe of middle body

Variates		9	10	11	12	13	14	15
Individual		2·1	2·25	1·2	—	—	1·3	1·35
specimens	*	2·8	—	1·7	3·1	2·25	1·85	2·0
	*	5·25	—	3·15	(5·6)	—	3·6	—

Pygidium (all measurements projected normally)

16 = sagittal length exclusive of articulating half-ring
17 = maximum width
18 = width of axis at anterior margin
19 = minimum transverse separation of post-axial furrows
20 = posterior margin to position of minimum transverse separation of post-axial furrows (sag.)

Variates	16	17	18	19	20
Individual specimens	1·8	—	0·95	0·55	0·95
	4·35	—	(2·25)	1·15	2·15
laciniatus holotype	**17·4**	**(26·8)**	**8·9?**	**4·9**	**10·4**

ONTOGENY. A cranidium 1·75 mm. long (Pl. 2, fig. 12; Text-fig. 2*b*) differs from larger specimens in having a relatively narrower glabella with proportionately shorter (exsag.) lateral lobes which reach only as far forwards as the inner ends of the prominent eye-ridges; on the central glabellar lobe there is a transverse furrow (presumably S_1) at the posterior ends of the lateral lobes, and further forwards are traces of paired furrows (presumably S_2); the occipital lobes are faintly defined.

A cranidium about 1·1 mm. long (Pl. 2, fig. II; Text-fig. 2*a*) is referred to the species on the basis of the strong eye-ridge palpebral lobe and well developed frontal lobe of the glabella, features which preclude reference to any of the other trilobites in the fauna. In front of the occipital furrow are two transverse glabellar furrows (presumably S_1 and S_2) and traces of paired furrows (presumably S_3) near the ends of the eye-ridges. Oblique furrows run back from near the outer ends of S_2 to join S_1 and apparently continue faintly back to define small lobes. The occipital ring is poorly preserved. The glabella is widest across the frontal lobe, and the axial furrows are deepened and widened to form anterior pits at the anterolateral corners of the glabella.

FIG. 2. Outline drawings of small cranidia of *Lichas laciniatus*, × 25. *a*, It 5012 (see Pl. 2, fig. 11); *b*, It 5021 (see Pl. 2, fig. 12).

If the smaller of these two specimens is correctly referred to *L. laciniatus* it seems that the small lobes near the back of the pre-occipital glabella at this stage correspond to the lateral (' bicomposite ') lobes of later stages; and that during development the lobes grow rapidly forwards (presumably pushing the axial furrows outwards as they go), the anterior ends of the lobes reaching the ends of the eye-ridges at a cranidial length of 1·75 mm. and ultimately extending considerably further forwards (Pl. 2, fig. 9). The forward extension of the lateral lobes during growth is illustrated by Text-fig. 3, a plot of the exsagittal length of the lateral lobes (measurement 8) against the sagittal length of the pre-occipital glabella (measurement 2). The fitted regression line clearly does not pass through the origin (the intercept on the ordinate axis being significantly different from zero, $p < \cdot 005$ one-sided), and the ratio of lateral lobe length to pre-occipital glabellar length decreases with decreasing size, slowly at first and progressively more rapidly until the lateral lobe would disappear at a pre-occipital glabellar length of about 0·48 mm. No specimen as small as this has been found at Keisley but it is interesting to note that the only known lichad protaspis, which has a pre-occipital glabellar length of about 0·37 mm., has no lateral lobes (Whittington : 1957 : text-fig. 13). At the other end of the size range the cranidium of *L. laciniatus* figured in profile by Warburg (1939 : pl. 9, fig. 3a), which is over twice as long as the longest measurable cranidium from Keisley, has lateral lobes proportionately longer than those of the Keisley specimens; this specimen plots close to (slightly above) the continuation of the regression line of Text-fig. 3.

Although there is strong evidence from the 1·75 mm. stage onwards for the forward growth of the lateral lobes relative to the rest of the glabella, the evidence for the earlier development of the lobes rests on a single specimen, the 1·1 mm. cranidium. Further evidence about the rapid early changes in the lateral lobes is clearly desirable. Such evidence would be provided by cranidia intermediate in size between these two stages, and, since the ratio of their lengths is 1·53, it is likely that such an intermediate instar may exist.

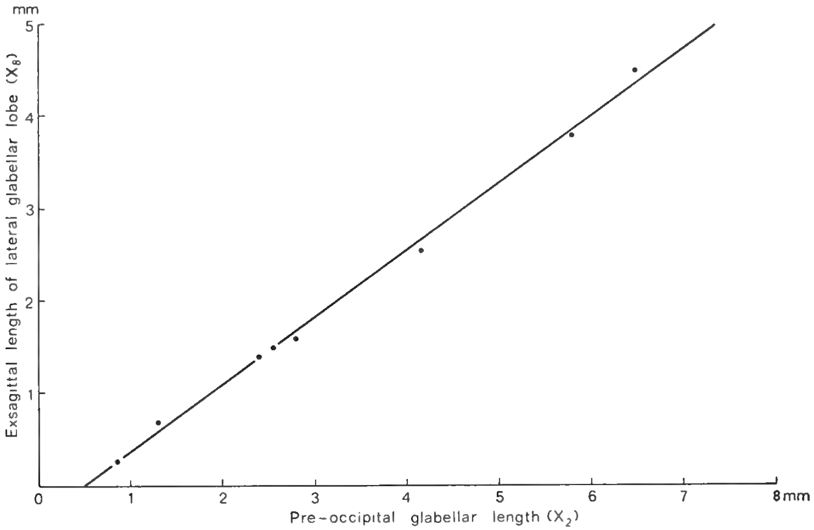

FIG. 3. A plot of measurements 8 and 2 on cranidia of *Lichas laciniatus* from Keisley. The fitted regression line has equation : $x_8 = 0{\cdot}726x_2 - 0{\cdot}350$.

The postulated development of the lateral lobes of *L. laciniatus* by forward growth from the back part of the pre-occipital glabella is quite different from the phylogenetic sequence normally assumed for the development of the lichad lateral lobes, i.e. by backward growth of the inner ends of S_3 (Reed 1902 : 66).

REMARKS. The strongly convex profile of the glabella, the relative width of the central lobe at its narrowest point (greater than the mean width of the lateral lobes measured along the same transverse line as the minimum central lobe width in 8 out of 10 specimens) and the relatively long axis of the pygidium suggest comparison of the Keisley material with *Lichas affinis* Angelin (see Warburg 1925 : 302, pl. 8, figs. 1–8, 11–13, 21, 23; 1939 : 16, pl. 9, figs. 13–15) rather than with *L. laciniatus*, as the two species have been interpreted by Warburg (1925 : 306). On the other hand, the neck of the central lobe is not raised above the lateral lobes and the post-axial furrows of the pygidium are not strongly divergent, features which are more suggestive of *L. laciniatus*, although the Keisley hypostome differs in its branched middle furrows from those attributed to either of the Swedish species. The Keisley material is referred to *L. laciniatus* because of the similarity of the pygidia to the holotype of Wahlenberg's species (Warburg 1939; pl. 9, fig. 1, refigured here as Pl. 3, fig. 5); quantitative comparison is precluded by the fragmentary nature of the Keisley material and the disparity in size with the much larger holotype.

Family **PROETIDAE** Salter 1864

Cranidium Type 1

(Pl. 4, figs. 1–4)

Description. Pre-glabellar area sub-horizontally disposed relative to tangent plane to posterior part of pre-occipital glabella; pre-glabellar field flat or slightly concave in section axially in front of glabella, becoming slightly convex abaxially; anterior border flat or slightly convex in section; anterior border furrow faint; pre-glabellar field usually slightly longer (sag.) than anterior border. Axial furrows not clearly incised around frontal lobe of glabella. Glabella widening slightly from occipital furrow around L_1, the effect being enhanced by bevelling and rounding of posterodistal corners of L_1. In front of L_1 glabella may appear slightly waisted but this is usually due to a point of inflection of the axial furrow rather than a true turning point. Glabella broadly rounded in front. S_1 very faint, inclined backwards but not circumscribing L_1; S_2 and S_3 not usually distinguishable with certainty but slight traces sometimes visible. Occipital ring narrowing (tr.) forwards and (exsag.) abaxially, bearing an axial tubercle and sometimes with traces of occipital lobes. Palpebral lobes poorly known, apparently long (extending from in front of S_2 to near posterior border furrows) and close to axial furrows. Pre-ocular facial sutures diverging usually strongly initially but converging near border furrow (sometimes almost at right angles to their earlier course) to cut margin along or within exsagittal line with front of palpebral lobe. Post-ocular fixed cheeks apparently very small and triangular. Outer surface of test smooth.

Cranidium Type 2

(Pl. 4, figs. 5–8, 12)

Description. Pre-glabellar area inclined obliquely downwards relative to tangent plane to posterior part of pre-occipital glabella; pre-glabellar field continuing slope of anterior part of frontal lobe of glabella, slightly convex in section; anterior border flat or slightly concave in section; anterior border furrow faint; pre-glabellar field usually slightly longer (sag.) than anterior border. Axial furrows clearly incised around frontal lobe of glabella. Glabella tapering forwards from just in front of occipital furrow, sometimes tapering less rapidly in front of S_2. Glabellar furrows well-marked: S_1 strong and oblique but not reaching occipital furrow; S_2 sub-parallel to S_1; S_3 short, less oblique, not reaching axial furrow. Occipital ring poorly known, bearing a small axial tubercle. Palpebral lobes poorly known, reaching apparently from about the ends of S_2 to near posterior border furrow. Preocular facial sutures and post-ocular fixed cheeks as in Type 1. Outer surface of test smooth.

Free cheeks

(Pl. 4, figs. 15, 16)

Two proetid and/or otarionid free cheeks are illustrated. It is not possible on the available material to demonstrate whether more than one type is represented.

Hypostome

(Pl. 4, figs. 9–11)

DESCRIPTION. Maximum width at anterior wings; outline waisted near mid-length. Anterior lobe of middle body very convex (but not pointed), sloping steeply from in front of its mid-length to anterior margin and more gently to middle furrow; anterolateral flanks of anterior lobe slightly bevelled. Middle furrow convex posteriorly, faint axially. Posterior lobe of middle body crescentic, continuing with slight independent convexity the downward (dorsal) backward slope of anterior lobe. Anterior border narrow (sag. & exsag.), upturned (ventrally). Details of anterior wings unknown. Lateral furrows absent opposite anterior wings; lateral and posterior furrows uniformly deep otherwise. Lateral border narrow, sloping up (ventrally) in side view to position opposite ends of middle furrows, sloping down behind around posterior lobe. Posterior border apparently sub-horizontally disposed, produced into 3 (?2) short spines on each side. Outer surface: anterior lobe of middle body with strong terraced lines diverging backwards from mid-line; lateral and posterior borders with strong terraced lines parallel to margin.

Pygidium Type 1

(Pl. 4, figs. 13, 20)

DESCRIPTION. Outline roundedly sub-triangular; ratio of maximum width to length about 1·4 : 1 in most complete specimen; maximum width situated slightly behind rounded anterolateral corners. Axis very convex, approximately semi-circular in transverse section; axis forming 38% of maximum pygidial width at anterior margin of most complete specimen, tapering evenly backwards, not reaching posterior margin; posterior end of axis declining and ill defined, sometimes passing into slight tapering axial ridge. First axial ring well defined by sinuous ring furrow; six or seven further axial rings defined by thin sinuous ring furrows each of which is more steep anteriorly than posteriorly; terminal piece. Pleural lobes gently convex, without border. Sutural furrows very faint or indistinguishable; up to six pleural furrows distinguishable, wide, curved, extending almost to margin of pygidium, all except the first lagging progressively further behind corresponding axial rings; pleural furrows inclined obliquely backwards from axial furrows, the posterior ones progressively more so. Outer surface smooth, but one specimen shows faint traces of terraced lines on pleural lobes, and another shows terraced lines on axis.

Pygidium Type 2

(Pl. 4, fig. 17)

Three specimens differ from the above description in being more elongated transversely (ratio of maximum width to length 1·7 : 1 and 2·2 : 1 in two specimens), with a less convex axis, the oblique furrows being apparently fewer (only four observed on the only specimen with well-preserved pleural lobes) and directed initially more transversely away from axial furrows.

Pygidium Type 3

(Pl. 4, figs. 14, 18, 19)

DESCRIPTION. Outline imperfectly known, apparently sub-semicircular. Axis very convex, approximately semicircular in transverse section, apparently tapering only slowly for much of its length, not reaching posterior margin. Axis with 8 rings in best-preserved specimen. Pleural lobes gently convex; in some cases a barely perceptible distal change in slope forms an incipient border; up to 8 pleurae distinguishable; pleurae not lagging behind axial rings. Sutural furrows well marked, relatively thin and faint proximally but becoming stronger distally where they reach beyond ends of pleural furrows almost to pygidial margin behind raised distal ends of posterior pleural bands; pleural furrows narrower and more transversely directed than in Type 1; anterior pleural bands narrower (exsag.) than posterior bands along most of their length except towards margin where pleural furrows turn obliquely back before dying out.

A single specimen differs from the above description in being more transversely elongated and in having a wide tapering axis.

MEASUREMENTS OF PROETIDAE.

Cranidium.

1 = sagittal length of glabella (normal projection)
2 = sagittal length of cranidium (projected as 1)
3 = sagittal length of occipital ring (projected as 1)
4 = sagittal length of anterior border (projected normal to sagittal length of pre-glabellar area)
5 = sagittal length of pre-glabellar field (projected as 4)
6 = maximum width of glabella
7 = maximum width (tr.) of occipital ring
8 = mid-point of occipital furrow to distal end of S_1 (exsag.) (projected as 1)
9 = mid-point of occipital furrow to distal end of S_2 (exsag.) (projected as 1)
10 = mid-point of occipital furrow to distal end of S_3 (exsag.) (projected as 1)

11 = transverse separation of distal ends of S_1
12 = transverse separation of distal ends of S_2
13 = transverse separation of distal ends of S_3

N.B. When the glabellar furrow does not reach the axial furrow the ' distal end ' in 8–10 and 11–13 is the point where the projection of the glabellar furrow along its distal length meets the axial furrow.

Variates		1	2	3	4	5	6	7	8	9	10	11	12	13
Individual specimens														
Type 1		1·1	1·5	0·25	0·15	0·3	0·75	0·65?	—	—	—	—	—	—
		1·2	1·65	0·25	0·1	0·3	1·0	—	0·35	0·55	0·65	0·95	0·8	0·7
	*	1·35	1·7	0·25	0·15	0·25	0·6	—	—	—	—	—	—	—
		1·85	2·35	—	0·55[a]	—	1·2	—	—	—	—	—	—	—
		2·25	2·9	0·45	0·65[a]	—	1·35	—	—	—	—	—	—	—
	*	2·3	3·0	0·5	0·3	0·35	1·75	1·6	0·6	1·0	—	1·65	1·5	—
	*	2·7	3·45	0·55	0·3	0·45	2·0?	—	0·75	1·25	1·6	1·9?	1·6	1·45
		3·4	4·25	0·6	0·5	0·45	—	—	—	—	—	—	—	—
Type 2?	*	1·95	2·6	0·35	0·3	0·45	1·1	—	0·6	0·85	1·05	1·0	0·85	0·85
		3·55	4·45	0·6	0·4	0·55	2·35	—	1·2	1·6	—	2·05	1·9	—
Type 2	*	0·8	1·1	0·1	0·2	0·2	0·6	—	0·25	0·35	0·45	0·6	0·55	0·55
	*	0·95	1·3	0·1	0·2	0·3	—	—	0·2	0·4	—	0·65	0·6	—
		—	—	—	0·2	0·35	—	—	—	—	—	1·05	0·95	0·85
	*	1·9?	2·5?	—	0·25	0·35	—	—	0·5	0·8	1·0	1·45	1·35	1·3
	*	2·05	2·8	—	0·35	0·5	—	—	0·5	0·95	—	1·5	1·35	—

[a] value for 4+5.

Hypostome (lengths projected normal to sagittal length).

1 = sagittal length
2 = anterior margin to posterior furrow (sag.)
3 = mid-point of anterior margin to position of minimum width (exsag.)
4 = width at anterior wings
5 = minimum width
6 = maximum width opposite posterior lobe of middle body
7 = minimum width of middle body
8 = maximum width of posterior lobe of middle body

Variates	1	2	3	4	5	6	7	8
Individual specimens	1·05	0·95	0·4	0·85?	0·6	0·7	0·45	0·6
	2·3	2·1	1·25	—	1·4	1·45	1·0	1·15
	2·8	2·55	1·55	—	—	—	—	—

Pygidium (lengths projected on to plane of margin).

1 = sagittal length excluding half-ring
2 = articulating furrow to ring furrow behind 5th axial ring (sag.)
3 = maximum width
4 = width of axis at anterior margin

5 = width of axis at ring furrow behind 5th axial ring
6 = score of 4th pleural furrow on scale of distal ends of ring furrows (articulating furrow counted as 1)
7 = width (perpendicular to length of pleura) of anterior band of 4th pleura at mid-length of pleura (projected normal to pleura)
8 = width (perpendicular to length of pleura) of posterior band of 4th pleura at mid-length of pleura (projected as 7)

Variates	1	2	3	4	5	6	7	8
Individual specimens								
Type 1	2·3	—	*(3·55)*	1·0	—	—	—	—
	5·4	2·85	7·7?	2·9	1·9	4·8	—	—
*	5·6	2·9	—	—	—	4·7?	—	—
Type 2	2·15	1·0	4·75?	1·45	0·9	5·0	—	—
*	2·7	1·5	4·7?	—	—	—	—	—
Type 3	1·25	0·7	2·4	0·6	0·35	4·2	—	—
	—	—	—	1·35?	0·95	4·3	0·19	0·23
	3·3	—	*(4·6)*	—	1·0	4·3	0·16	0·24
*	3·7	2·0	—	—	—	4·2	0·21	0·27

Remarks on Proetidae. Analysis of the proetid material is difficult. Of the three morphological types of pygidia which can be distinguished, Types 1 and 2 differ mainly in their width-relations and variation in this character may prove with larger collections to be continuous between the two morphotypes, while Type 3 differs considerably from both the others in segmentation and in the nature of the pleurae. The three pygidial morphotypes may, therefore, reduce to two basic types. Among cranidia also, two main morphotypes may be recognized, but their distinction is difficult and doubtfully objective. Provisionally, though, it may be accepted that both cranidia and pygidia show two morphotypes. On the other hand it is not possible to distinguish two types of proetid hypostome among the four available specimens, while the numerous proetacean free cheeks cannot even be separated with certainty into proetid and otarionid.

Of the two proetid cranidial morphotypes, Type 1 may be referable to *Proetidella* (see Dean 1963 : 243), a genus which Whittington (1966 : 81) has recently considered a synonym of *Astroproetus*. Type 2 would seem on current taxonomic practice to belong to a different, apparently undescribed, genus, but the possibility cannot be excluded that it represents a different morph of the same species as Type 1. There is no evidence as to association of the two (or three) pygidial morphotypes with cranidia.

Family **OTARIONIDAE** R. & E. Richter 1926

Genus ***OTARION*** Zenker 1833

Type species. *Otarion diffractum* Zenker 1833, by subsequent designation of R. & E. Richter (1926 : 95).

Otarion megalops (M'Coy, 1846)

(Pl. 5, figs. 1–5, 7–13, 15–19, 21, 22, ?20)

1846 *Harpes* (?) *megalops* M'Coy : 54, pl. 4, fig. 5.
1967 *Otarion megalops* (M'Coy, 1846) ; Whittington & Campbell : 461, pl. 19, figs. 1–14, 16.

HOLOTYPE. Internal mould of cranidium, G 110 : 1967/3, figured by M'Coy, 1846, pl. 4, fig. 5, from Upper Llandovery of Boocaun, near Cong, County Galway, Eire.

DESCRIPTION (of Keisley material). *Cranidium*: Sagittal and transverse convexity strong; glabella with strong independent convexity. Pre-glabellar field long, convex in profile, sloping down forwards as a continuation of slope of anterior part of glabella. Anterior border furrow broad; anterior border convex in profile and nearly horizontally disposed. Relative dimensions of glabella are summarized in quoted measurements. Glabella broadly rounded in front (see also ' Remarks ' below). Basal glabellar lobes relatively small, delimited axially by furrows deeper than adjacent parts of axial furrows. A slight inward thickening of axial furrows shortly in front of basal lobes may represent S_2. Palpebral lobes long, reaching back almost to mid-length of basal glabellar lobes. Anterior branches of facial suture diverging variably anteriorly in outwardly convex curves. From front end of palpebral lobe a vague ridge (? eye-ridge) flanked externally by a shallow groove runs obliquely forwards to axial furrow at front of glabella. Dorsal surface smooth; axial tubercle on occipital ring.

Free cheek: Not identified.

Hypostome: A single large hypostome is tentatively associated with the cranidium of *O. megalops*. It is too incomplete to warrant detailed description but is similar to one of the otarionid hypostomes from the Silurian of Maine described by Whittington & Campbell (1967 : 464, pl. 7, figs. 21–22).

Pygidium: Outline transversely elongated (ratio of maximum width to length about 2·2 : 1 in two specimens), evenly rounded posteriorly. Axis forming about 25% and 30% of maximum width at anterior margin in two specimens, tapering sharply to narrow rounded termination, not reaching posterior margin, not strongly convex. Axis with 6 or 7 axial rings and small terminal piece; anterior ring furrows branch over axial line. Pleural lobes nearly flat; in two specimens out of three a faintly raised border; 5 (?6) pleurae visible, the first directed initially transversely away from axial furrows, subsequent pleurae directed increasingly backwards from axial furrows; pleurae not lagging behind axial rings. Sutural furrows relatively narrow proximally, becoming stronger distally where they reach beyond ends of pleural furrows almost to pygidial margin behind raised distal ends of posterior pleural bands. Pleural furrows broader (exsag.) than sutural furrows. Anterior pleural bands as wide (exsag.) as posterior bands adjacent to axial furrows, widening outwards to become wider than parallel-sided posterior bands. Outer surface smooth but axial rings bear sagittal tubercles.

MEASUREMENTS.

Cranidium

1 to 7 as for Proetidae (p. 218)
8 = minimum width of central lobe of glabella
9 = transverse separation of axial furrows at distal ends of S_1
10 = mid-point of occipital furrow to distal end of S_1 (exsag.) (projected as 1)

Variates		1	2	3	4	5	6	7	8	9	10
Individual specimens	*	0·65	0·9	0·15	0·15	0·15	—	—	—	0·4	0·1
		0·7	—	0·15	—	—	0·5	—	0·2	0·5	0·15
		1·05	1·5	0·15	0·15	0·3	0·7	—	0·35	0·6	0·35
		1·2	1·75	0·25	0·25	0·25	1·0	—	0·45	0·75	0·35
		1·25	1·6	0·2	0·15	0·35	0·95	0·85	0·5	0·75	0·4
	*	1·5	2·05	0·25	0·2	0·4	1·25	1·05	0·75	1·05	0·55
	*	1·5	2·2	0·2	0·25	0·5	1·4?	1·15?	0·7	1·1?	0·65
	*	1·8	2·6	0·35	0·35	0·5	1·4	1·25?	0·6?	1·2?	0·5
	*	1·85	2·6	0·25	0·3	0·5	1·75	1·45	0·85	1·5	0·6
megalops topotypes		**2·9**	**3·85**?	**0·55**	—	**0·75**?	**2·8**	—	**1·55**?	**2·1**	**1·1**
		3·1	—	0·55	—	—	2·85	2·4	1·5	2·25	1·3
		3·35	4·6	0·6	0·5	0·95	3·0	—	1·55	2·25	1·3

Pygidium

1 to 8 as for Proetidae (p. 219)

Variates		1	2	3	4	5	6	7	8
Individual specimens	*	0·95	0·55	(*2·15*)	0·55	0·35	4·2	0·07	0·07
		1·35	0·75	(*3·05*)	0·75	0·45	4·4	0·12	0·10
		1·35	0·8	3·0	0·9	0·4	4·6	0·12	0·12

REMARKS. Two cranidia (It 5049 illustrated on Pl. 5, fig. 22; the other fragmentary) differ from other Keisley specimens in having a less inflated glabella with short (exsag.) basal lobes and tapering forwards to a sub-triangular preglabellar furrow, features which suggest comparison with *O. trigoda* Warburg sp. (1925 : 190, pl. 5, figs. 38–39).

Comparison of the Keisley cranidia with the original topotype material of M'Coy's species (redescribed by Whittington & Campbell 1967 : 461, pl. 19, figs. 1–11) is made difficult by the larger size of the Irish specimens. The effect of the size difference may in principle be overcome, on the assumption that the size eigenvector of the Keisley specimens would not change significantly at sizes larger than the largest cranidium in the sample, by comparisons of the scores of the Keisley and Irish specimens on the shape eigenvectors of the Keisley sample. However, the small size of the latter sample (7 complete specimens if variate 7 is excluded) and the fact that several of the specimens are distorted (albeit slightly) both affect adversely the accuracy of the sample estimates of the eigenvectors, and, when considerable size extrapolation is involved (from Keisley to Irish specimens), inaccuracy in the estimated size eigenvector will introduce a size element into intended shape comparisons along sample shape eigenvectors. Nevertheless, with all its limitations and inaccuracies, plotting of the specimens along the Keisley shape eigenvectors is a considerably better method of bridging the size gap between the two samples than either an intuitive assessment of changing cranidial proportions or the comparison of photographs enlarged to the same size, for the first of these alternatives is subjective as well as being excessively difficult while the second is illegitimate in that it takes no account of changing proportions. The scores of the two most complete Irish specimens (variate 4 being estimated on the holotype) on the second eigenvector of the Keisley 9-variate variance-covariance matrix almost straddle the spread of Keisley values, but for both the third and fourth eigenvectors the Irish specimens lie beyond the Keisley range (Text-fig. 4). The direction cosines of the maximum shape difference between the two samples relative to the Keisley size eigenvector for variates 1, 2, 3, 4, 5, 6, 8, 9 and 10 are (0·39, −0·01, 0·27, −0·17, −0·02, −0·01, 0·35, −0·66, 0·43). The Irish specimens may therefore, when allowance is made for the size difference, have glabellas which are narrower at the distal ends of S1 and somewhat longer, with

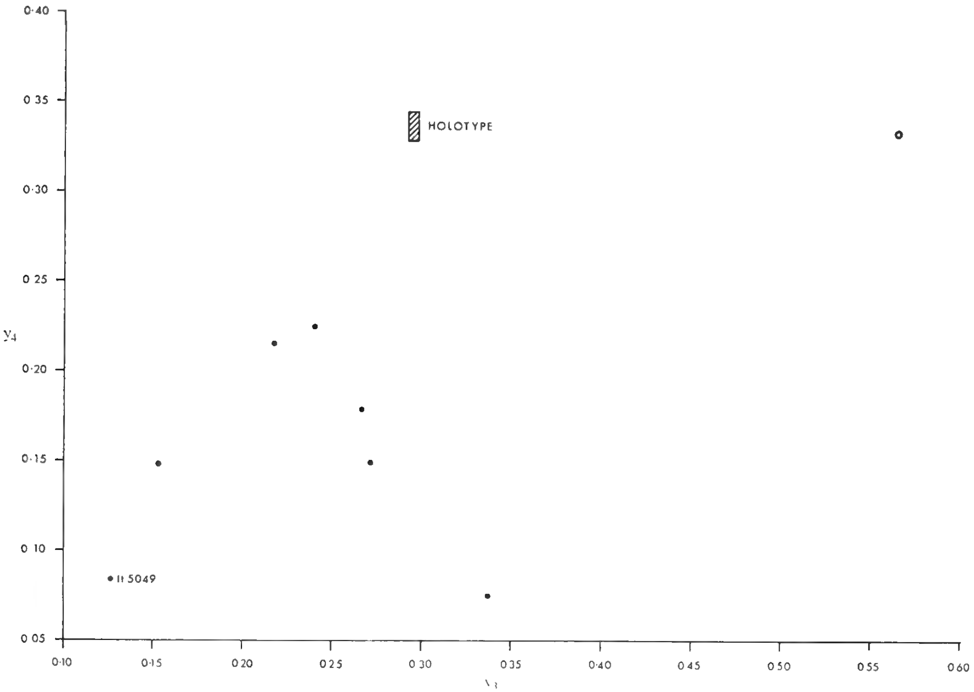

FIG. 4. Cranidia of *Otarion megalops* from Keisley (closed circles) and Ireland (holotype indicated; open circle is another topotype) plotted on the third (y_3) and fourth (y_4) eigenvectors of the variance-covariance matrix of the Keisley specimens. Transformed scale units correspond to original measurements in mm. See text for further explanation.

somewhat longer and narrower (tr.) basal lobes. It is interesting that, relative to y_3 and y_4, specimen It 5049 differs from other Keisley specimens in a direction opposite to that in which the Irish specimens differ; there appears, though, to be no reason for separating it from the rest of the sample.

An external mould of a cranidium on the same block as the holotype of *O. megalops* shows that the outer surface of the glabella, and possibly also of the pre-glabellar field, of the Irish species is finely tuberculate, in contrast to the smooth outer surface of the Keisley specimens.

In summary, accurate comparison of the Keisley specimens with *O. megalops* is not possible because of the size discrepancy, but such limited analysis as is possible indicates relatively slight differences and the Keisley material is referred to M'Coy's species. Attribution of the Keisley pygidia to *O. megalops* is provisional.

Family **AULACOPLEURIDAE** Angelin 1854

Genus ***AULACOPLEURA*** Hawle & Corda 1847

Type species. *Arethusa Koninckii* Barrande 1846 by monotypy.

Aulacopleura sp.

(Pl. 5, fig. 23)

A single fragmentary cranidium shows a short tapering glabella reaching a little over half the length of the cephalon and with strongly cut-off basal lobes, a thin eye-ridge, long horizontally disposed pre-glabellar field, broad anterior border furrow, and narrow upturned anterior border. The entire surface except for the furrows and the crest of the anterior border is covered with rounded tubercles about 0·125 mm. across at their bases.

The specimen is too poor for useful comparisons to be made. The strongly tuberculate surface is unusual in *Aulacopleura*.

Measurements.

sagittal length of pre-occipital glabella (normal projection), 2·6
mid-point of occipital furrow to anterior margin of cranidium (sag.) (projected as above), 5·0
mid-point of occipital furrow to distal end of S_1 (exsag.) (projected as above), 1·15

Family **CALYMENIDAE** Burmeister 1843

Genus ***FLEXICALYMENE*** Shirley 1936

Type species. *Calymene Blumenbachii* var. *Caractaci* Salter 1865 by original designation of Shirley (1936 : 395).

Flexicalymene sp.

(Pl. 6, figs. 1–17)

DESCRIPTION. *Cranidium* : Glabella reaches further forward than cheeks. No pre-glabellar field. Anterior border slopes slightly up forwards relative to tangent plane to posterior part (i.e. that opposite L_1 and L_2) of pre-occipital glabella ; anterior border slightly concave in section near border furrow, becoming convex towards margin. Well-developed anterior pit opposite frontal lobe of glabella ; faint transverse ridge sometimes observable across axial furrow behind anterior pit. Palpebral lobe opposite S_2 and L_2 in largest forms, relatively further forward in smaller forms. Relative dimensions of glabella and disposition of glabellar furrows are summarized in quoted measurements. S_3 faint.

Free cheek : Apparently almost vertically disposed. Visual surface not known ; base of eye passing gradually into cheek which has slight independent convexity. Border furrow broad. Border slopes outwards from steep inward (horizontal in life) slope adjoining border furrow ; border slightly convex in section, widening forwards along cheek margin. Doublure slightly narrower than border (and also widening forwards along cheek margin), disposed almost parallel to overall surface of cheek, slightly concave dorsally ; outer surface of doublure apparently smooth.

Hypostome : Anterior margin convex, posterior margin embayed. Minimum width at about mid-length. Middle body strongly convex, highest at about mid-length of anterior lobe ; middle body vaguely delimited anterolaterally, separated from anterior border axially by short (tr.) depression, more sharply defined posteriorly where posterior furrow reaches nearly to posterior margin axially ; middle body narrowest at about mid-length. Middle furrow continuous across axial line, running close and almost parallel to lateral-posterior furrow, cutting off narrow sub-crescentic posterior lobe with slight independent convexity. Anterior furrow vague ; anterior border turned almost vertically up (ventrally) and continued dorsolaterally into anterior wing which bears dorsolaterally directed sub-circular process. Lateral border narrow and high opposite mid-length of middle body, widening and flattening behind posterior wing towards pointed posterior prolongation. Doublure vertical opposite midlength of middle body, becoming overturned near posterior wing which is developed as a transverse ridge on dorsal surface of doublure. Outer surface of hypostome (except apparently anterior part of middle body) faintly granular.

Thoracic segment: Pleura with sharp transversely directed pleural furrow turning slightly back just before dying out near spatulate pleural tip. Posterior band considerably wider than anterior band; anterior band widening rapidly at its distal end towards pleural tip. Doublure of posterior pleural margin long, its inner margin sub-parallel to pleural furrow and then curving round parallel to tip of pleura; doublure of anterior pleural margin short, terminating abruptly and shortly inwards; doublure flat posteriorly and laterally, raised (ventrally) to form vincular notch outside anterior termination.

Pygidium: Width of axis at anterior margin forming 34·6, 39·1, 41·5 per cent of maximum pygidial width in three specimens. Axis with 5 or 6 rings defined by ring furrows and traces of at least one further ring indicated by row of tubercles. Pleural lobes with 5 distinguishable segments. Pleural furrows deeper and more curved than interpleural furrows (on internal moulds pleural furrows deep and conspicuous, interpleural furrows very faint, particularly proximally). Anterior pleural bands nearly parallel-sided, widening towards distal ends; posterior bands wider than anterior bands except at distal ends where widths of bands become sub-equal; both bands equally but not greatly convex. Doublure narrow, inclined upwards inwardly; outer surface of doublure apparently smooth.

Dorsal surface: Entire dorsal surface (except furrows) bears tubercles, closest and strongest around the periphery of the complete integument, i.e. at margins of anterior border and free cheeks, at tips of pleurae, and around lateral and posterior margins of pygidium. The tubercles are associated with approximately parallel-sided pores which also are strongest peripherally where they can be seen to pierce the integument. In pygidia about 1·5 mm. long the pleural tubercles form a single row on each of the anterior and posterior pleural bands; in slightly larger pygidia there is a single row on the anterior band and two rows roughly alternating in position on the posterior band; in the largest pygidia additional tubercles mask this arrangement.

MEASUREMENTS.

Cranidium (all lengths projected as 1)

1 = sagittal length of cranidium (normal projection)
2 = sagittal length of anterior border (measured on internal mould to vertical anterior margin of glabella)
3 = sagittal length of pre-occipital glabella (see 2)
4 = sagittal length of occipital ring
5 = mid-point of occipital furrow to posterior margin of eye (exsag.)
6 = mid-point of occipital furrow to anterior pit (exsag.)
7 = mid-point of occipital furrow to distal end of S_3 (exsag.)
8 = mid-point of occipital furrow to distal end of S_2 (exsag.)
9 = mid-point of occipital furrow to distal end of S_1 (exsag.)
10 = transverse separation of anterior pits
11 = transverse separation of distal ends of S_3
12 = transverse separation of distal ends of S_2
13 = transverse separation of distal ends of S_1
14 = width of glabella (maximum) across L_1

N.B. When the glabellar furrow does not reach the axial furrow the ' distal end ' in 7–9 and 11–13 is the point where the projection of the glabellar furrow along its length meets the axial furrow.

Variates		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Individual specimens	*	1·55	0·2	1·1	0·2	0·55	0·85	0·7	0·55	0·4	0·65	—	0·65	0·65	0·7
		1·6	0·2	1·2	0·25	0·5	0·85	0·75	0·55	0·35	0·85	0·85	0·9	0·9	0·95
	*	2·95	0·5	1·95	0·5	0·95	1·5	1·3	1·15	0·75	1·5	1·55	1·65	1·75	1·85
	*	4·25	0·75	2·85	0·65	1·2	2·25	2·0	1·65	1·05	1·75	—	2·0	2·25	2·4

Hypostome (all lengths projected as 15)
15 = sagittal length (normal projection)
16 = overall length (exsag.)
17 = anterior margin to middle furrow (sag.)
18 = sagittal length of posterior lobe of middle body
19 = width of hypostome at posterior wings
20 = width of hypostome at anterior wings (excluding processes)
21 = minimum width of hypostome

Variates		15	16	17	18	19	20	21
Individual specimens		—	—	—	0·3	0·85	—	0·75
	*	1·3	—	1·0	0·25	0·95	1·2	0·85
	*	1·35	1·45	1·0	0·25	—	—	0·95
	*	2·35	—	1·85	0·4	—	2·25	—
		—	—	—	0·5	(*2·1*)	—	1·75
		2·9	3·15	2·35	0·45	—	2·65	1·8

Pygidium (all lengths projected as 22)
22 = sagittal length excluding half-ring (normal projection)
23 = 22 minus thickness of integument
24 = sagittal length of axis excluding half-ring
25 = articulating furrow to ring furrow behind 5th axial ring (sag.)
26 = maximum width minus thickness of integument
27 = width of axis at anterior margin
28 = width of axis at ring furrow behind 5th axial ring
29 = width (perpendicular to length of pleura) of anterior band of 2nd pleura at mid-length of pleura (projected normal to pleura)
30 = width (perpendicular to length of pleura) of posterior band of 2nd pleura at mid-length of pleura (projected as 29)
31 = score of sutural furrow behind 3rd pleura on scale of distal ends of ring furrows (articulating furrow counted as 1)

Variates		22	23	24	25	26	27	28	29	30	31
Individual specimens	*	—	1·35	—	0·95	2·55	1·0	0·5	0·12	0·12	—
	*	—	1·5	1·3	—	3·2	1·1	—	—	—	—
		2·65	2·55	2·3	1·55	—	1·55	1·25	0·18	0·19	4·2
	*	3·6	3·4	3·1	—	(*5·8*)	2·4	—	—	—	—
		—	4·35	3·7	—	—	3·2	2·1	—	—	4·0
	*	—	4·65?	4·0	—	—	2·8	—	—	—	—
	*	—	—	—	—	—	—	—	0·27	0·39	—

ONTOGENY. Two small cranidia are known, 1·55 mm. and 1·6 mm. long respectively (Pl. 6, figs. 10, 11, 14). In these specimens the glabella is parallel-sided, the frontal lobe is proportionately long, there is a strong axial occipital tubercle, and the anterior border bears many small tubercles (of which in the smaller specimen two situated shortly within the prolongations of the axial furrows are prominent); the larger specimen appears to have a fixigenal spine. The strong occipital tubercle is not distinguishable in a cranidium 2·95 mm. long.

REMARKS. Accurate comparison of the Keisley species must await quantitative description of topotype material of such species as *F. caractaci* (Salter) and *F. cobboldi* Dean (see Dean 1963 : 217, 218). The Keisley material, although well preserved and allowing detailed qualitative description of much of the exoskeleton, is not considered abundant enough to form the basis for the erection of a new species.

There are too few cranidia to show whether the variation in glabellar width is discontinuous, but in any case some of the narrower specimens appear to have suffered lateral compression.

Family **DALMANITIDAE** Vogdes 1890

Genus ***DALMANITINA*** Reed 1905

TYPE SPECIES. *Phacops socialis* Barrande, 1846 by original designation of Reed (1905b : 224).

Dalmanitina mucronata brevispina Temple, 1952

(Pl. 5, figs. 6, 14, 24–26)

1952 *Dalmanitina mucronata* (Brongniart) var. *brevispina* Temple : 14, pl. 2, fig. 2.
1952 *Dalmanitina mucronata* var. *brevispina* Temple ; Temple : 16.

HOLOTYPE. Internal and external moulds of pygidium, A 36372a,b figured by Temple 1952 : pl. 2, fig. 2, from basal Silurian, Watley Gill, Cautley, Yorkshire.

REMARKS. This subspecies was described qualitatively in 1952 on the basis of material from Yorkshire. Measurements of topotype material are given here together with measurements of specimens from Keisley. The two collections, however, are small, and both the quantitative distinction of the subspecies from *D. mucronata mucronata* and the identity of the Yorkshire and Keisley forms should be considered only provisional.

In Keisley specimens the surface is seen to bear small tubercles. The terminal pygidial spine is variable in length and not always thorn-like. Two protaspides are known.

MEASUREMENTS.

Cranidium (all lengths projected as 1)

1 = sagittal length of glabella (normal projection)
2 = sagittal length of occipital ring
3 = mid-point of occipital furrow to inner end of S_3 (exsag.)
4 = inner end of S_3 to mid-point of pre-glabellar furrow (exsag.)
5 = maximum length (exsag.) of palpebral lobe
6 = maximum width of glabella
7 = maximum width (tr.) of occipital ring

8 = maximum transverse separation of outer margins of palpebral lobes

9 = posteriormost point of outer margin of palpebral lobe to posterior margin of cheek in exsagittal line

10 = score of transverse projection of posteriormost point of outer margin of palpebral lobe on scale of distal ends of glabellar furrows (occipital furrow counted as 0)

Variates		1	2	3	4	5	6	7	8	9	10
Individual specimens		1·9	0·35	0·7	0·85	0·95	1·6	—	—	—	—
		2·8	0·45	1·0	1·35	1·1	2·15	*(1·25)*	—	0·55	—
	*	4·25	0·55	1·25	2·5	1·3	—	1·65	4·25	0·45	0·25
brevispina paratype		5·6	0·8	1·75	3·05	—	4·6	2·6	(6·9)	—	—

Pygidium

11 = sagittal length excluding half-ring but including terminal spine (normal projection)

12 = articulating furrow to ring furrow behind 6th axial ring (sag.) (projected as 11)

13 = maximum width

14 = width of axis at anterior margin

15 = width of axis at ring furrow behind 6th axial ring

16 = width (perpendicular to length of pleura) of anterior band of 4th pleura at mid-length of pleura (projected normal to pleura)

17 = width (perpendicular to length of pleura) of posterior band of 4th pleura at mid-length of pleura (projected as 16)

18 = score of sutural furrow behind 5th pleura on scale of distal ends of ring furrows (articulating furrow counted as 1)

Variates		11	12	13	14	15	16	17	18
Individual specimens		—	0·8	—	—	0·35	0·07	0·05	6·3
	*	3·15	1·55	3·2	1·05	0·65	0·15	0·13	6·2
	*	—	1·95	5·0	1·4	0·75?	0·21	0·19	6·1
		—	2·15	—	—	1·0	—	—	6·2
brevispina topotypes		**4·35+**	**2·4**	(**6·1**?)	**2·0**	**1·25**	**0·21**	**0·26**	**6·2**
		—	2·4	(6·7?)	2·0	1·2	0·24	0·27	6·1

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MALET STREET
LONDON, W.C.1

PLATE 1

Diacanthaspis sladensis (Reed 1905)

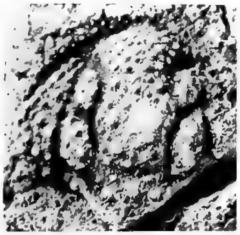
FIG. 1. Internal mould of cranidium, It 5001, × 7·5.
FIG. 2. Internal mould of cranidium, It 5002, × 7·5.
FIG. 3. Internal mould of cranidium, It 5003, × 7·5.
FIGS. 4, 5. Internal mould of cranidium in dorsal and anterior views, It 5004, × 10.
FIG. 6. Fragmentary internal mould of pygidium with nine pairs of marginal spines, It 5014, × 10.
FIG. 7. Internal mould of cranidium, It 5005, × 10.
FIG. 8. Internal mould of cranidium, A 52302, × 10.
FIG. 9. Internal mould of hypostome, It 5008, × 10.
FIG. 10. Internal mould of cranidium, It 5006, × 10.
FIG. 11. Latex cast of exterior of hypostome, It 5009, × 10.
FIG. 12. Internal mould of cranidium, It 5007, × 10.
FIG. 13. External mould of left free cheek, It 5010, × 10.
FIG. 14. Internal mould of Type 1 thoracic segment in anterodorsal view, It 5011, × 10.
FIG. 15. Internal mould of Type 2 thoracic segment in anterodorsal view, It 5013, × 10.
FIG. 16. Fragmentary internal mould of pygidium with eight pairs of marginal spines, It 5015, × 10.
FIG. 22. Internal mould of pygidium with eight pairs of marginal spines, It 5016, × 10.

Diacanthaspis sladensis (Reed 1905)

St. Martin's Cemetery Beds, Haverfordwest, Pembrokeshire

FIGS. 17, 18. Lectotype internal mould of cranidium in dorsal and anterior views, A 4646a (figured by Reed 1905a : pl. 4, fig. 8), × 10.
FIG. 19. Internal mould of hypostome, A 60382, × 10.
FIG. 20. External mould of doublure of right free cheek, A 60383, × 10.
FIG. 21. Syntype internal mould of pygidium with eight pairs of marginal spines, A 4645 (figured by Reed 1905a : pl. 4, fig. 11), × 10.


1 ×7·5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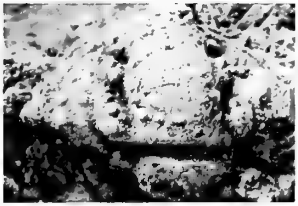
3 ×7·5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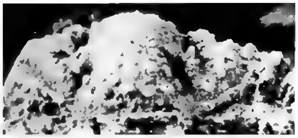
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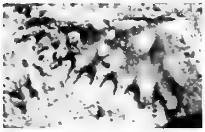
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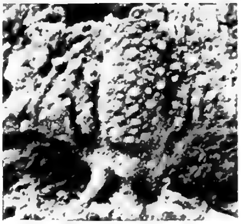
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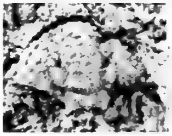
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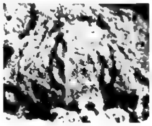
9 ×10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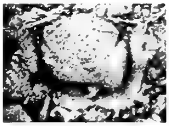
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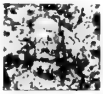
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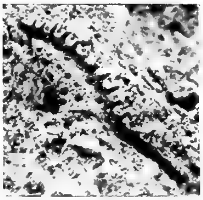
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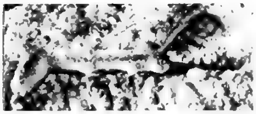
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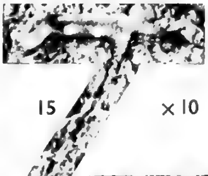
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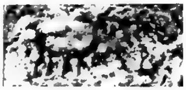
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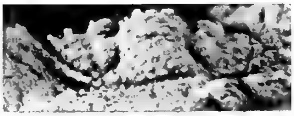
17 ×10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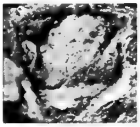
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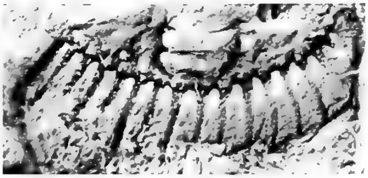
20 ×10


21 ×10


22 ×10

PLATE 2

Lichas laciniatus (Wahlenberg 1818)

FIG. 1. Internal mould of cranidium, It 5017, ×7·5.

FIGS. 2, 3. Internal mould of cranidium in anterior and dorsal views, It 5018, ×10.

FIGS. 4, 7, 8. Internal mould of cranidium in anterior, dorsal and left lateral views, It 5019, ×7·5.

FIGS. 5, 6, 9. Internal mould of cranidium in left lateral, anterior and anterodorsal views, It 5020, ×10.

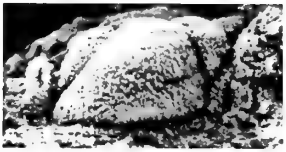
FIGS. 10, 13. Internal mould of left free cheek in dorsal and lateral views, It 5022, ×10.

FIG. 11. Internal mould of smallest cranidium, It 5012, ×15.

FIG. 12. Internal mould of cranidium, It 5021, ×10.

FIG. 14. Latex cast of exterior of left librigenal spine, It 5023, ×7·5.


1 ×7·5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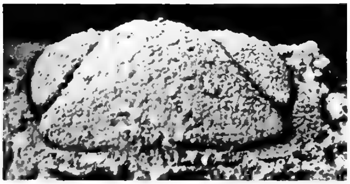
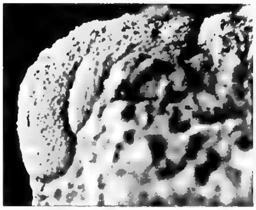
3 ×10

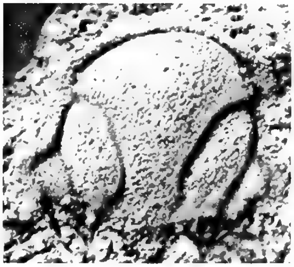

4 ×7·5


5 ×10

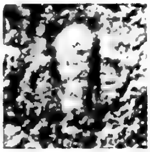

6 ×10


7 ×7·5


8 ×7·5


9 ×10


10 ×10


11 ×15


12 ×10


13 ×10


14 ×7·5

PLATE 3

Lichas laciniatus (Wahlenberg 1818)

FIG. 1. Internal mould of distorted hypostome, It 5024, ×7·5.

FIG. 2. Internal mould of hypostome, dissected posteriorly to show doublure and axial boss, It 5025, ×10.

FIG. 3. Internal mould of hypostome, It 5026, ×10.

FIG. 4. Fragmentary internal mould of pygidium, It 5027, ×7·5.

FIG. 6. Latex cast of exterior of almost complete pygidium, It 5028, ×10.

FIG. 7. Fragmentary internal mould of pygidium, It 5029, ×7·5.

FIG. 8. Fragmentary internal mould of pygidium, It 5030, ×7·5.

FIG. 9. Internal mould of small pygidium, It 5031, ×10.

FIG. 10. Internal mould of portion of thoracic segment, It 5032, ×7·5.

Lichas laciniatus (Wahlenberg 1818)

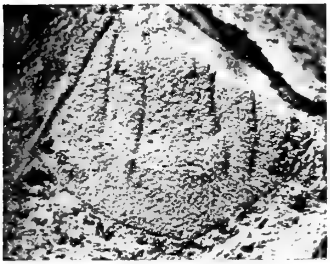
Dalmanitina Beds, Bestorp, Mösseberg, Västergötland, Sweden.

FIG. 5. Holotype internal mould of pygidium, ar. 1 (figured by Wahlenberg 1818: pl. 2, fig. 2*), ×3.

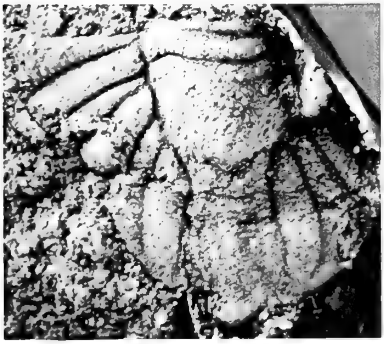

1 ×7·5


2 ×10


3 ×10


4 ×7·5


5 ×3


6 ×10


7 ×7·5


8 ×7·5


9 ×10

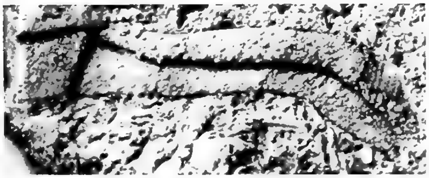

10 ×7·5

PLATE 4

Proetidae, **Cranidium** Type 1

FIGS. 1, 2. Internal mould in dorsal and lateral views, It 5033, ×7·5.
FIG. 3. Internal mould, It 5034, ×10.
FIG. 4. Internal mould, It 5035, ×10.

Proetidae, **Cranidium** Type 2

FIGS. 5, 6. Internal mould in dorsal and lateral views, It 5036, ×7·5.
FIG. 7. Fragmentary internal mould, It 5037, ×10.
FIG. 8. Distorted internal mould, It 5038, ×10.
FIG. 12. Internal mould, It 5039, ×10.

Proetidae, **Hypostome**

FIG. 9. Latex cast of exterior, It 5040, ×10.
FIG. 10. Internal mould, It 5041, ×10.
FIG. 11. Small internal mould, It 5042, ×10.

Proetidae, **Pygidium** Type 1

FIG. 13. Latex cast of exterior, It 5043, ×5.
FIG. 20. Internal mould, It 5048, ×10.

Proetidae, **Pygidium** Type 3

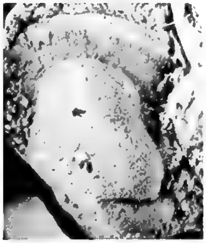
FIG. 14. Latex cast of exterior, It 5044, ×7·5.
FIG. 18. Fragmentary internal mould, It 5046, ×7·5.
FIG. 19. Fragmentary internal mould, It 5047, ×7·5.

Proetidae and/or Otarionidae, **Free cheeks**

FIG. 15. Internal mould, It 5050, ×10.
FIG. 16. Internal mould, It 5051, ×10.

Proetidae, **Pygidium** Type 2

FIG. 17. Internal mould, It 5045, ×7·5.


1 ×7·5


2 ×7·5


3 ×10

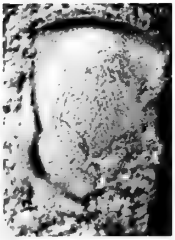

4 ×10


5 ×7·5


6 ×7·5


7 ×10


8 ×10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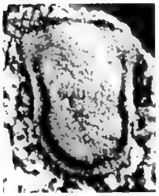
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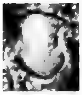
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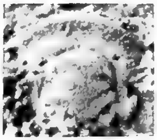
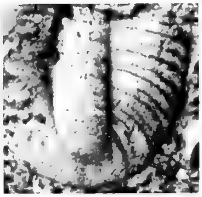

12 ×10


13 ×5


14 ×7·5


15 ×10


16 ×10


17 ×7·5


18 ×7·5


19 ×7·5

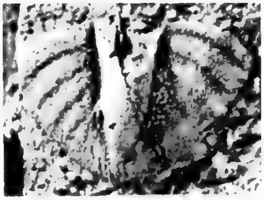

20 ×10

PLATE 5

Otarion megalops (M'Coy 1846)

FIGS. 1–4, 9. Internal mould of cranidium in dorsal, oblique, anterior, left lateral and anteroventral views, It 5054, × 10.

FIG. 5. Internal mould of referred pygidium, It 5052, × 10.

FIGS. 7, 8, 10–12. Internal mould of cranidium in dorsal, oblique, anteroventral, anterior and right lateral views, It 5056, × 10.

FIG. 13. Internal mould of referred pygidium, It 5053, × 10.

FIGS. 15–19. Internal mould of cranidium in dorsal, oblique, anteroventral, anterior and left lateral views, It 5055, × 10.

FIG. 20. Internal mould of referred hypostome, It 5058, × 10.

FIG. 21. Internal mould of cranidium, It 5057, × 10.

FIG. 22. Internal mould of cranidium, It 5049, × 10.

Dalmanitina mucronata brevispina (Temple 1952)

FIG. 6. Latex cast of exterior of cranidium, It 5060, × 10.

FIG. 14. Internal mould of pygidium with damaged or teratological pleurae in oblique lateral view, It 5061, × 7·5.

FIG. 24. Latex cast of exterior of pygidium with long axial spine, It 5062, × 10.

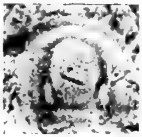
FIG. 25. Latex cast of exterior of pygidium in oblique lateral view, It 5063, × 10.

FIG. 26. Internal mould of pygidium, It 5064, × 7·5.

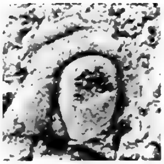
Aulacopleura sp.

FIG. 23. Fragmentary internal mould of cranidium, It 5059, × 7·5.


1 ×10


7 ×10


15 ×10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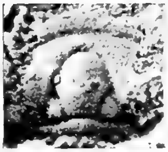
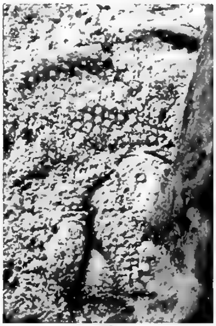

22 ×10


8 ×10


16 ×10

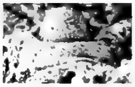

23 ×7·5


2 ×10


9 ×10


17 ×10


3 ×10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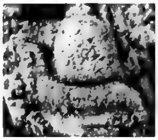
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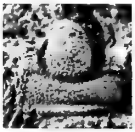
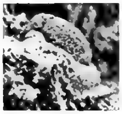
24 ×10


11 ×10


4 ×10


19 ×10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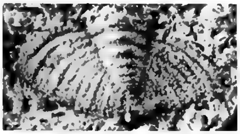
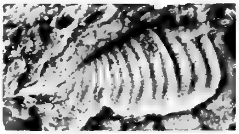

5 ×10


13 ×10


20 ×10


25 ×10


6 ×10


14 ×7·5

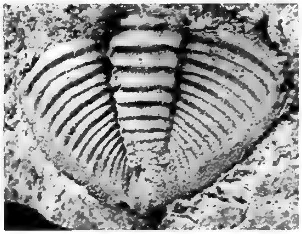

26 ×7·5

PLATE 6

Flexicalymene sp.

FIG. 1. Latex cast of exterior of cranidium, It 5065, × 7·5.

FIGS. 2, 6. Internal mould of cranidium in dorsal and lateral views, It 5066, × 7·5.

FIG. 3. Latex cast of exterior of same cranidium as figs. 2, 6, It 5066, × 7·5.

FIG. 4. Internal mould of right free cheek, It 5069, × 5.

FIG. 5. Internal mould of hypostome, It 5070, × 5.

FIG. 7. Internal mould of right pleura in lateral view (anterior of specimen to right of figure), It 5073, × 7·5.

FIG. 8. Internal mould of pygidium, It 5075, × 7·5.

FIG. 9. Latex cast of exterior of hypostome, It 5071, × 10.

FIGS. 10, 11. Internal mould of small cranidium in dorsal and anterior views, showing strong occipital tubercle, It 5067, × 10.

FIG. 12. Internal mould of right pleura in lateral view, dissected to show doublure (anterior of specimen to right of figure), It 5074, × 5.

FIG. 13. Internal mould of hypostome, It 5072, × 10.

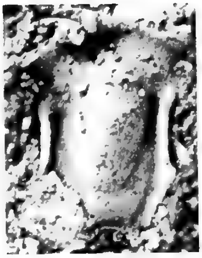
FIG. 14. Internal mould of small cranidium with narrow glabella, It 5068, × 10.

FIG. 15. Latex cast of exterior of pygidium in slightly lateral view, It 5076, × 7·5.

FIGS. 16–17. Internal mould of pygidium and latex cast of exterior of same specimen, It 5077, × 10.


1 ×7·5

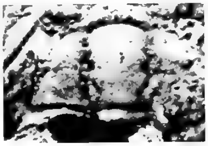

5 ×5


9 ×10


13 ×10


2 ×7·5


6 ×7·5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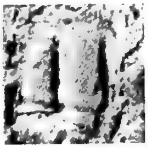
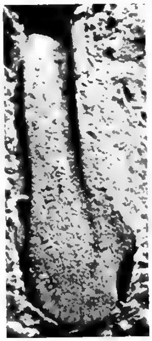

14 ×10

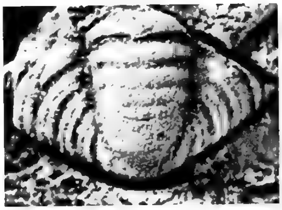

11 ×10


15 ×7·5


3 ×7·5

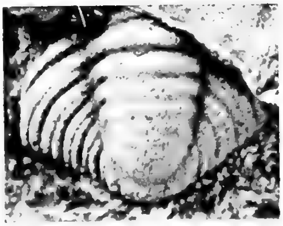

7 ×7·5


12 ×5


16 ×10


4 ×5


8 ×7·5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DINOFLAGELLATE CYSTS AND ACRITARCHS FROM THE BASAL KIMMERIDGIAN (UPPER JURASSIC) OF ENGLAND, SCOTLAND AND FRANCE

G. U. GITMEZ

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GEOLOGY Vol. 18 No. 7
LONDON: 1970

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BY

GULDEN USMAN GITMEZ

The University, Nottingham

Pp. 231–331; 14 *Plates*, 34 *Text-figures*

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DINOFLAGELLATE CYSTS AND ACRITARCHS FROM THE BASAL KIMMERIDGIAN (UPPER JURASSIC) OF ENGLAND, SCOTLAND AND FRANCE

By G. U. GITMEZ

CONTENTS

SYNOPSIS

The morphology of fossil dinoflagellate cysts and acritarchs from the base of the Kimmeridgian (Baylei Zone) of England, Scotland and France is described. The cysts are shown to fall into three broad groups—" proximate ", " chorate " and " cavate "—which are interpreted as indicating different modes of formation.

Two new genera and twelve new species, together with three new subspecies are proposed and described. The diagnosis of the genera *Cryptarchaeodinium* (Deflandre) and *Staplinium* (Jansonius), the species *Gonyaulacysta hyaloderma* (Deflandre) and *Leptodinium arcuatum* (Klement) are emended. The species *Hystrichosphaeridium capitatum* Cookson & Eisenack is transferred to the genus *Tenua* (Eisenack), and the species *Gonyaulacysta evitti* Dodékova to the genus *Occisucysta* gen. nov.

Seven species are recorded for the first time from Europe. Comparison is made with previously described specimens from Australia, France, Germany and England. Assemblages from the Kimmeridgian are found to be very close to the Upper Callovian and the Oxfordian assemblages of England and Normandy. A comparison with the Australian assemblages shows differences between the size of Australian and of Western European specimens.

I. INTRODUCTION

THE Kimmeridge Clay is seen in its typical facies in Dorset, the outcrop extending northwards into the southern Midlands of England. It is located above the Corallian and it is overlain by the Portland Sands and Portland Stone.

In France, beds of equivalent age are seen in the Boulonnais; the north-west and south-west of the Paris Basin ; Normandy ; and the Rhône Valley (Text-figure 1).

The Boulonnais is the nearest part of the European continent to the British Isles ; the exposures there are therefore of particular interest from the viewpoint of establishing international correlation. These beds have been subdivided by Ager (1963) into the Argiles de Moulin Wibert, Calcaires de Moulin Wibert, Grès de Châtillon and Schistes de Châtillon. The Argiles de Moulin Wibert are the lowest Jurassic strata exposed on this coast and form the core of the Crèche Anticline.

In Normandy and Le Havre, the Lower Kimmeridgian is only represented beneath the unconformable Cretaceous by clays and limestones with ammonites indicative of the Mutabilis, Cymodoce and Baylei Zones. At the junction between Kimmeridgian and Oxfordian, there is a thin bed of clay full of *Liostrea delta* Smith, comparable with that at Ringstead, Dorset.

Upper Jurassic rocks are known from a number of localities in the Hebridean region. In Scotland, on the Isle of Skye, beds of Kimmeridgian age are known only at Trotternish. Exposures on the coast, from Staffin Bay northwards, show Kim-

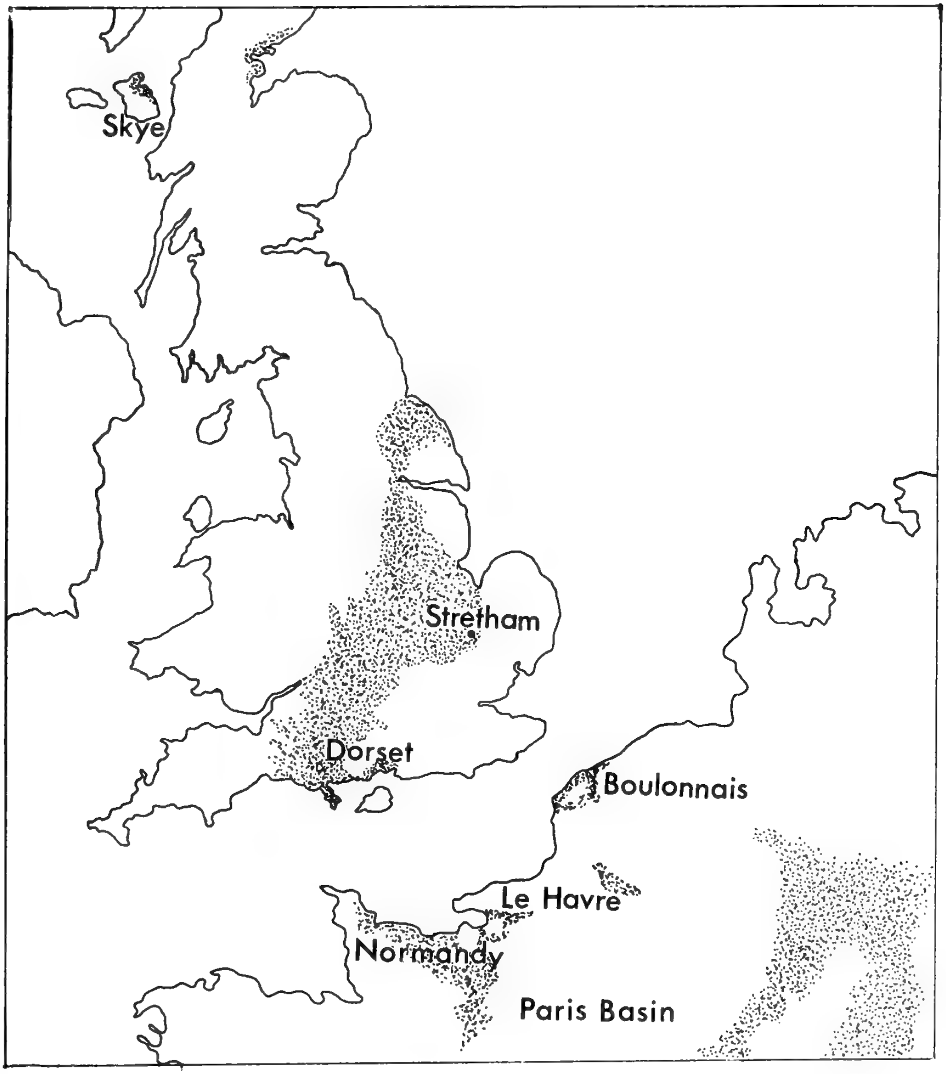

FIG. 1. Sketch map showing the Jurassic outcrops in England and Northern France, from which the samples were taken.

meridge Clay following the Corallian with little change in lithology. The ammonite fauna in the upper beds indicates the Baylei Zone.

Kimmeridgian microplankton were first described by Deflandre (1938); the first English assemblages were recorded by Downie (1957). Subsequently Lantz (1958) and Sarjeant (1960) gave incidental mention to Kimmeridgian forms.

Further research was considered necessary to increase our knowledge of the

Kimmeridgian microplankton. This is particularly so with respect to their potentiality as stratigraphical indicators in beds, whose subdivision and correlation present considerable difficulties. The plan of research adopted was to first of all examine assemblages from the type locality for the stage (Dorset), and then to examine comparative sections from regions to the north and south of this area, in order to assess the degree of lateral change in the assemblages.

This paper contains an account of the lowest zone (Baylei Zone) only. (The assemblages from higher zones will be described in a subsequent paper.)

Microplankton are here recorded for the first time from the Upper Jurassic of Scotland, the Boulonnais, Le Havre and the English Midlands.

Stage divisions of the Upper Jurassic : In 1962 the Jurassic system as a whole, and especially the Kimmeridgian–Portlandian boundary, was discussed at an International Colloquium held in Luxembourg. No firm decision was reached at this meeting, two alternative schemes being put forward. The first of the schemes was to retain the Kimmeridgian and the Portlandian in the sense of Arkell 1946; a second scheme visualized a short Kimmeridgian ending at the Gravesia Zone and followed by the Tithonian. The results of this meeting were discussed in papers published by D. V. Ager (1963), A. J. Lloyd (1964) and J. C. W. Cope, W. A. S. Sarjeant, D. A. E. Spalding and A. Zeiss (1963).

At a second meeting held in Luxembourg (1967), the problem of the Upper Jurassic stages was again discussed, but no firm decision was reached. For the present, it is here proposed to accept the Kimmeridgian in the original sense of d'Orbigny and of Arkell, i.e. commencing with the Baylei Zone and terminating with the Pallasioides Zone.

II. MATERIAL AND LOCALITY

The fossil microplankton assemblage here described were all obtained from the argillaceous facies of the Kimmeridge Clay. The samples consisted of either grey clay, shaly clay, black clay or argillaceous limestones. Seven samples were examined from Dorset, one sample from Cambridgeshire, and three samples from Staffin Bay, Isle of Skye, Scotland. French samples were taken from three parts of France: Normandy (one sample), Le Havre (two samples) and the Boulonnais (seven samples). The Dorset samples were collected by Dr. W. A. S. Sarjeant and Dr. J. C. W. Cope. The samples from Le Havre and Normandy and those from the Boulonnais were collected by Dr. W. A. S. Sarjeant under the guidance of M. Michel Rioult and Dr. D. V. Ager respectively. Samples of Kimmeridge Clay from Staffin Bay were collected by Dr. W. A. S. Sarjeant and Mr. D. Field.

Samples are numbered according to the system suggested by Dr. W. A. S. Sarjeant ; duplicate samples are stored in his collections (University of Nottingham).

All samples were collected from the Baylei Zone of Kimmeridgian.

1. OM 131—shaly clay, light olive grey in colour (5 Y 4/1) at the base of Kimmeridge Clay. *Liostrea delta* Bed, foreshore exposure immediately west of the slipway at Osmington Mills, Dorset.[1] (National grid reference : 734817).

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[1] Explanation of the samples colours are according to the "Rock Color Chart", produced by the Geological Society of America (1963) and based on the Munsell System.

2. OM 418—clay, greenish grey in colour (5 GY 6/1), from 10 ft. above Ringstead Coral Bed. Foreshore exposure, west of Osmington Mills, Dorset.

3. OM 419—clay, dark grey in colour (5 G 4/1), from 15 ft. above Ringstead Coral Bed. Foreshore exposure, west of Osmington Mills, Dorset.

4. OM 420—clay, light grey in colour (N 7), from 20 ft. above Ringstead Coral Bed. Foreshore exposure, west of Osmington Mills, Dorset.

5. HD 191—clay, light greenish grey in colour (5 GY 7/1), from 6 ft. below top of the Black Clay, Holworth, Dorset. (National grid reference : 763817).

6. RB 218—clay, dark greenish grey in colour (5 G 4/1), from between the Ringstead Waxy Clay and the Ringstead Coral Bed, Ringstead Bay, Dorset. (National grid reference : 757814).

7. RB 219—clay, medium light grey in colour (N 6), from the *Rhactorhynchia inconstans* Bed, Ringstead Bay, Dorset.

8. SC 444—clay, medium light grey in colour (N 6), from the Great Ouse River Board Pit, Stretham, Cambridgeshire. (National grid reference : 516743).

9. SS 625—shale, medium dark grey in colour (N 4), from 60 ft. above the second dolerite sill, Staffin Bay, east of Digg, Isle of Skye, Scotland. (National grid reference : 473696). (Pt. 2 in figure 2).

10. SS 626—shale, medium dark grey in colour (N 4), from 80 ft. above the second dolerite sill, Staffin Bay, east of Digg, Isle of Skye, Scotland.

11. SS 627—shale, between medium dark grey and dark grey in colour (N $3\frac{1}{2}$), from 100 ft. above the second dolerite sill, Staffin Bay, east of Digg, Isle of Skye, Scotland.

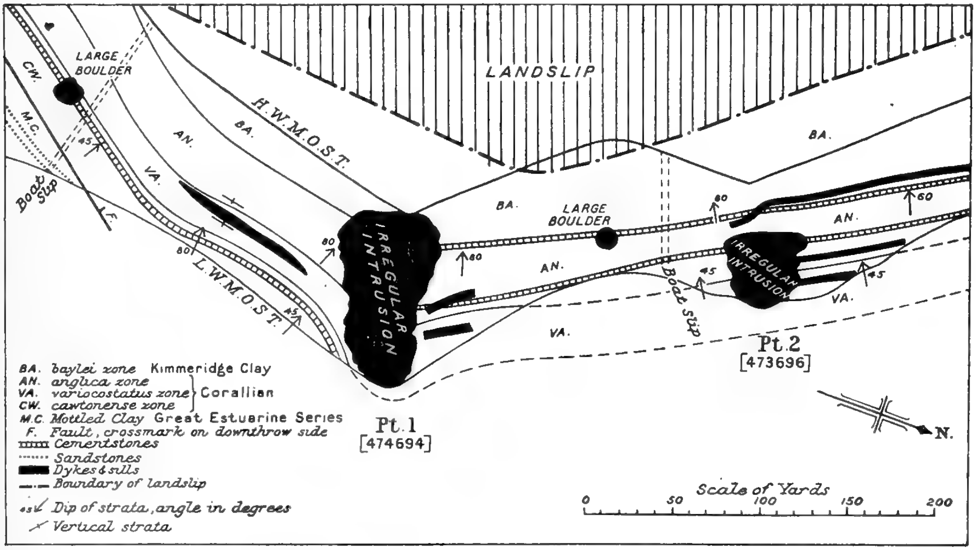

FIG. 2. Sketch map of Staffin Bay, coast of Digg, showing collection localities. (From "The Geology of Northern Skye", Geological Survey Memoir, pp. 49, fig. 8. Reproduced by permission of the Director of the Institute of Geological Sciences.)

12. VN 184—clay, medium light grey in colour (N 6), from the *Liostrea delta* Bed (equivalent to that at Ringstead), Villerville, Normandy, France.

13. CH 185—clay, light grey in colour (N 7), from Exogyra Marls, *c.* 1 m. above the Upper Hard Band, Cap de La Hève, Le Havre, France.

14. CH 186—clay, light grey in colour (N 7), from immediately below Upper Hard Band, Cap de La Hève, Le Havre, France.

15. CC 447—clay, medium dark grey in colour (N 4), from the Argiles de Moulin Wibert, lowest exposed level (20 ft. below the top) on the south side of Cap de La Crèche, Boulonnais, France.

16. CC 448—clay, light grey in colour (N 7), from the base of the Calcaires de Moulin Wibert, south side of Cap de La Crèche, Boulonnais, France.

17. CC 449—clay, light grey in colour (N 7), from *c.* 10 ft. top of the Calcaires de Moulin Wibert, south side of Cap de La Crèche, Boulonnais, France.

18. CC 450—clay, light olive grey in colour (5 Y 6/1), from the top of the Grès de Châtillon, south side of Audresselles, Boulonnais, France.

19. CC 451—clay, dark grey in colour (N 3), from 5 ft. above the base of Argiles de Châtillon, south side of Audresselles, Boulonnais, France.

20. CC 452—clay, dark greenish grey in colour (5 GY 4/1), from 5 ft. below the base of Grès de La Crèche, south side of Audresselles, Boulonnais, France.

21. CC 455—clay, greenish grey in colour (5 GY 6/1), from beneath Upper Nodule Bed dividing Argiles de La Crèche from Argiles de Wimereux ; *c.* 200 yds. north of Cap de La Crèche, Boulonnais, France.

III. TREATMENT

Every sample was cleaned first, then crushed mechanically and treated with 50% HCl acid to remove carbonates, washed to neutrality and then heated in HF acid of commercial strength. After being again washed to neutrality, the organic residue was heated in HCl acid and once more washed to neutrality. The residue was oxidized with Schulze solution and washed again ; to complete the maceration it was then treated with 10% NaOH solution, to remove humic compounds, and washed into a sintered glass filter funnel. After further washing with water the residue was stained with safranin. A small amount of the glycerine jelly was melted in a test tube and a few drops of the prepared sample in water suspension, added. The mixture was then vigorously agitated so as to disperse the microfossils. A drop of the solution was transferred, by a pipette, to a clean microscope slide and covered by a coverslip and allowed to dry for study.

IV. SYSTEMATIC SECTION

The full list of species present, together with their numerical distribution, is given in Table 4 A and B.

Proportions of the major components of the assemblage are given in Tables 1, 2 and 3.

The cysts are shown to fall into three broad groups, " proximate ", " chorate " and " cavate ", which are interpreted as indicating different modes of formation within the cell wall of the motile dinoflagellate. Only species that are new, or species about which additional information can be given, are dealt with in this section.

All type specimens and some of the figured specimens that are mentioned together with the British Museum (Natural History) slide numbers, are deposited in the Palaeontological collections of the British Museum (Natural History), London. The rest of the figured specimens and other representative slides are lodged in the collections of the Micropalaeontology Laboratory, Department of Geology, University of Nottingham.

Table 1

Proportion of the major components of the assemblages from England

Microfossil groups	No. of samples examined							
	OM 131	OM 418	OM 419	OM 420	HD 191	RB 218	RB 219	SC 444
	%	%	%	%	%	%	%	%
ACRITARCHA								
Micrhystridia	0·2	6·8	1·3	6·5	2·8	3·2	1·1	20·9
Total Acritarcha	5·4	11·8	4·0	15·4	8·5	14·2	9·4	24·8
DINOPHYCEAE								
Proximate cysts	33·1	37·2	35·6	45·8	17·4	24·3	35·3	21·3
Chorate cysts	12·2	20·5	12·1	8·4	2·8	33·3	8·0	2·8
Proximochorate cysts	0·2	—	0·4	1·7	—	—	—	0·5
Cavate cysts	11·2	9·3	9·9	13·6	2·8	2·5	1·1	2·1
Indeterminate cysts	8·1	8·0	10·3	8·3	42·8	5·2	13·2	2·5
Total Dinoflagellates	64·8	75·0	68·3	77·8	65·5	65·0	57·4	29·2
Pollen and Spores	29·0	13·2	25·4	6·8	25·7	20·5	28·1	36·0
Foraminiferal shell linings	—	—	2·3	—	—	—	—	10·0
Wood fragments	0·8	—	—	—	—	—	4·9	—

Table 2

Proportion of the major components of the assemblages from Scotland

Microfossil groups	No. of samples examined		
	SS 625	SS 626	SS 627
	%	%	%
ACRITARCHA			
Micrhystridia	0·5	0·8	1·4
Total Acritarcha	2·9	1·0	2·2
DINOPHYCEAE			
Proximate cysts	25·7	11·4	20·1
Chorate cysts	7·9	3·9	9·2
Proximochorate cysts	—	0·2	0·2
Cavate cysts	5·1	1·9	3·8
Indeterminate cysts	2·3	1·5	4·5
Total Dinoflagellates	41·1	18·9	37·8
Pollen and Spores	39·0	76·1	56·0
Foraminiferal shell linings	13·0	2·0	3·0
Wood fragments	4·0	2·0	1·0

TABLE 3

Proportion of the major components of the assemblages from France

Microfossil groups	No. of samples examined									
	VN 184	CH 185	CH 186	CC 447	CC 448	CC 449	CC 450	CC 451	CC 452	CC 455
	%	%	%	%	%	%	%	%	%	%
ACRITARCHA										
Micrhystridia	3·0	5·1	2·2	1·4	1·8	0·6	1·0	—	—	—
Total Acritarcha	11·9	13·1	2·7	12·0	8·2	3·4	2·0	35·7	—	—
DINOPHYCEAE										
Proximate Cysts	30·3	39·1	41·2	28·4	36·5	54·3	45·7	9·9	55·6	7·0
Chorate cysts	27·2	7·2	7·8	38·7	5·7	19·5	4·8	19·1	20·5	0·8
Proximochorate cysts	0·6	—	—	—	—	—	—	—	—	—
Cavate cysts	14·1	4·4	21·1	6·5	18·1	4·2	8·3	3·9	0·6	7·7
Indeterminate cysts	7·9	9·2	7·2	6·4	12·0	14·6	10·2	19·1	12·8	11·5
Total Dinoflagellates	80·1	59·9	77·3	80·0	72·3	92·6	69·0	52·0	89·5	27·0
Pollen and Spores	8·0	27·0	20·0	8·0	18·0	3·0	29·0	12·3	10·5	73·0
Foraminiferal shell linings	—	—	—	—	—	1·0	—	—	—	—
Wood fragments	—	—	—	—	1·5	—	—	—	—	—

Class *DINOPHYCEAE* Pascher
Sub-class *DINOFEROPHYCIDAE* Bergh
Order DINOPHYCIALES Lindemann
Cyst-Family **FROMEACEAE** Sarjeant & Downie, 1966
Genus ***CHYTROEISPHAERIDIA*** Sarjeant, emend. Downie, Evitt & Sarjeant, 1963

Chytroeisphaeridia chytroeides Sarjeant, 1962b
(Pl. 14, fig. 5)

1962b *Leiosphaeridia* (*Chytroeisphaeridia*) *chytroeides* Sarjeant, 493–494, pl. 70, figs. 13, 16; text-figs. 11, 12, tables 2, 3.
1963 *Chytroeisphaeridia chytroeides* (Sarjeant); Downie, Evitt & Sarjeant: 9.
1964 *C. chytroeides* (Sarjeant); Downie & Sarjeant: 103.
1967a *C. chytroeides* (Sarjeant); Sarjeant, table 3.
1968 *C. chytroeides* (Sarjeant); Sarjeant, pl. 3, fig. 10, table 2B.

This species has been previously recorded from the Oxfordian (Ampthill Clay) of England by Sarjeant (1962). It occurs in moderate abundance in the assemblages from the base of the Kimmeridgian of England, Scotland and France.

FIGURED SPECIMEN. BM(NH) slide V.53975(1). Shale from 80 ft. above the second dolerite sill, east of Digg, Staffin Bay, Skye (SS 626).

DIMENSIONS. There is a difference in range of dimensions between Oxfordian and

Kimmeridgian specimens: Diameters of Oxfordian specimens, as quoted by Sarjeant, are between 30–60 μ ; figured specimen's length (apex lacking) 45 μ, breadth 55 μ. Range of the measured specimens: length (apex lacking) 20–65 μ, breadth 18–75 μ. 154 specimens were measured.

Chytroeisphaeridia pococki Sarjeant, 1968

(Pl. 9, figs. 7, 8; Pl. 10, fig. 3)

1965 *Chytroeisphaeridia* sp. Sarjeant, pl. 1, fig. 13.
1968 *Chytroeisphaeridia pococki* Sarjeant, 230, pl. 3, fig. 9.

Chytroeisphaeridia pococki has been previously observed in both the Lower Callovian (*S. calloviense* Zone) and Upper Callovian (*L. lamberti* Zone) of Normandy by Sarjeant (1965, 1968). It has also been recorded from the base of Kimmeridgian of England, Scotland and France.

FIGURED SPECIMENS. BM(NH) slide V.53958(2). Clay from 20 ft. above Ringstead Coral Bed, west of Osmington Mills, Dorset (OM 420).

BM(NH) slide V.53619(1). Shale from 100 ft. above the second dolerite sill, Staffin Bay, Skye (SS 627).

BM(NH) slide V.53954(1). Clay from 10 ft. above the Ringstead Coral Bed, west of Osmington Mills, Dorset (OM 418).

DIMENSIONS. The observed range in dimensions was length (apex lacking) 30–80 μ, breadth 30–70 μ; somewhat larger than those of the holotype (holotype dimensions, quoted by Sarjeant: length -apex lacking- 45 μ, breadth 55 μ.). 32 specimens were measured.

Genus ***TENUA*** Eisenack, emend. Sarjeant, 1968

Tenua cf. ***capitata*** (Cookson & Eisenack), comb. nov.

(Pl. 10, fig. 4)

Hystrichosphaeridium capitatum has previously been recorded from the Oxfordian to the Kimmeridgian of Australia by Cookson and Eisenack. This species is placed in the genus *Tenua* on the basis of the shell outline, the presence of an apical archaeopyle, and the form and number of the processes. The distribution of the processes of this species does not reflect any tabulation ; also since they exceed 30, they are not the right number for the genus *Hystrichosphaeridium*.

DESCRIPTION. *Tenua* cf. *capitata* has a subspherical to elongate shell with an apical archaeopyle. It bears processes whose length is about one third of the shell breadth and up to fifty in number. The processes are hollow, capitate or somewhat bifurcate, their distribution appearing at random.

FIGURED SPECIMEN. BM(NH) slide V.53947(1). Clay from the base of Kimmeridge Clay, Ringstead Bay, Dorset (RB 219).

DIMENSIONS. Figured specimen: shell length (apex lacking) 50 μ, breadth 28 μ ; process length 7–9 μ. Range of the English specimens (6 specimens measured) : shell length 65 μ (apex lacking 50–57 μ), breadth 22–52 μ ; process length 7–10 μ ; French specimens (2 specimens measured) : shell length (apex lacking) 30–33 μ, breadth 25–40 μ ; process length 5–7 μ. These dimensions are similar to the dimensions of the Australian specimens (as quoted by Cookson and Eisenack : length 64–66 μ, breadth 28–44 μ).

REMARKS. Well-preserved specimens were observed in moderate number in the assemblages from Dorset, Le Havre and the Boulonnais. They are similar to the specimen figured by Cookson and Eisenack, but differ from it in the length and the number of the processes, the basal Kimmeridgian specimens having longer processes in greater number.

Tenua hystrix Eisenack, 1958

(Pl. 5, fig. 8 ; Pl. 10, fig. 7)

1958 *Tenua hystrix* Eisenack: 410, pl. 23, figs. 1–4 ; text-fig. 10.
1961a *T. hystrix* Eisenack ; Evitt: 398, pl. 1, fig. 2 ; pl. 5, fig. 1.
1964 *T. hystrix* Eisenack ; Downie & Sarjeant: 148.
1967a *T. hystrix* Eisenack ; Sarjeant, table 3.

Tenua hystrix has been recorded from the Aptian of Germany by Eisenack (1958). It is common in English, Scottish and French materials studied.

FIGURED SPECIMENS. BM(NH) slide V.53947(2). Clay from *Rhactorhynchia inconstans* Bed, Ringstead Bay, Dorset (RB 219) para. BM (NH) slide V.52794(2). Shaly clay from the base of Kimmeridge Clay, *Liostrea delta* Bed, Osmington Mills, Dorset (OM 131).

DIMENSIONS. Range of the dimensions : length (apex lacking) 35–80 μ, breadth 25–62 μ ; length of the spines 3–8 μ. 28 specimens were measured.

Tenua pilosa (Ehrenberg) emend. Sarjeant, 1968

(Pl. 4, fig. 5)

1843 *Xanthidium pilosum* Ehrenberg: 61–63.
1854 *X. pilosum* Ehrenberg ; Ehrenberg, pl. 37, fig. 8, no. 4.
1904 *Ovum hispidum* (*Xanthidium*) *pilosum* (Ehrenberg) ; Lohmann: 24–25.
1937 *Hystrichosphaeridium pilosum* (Ehrenberg) ; Deflandre: 31.
1960 *Baltisphaeridium pilosum* (Ehrenberg) ; Sarjeant, pl. 13, figs. 11, 12.
1961a *B. pilosum* (Ehrenberg) ; Sarjeant: 101–102, pl. 14, figs. 3–5.
1962a *B. pilosum* (Ehrenberg) ; Sarjeant, pl. 20, figs. 7–10 ; tables. 3, 4.
1964 *B. pilosum* (Ehrenberg) ; Downie & Sarjeant: 94.
1964a *B. pilosum* (Ehrenberg) ; Sarjeant, table 3.
1966 *Cleistosphaeridium pilosum* (Ehrenberg) ; Davey, Downie, Sarjeant & Williams, *nomen nudum*: 170.
1967a *Tenua pilosa* (Ehrenberg) ; Sarjeant, table 3.
1968 *T. pilosa* (Ehrenberg) ; Sarjeant: 231, pl. 2, fig. 7.
1969 *T. pilosa* (Ehrenberg) ; Davey, Downie, Sarjeant & Williams (in press).

This species of *Tenua* has been recorded from the Upper Callovian (*L. lamberti* Zone) and Oxfordian in Europe. Well preserved specimens were observed in the base of Kimmeridgian.

FIGURED SPECIMEN : BM(NH) slide V.52793(1). Shaly clay from immediately west of the slipway at Osmington Mills, Dorset (OM 131).

DIMENSIONS. Figured specimen : length 50 μ, breadth 40 μ ; length of the spines 6–8 μ. Range of the dimensions : English specimens length 40–70 μ, breadth 50 μ ; Scottish specimens length 35–40 μ, breadth 30–45 μ ; French specimens length 60 μ, breadth 50 μ. In all specimens, the length of the spines was 3–8 μ. 10 English, 1 French and 7 Scottish specimens were measured.

***Tenua* sp.**

(Pl. 9, fig. 3 ; Text-fig. 3)

DESCRIPTION. The spherical shell possesses spines that are uniformly distributed over the whole surface. These spines are very short, solid and conical. Neither tabulation nor longitudinal or transverse structure were seen. There is a large apical archaeopyle; however, the operculum remains attached on one side. Surface smooth between the spines. Spines are numerous, about 220.

FIGURED SPECIMEN. BM(NH) slide V.52796(1). Shaly clay from the base of Kimmeridge Clay, *Liostrea delta* Bed, Osmington Mills, Dorset (OM 131).

DIMENSIONS. Overall length 50 μ, breadth 50 μ ; apex lacking length 43 μ ; length of the spines 2 μ.

REMARKS. A single specimen was observed in the Dorset material, which is

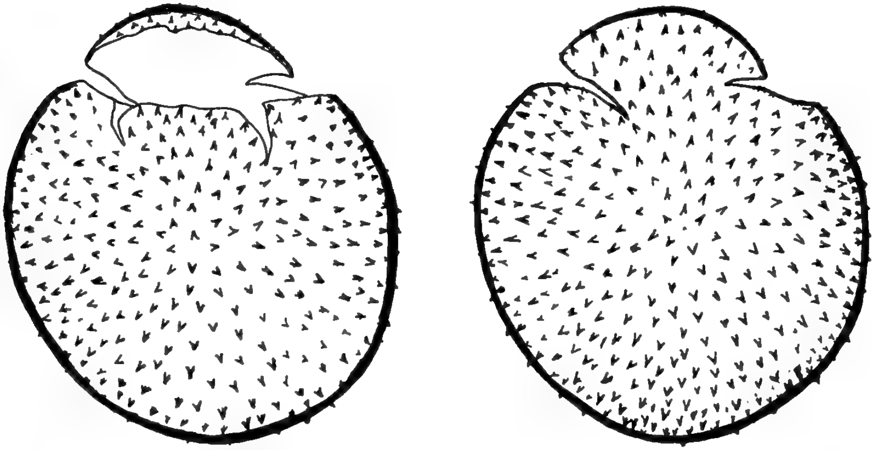

FIG. 3. *Tenua* sp. General appearance and the apical archaeopyle formation (the operculum remains attached on one side). ×*c.* 1280.

different from previously described species of *Tenua*, in its characteristic shape and spines. It may represent a new species, but further and better specimens are required before this can be decided.

Cyst-Family ***GONYAULACYSTACEAE*** Downie & Sarjeant, 1966

Genus ***CRYPTARCHAEODINIUM*** Deflandre, emend.

Emended diagnosis. Proximate dinoflagellate cysts, spherical, subspherical, broadly ovoidal or polygonal, with tabulation : 4′, 0–1a, 6″, 6c, 7‴, 2p, 0–1pv and 1⁗. Cingulum almost equatorial and slightly or strongly helicoid, laevorotatory. Sulcus generally broad, extending onto both epitract and hypotract. Apical horn rarely present ; median and antapical horns lacking. Sutures in the form of low ridges ; bearing crests of denticulate or spinous type. Archaeopyle formation, where developed, precingular and formed by loss of plate 3″.

Type species. *Cryptarchaeodinium calcaratum* Deflandre 1939. Upper Jurassic (Kimmeridgian) ; France.

Remarks. The generic diagnosis is emended to include reference to the tabulation, to the apical horn and to the mode of archaeopyle formation.

This genus, in view of inadequate knowledge of its morphology and in particular of its mode of archaeopyle formation was not attributed to any of dinoflagellate cyst-families, but was mentioned under " Cyst-Family Uncertain " by Downie & Sarjeant (1966). Since it has a tabulation of *Gonyaulax* type and a precingular archaeopyle, it is possible to reattribute this genus to the Cyst-Family *Gonyaulacystaceae*.

Cryptarchaeodinium calcaratum (Deflandre), emend.

(Pl. 1, figs. 1, 2 ; Text-fig. 4)

1939 *Cryptarchaeodinium calcaratum* Deflandre: 145, pl. 6, fig. 6.
1941 *C. calcaratum* Deflandre ; Deflandre: 19, pl. 5, figs. 7–9 ; text-figs. 9–10.
1952 *C. calcaratum* Deflandre ; Deflandre, fig. 92.
1964 *C. calcaratum* Deflandre ; Downie & Sarjeant: 104.
1964 *C. calcaratum* Deflandre ; Eisenack: 153–154.
1964a *C. calcaratum* Deflandre ; Sarjeant, table 2.
1967a *C. calcaratum* Deflandre ; Sarjeant, table 4.

Emended diagnosis. A *Cryptarchaeodinium* having a small, almost spherical shell, without either an apical or antapical process. Tabulation: 4′, 6″, 6c, 7‴, 2p, 1⁗. Plate boundaries bear short spiny crests. Cingulum almost equatorial, strongly spiral, laevorotatory. Shell wall thin, surface granular. Large precingular archaeopyle formed by loss of plate 3″.

Holotype. Specimen AP 17, Deflandre coll., Ecole Pratique des Hautes Etudes, Paris ; from Kimmeridgian of Orbagnoux, France.

Figured specimen. BM(NH) slide V.53959(1). Clay from Great Ouse River Board Pit, Stretham, Cambridgeshire (SC 444).

DIMENSIONS. Holotype : overall length 40 μ, breadth 40 μ ; length of the spines 3 μ. Figured specimen : overall length 34 μ, breadth 33 μ ; spines length 2–3 μ.

DESCRIPTION. Theca almost spherical, but having a somewhat polygonal appearance because of the angularly set spine rows on the plate boundaries.

Four apical plates are present. Plate 1′ is the largest ; the boundary between plates 1′ and 4′ was not clear. The six precingular plates, together with the apical plates form the epitract ; there is no anterior intercalary plate. Plate 1″ is reduced to accommodate of plate 2′. Plates 2″, 3″, 4″ and 5″ are more or less uniform in size and shape, but plate 6″ is different in shape because of the broadening sulcus.

The cingulum is occupied by six plates of moderate size. The sulcus extends onto the epitract and the hypotract, from apex to antapex ; it is narrow in its middle portion, being broad in its anterior and posterior portions.

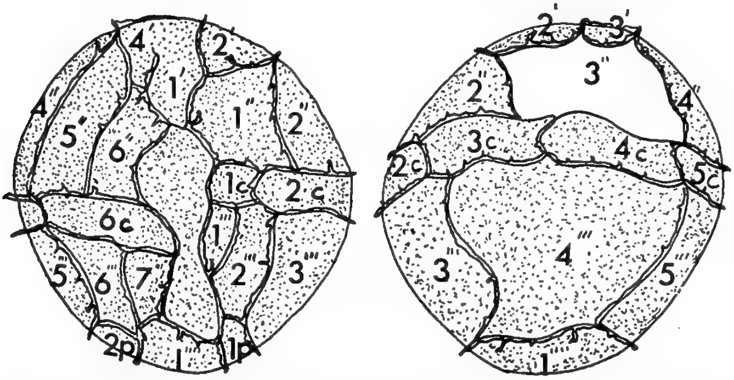

FIG. 4. *Cryptarchaeodinium calcaratum* (Deflandre). Specimen, showing the tabulation and the precingular archaeopyle (plate 3″ is missing). Left, ventral view; right, dorsal view. ×*c*. 1400.

Seven postcingular plates of variable size and shape are present. Plates 1″ ′, 6″ ′ and 7″ ′ are small, whereas plate 4″ ′ is largest of all the plates of the shell. Two posterior intercalary plates are located on the two sides of the posterior end of the sulcus. The single antapical plate 1″ ′ is a rather small plate.

REMARKS. The diagnosis of *C. calcaratum* is emended to include the presence of the archaeopyle and the detail of the tabulation. This study was based on a single but excellently preserved specimen from the Kimmeridge Clay of Stretham.

Deflandre first observed *C. calcaratum* in the assemblages from Orbagnoux in 1939 ; a fuller diagnosis was given in 1941 and quoted again in 1952. The Stretham specimen corresponds closely to the holotype, differing only in the number of the apical plates, which are hesitantly mentioned as 4 in number by Deflandre (1941), and in the presence of the precingular archaeopyle.

In 1957, Downie observed a very similar specimen in the Kimmeridge Clay of Dorset, which he mentioned and figured as *Cryptarchaeodinium* sp. Although it was similar in many respects to this genus, it differed in the presence of an anterior intercalary plate 1a and of several very small plates between the plates 1a and 6″. The position of the antapical plate 1″ ″ and the sutures were also different. Eisenack incorrectly cited Downie's species as *C. calcaratum* in his " Katalog der Fossilen Dinoflagellaten, Hystrichosphären und verwandten Mikrofossilen " in 1964. On the basis of Downie's figure and description, this is unjustified.

Cryptarchaeodinium sp.

(Pl. 6, figs. 4, 7 ; Text-fig. 5)

Description. A small shell, spherical with a short and broad, blunt apical horn. The cingulum is slightly laevorotatory, dividing the theca into two unequal parts with epitract larger than the hypotract. Both cingulum and sulcus are broad. Reflected tabulation : 4′, 1a, 6″, 6c, 7″ ′, 2p, 1pv and 1″ ″. Apical plate 1′ is elongate, as long as the sulcus, and extends along the anterior prolongation of the sulcus. The other apical plates are small. The single anterior intercalary plate 1a is large and nearly square. The precingular plates are relatively large, plate 6″ being reduced to accommodate the intercalary plate 1a.

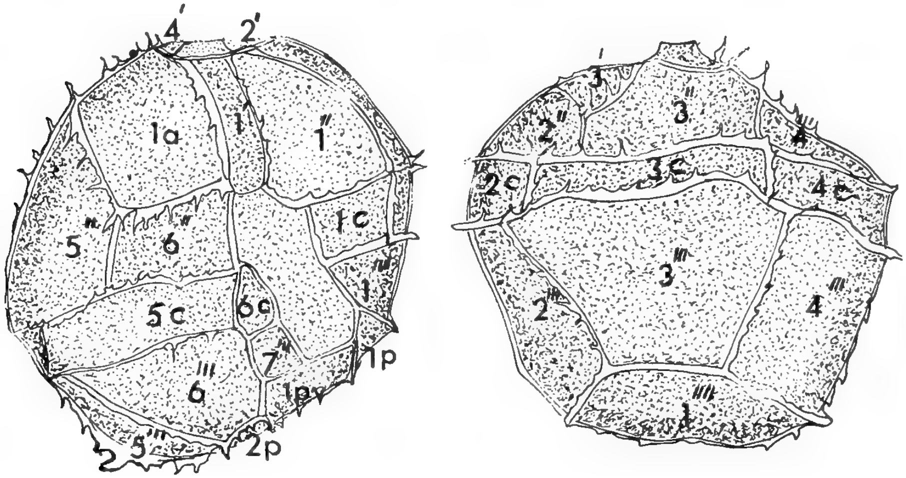

Fig. 5. *Cryptarchaeodinium* sp. Tabulation. Left, ventral view ; right, dorsal view. ×*c*. 1280.

Six plates make up the cingulum: plate 6c is very small, triangular in shape.

Seven postcingular plates, with three intercalary plates and an antapical plate from the hypotract. Plate 1″ ′ is small ; plates 2″ ′, 3″ ′, 4″ ′, 5″ ′ and 6″ ′ are relatively large; plate 7″ ′ is again rather small. The posterior intercalary plate 1pv is large and situated posterior to the sulcus and plate 7″ ′ ; this position is unusual, since similar plates in other species are normally confined to the posterior extension of the sulcus. The other posterior intercalary plates (1p and 2p) are small ; the single antapical plate 1″ ″ is, in contrast, rather large.

Denticulate crests rise up on the plate boundaries. The surface of the shell is finely but densely granular.

Archaeopyle formation was not observed.

Figured specimen. BM(NH) slide V.53972(2). Clay from Grès de Châtillon, south of Audresselles, Boulonnais (CC 450).

Dimensions. Figured specimen : overall length 40 μ, breadth 40 μ ; horn length 3·5 μ, breadth 5 μ ; cingulum 4–7 μ wide ; crests 4–8 μ high.

Remarks. Although represented by a single specimen, the clear characterization of this form distinguishes it from the described species of *Cryptarchaeoidinium*. It is probably a new species, but further specimens are required to confirm this.

Hitherto two forms of *Cryptarchaeodinium* were known ; both were from the Kimmeridgian. This form has a small apical horn. It differs from *C. calcaratum* in the number and the shapes of the plates, in the presence of plate 1a and the absence of the archaeopyle. The absence of the small plates on the epitract and the presence of the posterior intercalary plates on the hypotract differentiate it from *Cryptarchaeodinium* sp. Downie, 1957.

Genus ***GONYAULACYSTA*** Deflandre, emend. Sarjeant, 1969

Gonyaulacysta aculeata (Klement) Sarjeant, 1969

(Pl. 1, figs. 5, 6 ; Text-figs. 6a, b)

1960 *Gonyaulax aculeata* Klement: 42, pl. 5, figs. 6, 7; text-fig. 21.
1964 *G. aculeata* Klement ; Downie & Sarjeant: 113.
1964 *G. aculeata* Klement ; Eisenack: 313.
1964a *G. aculeata* Klement ; Sarjeant, table 2.
1966 *Gonyaulacysta aculeata* (Klement) ; Sarjeant, *nomen nudum*: 130.
1967b *Gonyaulax aculeata* Klement ; Vozzhennikova, table 11.
1967b *Gonyaulacysta aculeata* (Klement) ; Sarjeant, *nomen nudum*, table 1.
1969 *G. aculeata* (Klement) ; Sarjeant (in press).

Description. Specimens of *G. aculeata* from the base of Kimmeridgian possess an ovate shell, with the tabulation : 4′, 6″, 6c, 6″′, 1p and 1″″. The epitract and hypotract are more or less equal in size and separated by the laevorotatory cingulum. The sulcus is broader on the hypotract. Longer spines, which are longer than the sutural spines, occupy the apex ; one of them is particularly prominent and forms the so-called " apical protuberance " mentioned by Klement. The sutures are marked by rows of spines. The spines are mostly simple and acuminate, but they become complicated near the apex and the antapex. The surface of the shell is coarsely tuberculate. A precingular archaeopyle is formed by loss of plate 3″.

Figured specimen. BM(NH) slide V.53965(3). Clay from Argiles de Moulin Wibert, lowest exposed level (20 ft. below the top) on the south side of Cap de La Crèche, Boulonnais (CC 447).

Dimensions. Figured specimen : overall length 68 μ, breadth 50 μ ; apical processes 6 μ long ; length of the spines on the sutures 3–5 μ. Range of the other specimens : English specimen (1 specimen measured) : length 63 μ, breadth 55 μ ; spine length 3 μ. French specimens (3 specimens measured) : length 68–74 μ, breadth 63–65 μ ; length of apical processes 5–7 μ ; length of the spines 3–4 μ. Range of German specimens, as quoted by Klement : length 66–72 μ, breadth 61–63 μ ; length of the apical processes 6 μ, sutural spines length 4 μ.

REMARKS. *G. aculeata* has been previously recorded from the Malm Upper Alpha to Lower Delta of Germany by Klement (1960). It is rare in the assemblages from the base of Kimmeridgian ; the specimens are usually badly preserved. The basal Kimmeridgian specimens correspond closely to those figured from Germany, but plate 1ppl, which was mentioned by Klement, was not observed.

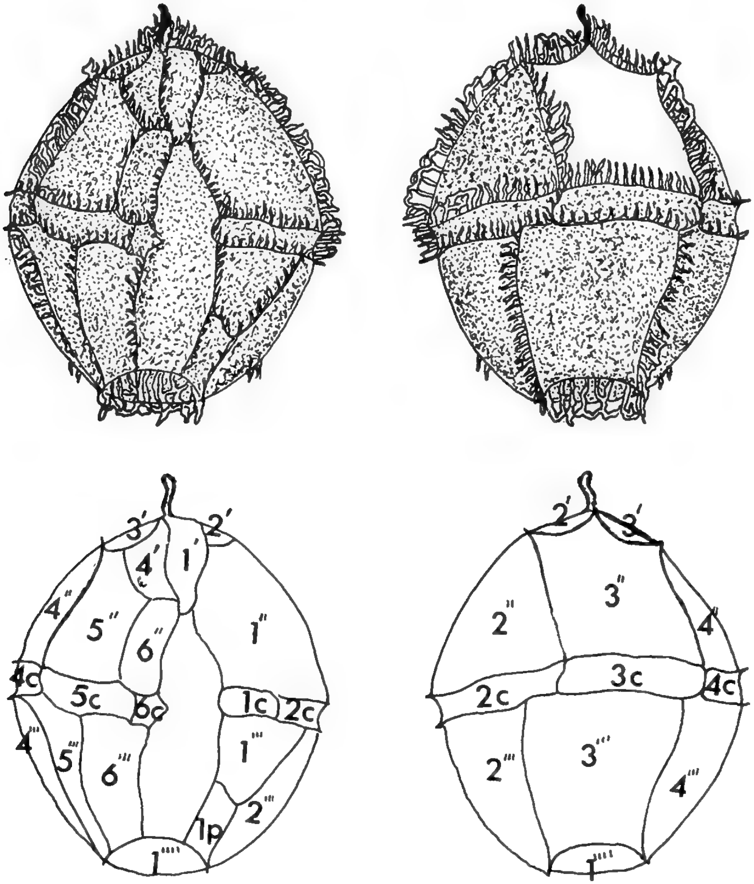

FIG. 6. *Gonyaulacysta aculeata* (Klement). A. General appearance and the archaeopyle formation ; left, ventral view ; right, dorsal view. ×*c*. 820. B. Tabulation. ×*c*. 820.

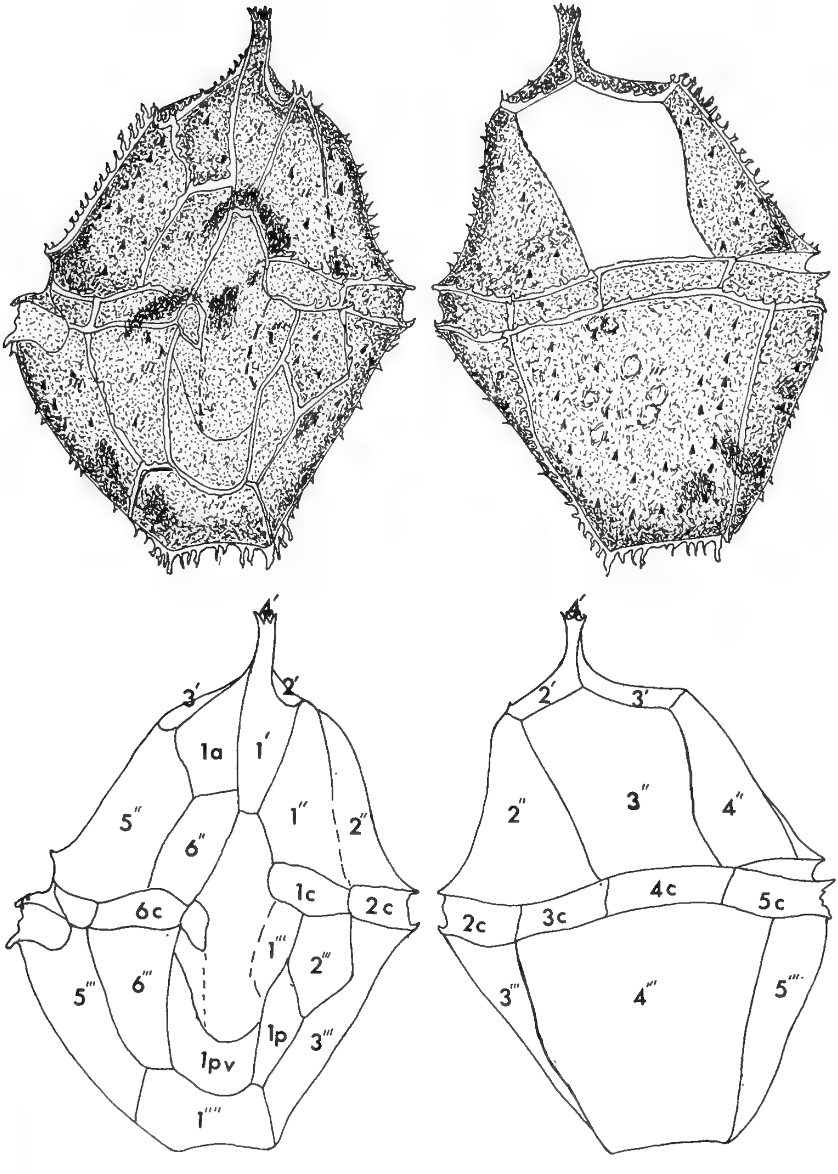

FIG. 7. *Gonyaulacysta angulosa* sp. nov. A. General appearance and the archaeopyle formation of the holotype. Left, ventral view; right, dorsal view. ×*c*. 1280. B. Tabulation. ×*c*. 1280.

Gonyaulacysta angulosa sp. nov.

(Pl. 2, figs. 4, 5 ; Text-fig. 7 a, b)

Derivation of the name. Latin, *angulosus*, angular, in reference to the shape of the cyst.

Diagnosis. *Gonyaulacysta* with a thick wall, composed of two layers ; the polygonal theca terminates in a strong apical horn formed from both shell layers. Tabulation : 4′, 1a, 6″, 6c, 6‴, 1p, 1pv, 1⁗. Plates are bordered by denticulate crests of moderate height. Cingulum laevoratotory. Sulcus broad, extending onto both parts of the shell. Surface granular ; simple, solid, short spines occasionally present. Single-plate precingular archaeopyle forms by loss of plate 3″.

Holotype. BM(NH) slide V.53934(1). Clay from the *Liostrea delta* Bed of Villerville, Normandy (VN 184).

Dimensions. Holotype : overall length 75 μ, breadth 58 μ ; horn length 7 μ, breadth 3 μ. Range of the dimensions : overall length 65–75 μ, breadth 50–58 μ ; horn length 6–8 μ. Measured specimens 3 in number.

Description. The elongate shell bears an apical horn which is developed from the apical plates 1′, 2′ and 3′ ; plate 4′ is placed on the top of the horn. Epitract is slightly longer than the hypotract. The nearly square anterior intercalary plate 1a is located between plates 3′ and 6″. Precingular plates are relatively large.

Six postcingular plates are present, with plates 1‴ and 2‴ reduced and angular in shape ; an elongate posterior intercalary plate between them and antapex. Plate 4‴ is very large and occupies nearly the whole dorsal side of the hypotract. A single, rather quadrate plate is present on the antapex; this antapical plate is separated from the sulcus by a crescent-shaped posterior ventral intercalary plate (1pv).

Remarks. This is an infrequent species : of four specimens encountered, one (holotype) is well preserved, the other three are severely damaged.

This new species, in general appearance, structure and the tabulation, agrees with those of the genus *Gonyaulacysta*.

G. angulosa may be compared with *G. cladophora* because of the structure of the sutures; but the tabulation, with plates 1a, 1pv, details of the plates 4′ and 1⁗ and presence of the small sulcal plates, is different.

Gonyaulacysta ehrenbergii sp. nov.

(Pl. 2, figs. 8, 9 ; Text-fig. 8)

Derivation of the name. Named after the microscopist Christian Gottfried Ehrenberg, who first discovered dinoflagellates in Jurassic and Cretaceous cherts and flints.

Diagnosis. *Gonyaulacysta* having an ovoidal theca of moderate wall thickness, with an apical horn. Tabulation : 4′, 1a, 6″, 6c, 7‴, 1p, 1pv, 1⁗ ; sutures in form of moderately high, membraneous crests giving rise occasionally to short, blunt spines.

Cingulum narrow, helicoid, laevorotatory ; sulcus of moderate breadth. Shell surface densely granular. Large precingular archaeopyle formed by loss of plate 3″.

HOLOTYPE. BM(NH) slide V.53968(1). Clay from the base of the Calcaires de Moulin Wibert, south side of Cap de La Crèche, Boulonnais (CC 448).

DIMENSIONS. Holotype : overall length 70 μ, breadth 50 μ ; horn length 8 μ ; breadth of the cingulum 5–8 μ. Range (5 specimens measured) : overall length 70–80 μ, breadth 50–65 μ ; horn length 6–9 μ.

DESCRIPTION. The shell is broadly ovoidal, giving rise to a strong apical horn ; this is formed by three of the four apical plates (plates 1′, 2′ and 4′). Apical plates 1′ and 4′ are larger than the other two plates ; 1′ is elongate. The single anterior intercalary plate 1a is large and located between the apical plates 3′, 4′ and precingular plates 4″, 5″, 6″. The precingular plates are generally large, plates 5″ and 6″ being reduced to accommodate the intercalary plate 1a.

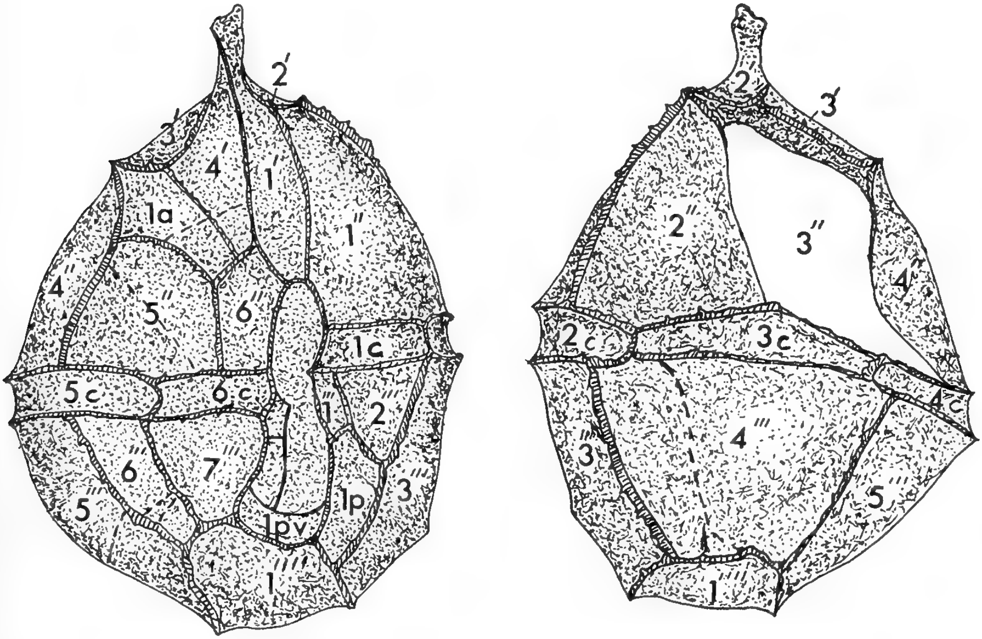

FIG. 8. *Gonyaulacysta ehrenbergii* sp. nov. Tabulation and the archaeopyle formation of the holotype (plate 3″ is missing). Left, ventral view ; right, dorsal view. × *c.* 1200.

Seven postcingular plates are present : Plates 1″′ and 2″′ are reduced because of the large intercalary plate 1p ; plates 6″′ and 7″′ are also reduced, since the large antapical plate 1″″ occupies a large area. The presence of posterior intercalary plate 1pv and the sulcal plates render the sulcus short and narrow.

REMARKS. Five specimens of this infrequent species were observed ; all of them are well preserved. All records were from French assemblages—from Normandy, and the Boulonnais.

The generic allocation of *Gonyaulacysta ehrenbergii* is questionable, in view of its possession of a seventh postcingular plate. The similarity in general morphology to a number of species of *Gonyaulacysta* resulted in its allocation to that genus. Since it possesses seven postcingular plates, there is a similarity between this species and the species of *Cryptarchaeodinium* ; but the *Cryptarchaeodinium* species so far observed have a slightly different tabulation, with plate 2p and without the sulcal plates. One species of that genus, described for the first time in this paper, bears a blunt apical horn ; but the apical horn of *G. ehrenbergii* is longer than the horn observed in *Cryptarchaeodinium*. *G. ehrenbergii* is twice the size of any described species of *Cryptarchaeodinium*.

With seven post-cingular plates, this new species is similar to *G. fetchamensis* and *G. palla* ; but it differs in details of tabulation, general aspect and size. The general structure and thick wall render this species similar to *G. scotti*, which was recorded from Lower Kimmeridgian of Australia by Cookson & Eisenack (1958) ; since Cookson and Eisenack were unable to determine the tabulation of *G. scotti*, of which they give a very incomplete description, and since the holotype was not available for study, the relationships between this latter species and *G. ehrenbergii* can not be commented on.

Gonyaulacysta eisenacki (Deflandre) Sarjeant, 1969
(Pl. 3, fig. 9)

1938a *Gonyaulax eisenacki* Deflandre: 171–173, pl. 6, fig. 7 ; text-figs. 3–4.
1958 *G. eisenacki* Deflandre ; Cookson & Eisenack: 30, pl. 2, fig. 11.
1960 *G. eisenacki* Deflandre ; Klement: 29–30, pl. 2, figs. 9–10.
1962a *G. eisenacki* Deflandre ; Sarjeant: 258, pl. 1, fig. 4 ; tables 3, 4.
1962b *G. eisenacki* Deflandre ; Sarjeant, pl. 69, fig. 3 ; tables 2, 3.
1964 *G. eisenacki* Deflandre ; Downie & Sarjeant: 114.
1964 *G. eisenacki* Deflandre ; Eisenack: 355.
1964a *G. eisenacki* Deflandre ; Sarjeant, table 2.
1965 *G. eisenacki* Deflandre ; Górka: 299–300, pl. 1, figs. 5 a–c.
1965 *Gonyaulacysta eisenacki* (Deflandre) ; Sarjeant, *nomen nudum*, table 1.
1966 *G. eisenacki* (Deflandre) ; Sarjeant, *nomen nudum*: 131.
1967 *G. eisenacki* (Deflandre) ; Dodekova: 18–19, pl. 2, figs. 9–11.
1967b *Gonyaulax eisenacki* Deflandre ; Vozzhennikova: 81, pl. 21, figs. 1–3 ; pl. 22, figs. 1–6 ; pl. 23, figs. 1–6 ; pl. 24, figs. 1–8, tables 2, 11.
1967a *Gonyaulacysta eisenacki* (Deflandre) ; Sarjeant, table 1, *nomen. nudum.*
1968 *G. eisenacki* (Deflandre) ; Sarjeant: 227, pl. 3, fig. 4, table 2a.
1969 *G. eisenacki* (Deflandre) ; Sarjeant (in press).

REMARKS. *G. eisenacki* has been recorded from the Middle Jurassic of East Prussia and Oxfordian of France by Deflandre (1938) ; from the Lower Oxfordian (Malm Alpha) of south-west Germany by Klement (1960), and from the Upper Jurassic of Moscow by Vozzhennikova (1967). In England it has previously been recorded from the Middle Callovian and Upper Oxfordian (Sarjeant, 1962, 1965). Recently Sarjeant observed it in the Upper Callovian and Lower Oxfordian of

Normandy (1968). This species characterized by the form of its high and denticulate crests and the character of apex and antapex, was observed in the Dorset assemblages.

FIGURED SPECIMEN. BM(NH) slide V.52800(1). Shaly clay from the *Liostrea delta* Bed, Osmington Mills, Dorset (OM 131).

DIMENSIONS. Figured specimen : overall length 85 μ, breadth 50 μ ; shell length 55 μ, breadth 45 μ. Range of the specimens observed : overall length 83–98 μ, breadth 48–60 μ ; shell length 58–68 μ, breadth 45–50 μ.

Dimensions of the French specimens, according to Deflandre : overall length 65–80 μ, breadth 57–60 μ ; according to Sarjeant : overall length 70–80 μ, breadth 50–60 μ. Klement recorded dimensions of 78–98 μ length and 52–58 μ breadth. Dimensions of the Russian specimens, as given by Vozzhennikova : overall length 59·4–67·5 μ, breadth 57–64·7 μ. There is thus little difference in dimensions between the French, German, English and Russian specimens from the Upper Jurassic.

***Gonyaulacysta* cf. *eisenacki* (Deflandre)**

(Pl. 2, fig. 10)

REMARKS. The specimens, observed in the basal Kimmeridgian assemblages of Dorset and the Boulonnais, resemble *G. eisenacki* in their denticulate crests and general appearance, but differ in that the apex is rounded and there is no antapical pericoel. This form may be an extreme variant of *G. eisenacki* or may be a new species ; further and better specimens are required before this can be decided.

FIGURED SPECIMEN. BM(NH) slide V.52792(1). Shaly clay from the *Liostrea delta* Bed, Osmington Mills, Dorset (OM 131).

DIMENSIONS. Figured specimen : overall length 59 μ, breadth 37 μ ; sutures 3–12 μ high. Other English specimens length 60–65 μ, breadth 50–55 μ. The French specimens were not measured because of their poor preservation.

***Gonyaulacysta granulata* (Klement) Sarjeant, 1969**

(Pl. 8, figs. 1, 2 ; Text-fig. 9)

1960 *Gonyaulax granulata* Klement: 39–41, pl. 4, figs. 10–13 ; text-figures 18–20.
1964 *G. granulata* Klement ; Downie & Sarjeant: 114.
1964 *G. granulata* Klement ; Eisenack: 357–358.
1964a *G. granulata* Klement ; Sarjeant, table 2.
1966 *G. granulata* Klement ; Schulz & Mai, table 1.
1966 *Gonyaulacysta granulata* (Klement) ; Sarjeant, *nomen nudum*: 131.
1967b *Gonyaulax granulata* (Klement) ; Vozzhennikova, table 11.
1967b *Gonyaulacysta granulata* (Klement) ; Sarjeant, *nomen nudum*, table 1.
1969 *G. granulata* (Klement) ; Sarjeant (in press).

DESCRIPTION. The broadly spherical shell is divided into two almost equal parts by the laevorotatory cingulum. A short apical horn is present. Tabulation : 4′, 6″, 6c, 6‴, 1p and 1⁗. Moderately low sutures rise up on the plate boundaries.

Sulcus is short and broad. The precingular archaeopyle forms through loss of the plate 3″. Surface of the shell finely granular.

Figured specimen. BM(NH) slide V.53969(1). Clay from top of the Grès de Châtillon, south of Audresselles, Boulonnais (CC 450).

Dimensions. Figured specimen : overall length 62 μ, breadth 55 μ ; horn length 7 μ. Other French specimens (15 specimens measured) : overall length 62–80 μ, breadth 55–65 μ; horn length 6–7 μ. Range of the English specimens (2 specimens measured) : overall length 68–73 μ, breadth 70–72 μ ; horn length 6–8 μ. (Dimensions of the type material : length 66 μ, breadth 63 μ ; horn length 9 μ.)

Remarks. Klement has recorded *G. granulata* from the Upper Jurassic (Lower Oxfordian to Upper Kimmeridgian) of Germany. It is present in the Dorset and Boulonnais assemblages. The specimens from these localities correspond closely in general morphology to the German material, differing only in details of the shape of plates 1′, 3′ and 1‴.

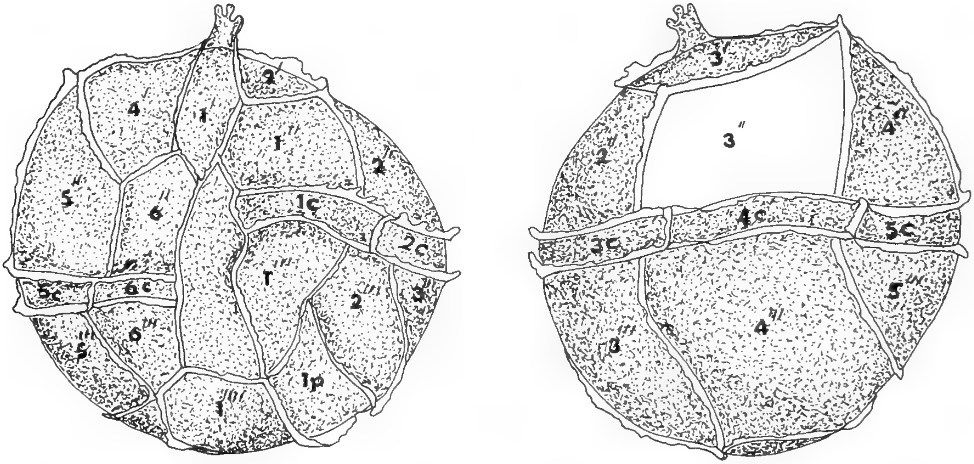

Fig. 9. *Gonyaulacysta granulata* (Klement). Tabulation. Left, ventral view ; right, dorsal view. Plate 3″ is missing to form the precingular archaeopyle. ×*c.* 1280.

Gonyaulacysta granuligera (Klement) Sarjeant, 1969

(Pl. 1, figs. 10, 11 ; Text-fig. 10)

1960 *Gonyaulax granuligera* Klement: 41–42, pl. 5, figs. 4, 5.
1964 *G. granuligera* Klement ; Downie & Sarjeant: 114.
1964 *G. granuligera* Klement ; Eisenack: 359.
1964a *G. granuligera* Klement ; Sarjeant, table 2.
1966 *G. granuligera* Klement ; Schulz & Mai, table 1.
1966 *Gonyaulacysta granuligera* (Klement) ; Sarjeant, *nomen nudum*: 131.
1967b *Gonyaulax granuligera* Klement ; Vozzhennikova, table 11.
1967b *Gonyaulacysta granuligera* (Klement) ; Sarjeant, table 1, *nomen nudum.*
1969 *G. granuligera* (Klement) ; Sarjeant (in press).

DESCRIPTION. Shell subspherical to elongate, with a long apical horn. Tabulation : $4'$, $6''$, 6c, $6'''$, $1''''$. Cingulum narrow and laevorotatory, dividing the shell into two unequal parts : epitract longer than the hypotract. Plate boundaries spiny ; spines short, solid and distally acute or blunt. Precingular archaeopyle forms by loss of the plate $3''$. Surface densely granular.

FIGURED SPECIMEN. BM(NH) slide V.53972(1). Clay from top of the Grès de Châtillon, south of Audresselles, Boulonnais (CC 450).

DIMENSIONS. Figured specimen : overall length 73 μ, breadth 65 μ ; horn length 8 μ ; length of the spines 1–3 μ. Range of the English specimens (15 specimens measured) : overall length 65–73 μ, breadth 50–75 μ. French specimens (25 specimens measured) : overall length 68–72 μ, breadth 60–65 μ. German specimens : length 72–84 μ, breadth 58–69 μ ; horn length 9–12 μ (quoted by Klement). English and French specimens are thus more spherical and their horns shorter than the type species.

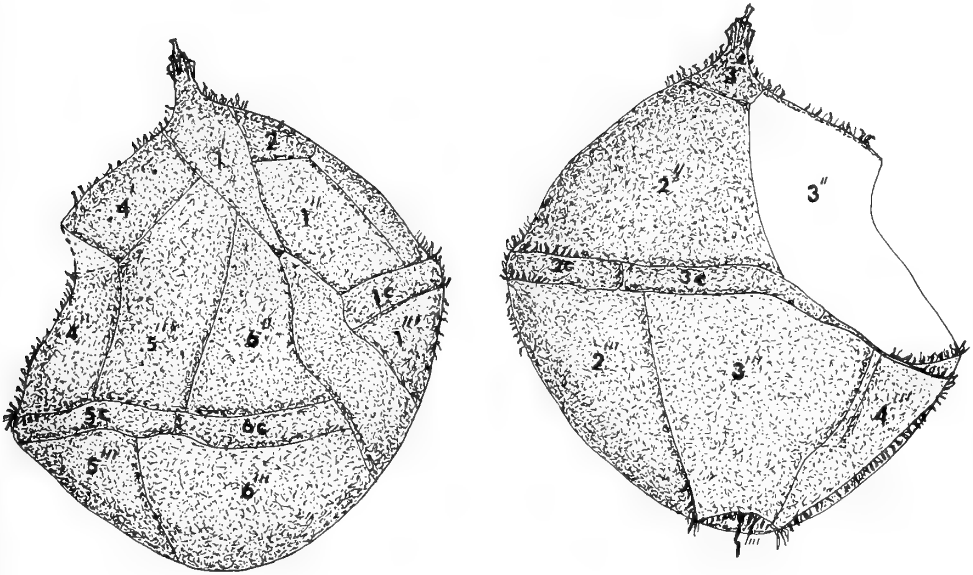

FIG. 10. *Gonyaulacysta granuligera* (Klement). Tabulation and the archaeopyle formation (plate $3''$ is missing). Left, ventral view ; right, dorsal view. × *c.* 1280.

REMARKS. *C. granuligera* has been recorded from Malm Upper Alpha to Lower Delta (Kimmeridgian) of Germany (Klement, 1960). The interpretation of the tabulation here made is slightly different from Klement's, as might be expected in view of the densely granular surface : plates 1p and 1ppl, mentioned by Klement, were not observed.

***Gonyaulacysta* cf. *helicoidea* (Eisenack & Cookson)**

(Pl. 2, figs. 1, 2; Text-fig. 11)

Description. An almost spherical theca with a short and broad, blunt apical horn. Tabulation : 4′, 1a, 6″, 6c, 6″ ′, 1p and 1″ ″. Denticulate crests rise up from the plate boundaries ; the height and character of denticulation are variable. The strongly spiral cingulum separates the epitract and the hypotract, which are almost equal in size. Sulcus sigmoidal. Surface of the shell tuberculate ; scattering of the tubercules irregular. Precingular archaeopyle forms by loss of plate 3″.

Figured specimen. BM(NH) slide V.53931(1). Clay from the *Liostrea delta* Bed of Villerville, Normandy (VN 184).

Dimensions. Figured specimen : overall length 45 μ, breadth 40 μ ; horn length 5 μ. Holotype dimensions (given by Eisenack and Cookson) are length 78 μ, breadth 56 μ. Range of English specimens (as quoted by Sarjeant) : overall length 44–53 μ, breadth 42–46 μ.

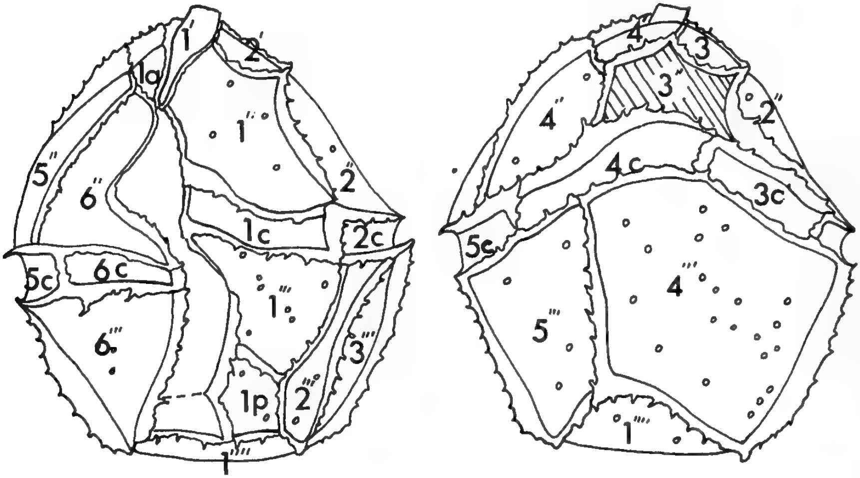

Fig. 11. *Gonyaulacysta* cf. *helicoidea* (Eisenack & Cookson). Tabulation. Left, ventral view ; right, dorsal view. ×*c*. 1360.

Remarks. *G. helicoidea* was originally recorded from the Lower Cretaceous (Aptian or older) of South Australia by Eisenack and Cookson (1960) ; subsequently Sarjeant observed it in the Speeton Clay of England (Lower Barremian), emended the diagnosis, and gave an exact tabulation of the species (1966). It was also observed in the Barremian of Russia by Vozzhennikova (1967).

A single, excellently preserved specimen was recorded from the basal Kimmeridgian of Normandy. This specimen is closely comparable with the specimen figured by Sarjeant ; the only difference is in the height of the apical horn (although it has been mentioned that the length of the horn is very variable, by Sarjeant, 1966c). Dimensions of the Kimmeridgian specimen similar to the English (Barremian) specimens, but both are smaller than the Australian (Aptian) holotype.

The stratigraphic range of *G. helicoidea* is from Barremian to Aptian ; therefore this is an unexpected observation in the base of Kimmeridgian assemblages. Since this form is different from the typical *G. helicoidea*, it is considered preferable not to place this specimen in the latter species until a larger assemblage of specimens is available for study.

Gonyaulacysta hyaloderma (Deflandre), emend.

(Pl. 9, figs. 9, 10 ; Text-fig. 12)

1939 *Plaeoperidinium hyalodermum* Deflandre: 144, pl. 6, figs. 3, 4.
1941 *P. hyalodermum* Deflandre ; Deflandre: 17, pl. 5, figs. 10–12.
1957 *P. hyalodermum* Deflandre ; Downie: 422, pl. 20, fig. 9.
1964 *P. hyalodermum* Deflandre ; Downie & Sarjeant: 137.
1964 *P. hyalodermum* Deflandre ; Eisenack: 603.
1964a *P. hyalodermum* Deflandre ; Sarjeant, table 2.
1965 *P. hyalodermum* Deflandre ; Coninck: 16, pl. 3, fig. 3.
1967a *Gonyaulacysta hyaloderma* (Deflandre) ; Sarjeant:252.
1967b *G. hyaloderma* (Deflandre) ; Sarjeant, table 1.

EMENDED DIAGNOSIS. A *Gonyaulacysta* with thin-walled, spherical to ovoidal shell terminating in a short, blunt horn. Tabulation : 4′, 6″, 6c, 6‴, 1p and 1⁗. Plate boundaries demarcated by moderately high, delicate crests with smooth or denticulate edges. Epitract and hypotract are almost equal in size and separated by laevorotatory helicoidal cingulum. Sulcus broadening posteriorly, weakly sigmoidal. Surface of the shell smooth. Precingular archaeopyle forms by loss of plate 3″.

HOLOTYPE. Specimen AP 2, Deflandre coll., Ecole Pratique des Hautes Etudes, Paris, from Kimmeridgian of Orbagnoux, France.

FIGURED SPECIMEN. BM(NH) slide V.53932(1). Clay from the *Liostrea delta* Bed of Villerville, Normandy (VN 184).

DIMENSIONS. Holotype : length 42 μ, breadth 35 μ ; length of the apical horn 3 μ. Figured specimen : overall length 44 μ, breadth 40 μ ; horn length 4 μ. Dimensions of the specimen from Eocene of Belgium (as quoted by Coninck) : length 42 μ, breadth 32 μ ; horn length 7 μ. According to these measurements, the dimensions of the specimens from the Kimmeridgian and Eocene are similar.

DESCRIPTION. Shell broadly ovoidal, with a short and broad horn at the apex, and the hypotract rounded. The crests separating the four apical plates meet at the apex. Plate 1′ occupies the anterior prolongation of the sulcus ; it is long and broadening towards the apex. Plate 2′ is the largest of the apical plates and forms the apical horn together with plate 1′. Six precingular plates are present ; they are moderately large. Plate 6″ is elongate and narrower than the others. The six postcingular plates are of variable size. Plate 1‴ is the smallest, triangular in shape ; plate 3‴ and 4‴ are larger, quadrate and occupy the whole dorsal side of the hypo-

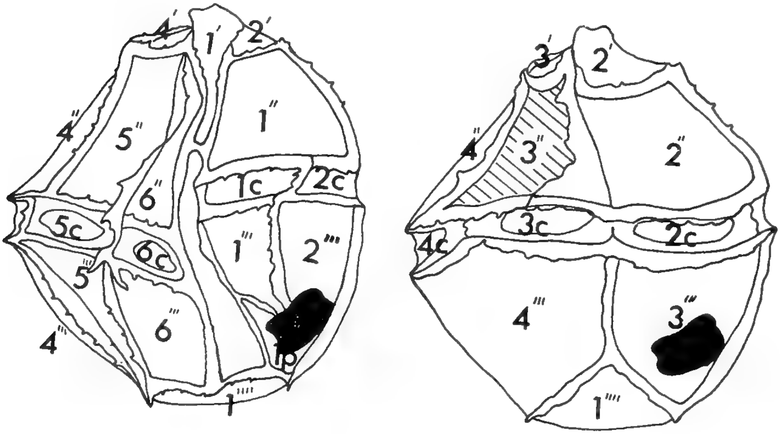

FIG. 12. *Gonyaulacysta hyaloderma* (Deflandre). Tabulation and the archaeopyle formation (plate 3″ is missing). Left, ventral view ; right, dorsal view. × *c.* 1300.

tract ; 6″ ′ is square in shape. A posterior intercalary plate (1p) separates plate 1″ ′ from the single, polygonal antapical plate (1″ ″). The shell wall and crests are delicate.

REMARKS. The diagnosis is emended to include reference to the tabulation. which was not determined by Deflandre. Downie attempted to reconstruct the tabulation on the basis of a single poorly preserved specimen ; however, he was doubtful about his reconstruction and prefaced most plate labels with a question mark. The reconstruction is here made on the basis of a single, excellently preserved specimen from the *Liostrea delta* Bed of Normandy. The species was not encountered in the English and Scottish assemblages.

G. hyaloderma was originally recorded from the Kimmeridgian of France (Deflandre, 1939b) ; subsequently, Downie observed it in the Kimmeridge Clay of Dorset and Coninck observed in the Eocene of Belgium. The specimens figured by Downie and Coninck both have longer apical horn than the holotype.

The systematic placing of this species was discussed by Sarjeant (1967) after he was able to examine the holotype, and it was redesignated as *Gonyaulacysta hyaloderma.*

Gonyaulacysta jurassica var. ***longicornis*** Deflandre, 1938

(Pl. 5, fig. 11)

1938a *Gonyaulax jurassica* var. *longicornis* Deflandre: 171, pl. 6, fig. 6.
1958 Peridinian Lantz, pl. 7, fig. 74.
1960 *G. jurassica* var. *longicornis* Deflandre ; Klement, pl. 2, figs. 6–8.
1961a *G. jurassica* var. *longicornis* Deflandre ; Sarjeant: 92–94 ; text-figs. 2, 3, 15.
1962a *G. jurassica* var. *longicornis* Deflandre ; Sarjeant: 258, pl. 1, fig. 3.
1964 *G. jurassica* var. *longicornis* Deflandre ; Downie & Sarjeant: 115.
1964 *G. jurassica* var. *longicornis* Deflandre ; Sarjeant, table 2.

1964 *Gonyaulacysta jurassica* var. *longicornis* (Deflandre) ; Deflandre: 5.
1967b *Gonyaulax jurassica* var. *longicornis* Deflandre ; Vozzhennikova: 85, pl. 19, fig. 5 ; tables 2, 11.

REMARKS. This variety of *G. jurassica* has been recorded from the Upper Jurassic of France, Germany, England and Russia. It was observed in the samples from the basal Kimmeridgian of Dorset, Le Havre and the Boulonnais.

FIGURED SPECIMEN. BM(NH) slide V.53939(1). Clay from Exogyra Marls, *c.* 1 m. above the Upper Hard Band, Cap de La Hève, Le Havre (CH 185).

DIMENSIONS. Figured specimen : overall length 75 μ, breadth 45 μ ; horn length 21 μ. Range : overall length 75–145 μ, breadth 40–80 μ ; horn length 18–25 μ. (Holotype dimensions : length 88 μ, breadth 54 μ ; horn length 30 μ, as quoted by Deflandre.) 6 specimens measured.

***Gonyaulacysta* cf. *mamillifera* (Deflandre)**

(Pl. 3, fig. 4)

DESCRIPTION. Relatively large shell, ovoidal in shape. The nearly circular cingulum divides the shell into two equal parts : epitract terminates in a mamelon form, that is broader than one is usual for an apical horn, and hypotract rounded. The plate boundaries are marked by low membraneous crests. Surface of the shell densely granular ; as a result tabulation not clear. On the dorsal side, a precingular archaeopyle is present, and possibly formed by loss of plate 3″.

FIGURED SPECIMEN. BM(NH) slide V.53965(1). Clay from Argiles de Moulin Wibert, 20 ft. below the top, south side of Cap de la Crèche, Boulonnais (CC 447).

DIMENSIONS. Figured specimen : length 88 μ, breadth 60 μ. Holotype (as measured by Deflandre) ; length 92 μ, breadth 84 μ.

REMARKS. *G. mamillifera* has only been recorded from the Kimmeridgian of France (Deflandre, 1939). A single specimen was observed in the basal Kimmeridgian assemblage from the Boulonnais. It is very similar to the holotype, but is narrower in size and is without the spinose sutures. Allocation to this species is therefore provisional only.

***Gonyaulacysta nuciformis* (Deflandre) Sarjeant, 1969**

(Pl. 6, fig. 1)

1938a *Palaeoperidinium nuciforme* Deflandre: 180, pl. 8, figs. 4–6.
1962a *P. nuciforme* Deflandre ; Sarjeant, pl. 1, fig. 8, tables 3, 4.
1962b *Gonyaulax nuciformis* (Deflandre) ; Sarjeant: 482–483, pl. 69, fig. 6 ; text-fig. 4; tables 2–3.
1964 *G. nuciformis* (Deflandre) ; Downie & Sarjeant: 115.
1964 *Palaeoperidinium nuciforme* Deflandre ; Eisenack: 609.
1964a *Gonyaulax nuciformis* (Deflandre) ; Sarjeant, table 2.
1965 *Palaeoperidinium nuciformoides* Gorka: 300–301, pl. 2, figs. 1–2.
1966 *? Gonyaulacysta nuciformis* (Deflandre) ; Sarjeant, *nomen nudum*: 132.

1967b *Gonyaulax nuciformis* (Deflandre) ; Vozzhennikova, table 11.
1967b *? Gonyaulacysta nuciformis* Deflandre ; Sarjeant, table 1, *nom. nud.*
1968 *G. nuciformis* (Deflandre) ; Sarjeant: 227, pl. 3, fig. 4.
1969 *? G. nuciformis* (Deflandre) ; Sarjeant (in press).

Gonyaulacysta nuciformis was first recorded from the Upper Jurassic of France by Deflandre (1938) ; he was uncertain as to its tabulation and placed it in the " waiting genus " *Palaeoperidinium.* Later Sarjeant observed it in the assemblages from Upper Callovian to Oxfordian of England and France (1962, 1964) ; on the basis of observation of its tabulation, he placed it in the genus *Gonyaulax* and has since transferred it to the cyst-genus *Gonyaulacysta.*

The geographic range of this species is extended to Poland by the observation in the Upper Jurassic assemblage of Magnuszew, Poland (Górka, 1965). The Polish specimens were described as a new species, but Sarjeant (1968) considers that this should be treated as a subjective junior synonym, since the diagnostic character (difficulty in observing tabulation) is thought to be inadequate.

It is present in moderate abundance in the assemblages from the basal Kimmeridgian of England, France and Scotland. The specimen of this type comparable with the specimen figured by Sarjeant (1962) ; having a spherical to ovoidal shape with thick-walled and densely granular surface are similar. Determination of the tabulation is difficult because of the wall structure of this species. A precingular archaeopyle is present, possibly formed by loss of plate 3″.

FIGURED SPECIMEN. BM(NH) slide V.52793(2). Shaly clay from the *Liostrea delta* Bed, Osmington Mills, Dorset (OM 131).

DIMENSIONS. Figured specimen : overall length 50 μ, breadth 43 μ ; horn length 7 μ. Range of English specimens (17 specimens measured) overall length 50–100 μ, breadth 40–85 μ ; horn length 4–16 μ. Range of French specimens (5 specimens measured) : overall length 49–60 μ, breadth 45–70 μ ; horn length 4–7 μ. Range of Scottish specimens (2 specimens measured) : overall length 70–80 μ, breadth 65–66 μ ; horn length 5–7 μ.

The following dimensions are quoted by Deflandre : overall length 60–65 μ, breadth 47–53 μ (approximately). Dimensions of the Callovian specimens (as quoted by Sarjeant) : overall length 56–58 μ, breadth 50–64 μ. Polish specimens ; overall length 38–54 μ, breadth 40–44 μ (as given by Górka).

Gonyaulacysta serrata (Cookson & Eisenack) Sarjeant, 1969a

(Pl. 5, fig. 7)

1958 *Gonyaulax serrata* Cookson & Eisenack: 34, pl. 3, fig. 2 ; text-figs. 12–14.
1960a *G. serrata* Cookson & Eisenack ; Cookson & Eisenack: 244.
1964 *G. serrata* Cookson & Eisenack ; Downie & Sarjeant, 115.
1964 *G. serrata* Cookson & Eisenack ; Eisenack: 403–404.
1964a *G. serrata* Cookson & Eisenack ; Sarjeant, table 2.
1966 *Gonyaulacysta serrata* (Cookson & Eisenack) ; Sarjeant, *nomen nudum*: 131.
1967b *Gonyaulax serrata* Cookson & Eisenack ; Vozzhennikova, table 11.
1967b *Gonyaulacysta serrata* (Cookson & Eisenack) ; Sarjeant, table 2, *nom. nud.*
1969 *G. serrata* (Cookson & Eisenack) ; Sarjeant (in press).

This species has been recorded from the Tithonian to Neocomian of Australia and New Guinea by Cookson and Eisenack. Badly preserved specimens, apparently attributable to it, were observed in the samples studied from Dorset, Scotland, Normandy and the Boulonnais.

These specimens agree with the diagnosis of the holotype in their general appearance and the character of the sutures. Holotype tabulation was not determined by Cookson and Eisenack ; the specimens from the basal Kimmeridgian likewise do not present a determinable tabulation.

Figured specimen. BM(NH) slide V.53935(1). Clay from the *Liostrea delta* Bed of Villerville, Normandy (VN 184).

Dimensions. Figured specimen : overall length 75 μ, breadth 70 μ. Range of English specimens (5 specimens measured) : overall length 80–109 μ, breadth 70–106 μ ; French specimens (7 specimens measured) : overall length 75–100 μ, breadth 70–100 μ ; Scottish specimen overall length 45 μ, breadth 50 μ. The range of Australian specimens (as given by Cookson and Eisenack) length 100–109 μ, breadth 94–100 μ.

Gonyaulacysta sp. A

(Pl. 3, fig. 3, Text-fig. 13)

Description. A thick-walled ovate cyst with an apical horn formed by three apical plates. Reflected tabulation : 3′, 1a, 6″, 6c, 6″ ′, 1p, 1pv and 1″ ″. Plate boundaries marked by low crests with poorly defined rows of low spines.

Plate 1′ is elongate, extending to the anterior end of the sulcus ; plates 2′ and 3′ are located above the plates 2″, 3″ and 4″. The single anterior intercalary plate (1a) is large and angular in shape. Precingular plates 1″, 2″, 3″ and 4″ are more or less of the same size ; 5″ is the largest of the precingular plates ; plate 6″ is smaller because of the presence of plate 1a. The cingulum is slightly laevorotatory and nearly equatorial, formed by six cingular plates, plate 1c being very small.

Postcingular plates 1″ ′ and 2″ ′ are pentagonal in shape ; 1″ ′ is the smallest of the postcingular plates. Plate 3″ ′, 4″ ′ and 5″ ′ are large, 6″ ′ is small and triangular-shaped. The posterior intercalary plate 1p is small and elongate. Plate 1pv separates the sulcus from the large, convex antapical plate 1″ ″.

The surface of the plates is densely granular and sparsely spiny ; these spines are higher than the sutural spines.

Precingular archaeopyle is present and forms by loss of plate 3″ ; on the figured specimen since the plate 3″ remains attached, the archaeopyle appears as a split.

Figured specimen. BM(NH) slide V.53930(1). Clay from the *Liostrea delta* Bed of Villerville, Normandy (VN 184).

Dimensions. Figured specimen : overall length 65 μ, breadth 42 μ ; horn length 5 μ ; length of the spines on the crests 1–2 μ, length of the surface spines 4 μ. The second specimen could not be measured, because of its bad preservation.

Remarks. Two specimens were observed ; the figured specimen is well preserved, but the second is not. From its general appearance and tabulation this may be an

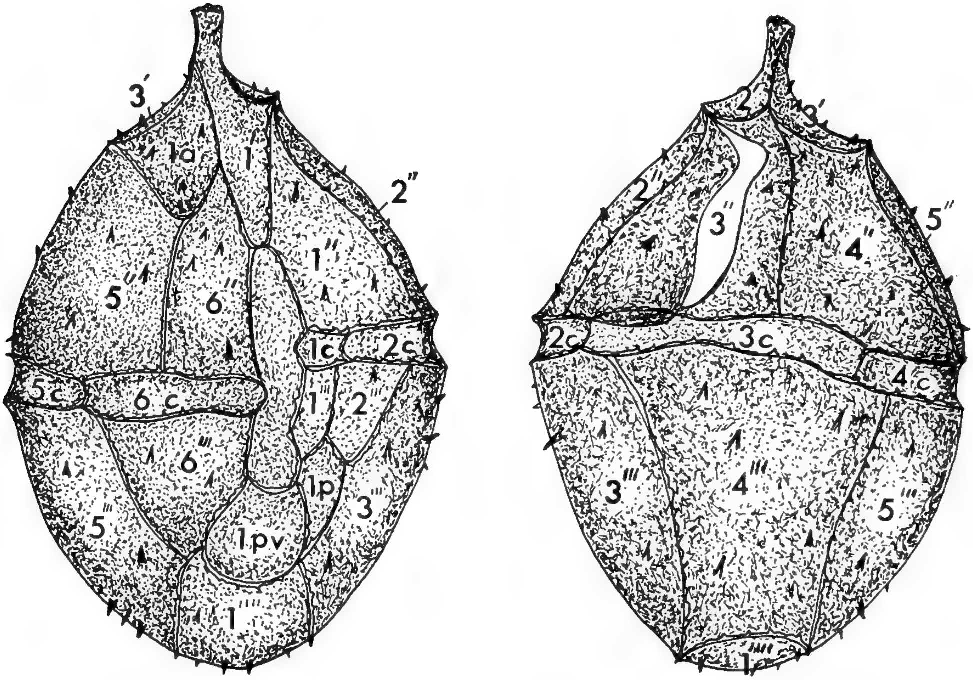

Fig. 13. *Gonyaulacysta* sp. A. Tabulation and the archaeopyle formation (plate 3″ remains attached). Left, ventral view ; right, dorsal view. ×*c*. 1280.

undescribed species of *Gonyaulacysta*. These two specimens differ from all previously described species in their tabulation and spiny surface.

Gonyaulacysta sp. B

(Pl. 6, fig. 3 ; Text-fig. 14)

Description. The broadly ovoidal theca terminates in a poorly developed apical horn. Tabulation: 4′, la, 6″, 6c, 6″ ′, lp, lpv and 1″ ″. Spiny crests of moderate height rise up on the plate boundaries. A slightly helicoid, laevorotatory cingulum of moderate breadth divides the theca into two unequal parts: the epitract is larger than the hypotract, almost $\frac{2}{3}$ of the shell length. The hypotract is dome-shaped. The sulcus is moderately broad, extending on both epitract and hypotract to the same length. The surface of the shell is densely granular.

Apical plate 1′ is elongate, its anterior and posterior ends being narrow ; together with plate 3′, it forms the apical horn. Plate 2′ is quite large ; 4′ is the smallest of the apical plates. The single anterior intercalary plate 1a is large ; as a result plate 6″ is reduced. Plate 1″ is long and narrow ; plates 2″, 3″, 4″ and 5″ are large.

Plate 1″ ′ is quadrate, as small as the single sulcal plate. All the other postcingular plates are relatively large. Posterior intercalary plate 1p is small and triangular,

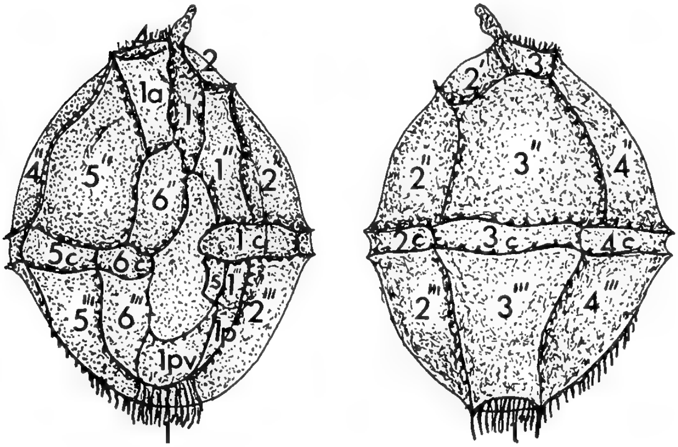

Fig. 14. *Gonyaulacysta* sp. B. Tabulation. Left, ventral view ; right, dorsal view. ×*c.* 950.

placed below plate 1″ ′. A crescent-shaped plate (1pv) separates the single antapical plate 1″ ″ from the sulcus. Plate 1″ ″ is characteristically surrounded by long (nearly three times longer than the sutural spines), thin, simple spines. No archaeopyle was seen.

Figured specimen. BM(NH) slide V.53965(2). Clay from Argiles de Moulin Wibert (20 ft. below the top) south side of Cap de La Crèche, Boulonnais (CC 447).

Dimensions. Figured specimen : overall length 78 μ, breadth 50 μ ; horn length 8 μ ; length of the sutural processes 3–5 μ, antapical processes 8 μ ; breadth of the cingulum 3–5 μ. The second specimen could not be measured.

Remarks. Only two specimens were encountered, one of them badly preserved but the other good enough for study. With their long processes around the antapex, these specimens are different from all described species of *Gonyaulacysta* ; this is probably a new species but, for fuller knowledge, more specimens must be examined.

Gonyaulacysta sp. C

(Pl. 4, figs. 10, 11 ; Text-fig. 15)

Description. This is an infrequent species. All the three specimens encountered are somewhat crushed, folded or covered by debris ; the one figured was the best oriented for study. The surface is densely granular ; because of the granulation and bad orientation, it was difficult to distinguish the tabulation.

The thick-walled theca is almost spherical, with a moderately long apical horn. Tabulation : 4′, 1a, 6″, 6–7c, 7″ ′, 1p, 1pv, 1″ ″. Plate 1′ occupies the anterior prolongation of the sulcus. Plates 2′ and 3′ are small ; the position of the boundary between them was not confirmed. Plate 4′ is almost as large as plate 1′. The single anterior intercalary plate is small, placed between the plates 4′ and 6″. The pre-

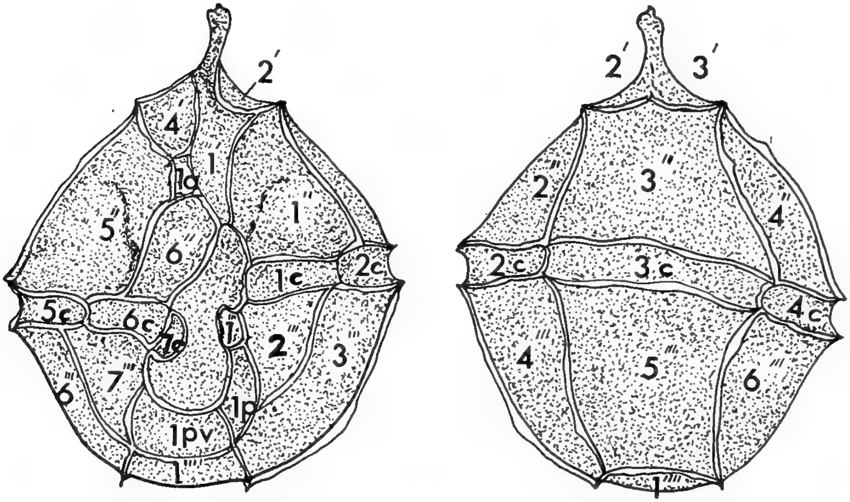

FIG. 15. *Gonyaulacysta* sp. C. Tabulation. Left, ventral view ; right, dorsal view. ×*c*. 800.

cingular plates are generally large, plate 6″ being of reduced size because of the intercalary plate 1a.

The postcingular plates are of variable size and shape : plates 1″ ′ and 1p are both small, plate 2″ ′ is also reduced and does not have a boundary with the antapical plate. Plates 3″ ′, 4″ ′, 5″ ′ and 6″ ′ are relatively large ; plate 7″ ′ is in contrast reduced, having nearly the same size as plate 2″ ′. The quite broad posterior intercalary plate 1pv separates the sulcus from the single antapical plate 1″ ″.

The plate boundaries are demarcated by delicate crests of variable height.

The cingulum is of moderate breadth, helicoid and laevorotatory. The number of the cingular plates is hesitantly mentioned because the character of the small plate beside 6c is doubtful ; it may be either a cingular plate or a sulcal plate. The sulcus is short, broadening posteriorly.

A precingular archaeopyle, formed by loss of plate 3″, was seen in one of the three specimens.

FIGURED SPECIMEN. BM(NH) slide V.53966(1). Clay from Argiles de Moulin Wibert, 20 ft. below the top, on the south side of Cap de La Crèche, Boulonnais (CC 447).

DIMENSIONS. Figured specimen : overall length 68 μ, breadth 62 μ ; horn length 8 μ ; height of the crests 4–5 μ. Range : overall length 65–68 μ, breadth 58–62 μ ; horn length 8–12 μ.

REMARKS. In its general form, this unnamed species of *Gonyaulacysta* differs from all described species. The most closely similar species is *G. palla*, which has similarly spherical shape and comparable tabulation ; but this form differs from it in its apical horn, sutural crests, absence of plate 1a, and presence of plate 1pv.

Because of its seventh postcingular plate it is comparable with *G. fetchamensis* and *G. ehrenbergii*, but its other morphologic features are different. The naming of this species is deferred until further, better specimens are available.

Genus ***OCCISUCYSTA*** gen. nov.

Derivation of the name. Latin, *occisus*, ruined, lost, undone ; with reference to loss of two precingular plates in archaeopyle formation. Greek, *kystis*, cell, cyst.

Diagnosis. Proximate dinoflagellate cysts, spherical, subspherical or broadly ovoidal, with the tabulation 4′, 0–1a, 6″, 6c, 6–7‴, 1p, 0–1pv, 1⁗. Cingulum strongly or weakly helicoid ; sulcus generally extending onto epitract. Strong apical horn present, median and antapical horns lacking. Sutures in form of high ridges, denticulate, fenestrate or spiny. Surface of the shell is granular or tuberculate. Precingular archaeopyle is normally present and forms by loss of two precingular plates (2″ and 3″).

Type species. *Occisucysta balios* sp. nov. Base of the Kimmeridgian (Upper Jurassic), Normandy.

Remarks. This genus is similar to *Gonyaulacysta* in its tabulation, but distinguished by the loss of two precingular plates in archaeopyle formation.

Two new species from the Kimmeridgian assemblages studied, accord with the diagnosis of this genus; a third species is transferred from the genus *Gonyaulacysta*, since it has a two-plate precingular archaeopyle.

Occisucysta balios sp. nov.

(Pl. 5, figs. 1, 2 ; Text-fig. 16)

Derivation of the name. Greek, *balios* spotted, with reference to the tubercules on the surface.

Diagnosis. *Occisucysta* having a subspherical shell terminating in a strong, thick apical horn. Antapex rounded, dome-shaped. Tabulation : 4′, 1a, 6″, 6c, 7‴, 1p, 1pv, 1⁗. The crests on the sutures are denticulate and fenestrate. Cingulum strongly helicoid, laevorotatory. Sulcus mainly confined to the epitract. Surface of the shell granular and sparsely tuberculate.

Holotype. BM(NH) slide V.53934(2). Kimmeridge Clay from the *Liostrea delta* Bed of Villerville, Normandy (VN 184).

Dimensions. Holotype : overall length 60 μ, breadth 60 μ ; shell length 50 μ, breadth 55μ ; horn length 8 μ, breadth 6 μ. Dimensions of French specimens (4 specimens measured) : length 58–62 μ, breadth 58–59 μ ; horn length 5–8 μ, breadth 5–7 μ. Tubercules approximately 0·5–1·2 μ in diameter. English specimen overall length 55 μ, breadth 63 μ ; horn length 10 μ.

Description. This proximate cyst has an apical horn which is formed by all four apical plates. Plate 1′ is elongate, narrowing as it approaches the horn ; the

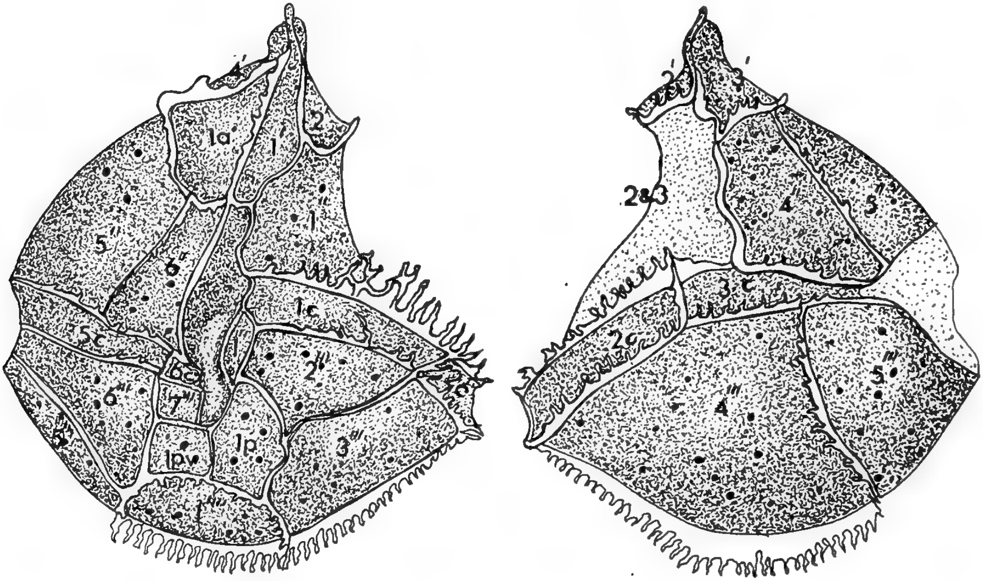

Fig. 16. *Occisucysta balios* sp. nov. Tabulation and the archaeopyle formation of the holotype (plates 2″ and 3″ are missing). Left, ventral view ; right, dorsal view. ×*c*. 1280.

other apical plates are relatively large, roughly triangular. Intercalary plate 1a is large, and the precingular plate 6″ is reduced. Plate 5″ is longer than the other surviving precingular plates. Identification of cingular plates was rendered problematical because of the poor preservation and the high crests, which partially obscure the shell itself.

Six postcingular plates are present. Plate 1″ ′ is very small. Plate 4″ ′ is largest and 7″ ′ is smallest of the plates ; because of its unusual situation, above the posterior intercalary plate 1pv, plate 7″ ′ could alternatively be regarded as sulcal plate. Posterior intercalary plate 1p is quite large, 1pv is tetragonal in shape. A single plate occupies the antapex, 1″ ″.

Surface of the plates granular with, in addition to, an irregular scatter of tubercles. The number of the tubercles on each plate is between 1 and 16 ; no tubercles were observed on the cingulum and sulcus. The membraneous crests on the sutures distally deeply denticulate or fenestrate.

Remarks. The specimens observed were broken and badly preserved, the holotype being the best preserved. (It is probable that the large archaeopyle may help to render this species especially susceptible to further damage.) It is similar to the species of *Gonyaulacysta* in its tabulation, but it is easily distinguished from all previously described species by its tuberculate surface and the archaeopyle formation by loss of two precingular plates.

Occisucysta sp.

(Pl. 7, fig. 8)

DESCRIPTION. This proximate cyst is spherical in shape, with a long apical horn and flattened antapex. The cingulum divides the theca into two parts, with the epitract slightly smaller than the hypotract. Because of the poor preservation, the tabulation was not fully determinable, but it appears to be typical for the genus. The plates on the dorsal side only were determinable : 3 apical, 4 precingular, 3 cingular, 4 postcingular and 1 antapical plates were observed. Two precingular plates, probably 2″ and 3″, are lost to form the large archaeopyle which is characteristic for the genus. The plate boundaries bear complex spines ; also there are some spines at the tip of the horn. The surface of the shell is densely granular.

FIGURED SPECIMEN. BM(NH) slide V.53945(1). Clay from the immediate base of the Kimmeridge Clay, Ringstead Bay, Dorset (RB 219).

DIMENSIONS. Figured specimen : overall length 78 μ, breadth 77μ ; horn length 25 μ, sutures 5–7 μ high.

REMARKS. Only a single poorly preserved specimen was available for study : it was attributed to the genus *Occisucysta*, since it has a large archaeopyle formed by loss of two plates. It differs from *O. balios*, in its long apical horn, details of the plates, and form of the crests. This new form is similar to *G. cladophora* in suture ornament and proportions, but it differs in the mode of archaeopyle formation. Better specimens are needed to determine fully the tabulation ; however, it is attributed to the genus *Occisucysta* without hesitation.

Occisucysta evitti (Dodekova) comb. nov.

1969 *Gonyaulacysta evitti* Dodekova, 14–15, pl. 1, figs. 1–8; table 1

REMARKS. This species, recently described from the Tithonian of Bulgaria, is characterised by a two-plate precingular archaeopyle. Although Dodekova did not mention the anterior intercalary plate 1a, the photographs of the holotype specimen of *G. evitti* show that the plate above plate 6″, which was indicated as plate 4′, is in fact the intercalary plate 1a, and that a boundary is present.

Genus ***LEPTODINIUM*** Klement, emend. Sarjeant, 1969

Leptodinium amabilis (Deflandre) Sarjeant, 1969

Plate 12, figs. 1, 2

1939 *Gonyaulax amabilis* Deflandre: 141–145, pl. 6, fig. 8.
1941 *G. amabilis* Deflandre ; Deflandre: 11, pl. 3, figs. 8, 9 ; text-figs. 1, 2.
1964 *G. amabilis* Deflandre ; Downie & Sarjeant: 113.
1964 *G. amabilis* Deflandre ; Eisenack: 315–316.
1964a *G. amabilis* Deflandre ; Sarjeant, table 2.
1966 *Gonyaulacysta amabilis* (Deflandre) ; Sarjeant, *nomen nudum*: 130.

1967b *Gonyaulax amabilis* Deflandre ; Vozzhennikova, 91 table 11.
1967a *Gonyaulacysta amabilis* (Deflandre) ; Sarjeant, *nomen nudum*, table 1.
1969 *Leptodinium amabilis* (Deflandre) ; Sarjeant (in press).

REMARKS. *Leptodinium amabilis* has been recorded from the Kimmeridgian of France by Deflandre (1939, 1941). It was observed also in the assemblages from England and France. Their general structure and the number of the plates correspond closely to Deflandre's holotype, but the preservation of the basal Kimmeridgian specimens was not good enough for fuller study.

FIGURED SPECIMEN. BM(NH) slide V.52805(1). Clay from 15 ft. above Ringstead Coral Bed. West of Osmington Mills, Dorset (OM 419).

DIMENSIONS. Figured specimen : length 43 μ, breadth 35 μ ; second English specimen length 40 μ, breadth 36 μ. Length of French specimen 50 μ, breadth 45 μ. These specimens are larger than the holotype (as quoted by Deflandre) length 38 μ, breadth 32 μ.

Leptodinium arcuatum (Klement), emend.

(Pl. 7, figs. 1, 2 ; Text-fig. 17)

1960 *Leptodinium arcuatum* Klement: 48, pl. 6, figs. 5, 6.
1964 *L. arcuatum* Klement ; Downie & Sarjeant: 126.
1964 *L. arcuatum* Klement ; Eisenack: 489.
1964a *L. arcuatum* Klement ; Sarjeant, table 2.
1966 *L. arcuatum* Klement ; Sarjeant, *nomen nudum*: 135.
1967a *L. arcuatum* Klement ; Sarjeant, *nomen nudum*, table 2.
1969 *L. arcuatum* Klement ; Sarjeant (in press).

EMENDED DIAGNOSIS. A *Leptodinium* having a relatively large, subspherical shell. Tabulation : 4′, 1a, 6″, 6c, 5‴, 1p and 1⁗ ; plates bordered by delicate, high crests. Cingulum helicoid, laevorotatory ; sulcus long, extending on the epitract and hypotract for nearly equal lengths and broadening on the hypotract. Surface of the shell very finely granular or smooth. A large precingular archaeopyle forms by loss of plate 3″.

HOLOTYPE. Specimen Pr. 1149/67, Tübingen, Geol.-Paläont. Institut ; from Malm Upper Alpha (Oxfordian), borehole core between 1783·1 and 1785·9 m. depth. South Germany.

FIGURED SPECIMEN. BM(NH) slide V.52799(1). Shaly clay from the base of Kimmeridge Clay, *Liostrea delta* Bed, Osmington Mills, Dorset (OM 131).

DIMENSIONS. Holotype : overall length 74 μ, breadth 77 μ. Figured specimen : overall length 80 μ, breadth 78 μ ; shell length 74 μ, breadth 70 μ. Range of the English specimens (5 specimens measured) : overall length 65–73 μ, breadth 60–80 μ ; French specimens (3 specimens measured) : overall length 65–73 μ, breadth 50–55 μ.

DESCRIPTION. The subspherical shell is divided by the laevorotatory cingulum into two parts. The epitract is approximately hemispherical, the hypotract is in the form of a truncated cone. The crests are thin and high ; their distal edge is always smooth.

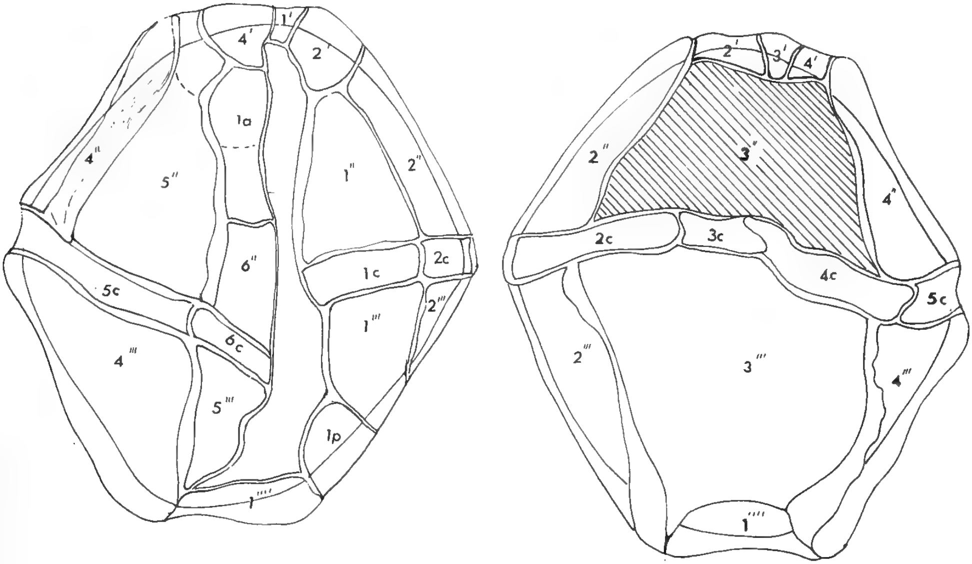

FIG. 17. *Leptodinium arcuatum* (Klement). Tabulation and the archaeopyle formation (plate 3″ is missing). Left, ventral view ; right, dorsal view. ×*c*. 1280.

The crests separate the four apical plates at the apex : plate 1′ and 3′ are smaller than plates 2′ and 4′. Precingular plates are large, only plate 6″ is somewhat reduced to accommodate intercalary plate 1a, which is long.

Five well-developed postcingular plates are present, plate 5″ ′ being smaller than the other postcingular plates. Posterior intercalary plate 1p is placed between the plates 1″ ′ and 1″ ″. The antapex is occupied by a single antapical plate 1″ ″.

The sulcus is long, extending between the apex and the antapex and broadening posteriorly.

REMARKS. The diagnosis is emended to include reference to the tabulation and the mode of archaeopyle formation, which were not mentioned by Klement.

L. arcuatum was originally recorded from the Oxfordian of Germany by Klement (1960). Well-preserved specimens were observed infrequently in both English (Dorset) and French (Normandy and the Boulonnais) assemblages.

Leptodinium clathratum (Cookson & Eisenack) Sarjeant, 1969

(Pl. 11, fig. 8)

1960a *Gonyaulax clathrata* Cookson & Eisenack: 246–247, pl. 37, fig. 5 ; text-fig. 2.
1964 *G. clathrata* Cookson & Eisenack ; Downie & Sarjeant: 114.
1964 *G. clathrata* Cookson & Eisenack ; Eisenack: 339.
1964a *G. clathrata* Cookson & Eisenack ; Sarjeant, table 2.
1966 *Gonyaulacysta clathrata* (Cookson & Eisenack) ; Sarjeant, *nomen nudum*: 130.
1967b *G. clathrata* (Cookson & Eisenack) ; Vozzhennikova, table 11.

1967a *G. clathrata* (Cookson & Eisenack) ; Sarjeant, table 1, *nomen nudum*
1969 *Leptodinium clathratum* (Cookson & Eisenack) ; Sarjeant (in press).

DESCRIPTION. The relatively large shell is divided into two equal parts by the cingulum. Apical tabulation is not clear in this material ; tabulation : ?′, ?Oa, 6″, 6″′, 1p and 1″″. The precingular archaeopyle is present on the dorsal side, possibly formed by loss of plate 3″. Cingulum and sulcus are narrow, the cingulum being almost planar. Processes and apical horn lacking. The plate boundaries bear moderately high, delicate, membraneous crests.

FIGURED SPECIMEN. BM(NH) slide V.53971(1). Clay from top of the Grès de Châtillon, south side of Audresselles, Boulonnais (CC 450).

DIMENSIONS. Figured specimen : overall length 105 μ, breadth 105 μ, crests 8–10 μ high. Diameters of the holotype (100×100 μ), as quoted by Cookson and Eisenack, are similar to these.

REMARKS. *L. clathratum* has been previously recorded from the Upper Jurassic (probably Tithonian) of Australia and New Guinea (Cookson & Eisenack, 1960). This is the first time it has been observed in Europe. Unfortunately only one poorly preserved specimen was encountered.

This species is transferred to the genus *Leptodinium* by Sarjeant (1969, in press), since it has no apical horn.

Leptodinium egemenii sp. nov.

(Pl. 10, figs. 5, 6 ; Text-fig. 18)

DERIVATION OF THE NAME. Named in honor of Dr. Recep Egemen, of the Geology Department of Ege University, Izmir, Turkey.

DIAGNOSIS. *Leptodinium* with proximate cyst polygonal in outline ; with the reflected tabulation 4′, 6″, 6c, 6″′, 2p and 1″″. Processes and apical horn lacking. Cingulum slightly spiral, sulcus approximately spindle-shaped. Endophragm and periphragm are in contact except at the apex and antapex : a pronounced antapical pericoel is present, but the degree of separation at the apex is small. Surface of the shell smooth. Precingular archaeopyle formed by loss of plate 3″.

HOLOTYPE. BM(NH) slide V. 52794(1). Shaly clay from the *Liostrea delta* Bed, Osmington Mills, Dorset (OM 131).

DIMENSIONS. Holotype : overall length 70 μ, breadth 58 μ, shell length 54 μ, breadth 58 μ. Range of the English specimens (10 specimens measured) : length 50 (42)-80 (57) μ, breadth 40–50 μ ; French specimens (10 specimens measured) : length 55 (35)–78 (50) μ, breadth 43–52 μ ; Scottish specimen : length 65 (45) μ, breadth 48 μ (1 specimen measured). [The length of the endoblast is shown in parenthesis.]

DESCRIPTION. The thin-walled polygonal theca is divided into an approximately hemispherical epitract and a hypotract in the form of a truncated cone, the antapex being quite flat.

The first apical plate (1′) is elongate, situated in the anterior prolongation of the

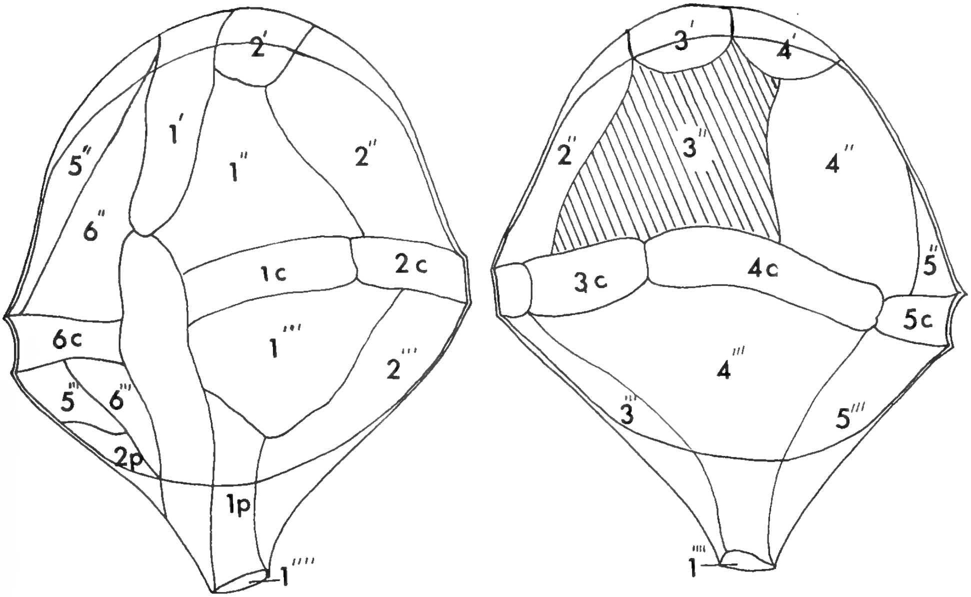

Fig. 18. *Leptodinium egemenii* sp. nov. Tabulation and the archaeopyle formation of the holotype (plate 3″ is missing). Left, ventral view ; right, dorsal view. ×*c.* 1280.

sulcus ; the three other apical plates are more or less uniform in size and smaller than plate 1′. Six precingular plates, without any intercalary plate, together with the apical plates occupy the epitract. Plates 1″ and 2″ are larger than the others ; plate 3″ lost to form the precingular archaeopyle ; plates 4″ and 5″ are elongate, 6″ is approximately triangular in shape.

Six postcingular plates are present : the first (plate 1″ ′) is small and more or less tetragonal; 2 ″ ′ is narrow and elongate, plate 3″ ′ is also elongate. Plate 4″ ′ is largest of the postcingular plates. Plate 5″ ′ is large and P-shaped as a result of the presence of the posterior intercalary plate 2p. Plate 6″ ′ is smaller of the postcingular plates and triangular-shaped. One of the two posterior intercalary plates, 1p, is elongate and long ; because of its accommodation, plate 1″ ′ is reduced. Plate 2p is small and placed posterior to plates 5″ ′ and 6″ ′. The single antapical plate 1″ ″ is very small and flattened.

The sutures are poorly marked by low crests, their distal edge is always smooth.

Remarks. *L. egemanii* is characterized by its tabulation, lack of an apical horn, and presence of an antapical pericoel. The tabulation was difficult to determine because the crests were poorly marked, and the preservation generally not good. It was observed in the Dorset, Scottish and Le Havre assemblages in moderate abundance.

Although it has a *Gonyaulacysta*-type tabulation, it is not a species of *Gonyaulacysta* because of the absence of an apical horn, according to the emended diagnoses of *Gonyaulacysta* and *Leptodinium* (Sarjeant, 1969) ; it is therefore attributed to the genus *Leptodinium*.

This new species of *Leptodinium* compares with the species of the genus *Psaligonyaulax* and *Tubotuberella*, since it has a pronounced antapical pericoel. In the lack of apical horn and in the detail of the tabulation, it differs from *Psaligonyaulax*. Because Vozzhennikova was unable to give the tabulation of the genus *Tubotuberella*, it is impossible to be certain regarding the generic assignation for this new species.

***Leptodinium* cf. *subtile* (Klement)**

(Pl. 11, figs. 1, 2 ; Text-fig. 19)

DESCRIPTION. This form has a subspherical shell, without apical horn or processes. The cingulum is nearly circular, dividing the theca into two slightly unequal parts, the hypotract being larger than the epitract. Tabulation : 4′, 1a, 6″, 6c, 5″ ′, 2p and 1″ ″. Apical plate 1′ is long and situated in the anterior extension of the sulcus ; the three other apical plates are small. Intercalary plate 1a is placed between plates 4′ and 6″, the latter plate is reduced to accommodate it. The other precingular plates are large.

Three of the postcingular plates (2″ ′, 3″ ′ and 4″ ′) are large ; plates 1″ ′ and 5″ ′ are small because of the intercalary plates 1p and 2p : 1p placed below the first postcingular plate, 2p placed below the fifth postcingular plate. Both of the intercalary plates are rather large. The single antapical plate 1″ ″ is slightly polygonal and convex.

The sutures between the plates, have high, membraneous crests, distal edge of the

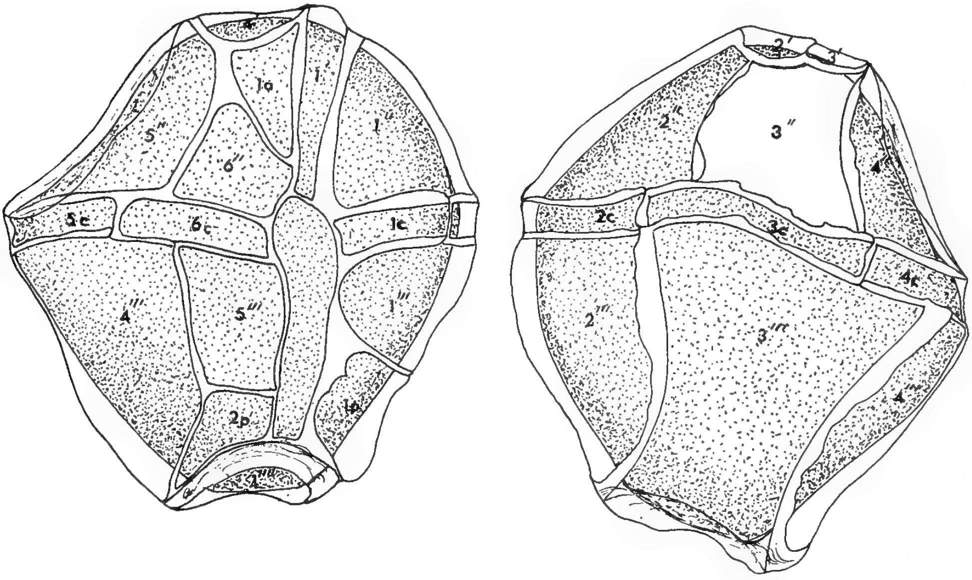

FIG. 19. *Leptodinium* cf. *subtile* (Klement). Tabulation and the archaeopyle formation (plate 3″ is missing). Left, ventral view ; right, dorsal view. × *c*. 1280.

crests is smooth. The surface of the shell is finely granular. A large precingular archaeopyle is present on the dorsal side, formed by loss of plate 3″.

FIGURED SPECIMEN. BM(NH) slide V.52803(1). Shaly clay from the base of Kimmeridge clay, *Liostrea delta* Bed, Osmington Mills, Dorset (OM 131).

DIMENSIONS. Figured specimen : overall length 80 μ, breadth 85 μ ; shell length 70 μ, breadth 60 μ. Dimensions of the second specimen : length 70 μ, breadth 72 μ.

The holotype of *L. subtile* has 74 μ length and 77 μ breadth, as quoted by Klement. In this view there is no difference between English and German specimens.

REMARKS. *L. subtile* has been previously recorded from the Oxfordian of Germany by Klement (1960). Two well-preserved specimens, observed from the Dorset assemblage, correspond in general structure, crests and dimensions to the holotype as figured by Klement ; however, they differ in the detail of the apical plates and the presence of intercalary plate 1a. These specimens are therefore compared with, but not placed in, Klement's species.

Cyst-Family **MICRODINIACEAE** Eisenack, emend. Sarjeant & Downie, 1966

Genus ***BELODINIUM*** Cookson & Eisenack, 1960a

Belodinium dysculum Cookson & Eisenack, 1960a

(Pl. 7, fig. 3)

1960a *Belodinium dysculum* Cookson & Eisenack: 250, pl. 37, fig. 14.
1964 *B. dysculum* Cookson & Eisenack ; Downie & Sarjeant: 99.
1964 *B. dysculum* Cookson & Eisenack ; Eisenack: 54.
1964a *B. dysculum* Cookson & Eisenack ; Sarjeant, table 2.
1967a *B. dysculum* Cookson & Eisenack ; Sarjeant, table 2.

REMARKS. A single specimen, observed in the base of Kimmeridgian of Dorset, is closely similar to *B. dysculum*, previously recorded from probable Tithonian of Western Australia by Cookson & Eisenack (1960).

FIGURED SPECIMEN. BM(NH) slide V.52798(1). Shaly clay from the base of Kimmeridge Clay, *Liostrea delta* Bed, Osmington Mills, Dorset (OM 131).

DIMENSIONS. Figured specimen : overall length 95 μ, breadth 55 μ. This is similar to the holotype dimensions as quoted by Cookson and Eisenack (length 97 μ, breadth 42 μ).

Genus ***DICTYOPYXIS*** Cookson & Eisenack, 1960b

Dictyopyxis sp.

(Pl. 4, fig. 1)

DESCRIPTION. This form is characterized by the highly reticulate surface. Each small field is separated by high sutures from the others. There is no obvious tabulation ; but some small fields on the equatorial plane together form a median line, which may well be equivalent to the cingulum of a motile dinoflagellate. The apex is lost in archaeopyle formation.

FIGURED SPECIMEN. BM(NH) slide V.53956(1). Kimmeridge Clay from the west of Osmington Mills, Dorset, which is 20 ft. above the Ringstead Coral Bed (OM 420).

DIMENSIONS. Figured specimen : overall length (apex lacking) 55 μ, breadth 50 μ. Range of the English specimens (4 specimens measured) : overall length (apex lacking) 30–36 μ, breadth 40–42 μ. Single French specimen is overall length (apex lacking) 50 μ, breadth 52 μ.

REMARKS. The specimens observed were generally badly preserved. They differ from previously known species of *Dictyopyxis* (*D. areolata* and *D. reticulata*) and possibly represent a new species, but better specimens are needed before this can be confirmed.

Genus ***HISTIOPHORA*** Klement, 1960

Histiophora cf. ***ornata*** (Klement)

(Pl. 11, fig. 3)

REMARKS. *Histiophora ornata* has previously been recorded from Malm Lower Delta of Germany by Klement (1960). Observed specimens, one from Stretham and two from the Boulonnais, are generally similar to Klement's species, in that they have ellipsoidal shells, bearing four quadrilateral isolated fields, and develop an apical archaeopyle. They differ only in the form of the crests, which are deeply denticulate, having almost the aspect of processes.

FIGURED SPECIMEN. BM(NH) slide V.52964(1). Clay from Argiles de Moulin Wibert, 20 ft. below the top, south side of Cap de La Crèche, Boulonnais (CC 447).

DIMENSIONS. Figured specimen : overall length (apex lacking) 55 μ, breadth 45 μ ; height of the crests 5–7 μ. The second specimen from the Boulonnais has length 35 μ (apex lacking) and breadth 32 μ. Length of the Stretham specimen (apex lacking) 35 μ, breadth 35 μ. On both height of the crests 5–7 μ. These are smaller than the German specimen, which was quoted by Klement (length 60 μ, breadth 43 μ).

Genus ***MEIOUROGONYAULAX*** Sarjeant, 1966

Meiourogonyaulax staffinensis sp. nov.

(Pl. 3, fig. 1 ; Text-fig. 20 a, b)

DERIVATION OF THE NAME. Named after the type locality, Staffin Bay, Skye, Scotland.

DIAGNOSIS. *Meiourogonyaulax* having a subspherical to elongate theca, lacking the apex in all specimens seen. Tabulation : ?′, ? Oa, 6″, 6c, 6‴, 2p, 1pv and 1⁗. Crests are moderately high, slightly granulate with smooth distal edges. Cingulum

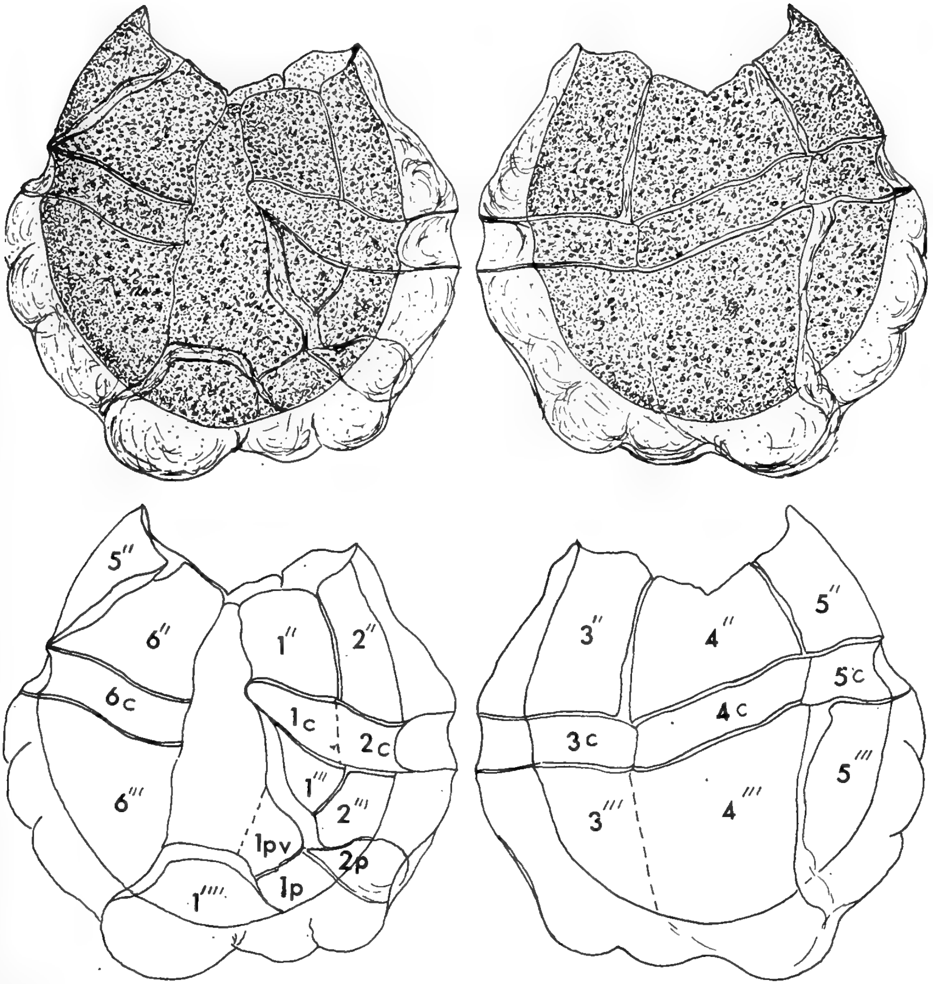

FIG. 20. *Meiourogonyaulax staffinensis* sp. nov. A. General appearance and the apical archaeopyle of the holotype. Left, ventral view; right, dorsal view. ×*c.* 1320. B. Tabulation (the apical plates are lost in the archaeopyle formation). ×*c.* 1320.

and sulcus are characteristically marked by deep furrows. The cingulum is slightly helicoid, laevorotatory, the sulcus broads towards the antapex. The shell surface is densely granular, sometimes tuberculate.

HOLOTYPE. BM(NH) slide V.53620(1). Shale from 100 ft. above the second dolerite sill, Staffin Bay, Skye (SS 627).

DIMENSIONS. Holotype: overall length (apex lacking) 50 μ, breadth 55 μ; crests 3–8 μ high; cingulum *c.* 6 μ broad. Range of the English specimens (7 specimens measured): overall length (apex lacking) 48–80 μ, breadth 50–78 μ; French specimens (6 specimens measured): overall length (apex lacking) 65–75 μ, breadth 58–80 μ ; Scottish samples (4 specimens measured) : overall length (apex lacking) 50–60 μ, breadth 45–70 μ.

DESCRIPTION. A proximate cyst of subspherical to elongate outline, with a dome-shaped hypotract. Because of the densely granulate surface, determination of the tabulation was difficult. The apex, with all the apical plates, was always lost to form the apical archaeopyle. No intercalary plate was observed. Six precingular plates are present : plate 1″ is the smallest of the precingular plates, the others being almost uniform of size.

Six postcingular plates are also present, plates 1″′ and 2″′ being reduced to accommodate posterior intercalary plates, 1p, 2p and 1pv ; plate 6″′ is much larger. The positions of the boundaries between the plates 3″′ and 4″′, and between the sulcus and plate 1pv, could not be confirmed. The antapex is occupied by a single plate 1″″.

The cingulum is broad, not less than one tenth of the shell length, being slightly laevorotatory spiral. The sulcus is likewise broad, extending onto both epitract and hypotract, being much broader towards the posterior.

The shell surface is densely granular and sometimes coarsely tuberculate. The tubercles have a diameter of approximately 0·5–1 μ ; they are scattered at random over the generally finely granulate surface.

The crests on the sutures are moderately high, smooth or slightly granulate and faintly striate.

REMARKS. Specimens were observed in the assemblages from England, Scotland and France ; they differ in the nature of the crests, surface ornamentation and general aspect from all previously described species of *Meiourogonyaulax*.

Meiourogonyaulax sp.

(Pl. 13, fig. 10, text-fig. 21)

DESCRIPTION. Shell elongate, lacking the apex. Antapex rounded. Without the apex, epitract and hypotract are more or less of the same length. Tabulation : ?4′, 1a, 6″, 6c, 6″′, 1p and 1″″.

Apical plates are lost in the archaeopyle formation. Plate 1a is located between plates 4′ and 5″, plate 5″ being therefore reduced. First precingular plate 1″ is almost quadrate in shape. The precingular plates on the dorsal side, are larger than the others.

Postcingular plate 1″′ is tetragonal and large. Plate 2″′ being reduced and elongate, separated from the antapex by a posterior intercalary plate (1p). Plate 3″′ is largest of the postcingular plates. Plate 4″′ and 5″′ are reduced, since the large antapical plate 1″″ occupies a large area. Plate 6″′ is small.

The cingulum is almost planar, occupied by 6 cingular plates of relatively uniform size. The sulcus is broad, extending between apex and antapex.

The crests on the sutures are high and delicate, with smooth or denticulate edges ; around the antapical plate 1″″ being formed of distally bifid, process like projections.

The surface of the shell is smooth.

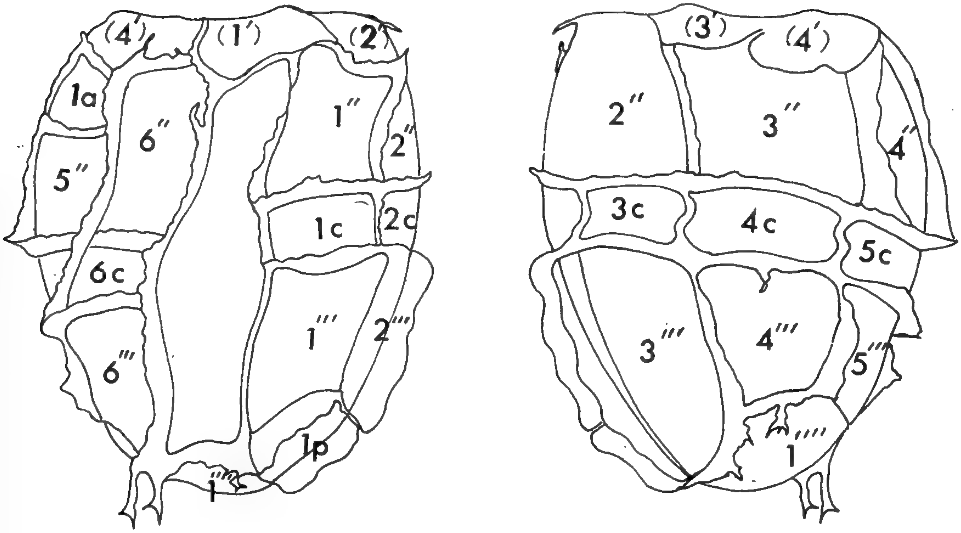

FIG. 21. *Meiourogonyaulax* sp. Tabulation (the apical plates are lost in the archaeopyle formation). Left, ventral view ; right, dorsal view. ×*c*. 1600.

FIGURED SPECIMEN. BM(NH) slide V.53973(1). Shale from 60 ft. above the second dolerite sill, Staffin Bay, Skye (SS 625).

DIMENSIONS. Figured specimen : overall length (apex lacking) 45 μ, breadth 35 μ ; crests 3–6 μ high ; antapical projections length 8 μ. Second specimen overall length (apex lacking) 60 μ, breadth 48 μ ; crests 4–6 μ high.

REMARKS. Two specimens observed were small and transparent, which makes the plates difficult to identify ; the tabulation is also masked by the high crests.

In its small size and apical archaeopyle, it is close to *Microdinium* species, but the number of the apical plates was obviously more than one : from the angular profile of the archaeopyle, the former presence of four apical plates is deduced. This species is accordingly attributed to *Meiourogonyaulax*. The finding of further specimens of this morphological type is necessary before its correct systematic place can be determined and, for this reason, no specific name is given here.

Cyst-Family **PAREODINIACEAE** Gocht, emend. Sarjeant & Downie, 1966

Genus ***APTEODINIUM*** Eisenack 1958

Apteodinium granulatum Eisenack, 1958

(Pl. 4, fig. 6)

? 1935 *Palaeoperidinium ventriosum* O. Wetzel ; Deflandre: 228, pl. 15, fig. 5.
? 1936 *P. ventriosum* O. Wetzel ; Deflandre: 27, pl. 15, figs. 1–4.
? 1936 *P. ventriosum* O. Wetzel ; Deflandre, fig. 100.
1958 *Apteodinium granulatum* Eisenack: 386, pl. 23, figs. 8–14 ; text-fig. 3.

1959 *A. granulatum* Eisenack ; Gocht: 64, pl. 5, fig. 2; table l.
1961 *A. granulatum* Eisenack ; Alberti: 24, pl. 4, figs. 4–6, table c.
1963 *A. granulatum* Eisenack ; Balteş: 584, pl. 4, fig. 11.
1964 *A. granulatum* Eisenack ; Downie & Sarjeant: 82.
1964 *A. granulatum* Eisenack ; Eisenack: 37.
1966 *A. granulatum* Eisenack ; Davey, (Ph.D. Thesis): 88–89, pl. 3, figs. 7–9.
1967b *A. granulatum* Eisenack ; Vozzhennikova: 61, pl. 17, fig. 3; table 2.
1967a *A. granulatum* Eisenack ; Sarjeant, table 2.
1969 *A. granulatum* Eisenack; Davey: 130–131, pl. 3, figs. 5, 6.

DESCRIPTION. The spheroidal to ovoidal shell is relatively thick-walled (1·5–2 μ) and bears a strong apical horn. Antapex is rounded. There is no definite indication of tabulation. A cingulum is weakly indicated, sometimes also a sulcus. On the dorsal side a precingular archaeopyle is present, forming by loss of probably plate 3″. The surface is finely granular.

FIGURED SPECIMEN. BM(NH) slide V.53949(1). Kimmeridge Clay from the base, Ringstead Bay, Dorset (RB 219).

DIMENSIONS. Figured specimen : overall length 87 μ, breadth 80 μ ; horn length 13 μ. Range of the English specimens (6 specimens measured) : overall length 80–90 μ, breadth 75–80 μ ; horn length 8–13 μ ; French specimens (6 specimens measured) : overall length 78–83 μ, breadth 70–79 μ. The dimensions of the holotype, as quoted by Eisenack, are length 75 μ, breadth 64 μ ; horn length 12 μ.

REMARKS. This proximate cyst has been previously recorded from the Aptian of Germany by Eisenack (1958). In Europe its stratigraphic range extends into the Cenomanian, since Davey observed *A. granulatum* in the English Cenomanian assemblages (1966). Vozzhennikova observed it in assemblages from the Moscow province, for the first time from the Upper Jurassic (Volgian). It is also present in the basal Kimmeridgian assemblages of Dorset, Stretham, Normandy and the Boulonnais, but the specimens were badly preserved.

Palaeoperidinium ventriosum O. Wetzel, as figured by Deflandre (1935, 1936), has been compared with *A. granulatum* from Aptian and Cenomanian by Davey (1966). The holotype of *P. ventriosum* O. Wetzel has been re-examined and described as having a distinct tabulation by Lejeune-Carpentier (1946) ; it was designated as *Gonyaulax obscura*. Since the specimens attributed by Deflandre do not possess a tabulation, they have hesitantly been re-attributed to *A. granulatum* by Davey.

***Apteodinium* cf. *maculatum* (Cookson & Eisenack)**

(Pl. 12, fig. 8)

DESCRIPTION. The nearly spherical shell has a small horn at the apex. There is no indication of a tabulation, cingulum, sulcus or of archaeopyle formation. The surface of the shell is coarsely granular.

FIGURED SPECIMEN. BM(NH) slide V.53970(1). Clay from Grès de Châtillon, south of Audresselles, Boulonnais (CC 450).

DIMENSIONS. Figured specimen : overall length 50 μ, breadth 48 μ. It is smaller than *A. maculatum*, as recorded from the assemblages of Australia. (Range of dimensions as given by Cookson and Eisenack are length 74–105 μ, breadth 70–105 μ.)

REMARKS. One specimen was observed in the assemblage from the Boulonnais which is similar to *A. maculatum*, as recorded from Albian and described by Cookson & Eisenack (1960). It is compared with the latter species, but not placed in it, in absence of knowledge of the possible range of dimensions and of certain major morphologic features and because of the stratigraphic gap : Its observation in the Lower Barremian assemblages from Yorkshire (Sarjeant, 1966) made a considerable extension in the geographic and stratigraphic range of *A. maculatum* ; but still, its presence in the base of the Kimmeridgian is unexpected.

Genus ***PAREODINIA*** Deflandre, 1947

Pareodinia ceratophora Deflandre, 1947

(Pl. 6, figs. 5, 6 ; Pl. 14, fig. 6)

1947 *Pareodinia ceratophora* Deflandre, 4, text-figs. 1–3.
1953 *P. ceratophora* Deflandre ; Valensi: 30, pl. 13, fig. 4.
1959b *P. ceratophora* Deflandre ; Sarjeant: 336–337.
1961a *P. ceratophora* Deflandre ; Sarjeant: 99, pl. 13, fig. 6; text-fig. 15.
1961 *P. ceratophora* Deflandre ; Alberti: 23, pl. 12, fig. 14; table d.
1962a *P. ceratophora* Deflandre ; Sarjeant: 263, pl. 1, fig. 13, tables 3, 4.
1962b *P. ceratophora* Deflandre ; Sarjeant: 483, pl. 69, fig. 8 ; text-fig. 5.
1964 *P. ceratophora* Deflandre ; Downie & Sarjeant: 138.
1964 *P. ceratophora* Deflandre ; Eisenack: 633.
1964a *P. ceratophora* Deflandre ; Sarjeant, table 2.
1965 *P. ceratophora* Deflandre ; Sarjeant, table 1.
1966 *P. ceratophora* Deflandre ; Schulz & Mai, table 1.
1967b *P. ceratophora* Deflandre ; Sarjeant, table 2.
1968 *P. ceratophora* Deflandre ; Sarjeant, table 2A.

REMARKS. This species was first recorded from the Callovian of the Baltic region and Bajocian of France by Deflandre (1947). In England it has been recorded from Middle Callovian to Upper Oxfordian (Sarjeant, 1961, 1962). It occurs in moderate abundance in the assemblages from the base of the Kimmeridgian of France, England and Scotland.

FIGURED SPECIMENS. BM(NH) slide V.52802(1). Shaly clay from base of the Kimmeridge Clay, *Liostrea delta* Bed, Osmington Mills, Dorset (OM 131).

BM(NH) slide V.53938(1). Clay from Exogyra Marls, 1 m. above the Upper Hard Band, Cap de la Hève, Le Havre (CH 185).

BM(NH) slide V.53948(1). Clay from *Rhactorhynchia inconstans* Bed, Ringstead Bay, Dorset (RB 219).

DIMENSIONS. Range of the English specimens (42 specimens measured) : overall length 45–110 μ, breadth 32–80 μ ; horn length 8–25 μ. French specimens (31 specimens measured) : overall length 58–96 μ, breadth 42–76 μ ; horn length 7–23 μ. Scottish specimens (5 specimens measured) : overall length 60–75 μ, breadth 32–60 μ ; horn length 8–15 μ.

Genus ***TRICHODINIUM*** Eisenack & Cookson, 1960

Trichodinium sp.

(Pl. 4, fig. 2)

Description. A proximate cyst having a broadly ovoidal shell with a short, branched apical horn. There is no indication of a longitudinal furrow and no definite tabulation ; the rather distinct cingulum is equatorial and almost plannar.

The shell membrane is relatively thick (*c.* 1·5–2 μ) ; its surface is granular, bearing processes at random, which are solid, simple conical or rarely branched, generally broad-based.

No archaeopyle was observed in the specimen studied.

Figured specimen. BM(NH) slide V.53960(1). Clay from Great Ouse River Board Pit, Stretham, Cambridgeshire (SC 444).

Dimensions. Figured specimen : overall length 53 μ, breadth 45 μ ; horn length 6 μ ; length of the processes 5–8 μ.

Remarks. This observation was based on a single, but well preserved specimen. It is characterized by bearing processes over the whole shell surface. It differs from all described species of the genus in the form and distribution of its processes and in the absence of an archaeopyle ; and it obviously represents an undescribed species of this genus ; for fuller knowledge, further and better specimens must be awaited.

Cyst-Family uncertain

Genus ***IMBATODINIUM*** Vozzhennikova, 1967b

Translation of original diagnosis. The shell is strongly elongate, laterally slightly compressed. The cingulum may be shallow or deep and is displaced towards the posterior end of the cell.

The sulcus is curved and S-shaped, shallow or deep, and extends from the base of the apical horn to the end of the antapex. The epitract is big, with a finger-shaped apical horn, on the distal end of which there is often a fibre-like growth tentacle finishing in a small bulge of button-like appearance. The hypotract represents $\frac{1}{3}$–$\frac{1}{4}$ of the length of the shell, with a small antapical projection, uniform or variable in form and size. The wall is typically thin, more rarely thick. The surface is smooth, grainy, knobbly or covered with fibres, small spines or other growths. The archaeopyle is oval in shape and intercalary in position.

Type species. *Imbatodinium kondratjevi* Vozzhennikova. Upper Jurassic western Siberia (Verkhnye-Imbatskoye).

Remarks. Since the diagnosis of this genus has only previously been published in Russian, a translation is given here.

Imbatodinium sp.

(Pl. 7, fig. 5)

Description. A proximate cyst, ovoidal in shape, with a finger-shaped apical horn. There is no definite indication of tabulation or of a sulcus ; the cingulum is weakly developed. The epitract is longer than the hypotract, which is almost $\frac{3}{4}$ of the overall length. The surface of the shell is coarsely granular. An intercalary archaeopyle was seen on the epitract of one specimen.

Figured specimen. BM(NH) slide V.52799(2). Shaly clay from *Liostrea delta* Bed, west of Osmington Mills, Dorset (OM 131).

Dimensions. Figured specimen : overall length 80 μ, breadth 45 μ ; horn length 12 μ. Second specimen overall length 75 μ, breadth 38 μ ; horn length 18 μ.

Remarks. Two specimens, observed in the basal Kimmeridgian assemblages, are similar to the species of *Pareodinia*, but their apical horn is different. These specimens are possibly representatives of an undescribed species of *Imbatodinium*, since they differ from existing species in the characteristics above described. Further and better specimens are required before this can be decided.

Genus ***NANNOCERATOPSIS*** Deflandre, 1938a

Nannoceratopsis pellucida Deflandre, 1938a

(Pl. 7, fig. 4)

1938a *Nannoceratopsis pellucida* Deflandre, 183: pl. 8, fig. 10.
1952 *N. pellucida* Deflandre ; Deflandre, fig. 81.
1958 *N. pellucida* Deflandre ; Cookson & Eisenack: 52, pl. 10, figs. 5, 6 ; text-fig. 19.
1960 *N. pellucida* Deflandre ; Sarjeant: 392, pl. 12, figs. 7–10.
1961b *N. pellucida* Deflandre ; Evitt: 312, pl. 1, fig. 15 ; pl. 2, figs. 30–31.
1962a *N. pellucida* Deflandre ; Sarjeant, tables 3, 4.
1962b *N. pellucida* Deflandre ; Sarjeant, pl. 69, figs. 9–10 ; tables 2, 3.
1964 *N. pellucida* Deflandre ; Downie & Sarjeant: 134.
1964 *N. pellucida* Deflandre ; Eisenack: 535–536.
1964a *N. pellucida* Deflandre ; Sarjeant, table 2.
1966 *N. pellucida* Deflandre ; Schulz & Mai, table 1.
1967b *N. pellucida* Deflandre ; Sarjeant, table 4.

Remarks. This species has been recorded from Oxfordian to Lower Kimmeridgian of Australia and Europe. Two specimens were observed in the Dorset assemblages only.

Figured specimen. BM(NH) slide V.52800(2). Shaly clay from the base of Kimmeridge Clay, *Liostrea delta* Bed, west of Osmington Mills, Dorset (OM 131).

Dimensions. Figured specimen : overall length 120 μ, breadth 55 μ ; apical horn length 12 μ, antapical horn length 40 μ. Second specimen : overall length 115 μ, breadth 60 μ ; apical horn length 10 μ, antapical horns length 36 μ.

Cyst-family **HYSTRICHOSPHAERIDIACEAE** Evitt, emend. Sarjeant & Downie, 1966

Genus ***CLEISTOSPHAERIDIUM*** Davey, Downie, Sarjeant & Williams, 1969

Cleistosphaeridium ehrenbergi (Deflandre) Davey, Downie, Sarjeant & Williams, 1969

(Pl. 4, fig. 7 ; Text-fig. 22a)

1938a *Hystrichosphaeridium* cf. *hirsutum* Deflandre, pl. 10, fig. 9.
1947 *Hystrichosphaeridium ehrenbergi* Deflandre, fig. 1, no. 5.
1952 *H. ehrenbergi* Deflandre ; fig. 9.
1955 *H. ehrenbergi* Deflandre ; Valensi: 587, pl. 3, fig. 1.
1963 *Baltisphaeridium ehrenbergi* (Deflandre) ; Sarjeant: 486–487, pl. 70, fig. 1 ; text-fig. 6a.
1964 *B. ehrenbergi* (Deflandre) ; Downie & Sarjeant: 90.
1964a *B. ehrenbergi* (Deflandre) ; Sarjeant, table 3.
1966 *Cleistosphaeridium ehrenbergi* (Deflandre) ; Davey, Downie, Sarjeant and Williams, *nomen nudum*, 170.
1967a *C. ehrenbergi* (Deflandre) ; Sarjeant, table 5, *nomen nudum*.
1968 *C. ehrenbergi* (Deflandre) ; Sarjeant, table 2B, *nomen nudum*.
1969 *C. ehrenbergi* (Deflandre) ; Davey, Downie, Sarjeant & Williams (in press).

DESCRIPTION. The subspherical shell bears simple straight, solid, conical and distally closed processes in large number (30–44). The shell surface is smooth. Sometimes an apical archaeopyle is developed.

FIGURED SPECIMEN. BM(NH) slide V.52801(1). Shaly clay from the base of Kimmeridge Clay, *Liostrea delta* Bed, Osmington Mills, Dorset (OM 131).

DIMENSIONS. Figured specimen : shell length 35 μ, breadth 38 μ ; process length 15–18 μ. Range of the English specimens (9 specimens measured) : shell length 45–62 μ, breadth 45–50 μ ; French specimens (2 specimens measured) : shell length 48–65 μ, breadth 45–50 μ. In all specimens, length of the process 15–25 μ, breadth 1·5 μ. Dimensions of the Scottish specimen : shell length 30 μ, breadth 30 μ ; process length 16 μ.

REMARKS. This chorate cyst has previously been recorded from the Lower Oxfordian of Normandy and England. It is abundant in the Dorset assemblages, but rare in Scottish and French material.

Cleistosphaeridium polyacanthum sp. nov.

(Pl. 12, fig. 10 ; Text-fig. 22b)

DERIVATION OF THE NAME. Greek, *polys*, many, very ; and *acanthus*, thorny, with reference to the number of the processes of the shell.

DIAGNOSIS. A *Cleistosphaeridium* having an ellipsoidal to ovoidal shell bearing numerous processes (50–70 in number). All processes of approximately same length (not less than half of the shell length), simple, straight, hollow and acuminate. Shell surface smooth. Apical archaeopyle sometimes present.

HOLOTYPE. BM(NH) slide V.53943(1). Kimmeridge Clay from between the Ringstead Waxy Clay and the Coral bed, Ringstead Bay, Dorset (RB 218).

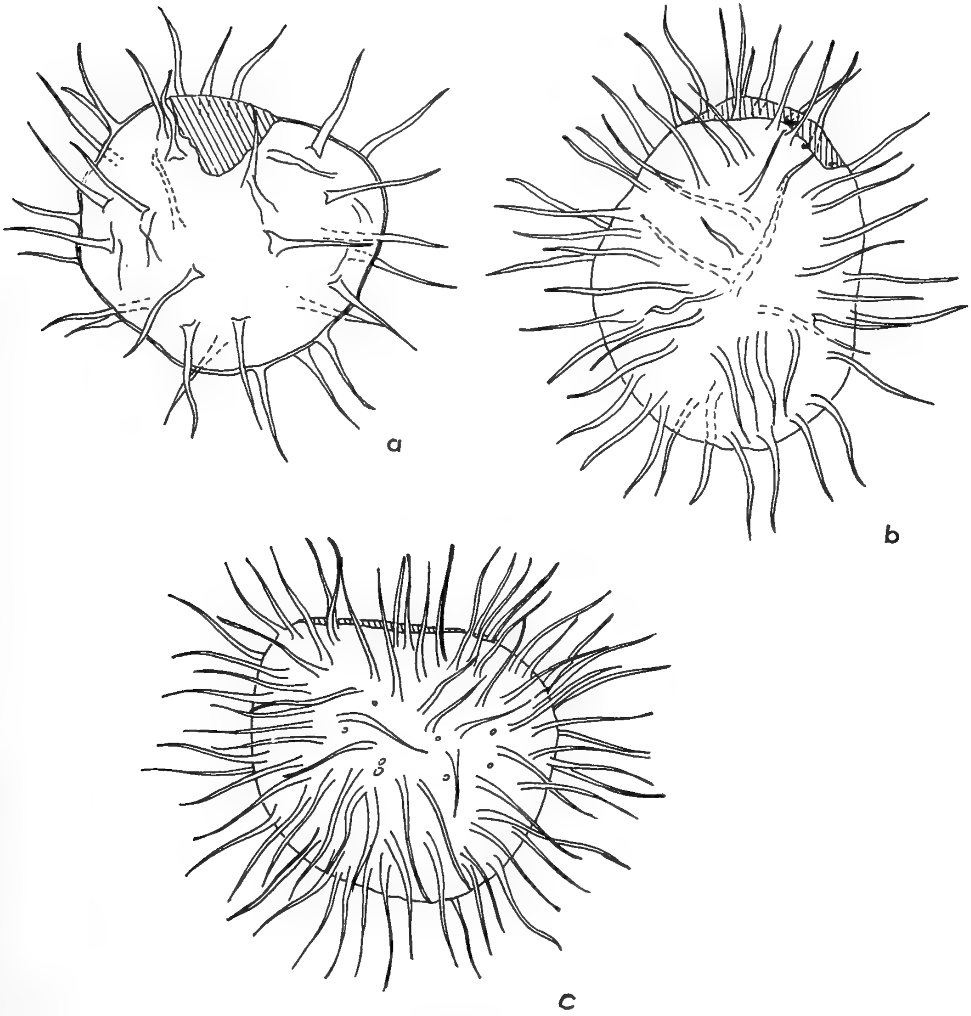

FIG. 22. Three similar species of *Cleistosphaeridium*. A. *Cleistosphaeridium ehrenbergi* (Deflandre). ×*c.* 1280. B. *Cleistosphaeridium polyacanthum* sp. nov. Holotype. ×*c.* 1400. C. *Cleistosphaeridium polytrichum* (Valensi). ×*c.* 1280.

DIMENSIONS. Holotype : shell length 40 μ, breadth 30 μ ; length of the processes 20–22 μ. Range of the English specimens (5 specimens measured) : shell length 33–42 μ, breadth 28–35 μ ; French specimens (4 specimens measured) : shell length 30–45 μ, breadth 25–38 μ ; length of the processes 16–20 μ.

DESCRIPTION. This chorate cyst has processes in variable number, 50–70, their cavity directly connected to the shell interior. There are no fields or plates identifiable on the shell.

REMARKS. This new form of *Cleistosphaeridium* should be placed morphologically between *C. ehrenbergi* and *C. polytrichum*. It differs from them consistently in shell shape and in the number of the processes. These three species do not seem to be part of a continuously varying plexus, at least at this horizon, since intermediate forms were not encountered (Table 5).

TABLE 5
Comparison of dimensions of three similar species of *Cleistosphaeridium*

	Dimensions	Length of Processes	Thickness of Processes	Number of Processes
C. ehrenbergi	Length 30–65 μ Breadth 30–50 μ	15–25 μ	1·5 μ	30–44 μ
C. polyacanthum	Length 30–45 μ Breadth 25–38 μ	16–20 μ	1 μ	50–70 μ
C. polytrichum	Length 28–30 μ Breadth 33–35 μ	12–15 μ	1·2 μ	86–100 μ

C. polyacanthum is comparable with *C. flexuosum*, which was recorded from Cenomanian of England by Davey, Downie, Sarjeant & Williams (1966), in its ovoidal shape and simple acuminate processes in large number. Since the processes of *C. flexuosum* are slightly fibrous and always flexuous, this new species is different ; moreover, archaeopyle formation was not observed in *C. flexuosum*.

Cleistosphaeridium polytrichum (Valensi), Davey, Downie, Sarjeant & Williams, 1969

(Pl. 4, fig. 4 ; Text-fig. 22c)

1947 *Hystrichosphaeridium polytrichum* Valensi, fig. 4.
1953 *H. polytrichum* Valensi ; Valensi, pl. 4, fig. 6 ; pl. 13, fig. 12.
1955 *H. polytrichum* Valensi ; Deflandre & Cookson, pl. 2, fig. 2.
1962b *Baltisphaeridium polytrichum* (Valensi) ; Sarjeant: 487, pl. 70, fig. 2 ; text-fig. 66.
1963 *Hystrichosphaeridium polytrichum* Valensi ; Górka, pl. 9, figs. 1–3.
1964 *Baltisphaeridium polytrichum* (Valensi) ; Downie & Sarjeant: 95.
1964a *B. polytrichum* (Valensi) ; Sarjeant, table 3.
1966 *B. polytrichum* (Valensi) ; Schulz & Mai, table 1.
1966 *Cleistosphaeridium polytrichum* (Valensi) ; Davey, Downie, Sarjeant & Williams, *nomen nudum*: 170.
1967a *C. polytrichum* (Valensi) ; Sarjeant, table 5, *nomen nudum*.
1968 *Baltisphaeridium polytrichum* (Valensi) ; Horowitz: 55, pl. 7, fig. 7 ; table 3.
1969 *Cleistosphaeridium polytrichum* (Valensi) ; Davey, Downie, Sarjeant & Williams (in press).

DESCRIPTION. The subspherical shell bears a large number of processes (about 86–100) ; they are simple, conical, solid and distally closed. An apical archaeopyle is usually present.

FIGURED SPECIMEN. BM(NH) slide V.52799(3). Shaly clay from the base of Kimmeridge Clay, *Liostrea delta* Bed, west of Osmington Mills, Dorset (OM 131).

Dimensions. Figured specimen : shell length (apex lacking) 28 μ, breadth 35 μ ; process length 12–15 μ, breadth 1·2 μ. Range : (5 specimens measured) : shell length 28–35 μ, breadth 33–35 μ ; process length 12–15 μ.

Remarks. *C. polytrichum* has previously been recorded from the Bathonian of France, the Oxfordian and Kimmeridgian of England. It was observed in the basal Kimmeridgian from Dorset assemblages only.

Cleistosphaeridium tribuliferum (Sarjeant), Davey, Downie, Sarjeant & Williams, 1969

(Pl. 9, fig. 2 ; Pl. 12, fig. 9 ; Text-fig. 23)

1962b *Baltisphaeridium tribuliferum* Sarjeant: 487–488, pl. 70, fig. 4 ; text-figs. 6c, 7.
1964 *B. tribuliferum* Sarjeant ; Downie & Sarjeant: 97.
1964a *B. tribuliferum* Sarjeant ; Sarjeant, table 3.
1966 *Cleistosphaeridium tribuliferum* (Sarjeant) ; Davey, Downie, Sarjeant & Williams, *nomen nudum*, 170.
1967a *C. tribuliferum* (Sarjeant) ; Sarjeant, table 5, *nomen nudum*.
1968 *C. tribuliferum* (Sarjeant); Sarjeant, table 2B, *nomen nudum*.
1969 *C. tribuliferum* (Sarjeant) ; Davey, Downie, Sarjeant & Williams (in press).

Description. The central body is subspherical to ovoidal in shape, bearing moderately numerous processes. The processes are conical, hollow, distally closed

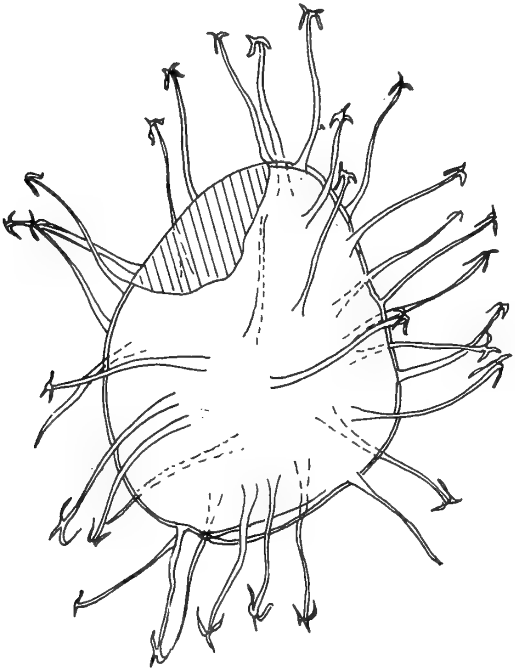

Fig. 23. *Cleistosphaeridium tribuliferum* (Sarjeant). A specimen from the basal Kimmeridgian of Ringstead Bay. ×*c.* 1280.

and recurved, between 28–60 in number. The surface of the shell is smooth. An apical archaeopyle is present.

FIGURED SPECIMENS. BM(NH) slide V.53951(1) and V.53978(1). Both specimens from immediate base of the Kimmeridge Clay, *Rhactorhynchia inconstans* Bed, Ringstead Bay, Dorset (RB 219).

DIMENSIONS. Range of the English specimens (20 specimens measured) : shell length 33–62 μ, breadth 25–53 μ ; process length 17–35 μ. Dimensions of the single Scottish specimen observed : shell length 35 μ, breadth 33 μ ; process length 15 μ.

REMARKS. *C. tribuliferum* has previously been recorded from the Ampthill Clay and Oxford Clay of England (Oxfordian) by Sarjeant. It is abundant in Dorset assemblages, but only one specimen was observed in the Scottish material, none from France.

C. tribuliferum is comparable in general appearance and by its similar processes with *Hystrichosphaeridium recurvatum*, which has hollow, distally open, recurved or aculeate processes ; but *C. tribuliferum* possesses processes in larger number which are distally closed.

Cleistosphaeridium sp.

(Pl. 1, fig. 7)

DESCRIPTION. A chorate dinoflagellate cyst having a subspherical to ovoidal shell bearing numerous processes, typically closed distally and without communication to the endocoel. The number of processes is about 70–80 ; they are simple, broad based, oblate and short ($\frac{1}{5}$ of the shell breadth). The surface of the shell is finely granular. An apical archaeopyle is present.

FIGURED SPECIMEN. BM(NH) slide V.53958(1). Clay from 20 ft. above Ringstead Coral Bed, west of Osmington Mills, foreshore exposure, Dorset (OM 420).

DIMENSIONS. Figured specimen : shell length (apex lacking) 38 μ, breadth 40 μ ; process length 8–10 μ, breadth (at the base) 3–3·5 μ, (at the top) 1–1·5 μ. Dimensions of the French specimens (2 specimens measured) : shell length 38–55 μ, breadth 45–55 μ ; process length 5–10 μ.

Dimensions of the Dorset specimen : shell length (apex lacking) 38 μ, breadth 45 μ ; process length 8–10 μ. Scottish specimen's length 50 μ, breadth 43 μ.

REMARKS. Five specimens were recorded from the basal Kimmeridgian assemblages, which are different from all previously known species of the genus in the nature of their processes. These specimens, with their broad-based, oblate processes and finely granular surface, are closest to *Exochosphaeridium pseudhystrichodinium* ; this species was originally recorded from the Upper Cretaceous by Deflandre (1937), as *Hystrichosphaeridium pseudhystrichodinium*, and tentatively re-attributed to the genus *Exochosphaeridium* by Davey, Downie, Sarjeant & Williams (1966). They differ, however in their mode of archaeopyle formation : *E. pseudhystrichodinium* has a precingular archaeopyle, but *Cleistosphaeridium* sp. has an apical archaeopyle.

Genus ***HYSTRICHOSPHAERIDIUM*** Deflandre, emend. Davey & Williams (in Davey, Downie, Sarjeant & Williams), 1969

Hystrichosphaeridium petilum sp. nov.

(Pl. 9, figs. 1, 6 ; Text-fig. 24)

DERIVATION OF THE NAME. Latin, *petilus*, thin, slender, with reference to the thin-walled shell.

DIAGNOSIS. A *Hystrichosphaeridium* having a subspherical delicate thin-walled shell. Processes very slender, tubular, open distally, with 4–6 aculeate spines around the process mouths. Reflected tabulation : 4′, 6″, 6c, 0–1s, 6″′, 1p and 1″″. Surface of the shell smooth. An apical archaeopyle is usually present.

HOLOTYPE. BM(NH) slide V.53944(1). Clay from between Ringstead Waxy Clay and Ringstead Coral Bed, Ringstead Bay, Dorset (RB 218).

DIMENSIONS. Holotype : shell length (apex lacking) 35 μ, breadth 35 μ ; process length 17–20 μ, breadth up to 3 μ. Range of the English specimens (20 specimens measured) : length 30–35 μ, (apex lacking) 28 μ, breadth 25–35 μ. French specimens (2 specimens measured) : length 33–35 μ, breadth 25–35 μ. Scottish specimens (10 specimens measured) : length 22–32 μ, (apex lacking) 20–30 μ, breadth 16–35 μ ; process length 12–20 μ.

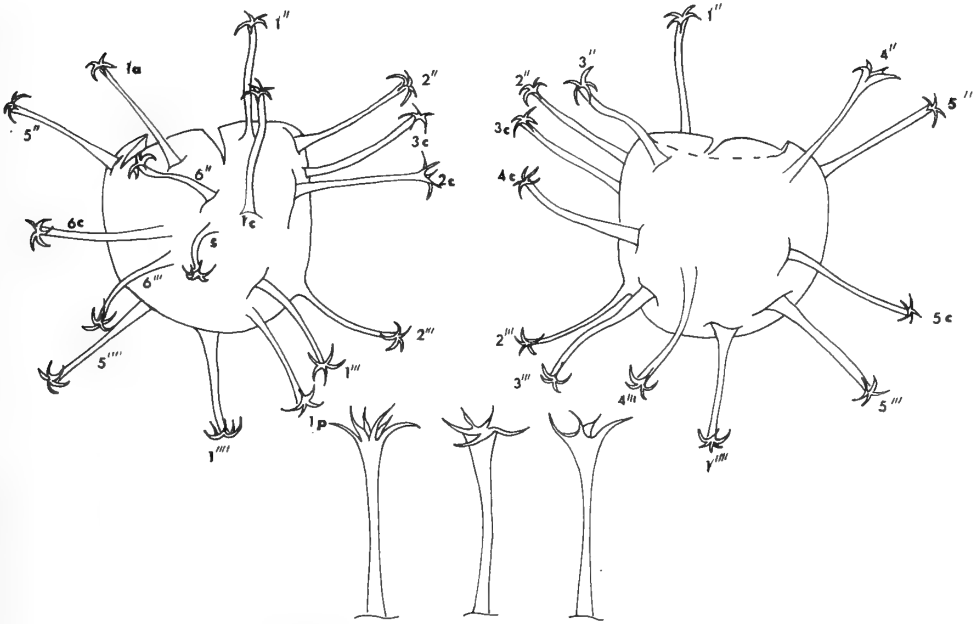

FIG. 24. *Hystrichosphaeridium petilum* sp. nov. Tabulation of the holotype. Upper left, ventral view ; upper right, dorsal view (by transparency). ×*c*. 1280. Lower centre, the processes. ×*c*. 1830.

DESCRIPTION. The central body and the processes are characteristically thin-walled. The central body is composed of two membranes, an inner endophragm and an outer periphragm, the periphragm only comprising the processes. The tubular processes are usually curved or bent to some extent, probably as a result of preservation. They are usually, at least, two-thirds of the shell length. The spines on the tube mouths are up to 4 μ in length and 4–6 in number. An apical archaeopyle is usually present, formed by loss of the apex with four apical processes.

REMARKS. This new chorate cyst was attributed to *Hystrichosphaeridium* without hesitation in view of the features described above. It is similar to *H. tubiferum*, *H. recurvatum*, *H. bowerbanki* and *H. sheppeyense*, but differs in details and the number of the processes : *H. tubiferum* has 4–5 sulcal processes, whereas in *H. petilum* either only one sulcal process or none at all are present. The processes of *H. tubiferum* are thicker and distally have an entire or serrate circular margin. *H. recurvatum* has 3–6 sulcal processes. The processes of *H. sheppeyense* are relatively thick-walled and, at the base of some of the processes, there are small proximal elevations or swellings. *H. bowerbanki* is ovoidal to elongate in shape and has 5 sulcal processes. *H. petilum* therefore is significantly different from all these species. It was observed in the basal Kimmeridgian assemblages from England, Scotland and France in moderate number.

Genus ***OLIGOSPHAERIDIUM*** Davey & Williams, 1966

Oligosphaeridium pulcherrimum (Deflandre & Cookson), Davey & Williams (in Davey, Downie, Sarjeant & Williams), 1966

(Pl. 7, fig. 7)

1955 *Hystrichosphaeridium pulcherrimum* Deflandre & Cookson: 270, pl. 1, fig. 8 ; text-fig. 21.
1955 *H. pulcherrimum* Deflandre & Cookson ; Valensi: 592, pl. 4, fig. 1.
1964 *H. pulcherrimum* Deflandre & Cookson ; Downie & Sarjeant: 121.
1966 *Oligosphaeridium pulcherrimum* (Deflandre & Cookson) ; Davey & Williams: 75–76, pl. 10, fig. 9 ; pl. 11, fig. 5.
1967b *Oligosphaeridium pulcherrimum* (Deflandre & Cookson) ; Sarjeant, table 6.

REMARKS. This species was first recorded from the Lower Cretaceous of Australia. In England it has been recorded from the London Clay. It was observed in Dorset and the Boulonnais assemblages, but all specimens are badly preserved.

FIGURED SPECIMEN. BM(NH) slide V.53946(1). Clay from immediately base of the Kimmeridge Clay, *Rhactorhynchia inconstans* Bed, Ringstead Bay, Dorset (RB 219).

DIMENSIONS. Figured specimen : shell length 50 μ, breadth 48 μ, process length 18–35 μ. The other three specimens were not measured because of their poor preservation.

Genus *POLYSTEPHANEPHORUS* Sarjeant, 1961

Polystephanephorus sarjeantii sp. nov.

(Pl. 11, fig. 4 ; Text-fig. 25)

Derivation of the name. Named in honour of Dr. William A. S. Sarjeant, who established the genus.

Diagnosis. *Polystephanephorus* having a spherical to subspherical shell, bearing 14 groups of processes together with 2 single processes. There is no connection between the adjacent groups. All processes of each group are connected distally by a ring trabecula. The number of the processes in the groups is variable, between 2 and 6. Reflected tabulation : ?′, 6″, 6″′, lp, 2s and 1″″. Surface of the shell smooth and transparent. Apical archaeopyle developed.

Holotype. BM(NH) slide V.52792(2). Shaly clay from the base of the Kimmeridge Clay, *Liostrea delta* Bed, Osmington Mills, Dorset (OM 131).

Dimensions. Holotype : shell length 40 μ, breadth 45 μ ; process length 20–25 μ. Range of the English specimens (10 specimens measured) : shell length 40–70 μ, breadth 35–60 μ ; process length 20–28 μ. French specimens (6 specimens measured) : shell length 42–60 μ, breadth 40–55 μ ; process length 22–28 μ.

Description. Central body subspherical or spherical in shape, with groups of complicated processes. In addition to the groups of processes, two single processes were observed, which are positional equivalents of the sulcus. These two single processes are foliate and furcate towards their distal ends. All the processes of each group separately rise up from the central body and are subsequently connected by

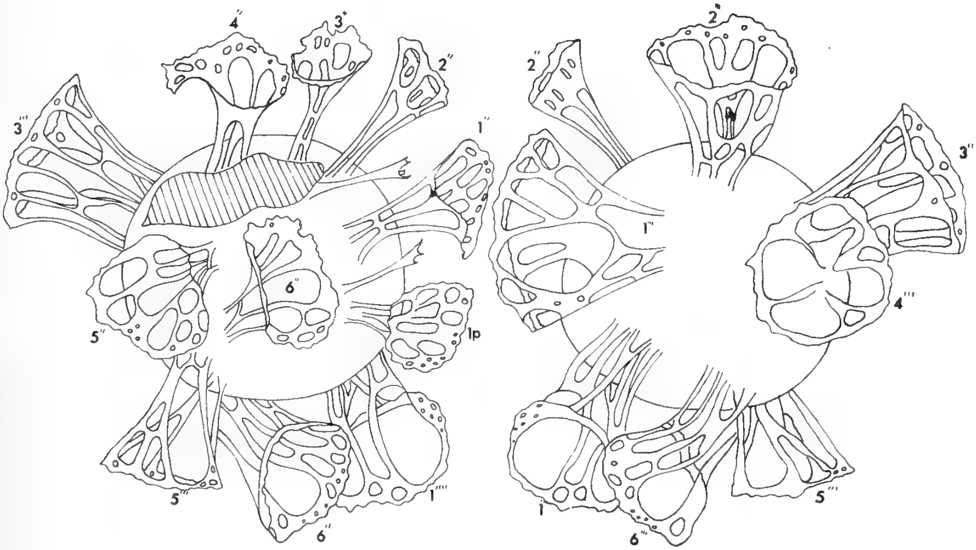

Fig. 25. *Polystephanephorus sarjeantii* sp. nov. Holotype, showing the tabulation. Left, ventral view ; right, dorsal view (by transparency). × c. 1530.

bridge-like strands ; near to their tips, they are foliate and fenestrate ; at their tips, they are connected by a ring trabecula with denticulate edges. All the processes are solid.

The surface of the shell appears smooth and transparent ; because of their transparency, identification of the processes was extremely difficult. An apical archaeopyle, slightly polygonal in shape, was seen in some of the specimens studied.

REMARKS. This new species of the genus *Polystephanephorus* differs from the previously described species in its more complicated processes. The processes are not connected proximally, as in *P. urnaformis*, and the branches are longer than the branches of *P. calathus* and *P. paracalathus* ; they are not directed parallel to the shell surface ; however the processes are linked by a ring trabecula as the other species of the genus.

P. sarjeantii is similar to *Adnatosphaeridium caulleryi*, but the arrangement and the manner of linkage of the processes are different.

This new species was observed in moderate number in the assemblages from Dorset and the Boulonnais, but none from Scotland.

Genus ***PROLIXOSPHAERIDIUM*** Davey, Downie, Sarjeant & Williams, 1966

Prolixosphaeridium cf. ***deirense*** (Davey, Downie, Sarjeant & Williams)

(Pl. 13, fig. 9)

DESCRIPTION. This chorate cyst is elongate to ovoidal in shape. The apical pole is lost to form the archaeopyle. The shell is thick-walled and granular, bearing simple, solid, conical processes, about 46 in number.

FIGURED SPECIMEN. BM(NH) slide V.53950(1). Clay from Ringstead Bay, *Rhactorhynchia inconstans* Bed, Dorset (RB 219).

DIMENSIONS. Figured specimen : shell length (apex lacking) 55 μ, breadth 37 μ ; length of the processes 12–15 μ. The other specimen length 69 μ, breadth 42 μ ; process length 14–16 μ.

REMARKS. Two specimens observed from the Dorset assemblages were similar to *P. deirense*, as described by Davey, Downie, Sarjeant & Williams (1966). However the enlarged antapical processes were not clear and the other processes did not appear to be arranged in rows ; therefore the species assignation remains uncertain.

Prolixosphaeridium granulosum (Deflandre), Davey, Downie, Sarjeant & Williams, 1966

(Pl. 2, fig. 6 ; Pl. 5, fig. 3 ; Pl. 13, fig. 7)

1935 *Hystrichosphaera xanthiopyxides* Deflandre, pl. 9, fig. 7.
1937 *Hystrichosphaeridium xanthiopyxides* var. *granulosum* (Deflandre) ; Deflandre: 29, pl. 16, fig. 4.
1955 *H. xanthiopyxides* var. *granulosum* (Deflandre) ; Valensi: 589, pl. 3, fig. 7 ; pl. 5, fig. 16.

1957 *H. xanthiopyxides* var. *granulosum* (Deflandre) ; Downie: 426, text-fig. 49.
1960 *Baltisphaeridium xanthiopyxides* var. *granulosum* (Deflandre) ; Klement: 59.
1962a *Baltisphaeridium granulosum* (Deflandre) ; Sarjeant: 264, pl. 2, fig. 14 ; text-fig. 8c ; tables 3, 4.
1964 *B. granulosum* (Deflandre) ; Downie & Sarjeant: 91.
1964a *B. granulosum* (Deflandre) ; Sarjeant, table 3.
1966 *Prolixosphaeridium granulosum* (Deflandre) ; Davey, Downie, Sarjeant & Williams: 172–173.
1967 *Baltisphaeridium granulosum* (Deflandre) ; Clarke & Verdier: 74, pl. 12, figs. 7–9.
1967b *Prolixosphaeridium granulosum* (Deflandre) ; Sarjeant, table 7.

REMARKS. This species has a known range from Oxfordian to Eocene. Deflandre first observed it in Cretaceous (?Aptian) flints from France (1937). Valensi described specimens of larger size from Cretaceous flints (1955). A closely similar form was recorded from the Kimmeridgian by Downie (1957), which was the first English and Jurassic specimen ; widening the geographic and stratigraphic range. Subsequently more representatives of *P. granulosum* were recorded from the Ringstead Waxy Clay (Oxfordian ; Sarjeant, 1962a) and the Eocene London Clay (1966) ; both from southern England. It was observed in the basal Kimmeridgian assemblages from England, Scotland and France in moderate abundance.

FIGURED SPECIMENS. BM(NH) slide V.52799(4). Shaly clay from *Liostrea delta* Bed, west of Osmington Mills, Dorset (OM 131).

BM(NH) slide V.53960(2). Clay from Great Ouse River Board Pit, Stretham, Cambridgeshire (SC 444).

Specimen RB 218/12–215 ; clay from between the Ringstead Waxy Clay and Ringstead Coral Bed, Ringstead Bay, Dorset (RB 218).

DIMENSIONS. Range of the English specimens (24 specimens measured) : shell length (apex lacking) 45–55 μ, with apex 40–62 μ, breadth 18–35 μ, process length 8–12 μ. French specimens (4 specimens measured) : shell length 38–58 μ, breadth 20–35 μ ; process length 9–11 μ. Dimensions of the Scottish specimens (10 specimens measured) : shell length 45–50 μ, (apex lacking) 30–55 μ, breadth 25–35 μ ; process length 6–18 μ.

Prolixosphaeridium parvispinum (Deflandre), Davey, Downie, Sarjeant & Williams, 1966

(Pl. 2, fig. 3)

1937 *Hystrichosphaeridium xanthiopyxides* var. *parvispinum* Deflandre: 29, pl. 16, fig. 5.
1941 *H. xanthiopyxides* var. *parvispinum* Deflandre ; Conrad: 2.
1952 *H. xanthiopyxides* var. *parvispinum* Deflandre ; Deflandre, fig. 13.
1958 *Histrichosphaeridium parvispinum* (Deflandre) ; Cookson & Eisenack: 45, pl. 7, figs. 10–12.
1960 *Baltisphaeridium parvispinum* (Deflandre) ; Klement: 59.
1962b *B. parvispinum* (Deflandre) ; Sarjeant: 488, text-fig. 9d.
1964 *B. parvispinum* (Deflandre) ; Downie & Sarjeant: 94.
1964a *B. parvispinum* (Deflandre) ; Sarjeant, table 3.
1966 *Prolixosphaeridium parvispinum* (Deflandre) ; Davey, Downie, Sarjeant & Williams: 173.
1967a *P. parvispinum* (Deflandre) ; Sarjeant, table 7.

DESCRIPTION. The shell is elongate to oval in shape, bearing short, conical, simple processes in large number. The apical pole is lost in archaeopyle formation. The surface of the shell is densely granular.

FIGURED SPECIMEN. BM(NH) slide V.53956(2). Kimmeridge Clay from 20 ft. above the Ringstead Coral Bed, west of Osmington Mills, Dorset (OM 420).

DIMENSIONS. Figured specimen : shell length (apex lacking) 44 μ, breadth 30 μ ; process length 3–5 μ. Range (3 English specimens measured) : shell length (apex lacking) 35–44 μ, breadth 15–30 μ ; (one Scottish specimen measured) : shell length 35 μ, breadth 15 μ ; process length 4 μ.

REMARKS. This species was observed only in Dorset and Scottish assemblages and is here described for the first time from the Kimmeridgian. It has a very wide stratigraphic and geographic range. Deflandre observed it in the Lower Cretaceous (Aptian) assemblages of France (1937), and described as a variety of *Hystrichosphaeridium xanthiopyxides* O. Wetzel. Conrad recorded it from the Upper Cretaceous (Maestrichtian) of Belgium (1941). A similar species was observed in the Lower Cretaceous (Aptian-?Albian) of Australia and New Guinea (Cookson & Eisenack, 1958) ; it was differentiated from *H. xanthipyxides* and created a new species, *H. parvispinum*, whose basionym was *H. xanthiopyxides* var. *parvispinum* Deflandre. Klement transferred this new species to the genus *Baltisphaeridium*. It was recorded for the first time from Ampthill Clay (Oxfordian), England, by Sarjeant (1962). When Davey, Downie, Sarjeant and Williams established the new genus, *Prolixosphaeridium*, the species *parvispinum* was transferred to it on the basis of shape, character of processes and possession of an apical archaeopyle.

Genus ***SYSTEMATOPHORA*** Klement, 1960

Systematophora areolata Klement, 1960

(Pl. 8, fig. 6 ; Pl. 11, fig. 10)

1960 *Systematophora areolata* Klement: 62–64, pl. 9, figs. 1–8 ; text-fig. 32.
1961a *S. areolata* Klement ; Evitt: 398, pl. 9, figs. 1, 2.
1964 *S. areolata* Klement ; Downie & Sarjeant: 146.
1964a *S. areolata* Klement ; Sarjeant, table 3.
1967 *S. areolata* Klement ; Dodekova: 23–24, pl. 3, figs. 7, 8.
1967a *S. areolata* Klement ; Sarjeant, table 7.

DESCRIPTION. Shell spherical to ellipsoidal in shape, bearing groups of processes together with single processes. The processes of the groups are placed so as to divide the whole surface into more or less polygonal or circular plate-like areas or fields. These fields are bordered by narrow crests. Solid, distally closed simple or furcate processes rise up from the crest in each field ; they are somewhat flexuous. These processes are not connected at their tips. Some simple, isolate processes are present equatorially between the fields. The surface of the central body is smooth or finely granular. An apical archaeopyle was observed in some specimens.

FIGURED SPECIMENS. BM(NH) slide V.53937(1). Clay from *Liostrea delta* Bed of Villerville, Normandy (VN 184).

Specimen SS 625/7–160. Shale from 60 ft. above the second dolerite sill, Staffin Bay, Isle of Skye.

DIMENSIONS. Range of the English specimens (20 specimens measured) : shell length 32–53 μ, breadth 26–56 μ ; processes length 18–23 μ. French specimens (100 specimens measured) : shell length 30–55 μ, breadth 25–55 μ ; process length 15–25 μ. 10 Scottish specimens measured : shell length 45–60 μ, breadth 40–67 μ, process length 12–25 μ.

REMARKS. *S. areolata* was originally described by Klement from the Malm Delta of Germany. It is abundantly present in the basal Kimmeridgian assemblages of England, France and Scotland.

Systematophora orbifera Klement, 1960

(Pl. 4, fig. 3)

1960 *Systematophora orbifera* Klement: 66–67, pl. 9, figs. 9–10 ; pl. 10, fig. 7.
1961a *S. orbifera* Klement ; Evitt: 398.
1964 *S. orbifera* Klement ; Downie & Sarjeant: 146.
1964a *S. orbifera* Klement ; Sarjeant, table 3.
1966 *S. orbifera* Klement ; Schulz & Mai, table 1.
1967 *S. orbifera* Klement ; Dodekova: 25–26, pl. 3, fig. 6.
1967b *S. orbifera* Klement ; Sarjeant, table 7.

DESCRIPTION. Subspherical to ovate shell with oriented small fields distributed over the whole shell surface. These circular fields are enclosed by solid, distally closed processes. In each group the processes rise up very close together ; they are interconnected in complex fashion at their tips. Between the fields some simple, isolate, single processes are present, which are placed equatorially.

Shell surface smooth or finely granular. An apical archeopyle is sometimes present.

FIGURED SPECIMEN. BM(NH) slide V.53936(1). Clay from *Liostrea delta* Bed of Villerville, Normandy (VN 184).

DIMENSIONS. Figured specimen : shell length (apex lacking) 62 μ, breadth 50 μ ; length of the processes 25–30 μ. Range of the English specimens (26 specimens measured) : shell length 48–60 μ, (apex lacking) 40–55 μ, breadth 33–55 μ ; process length 25–28 μ. French specimens (43 specimens measured) : shell length 48–62 μ, breadth 45–50 μ, shell length (apex lacking) 45–57 μ ; process length 20–31 μ. 6 Scottish specimens measured : shell length 40–70 μ, breadth 36–55 μ ; process length 12–20 μ.

REMARKS. *S. orbifera* was originally described from the Malm Alpha of Germany. It was observed in abundance in all the assemblages from Dorset, Normandy, Boulonnais and Scotland.

This species has a more elongate shell than *S. areolata* and differs from all the other species in the character of its processes.

Systematophora sp.

(Pl. 8, fig. 5)

Description. *Systematophora* having an elongate shell bearing groups of processes. One pole (apical) of the shell is lost in archaeopyle formation, the opposite pole is rounded. The shell wall is composed of two layers, the periphragm forming the processes. The surface of the shell is finely granular.

The processes in the groups are short, their length not more than one fourth of the shell breadth. They are broad-based, foliate and deeply forked at their distal end. There is no connection between the processes on their proximal and distal tips. They rise up separately from each other, showing a polygonal orientation on the periphragm and giving an aspect of small fields. There are four groups on the epitract, four groups on the hypotract and a small group on the antapex ; in each group the number of the processes is between 5 and 7.

Figured specimen. BM(NH) slide V.53962(1). Kimmeridge Clay from Great Ouse River Board Pit, Stretham, Cambridgeshire (SC 444).

Dimensions. Figured specimen : shell length (apex lacking) 35 μ, breadth 28 μ ; process length 6–8 μ.

Remarks. A single, well-preserved specimen was observed in the base of Kimmeridge Clay of Stretham. Because of its small fields on the shell, it resembles known species of *Systematophora*, but on the basis of the shape and character of its processes, it differs from all previously described species of the genus. It clearly represents a new species, for fuller knowledge of which further specimens must be awaited.

Genus ***TAENIOPHORA*** Klement, 1960

Taeniophora iunctispina Klement, 1960

(Pl. 9, fig. 5)

1960 *Taeniophora iunctispina* Klement: 68, pl. 10, figs. 1–6.
1964 *T. iunctispina* Klement ; Downie & Sarjeant: 146.
1964a *T. iunctispina* Klement ; Sarjeant, table 3.
1967b *T. iunctispina* Klement ; Sarjeant, table 7.

Description. This chorate cyst is spherical to broadly ovoidal in shape, bearing processes in groups randomly oriented on the surface of the shell. These processes are long, solid, simple or branched near to their distal ends. They are proximally connected by narrow basal ridges, surrounding fields of circular outline. The surface of the shell is finely granular. There is no tabulation, but a patch clear of processes, suggesting a sulcus, is present, defined by the arrangements of the groups of processes. An apical archaeopyle was developed by some of the specimens.

Figured specimen. BM(NH) slide V.52800(3). Shaly clay from *Liostrea delta* Bed of Osmington Mills, Dorset (OM 131).

Dimensions. Figured specimen : shell length (apex lacking) 45 μ, breadth 48 μ ; process length 22–27 μ. Range of the English specimens (9 specimens measured) : shell length 45–65 μ, breadth 40–50 μ ; process length 15–26 μ. French specimens

(10 specimens measured) : shell length 45–55 μ, breadth 40–50 μ ; process length 15–24 μ. 3 specimens from the Scottish assemblages were observed and measured : shell length 45–60 μ, breadth 35–50 μ ; process length 15–17 μ .

REMARKS. *T. iunctispina* has been recorded from the Upper Jurassic (Malm Alpha) of Germany by Klement (1960). It is observed in the Dorset, Scottish and French assemblages for the first time.

Cyst-Family Uncertain

Genus ***STEPHANELYTRON*** Sarjeant, 1961

Stephanelytron cf. ***scarburghense*** (Sarjeant)

(Pl. 10, fig. 2 ; Pl. 13, fig. 8)

DESCRIPTION. Shell spherical to ovoidal in shape with smooth surface, bearing numerous rows of tubes. These tubes are hollow and distally open. There is a large membraneous corona on one pole, a polygonal opening on the opposite pole.

FIGURED SPECIMENS. BM(NH) slide V.52792(3) and slide OM 131/1-267. Both from the *Liostrea delta* Bed of Osmington Mills, Dorset (OM 131).

DIMENSIONS. Range of the observed specimens : length 36–48 μ, breadth 35–40 μ ; length of tubes 5–6 μ; height of corona 10–12 μ. Measured specimens 6 in number. These are comparable with the holotype dimensions of *S. scarburghense* : overall length 45 μ, breadth 40 μ ; corona 12 μ high and the length of the tubes 5 μ (quoted by Sarjeant, 1961).

REMARKS. *S. scarburghense* has been previously recorded from the Oxford Clay of England. The specimens observed are similar to *S. scarburghense* as figured by Sarjeant ; processes appear thinner, however, and for this reason these forms are compared with, rather than placed in, Sarjeant's species. The specimens are few in number and generally badly preserved.

L. E. Stover (personal communication to W. A. S. Sarjeant) has recently demonstrated the dinoflagellate affinity of this genus. His results are not yet published.

Cyst-Family **HYSTRICHOSPHAERACEAE** O. Wetzel, emend. Sarjeant & Downie, 1966

Genus ***HESLERTONIA*** Sarjeant, 1966

Heslertonia pellucida sp. nov.

(Pl. 4, fig. 12 ; Pl. 14, fig. 2 ; Text-fig. 26)

DERIVATION OF THE NAME. Latin, *pellucidus*, transparent, in reference to the thin shell wall.

DIAGNOSIS. *Heslertonia* having a spheroidal to polyhedral shell without an apical horn. Tabulation : 4′, 6″, 6c, 6‴, 1p, 1pv and 1⁗. Borders of the plates characteristically formed by broad winged edges. Cingulum broad and slightly laevorotatory ; sulcus broad and short, mainly extending on the hypotract. Shell wall transparent and surface smooth. Precingular archaeopyle present, formed by loss of plate 3″.

Holotype. BM(NH) slide V.53620(2). Kimmeridge Clay from 100 ft. above the second dolerite sill, east of Digg, Staffin Bay, Skye (SS 627).

Dimensions. Holotype : shell diameter 30×30 μ ; height of the crests 4–8 μ ; breadth of the cingulum 5–6 μ. Dimensions of the second specimen : shell diameter 28×28 μ ; height of the crests 6–8 μ ; breadth of the cingulum 5–6 μ.

Description. A small proximochorate cyst, characterized by the high crests rising from the plate boundaries. Neither an apical horn nor any appendages are developed.

Four apical and six precingular plates form the epitract. Plate 1′ is elongate ; the other three apical plates are polygonal in shape. Plate 3′ is larger than plates 2′ and 4′, which are almost equal in size. No anterior intercalary plate was observed. The precingular plates are polygonal and more or less uniform in size.

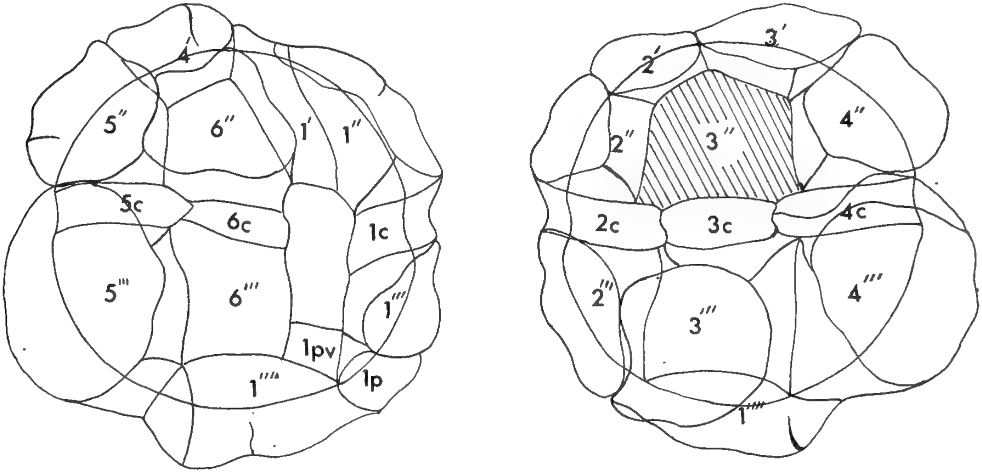

Fig. 26. *Heslertonia pellucida* sp. nov. Holotype, showing the tabulation and the archaeopyle formation. Left, ventral view ; right, dorsal view. ×*c.* 1580.

The slightly laevorotatory cingulum is occupied by six cingular plates : plate 1c is smallest, plate 4c is longest of the cingular plates. The ends of the cingulum are widely separated by a broad sulcus.

Six postcingular plates are present. Plate 1″ ′ is reduced to accommodate the posterior intercalary plate 1p. The other postcingular plates are relatively large. The two posterior intercalary plates are small ; plate 1pv is tetragonal and placed in the posterior prolongation of the sulcus. A single large antapical plate occupies the antapex.

Remarks. The remarkably well preserved, but transparent specimens were observed in the basal Kimmeridgian assemblages (one from Stretham and one from

Staffin Bay). Tabulation is difficult to determine because of the high crests between the plates and the transparent shell wall.

This new species of *Heslertonia* differs from the only previously known species of the genus (*H. heslertonensis*) in the form of its crests and the tabulation. This is the first species of the genus recorded from Jurassic strata. Although only two specimens were found, it was considered that their excellent preservation and clearly distinguishable characters fully justified their differentiation as a second species of this genus.

Cyst-Family Uncertain

Genus ***EPIPLOSPHAERA*** Klement, 1960

Epiplosphaera reticulospinosa Klement, 1960

(Pl. 1, fig. 4)

1960 *Epiplosphaera reticulospinosa* Klement: 75–76, pl. 8, figs. 10–12.
1964 *E. reticulospinosa* Klement ; Downie & Sarjeant: 112.
1964a *E. reticulospinosa* Klement ; Sarjeant, table 3.
1966 *E. reticulospinosa* Klement ; Schulz & Mai, table 1.
1967b *E. reticulospinosa* Klement ; Sarjeant, table 9.

Description. The spherical or subspherical shell shows a small-meshed reticulation on the surface. The processes arise at the point of junction of the reticulum ; they are simple, hollow, distally closed, bifid or briefly bifurcate. The shell wall is composed of two layers, the endophragm forming the processes. The surface of the shell is smooth. An apical archaeopyle is present.

Figured specimen. BM(NH) slide V.53932(2). Clay from *Liostrea delta* Bed, Villerville, Normandy (VN 184).

Dimensions. Figured specimen : shell length 45 μ, breadth 40 μ ; process length 8 μ. Range (4 English specimens were measured) : shell length 38–60 μ, breadth 38–65 μ ; process length 5–12 μ ; (2 French specimens were measured) : shell length 35–45 μ, breadth 25–40 μ ; process length 7–8 μ. Klement gave the following dimensions for this species : shell length 52–55 μ, breadth 46–49 μ ; process length 12–15 μ. The French specimens are thus smaller than English and German specimens. The processes of the German specimens are longer than the basal Kimmeridgian specimens.

Remarks. This species has been recorded from Malm Delta of Germany (Klement, 1960). It was observed in the assemblages from Dorset, Stretham and Normandy in small numbers. It differs from *E. areolata* in that it does not show a regular quadrilateral structure on the shell surface. It also differs from *E. bireticulata* in the absence of a second reticulum superimposed on the first.

Cyst-Family **ENDOSCRINIACEAE** Vozzhennikova, emend. Sarjeant & Downie, 1966

Genus ***ENDOSCRINIUM*** Klement, emend. Vozzhennikova, 1967a

Endoscrinium cf. ***campanula*** (Gocht)

(Pl. 5, figs. 9, 10 ; Text-fig. 27)

DESCRIPTION. A broadly ovate theca with a blunt, broad apical horn. Tabulation : 4′, 6″ 6c, 5″′, ?1p, 0″″. The crests are moderately high and irregularly perforated ; their distal edges are smooth. The cingulum forms a strong laevorotatory spiral, dividing the theca into two more or less equal parts. The epitract is pyramidal, the hypotract hemispherical. An endoblast, of similar shape to the shell, is present. The well developed sulcus broadens markedly towards the antapex. The surface of the periphragm is granular. A precingular archaeopyle forms by loss of plate 3″.

FIGURED SPECIMEN. BM(NH) slide V.52795(1). Shelly clay from *Liostrea delta* Bed, west of Osmington Mills, Dorset (OM 131).

DIMENSIONS. Figured specimen : overall length 90 μ, breadth 85 μ ; endoblast length 76 μ, breadth 70 μ. Range of the English specimens (6 specimens measured) : overall length 75–96 μ, breadth 60–85 μ ; endoblast length 50–78 μ, breadth 48–75 μ. French specimens (12 specimens measured) : overall length 78–105 μ, breadth 68–82 μ ; endoblast length 55–75 μ, breadth 50–75 μ. Only one specimen from the Scottish material was observed and measured : overall length 93 μ, breadth 85 μ ; endoblast length 73 μ, breadth 65 μ.

E. campanula holotype dimensions, as quoted by Gocht, are overall length 104 μ, breadth 91 μ. The basal Kimmeridgian specimens from France are of similar size to the holotype, but the Scottish and English specimens are a little smaller.

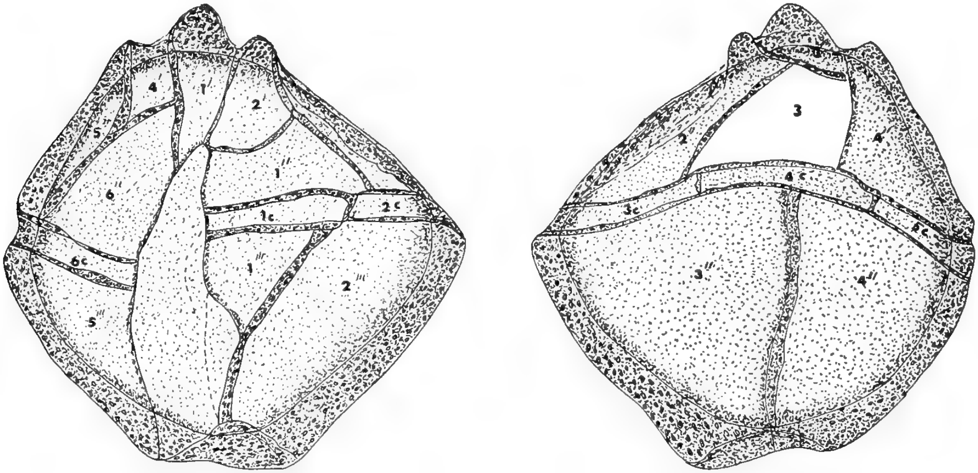

FIG. 27. *Endoscrinium* cf. *campanula* (Gocht). Tabulation and the archaeopyle formation. Left, ventral view ; right, dorsal view. ×*c*. 1280.

REMARKS. *E. campanula* has been recorded from the Lower Cretaceous (Lower and Upper Hauterivian) of Germany by Gocht (1959) and Alberti (1961), and also described from the Middle Cretaceous (Upper Albian and Lower Cenomanian) by Cookson and Hughes (1964) ; from Albian, Cenomanian and Turonian of England (Davey, 1966). Vozzhennikova observed it in the Barremian assemblages of Russia.

Similar specimens to this species were observed in the basal Kimmeridgian assemblages from Dorset, Scotland and the Boulonnais. These specimens are comparable with the specimens described as *E. campanula,* in their general morphologic features, but differ in the following few points : the surface of the shell of *E.* cf. *campanula* is granular, its crests perforate and endoblast rounded at the apex, and the apical horn forms from the periphragm only.

Endoscrinium galeritum (Deflandre) Vozzhennikova, 1967a

(Pl. 3, figs. 7, 8 ; Pl. 8, fig. 3)

1938a *? Gymnodinium galeritum* Deflandre: 167, pl. 5, figs. 7–9 ; pl. 6, fig. 1 ; text-fig. 1.
1957 *Scriniodinium galeritum* (Deflandre) ; Klement: 110.
1960 *S.* (*Endoscrinium*) *galeritum* (Deflandre) ; Klement: 22–27, pl. 1, figs. 4–12 ; pl. 2, figs. 1–2; text-figs. 4–5.
1961a *S. galeritum* (Deflandre) ; Sarjeant: 98–99, pl. 14, fig. 6.
1962a *S. galeritum* (Deflandre) ; Sarjeant, tables 3, 4.
1962b *S. galeritum* (Deflandre) ; Sarjeant, tables 2, 3.
1964 *S. galeritum* (Deflandre) ; Downie & Sarjeant: 144.
1964 *S. galeritum* (Deflandre) ; Eisenack: 359–760.
1964a *S. galeritum* (Deflandre) ; Sarjeant, table 2.
1966 *S. galeritum* (Deflandre) ; Schulz & Mai, table 1.
1967a *Endoscrinium galeritum* (Deflandre) ; Vozzhennikova: 137, figs. 44a, b.
1967b *E. galeritum* (Deflandre) ; Vozzhennikova: 176, pl. 93, fig. 7, table 2.
1967 *Scriniodinium galeritum* (Deflandre) ; Dodekova: 13–14, pl. 1, figs. 1–5.
1967b *Endoscrinium galeritum* (Deflandre) ; Sarjeant, table 11.
1968 *E. galeritum* (Deflandre) ; Sarjeant: 236, pl. 1, fig. 11, table 2B.

REMARKS. This species of *Endoscrinium* is known from the Middle-Upper Jurassic only ; having been described from the Callovian of Normandy (Sarjeant, 1968) ; Oxfordian of France (Calvados) by Deflandre (1938) and England (Dorset and Yorkshire) by Sarjeant (1961, 1962) ; Malm Alpha of Germany (Klement, 1960) and Volgian of Russia (Moscow) by Vozzhennikova (1967). It was observed in the assemblages from Dorset and the Boulonnais ; it is infrequent and badly preserved, the figured specimen being the best one found.

FIGURED SPECIMENS. BM(NH) slide V.52800(4). Shaly clay from *Liostrea delta* Bed, west of Osmington Mills, Dorset (OM 131).

Slide RB 219/1–7, from the base of Kimmeridge Clay, *Rhactorhynchia inconstans* Bed, Ringstead Bay, Dorset.

DIMENSIONS. Range of the English specimens (3 specimens measured) : overall length 78–90 μ, breadth 72–78 μ ; endoblast length 72–80 μ, breadth 67–75 μ. 2 French specimens were measured : overall length 75–86 μ, breadth 65–75 μ.

Endoscrinium luridum (Deflandre), emend. Vozzhennikova, 1967b

(Pl. 3, fig. 2 ; Text-fig. 28)

1938a *Gymnodinium luridum* Deflandre: 166, pl. 5, figs. 4–6.
1957 *Scriniodinium luridum* (Deflandre); Klement: 109–110.
1958 *Gymnodinium luridum* Deflandre; Cookson & Eisenack: 24, pl. 1, figs. 3, 4.
1960 *Scriniodinium luridum* (Deflandre); Sarjeant, pl. 12, fig. 2.
1960 *Scriniodinium* (*Endoscrinium*) *luridum* (Deflandre); Klement: 20–22, pl. 1, figs. 1–3; text-figs. 2–3.
1962a *S. luridum* (Deflandre); Sargeant: 259–261, pl. 1, fig. 14, tables 3, 4.
1962b *S. luridum* (Deflandre); Sarjeant, pl. 69, fig. 7.
1964 *S. luridum* (Deflandre); Downie & Sarjeant: 144.
1964 *S. luridum* (Deflandre); Eisenack: 767–768.
1964a *S. luridum* (Deflandre); Sarjeant, table 2.
1967 *S. luridum* (Deflandre); Dodekova: 12–13, pl. 1, fig. 3.
1967b *Endoscrinium luridum* (Deflandre); Vozzhennikova: 175.
1967b *E. luridum* (Deflandre); Sarjeant, table 11.
1968 *E. luridum* (Deflandre); Sarjeant, table 2B.

REMARKS. This species was recorded from the Upper Jurassic (Oxfordian–Kimmeridgian) of England, France, Germany, Bulgaria and Australia. It is extremely infrequent in assemblages from Dorset, Normandy and the Boulonnais, but quite frequent in the Scottish material.

FIGURED SPECIMEN. BM(NH) slide V.53934(3). Clay from *Liostrea delta* Bed of Villerville, Normandy (VN 184).

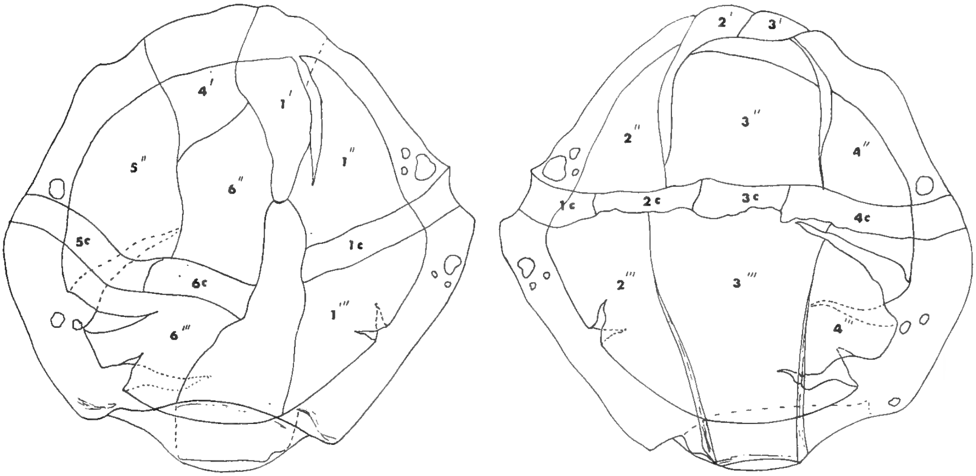

FIG. 28. *Endoscrinium luridum* (Deflandre). Tabulation and the archaeopyle formation (plate $3''$ remains attached). Left, ventral view ; right, dorsal view. ×*c.* 1280.

DIMENSIONS. Figured specimen : overall length 92 μ, breadth 68 μ ; endoblast length 76 μ, breadth 55 μ. Other two French specimens overall length 55–90 μ, breadth 52–85 μ ; endoblast length 45–75 μ, breadth 46–70 μ. Range of the English specimens (3 specimens measured) : overall length 90–120 μ, breadth 80–110 μ ;

endoblast length 63–90 μ, breadth 62–85 μ. Scottish specimens (5 specimens measured) : overall length 50–90 μ, breadth 48–90 μ ; endoblast length 45–70 μ, breadth 40–70 μ.

Endoscrinium oxfordianum (Sarjeant) Vozzhennikova, 1967a

(Pl. 5, fig. 6)

1960 *Scriniodinium* sp. Sarjeant: 394, pl. 13, fig. 2.
1962a *Scriniodinium* (*?Endoscrinium*) sp. Sarjeant; Sarjeant: 263, pl. 1, fig. 15.
1962b *Scriniodinium* (*?Endoscrinium*) *oxfordianum* Sarjeant; Sarjeant: 485–486, pl. 69, figs. 13–14; tables 2–3.
1964 *Scriniodinium oxfordianum* Sarjeant; Downie & Sarjeant: 144.
1964 *S.* (*?Endoscrinium*) *oxfordianum* Sarjeant; Eisenack: 769.
1964a *S. oxfordianum* Sarjeant; Sarjeant, table 2.
1967a *Endoscrinium oxfordianum* (Sarjeant); Vozzhennikova: 175.
1967 *E. oxfordianum* (Sarjeant); Sarjeant, table 11.

REMARKS. This species was previously recorded from the Oxfordian of England. It is infrequent in the basal Kimmeridgian assemblages and generally the preservation was not good.

FIGURED SPECIMEN. BM(NH) slide V.53933(1). Clay from *Liostrea delta* Bed of Villerville, Normandy (VN 184).

DIMENSIONS. Figured specimen : overall length 80 μ, breadth 68 μ ; endoblast length 63 μ, breadth 60 μ. The other French specimens and the English specimens were not capable of measurement. Range of the Scottish specimens (4 specimens measured) : overall length 60–100 μ, breadth 40–85 μ ; endoblast length 48–75 μ, breadth 32–75 μ.

Genus ***PSALIGONYAULAX*** Sarjeant, 1969

Psaligonyaulax apaleta (Cookson & Eisenack), Sarjeant, 1969

(Pl. 6, fig. 8 ; Text-fig. 29)

1960a *Scriniodinium apatelum* Cookson & Eisenack: 249, pl. 37, figs. 12–13.
1964 *S. apatelum* Cookson & Eisenack; Downie & Sarjeant: 144.
1964 *S. apatelum* Cookson & Eisenack; Eisenack: 747.
1964 *S. apatelum* Cookson & Eisenack; Manum & Cookson: 20, pl. 4, fig. 4.
1964a *S. apatelum* Cookson & Eisenack; Sarjeant, table 2.
1966 *Psaligonyaulax apaleta* (Cookson & Eisenack); Sarjeant, *nomen nudum*: 138
1967b *P. apaleta* (Cookson & Eisenack); Sarjeant, table 11: *nomen nudum.*
1969 *P. apaleta* (Cookson & Eisenack); Sarjeant (in press).

DESCRIPTION. The shell is elongate and bears a small apical horn and a pronounced antapical pericoel ; this is posteriorly narrow, with a spine-like projection at the antapex. The endoblast follows the outline of the shell except at the apex and antapex. There is an apical bulge on the endoblast. There is no tabulation ; the surface of the shell is smooth. A precingular archaeopyle is present, whose plate equivalence is uncertain.

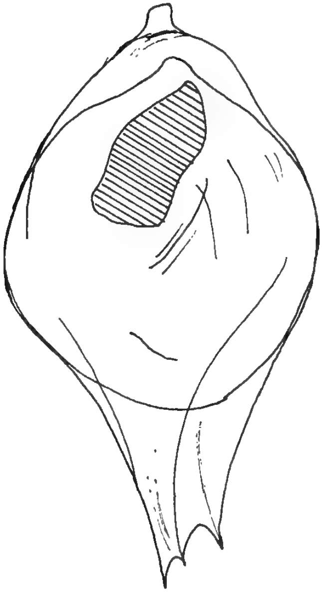

FIG. 29. *Psaligonyaulax apaleta* (Cookson & Eisenack). A specimen from the basal Kimmeridgian of Osmington Mills. ×*c.* 850.

FIGURED SPECIMEN. BM(NH) slide V.52804(1). Clay from 15 ft. above the Ringstead Coral Bed, west of Osmington Mills, Dorset (OM 419).

DIMENSIONS. Figured specimen : overall length 87 μ, breadth 50 μ ; endoblast length 55 μ, breadth 50 μ. Range of the English specimens (9 specimens measured) : overall length 75–105 μ, breadth 35–53 μ ; endoblast length 48–68 μ, breadth 35–53 μ. French specimens (5 specimens measured) : overall length 70–100 μ, breadth 37–60 μ ; endoblast length 45–65 μ, breadth 30–58 μ. Holotype dimensions (as quoted by Cookson and Eisenack) : overall length 120 μ, breadth 58 μ ; endoblast length 80 μ, breadth 58 μ. The Australian specimen is thus larger than the European specimens.

REMARKS. *P. apaleta* has previously been recorded from the Oxfordian to Lower Kimmeridgian of Australia and New Guinea. It was observed in the assemblages from Dorset, Stretham, Normandy and the Boulonnais, but it was not observed in the Scottish material.

Psaligonyaulax sp.

(Pl. 3, fig. 6 ; Text-fig. 30)

DESCRIPTION. The elongate shell bears an apical horn which is formed by the periphragm only. There is no determinable tabulation. A large precingular archaeopyle is present on the dorsal side. The surface of the shell is smooth.

FIGURED SPECIMEN. BM(NH) slide V.53956(3). Clay from 20 ft. above the Ringstead Coral Bed, Osmington Mills, Dorset (OM 420).

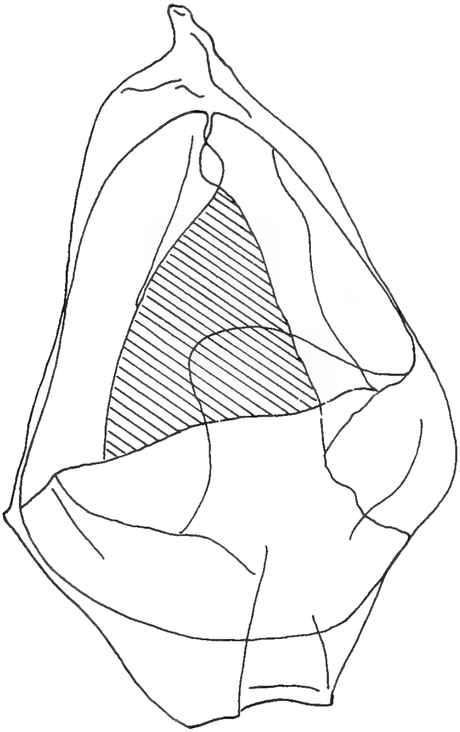

FIG. 30. *Psaligonyaulax* sp. A specimen from Osmington Mills, showing the precingular archaeopyle. ×*c*. 1280.

DIMENSIONS. Figured specimen : overall length 70 μ, breadth 45 μ ; endoblast length 50 μ, breadth 43 μ.

REMARKS. A single specimen was observed, which is closely similar to *P. apaleta* in its general appearance but differs in having a broader and more ovoidal shell. It may be an undescribed species ; for fuller knowledge, further specimens must be awaited.

Cyst-Family **HEXAGONIFERACEAE** Sarjeant & Downie, 1966

Genus ***HEXAGONIFERA*** Cookson & Eisenack, 1962

Hexagonifera sp.

(Pl. 1, fig. 12)

DESCRIPTION. A species of *Hexagonifera* which has a thick-walled, broadly ovoidal shell, with 6-sided apical archaeopyle. The surface of the shell is densely granular with occasional tubercles. The shell is completely enclosed in a smooth, delicate membrane. The circular, equatorial cingulum divides the shell into two equal parts. There is no definite indication of sulcus or of tabulation.

FIGURED SPECIMEN. BM(NH) slide V.53621(1). Shale from 100 ft. above the second dolerite sill, Staffin Bay, Skye (SS 627).

DIMENSIONS. Figured specimen : overall length (apex lacking) 46 μ, breadth 50 μ ; endoblast length (apex lacking) 40 μ, breadth 42 μ. Range of the English specimens (2 specimens measured) : overall length (apex lacking) 43–50 μ, breadth 48–52 μ ; endoblast length (apex lacking) 38–40 μ, breadth 42–52 μ. Range of the French specimens (3 specimens measured) : overall length (apex lacking) 42–50 μ, breadth 35–50 μ ; endoblast length (apex lacking) 38–46 μ, breadth 35–40 μ.

REMARKS. Well-preserved specimens are present, relatively infrequently, in assemblages from Dorset, Scotland, Le Havre and the Boulonnais. They are distinguished from the described species of *Hexagonifera* by the presence of a cingulum and the type of sculpture.

These specimens are similar to *Ascodinium verrucosum*, but A. *verrucosum* has one or two antapical horns whereas *Hexagonifera* sp. has a rounded antapex without any projection. Also the cingulum was not mentioned in A. *verrucosum*, whereas it is obvious in *Hexagonifera* sp. Therefore they appear to be different, and this new form is placed in the genus *Hexagonifera* ; possibly it is a new species of the latter genus ; but, before this can be decided, further specimens must be examined.

Genus ***PARVOCAVATUS*** gen. nov.

DERIVATION OF THE NAME. Latin, *parvus*, little small ; *cavo-atus*, hollow out, with reference to the cavate cyst of microfossil.

DIAGNOSIS. Cavate dinoflagellate cysts, subspherical, ovate to elongate, with the tabulation 4′, 6″, 6c, 6‴ and 1⁗. Cingulum circular, and nearly equatorial. Sulcus long and extending onto epitract and hypotract to equal length. Apical horn present and formed by the periphragm ; this is hollow and has a hole at its tip. Thin periblast surrounding a spheroidal endoblast ; the latter is thick-walled. Archaeopyle apical, the operculum remaining attached. Surface of periphragm smooth, but surface of the endophragm densely tuberculate.

TYPE SPECIES. *Parvocavotus tuberosus* sp. nov. Base of Kimmeridgian, Osmington Mills, Dorset.

REMARKS. A group of cavate cysts from the base of the Kimmeridge Clay are characterized by the incipient apical archaeopyle formation and the tabulation. Because of the mode of archaeopyle formation, these microfossils are attributed to Cyst-family Hexagoniferaceae in spite of their possession of tabulation. However, the tabulation, cingulum and sulcus are all poorly marked.

Parvocavatus tuberosus sp. nov.

(Pl. 6, fig. 9 ; Text-fig. 31)

Derivation of the name. Latin, *tuberosus*, full of lumps or protuberances.

Diagnosis. *Parvocavatus* having an ovoidal-polygonal periblast, with a spheroidal endoblast inside. There is a hollow apical horn at the apex, which is formed by the periphragm only and has a hole at its tip. Reflected tabulation : 4′, 6″, 6c, 6″ ′, and 1″ ″. Periphragm thin, endophragm thick, with a densely tuberculate surface. A circular cingulum divides the shell into two nearly equal parts. Apical archaeopyle developed, the operculum typically remaining attached.

Holotype. BM(NH) slide V.53956(4). Kimmeridge Clay from 20 ft. above the Ringstead Coral Bed, Osmington Mills, Dorset (OM 420).

Dimensions. Holotype : overall length 55 μ, breadth 45 μ ; endoblast diameters 40 × 40 μ. Other English specimens (2 specimens measured) : overall length 52–56 μ, breadth 46–48 μ ; endoblast diameters 38–40 μ. Range of the French specimens (40 specimens measured) : overall length 50–55 μ, breadth 43–45 μ ; endoblast diameters 35–45 μ. All the observed specimens were not capable of measurement.

Description. The periblast is ovoidal with a short, blunt apical horn ; the endoblast is spherical ; both periblast and endoblast have a rounded antapex. The epitract and hypotract are nearly equal in size. The sulcus extends between apex and antapex. On the ventral surface there is a split between the apical and precingular plates, which suggests incipient archaeopyle formation. The presence of a hole at the tip of the apical horn is also noteworthy. The precingular plates are

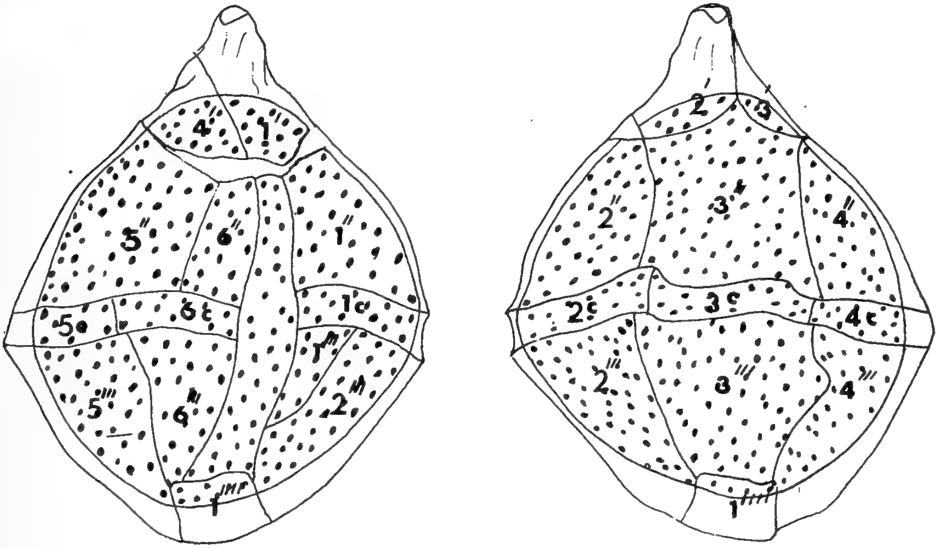

Fig. 31. *Parvocavatus tuberosus* sp. nov. Holotype, showing the tabulation and the archaeopyle formation. Left, ventral view ; right, dorsal view. ×*c.* 1280.

generally large : plate 6″ is smaller than the others. Six postcingular plates are present, plate 1″ ′ small and triangular-shaped. A single antapical plate is present ; it is quite large and convex.

REMARKS. *Parvocavatus tuberosus* is similar to *Gardodinium trabeculosum*, but differs in having no processes connecting the two membranes. This new species differs from all previously described species in its combination of the characteristic hole at the tip of the apical horn, archaeopyle formation and tabulation.

P. tuberosus is common in the French material, but it is rare in Dorset and Scottish assemblages. Generally the specimens are badly preserved, so that it was difficult to determine the details of the tabulation.

Cyst-Family **NELSONIELLACEAE** Eisenack, emend. Sarjeant & Downie, 1966

Genus ***SCRINIODINIUM*** Klement, 1957

Scriniodinium bicuneatum (Deflandre), Sarjeant, 1967a

(Pl. 5, fig. 5)

1938a *Palaeoperidinium bicuneatum* Deflandre: 180, pl. 8, fig. 7.
1957 *P. bicuneatum* Deflandre; Downie: 422, pl. 20, fig. 2.
1964 *P. bicuneatum* Deflandre; Downie & Sarjeant: 137.
1964 *P. bicuneatum* Deflandre; Eisenack: 591–592.
1964a *P. bicuneatum* Deflandre; Sarjeant, table 2.
1967b *P. bicuneatum* Deflandre; Vozzhennikova: 101.
1967a *?Scriniodinium bicuneatum* (Deflandre); Sarjeant: 248.
1967b *S. bicuneatum* (Deflandre); Sarjeant, table 11.

REMARKS. This species has been recorded from the Oxfordian of France (Deflandre, 1938) and Kimmeridgian of England (Downie, 1957) as *Palaeoperidinium bicuneatum* ; Sarjeant (1967) re-attributed to the genus *Scriniodinium* since presence of a tabulation not been confirmed.

Poorly preserved specimens were observed in small numbers in the basal Kimmeridgian assemblages of Dorset.

FIGURED SPECIMEN. BM(NH) slide V.53952(1). Clay from 10 ft. above the Ringstead Coral Bed, west of Osmington Mills, Dorset (OM 418).

DIMENSIONS. Figured specimen : overall length 105 μ, breadth 100 μ. Range : length 88–105 μ, breadth 75–100 μ. 2 specimens were measured.

Scriniodinium crystallinum (Deflandre), emend. Klement, 1957

(Pl. 7, fig. 6 ; Text-fig. 32)

1938a *Gymnodinium crystallinum* Deflandre: 165, pl. 5, figs. 1–3.
1938b *G. crystallinum* Deflandre; Deflandre: 688, fig. 1.
1957 *Scriniodinium crystallinum* (Deflandre); Klement: 109–110, fig. 1.
1958 *G. crystallinum* Deflandre; Cookson & Eisenack, pl. 1, figs. 1–3.
1960 *Scriniodinium crystallinum* (Deflandre); Klement: 18, pl. 1, fig. 1; text-fig. 1.

1961a *S. crystallinum* (Deflandre); Sarjeant: 98, pl. 14, figs. 9–12.
1962a *S. crystallinum* (Deflandre); Sarjeant: 259–261, pl. 2, fig. 2.
1964 *S. crystallinum* (Deflandre); Downie & Sarjeant: 145.
1964 *S. crystallinum* (Deflandre); Eisenack: 753–754.
1964a *S. crystallinum* (Deflandre); Sarjeant, table 2.
1966 *S. crystallinum* (Deflandre); Schulz & Mai, table 1.
1967 *S. crystallinum* (Deflandre); Dodekova: 11–12, pl. 1, figs. 1, 2.
1967b *S. crystallinum* (Deflandre); Sarjeant, table 11.
1968 *S. crystallinum* (Deflandre); Sarjeant, table 2B.

REMARKS. This species has been recorded from the Oxfordian of France (Deflandre, 1938a, b) and England (Sarjeant, 1961, 1962) ; Upper Callovian to Lower Oxfordian of Normandy (Sarjeant, 1968) ; Oxfordian to Middle Kimmeridgian of Australia (Cookson & Eisenack, 1957) and Malm Alpha of Germany (Klement, 1957, 1960). It is quite frequent in the basal Kimmeridgian assemblages, but all the specimens encountered are severely damaged, folded or covered by fine debris.

FIGURED SPECIMEN. BM(NH) slide V. 53942(1). Clay from between the Ringstead Coral Bed and Ringstead Waxy Clay, Ringstead Bay, Dorset (RB 219).

DIMENSIONS. Figured specimen : overall length 105 μ, breadth 75 μ ; endoblast length 95 μ, breadth 70 μ. Range of the English specimens (15 specimens measured) : overall length 90–100 μ, breadth 70–95 μ ; endoblast length 69–95 μ, breadth 62–90 μ. French specimens (8 specimens measured) : overall length 55–92 μ, breadth 52–95 μ ; endoblast length 45–76 μ, breadth 46–68 μ. Scottish specimens (5 specimens meas-

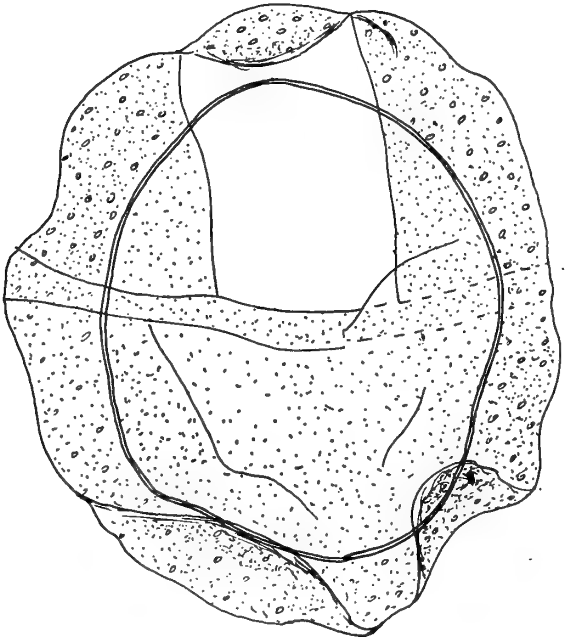

FIG. 32. *Scriniodinium crystallinum* (Deflandre). Dorsal view, showing the precingular archaeopyle. × *c*. 860.

ured) : overall length 55–105 μ, breadth 50–95 μ ; endoblast length 45–98 μ, breadth 45–75 μ.

Holotype dimensions, as quoted by Deflandre : length 65–92 μ, breadth 58–85 μ. Klement gave the following measurements for German specimens : length 81–127 μ, breadth 72–98 μ. The Kimmeridgian specimens thus accord with those from the European Oxfordian, whereas the Australian specimens are markedly larger.

Scriniodinium dictyotum Cookson & Eisenack, 1960a

1960a *Scriniodinium dictyotum* Cookson & Eisenack: 248–249, pl. 37, figs. 8, 9.
1962a *S. dictyotum* Cookson & Eisenack; Sarjeant: 262, pl. 1, fig. 9, tables 3, 4.
1962b *S. dictyotum* Cookson & Eisenack; Sarjeant, pl. 69, fig. 11.
1964 *S. dictyotum* Cookson & Eisenack, Downie & Sarjeant: 145.
1964 *S. dictyotum* Cookson & Eisenack; Eisenack: 755.
1964a *S. dictyotum* Cookson & Eisenack; Sarjeant, table 2.
1967b *S. dictyotum* Cookson & Eisenack; Sarjeant, table 11.
1968 *S. dictyotum* Cookson & Eisenack; Sarjeant: 236, pl. 1, fig. 7; table 2b.

REMARKS. *S. dictyotum* was originally recorded from Upper Jurassic with a stratigraphic range from Upper Callovian to Lower Kimmeridgian.

Scriniodinium dictyotum subsp. ***dictyotum*** Cookson & Eisenack

DIAGNOSIS. The typical subspecies of *Scriniodinium dictyotum*, with shell flat, oval, divided by a distinct and relatively broad girdle into an epitheca and hypotheca of approximately equal size ; epitheca prolonged into a broadly based, short, blunt apical projection. Capsule oval with a short apical prominence. The wall of the capsule bears numerous thin perpendicular ledges which form a small-meshed supporting reticulum for the thin outer membrane. The meshes of the reticulum vary considerably in size and reach the girdle. [Diagnosis as given, for the type material, by Cookson and Eisenack (1960).]

HOLOTYPE. *Scriniodinium dictyotum* Cookson & Eisenack, Melbourne Nat. Mus. Victoria, P 17768. Probably Tithonian, west of Australia.

REMARKS. The specimens encountered from the basal Kimmeridgian of Dorset and Le Havre show variation in the character of their apical structure. It is considered necessary, therefore, that the species be subdivided into a number of subspecies, to differentiate these new forms from the specimens within the range of the typical *S. dictyotum* Cookson & Eisenack. The latter forms are redesignated as *S. dictyotum* subsp. *dictyotum*.

Scriniodinium dictyotum subsp. ***osmingtonensis*** nov.

(Pl. 1, fig. 3 ; Pl. 8, fig. 12)

DERIVATION OF THE NAME. Named after the type locality, Osmington Mills, Dorset.

DIAGNOSIS. *Scriniodinium dictyotum* without any prominence at the apex.

HOLOTYPE. BM(NH) slide V.52797(1). Shaly clay from *Liostrea delta* Bed, west of Osmington Mills, Dorset (OM 131).

DIMENSIONS. Holotype : overall length 90 μ, breadth 82 μ ; endoblast length 80 μ, breadth 70 μ. Range of the other specimens (6 specimens measured) : overall length 75–90 μ, breadth 75–82 μ.

DESCRIPTION. The shell is broadly ovate with an endoblast. There is no apical horn. Periblast irregularly reticulate. The cingulum is circular and equatorial. A large precingular archaeopyle is present on the dorsal side. 9 specimens were observed in the materials from Dorset with these structures.

Scriniodinium dictyotum subsp. ***papillatum*** nov.

(Pl. 9, fig. 11)

DERIVATION OF THE NAME. Latin, *papilla* teat, nipple, bud ; with reference to the apical projection shape.

DIAGNOSIS. *Scriniodinium dictyotum* characterized by its blunt, mamelon-shaped apical prominence. The endophragm has the same shape as the periphragm.

HOLOTYPE. BM(NH) slide V.53940(1). Clay from 20 ft. above the Ringstead Coral Bed, west of Osmington Mills, Dorset (OM 420).

DIMENSIONS. Holotype : overall length 88 μ, breadth 70 μ. Range (2 specimens measured) : overall length 86–90 μ, breadth 65–85 μ.

DESCRIPTION. The shell is broadly ovoidal in shape, terminating in a mamelon form. The surface of the periphragm is irregularly reticulate.

Scriniodinium dictyotum subsp. ***pyrum*** nov.

(Pl. 13, figs. 1, 2 ; Pl. 10, fig. 1 ; Text-fig. 33 a, b)

DERIVATION OF THE NAME. Latin, *pyrum* pear, with reference to the pear-shape of the shell.

DIAGNOSIS. *Scriniodinium dictyotum* with shell elongate, roughly pear-shaped, with a strong apical horn and rounded antapex. The endophragm follows the periphragm except at the apex. The apical prominence of the endoblast is shorter and terminates in a mamelon form. Reflected tabulation : 5′, 6″, 6c, 6″ ′, 1p and 1″ ″. A circular cingulum divides the theca into two unequal parts, with epitract longer than the hypotract. Sulcus approximately sigmoidal. A precingular archaeopyle is present.

HOLOTYPE. BM(NH) slide V.53949(2). Clay from *Rhactorhynchia inconstans* Bed, Ringstead Bay, Dorset (RB 219).

DIMENSIONS. Holotype : overall length 108 μ, breadth 74 μ ; horn length 20 μ. Range of the English specimens (5 specimens measured) : overall length 108–125 μ,

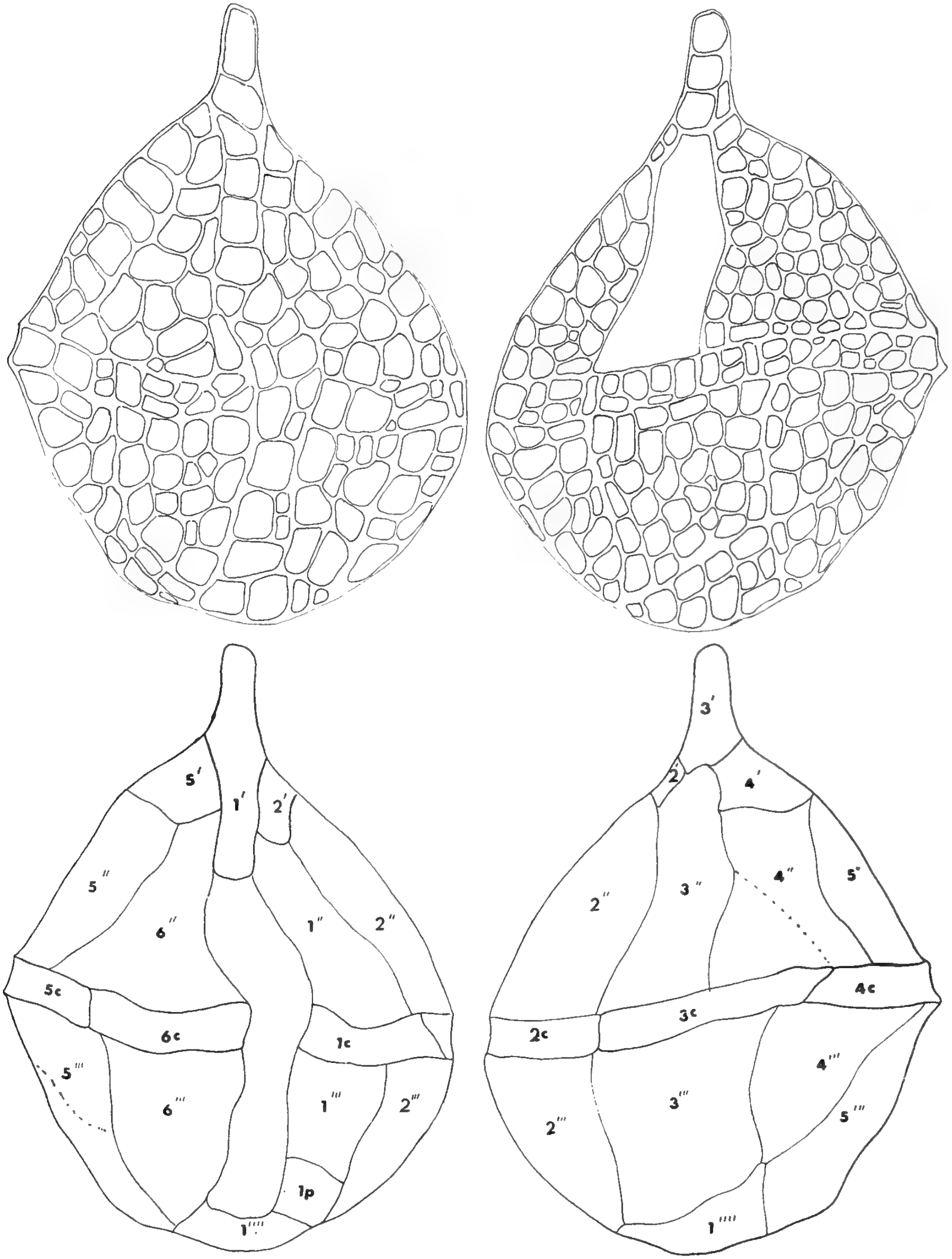

Fig. 33. *Scriniodinium dictyotum* subsp. *pyrum* nov. A. Holotype, showing the general appearance and the archaeopyle. Left, ventral view ; right, dorsal view. ×*c.* 1280. B. Reconstruction of original tabulation from the pattern of reticulation of the cyst. ×*c.* 1280.

breadth 74–90 μ ; horn length 20–30 μ. Dimensions of the French specimen : overall length 106 μ, breadth 70 μ ; horn length 14 μ.

Description. The rather large shell has a strong apical horn. The reflected tabulation is based on the alignment of some field boundaries ; along the boundaries of the plates, the series of alveoli are better developed and so reflect the tabulation. Apical plate 1′ is long and forms the horn, together with plate 3′. Plate 2′ is the smallest of the apical plates ; plates 4′ and 5′ are rather large. The precingular plates are more or less uniform in size. Plate 3″ is lost in archaeopyle formation.

The cingulum is moderately wide and occupied by six plates. The sulcus extends between the apex and the antapex, in moderate breadth and approximately sigmoidal in shape.

The postcingular plates are likewise large, plate 1″ ′ being reduced to accommodate the single posterior intercalary plate 1p. The antapex is occupied by a single, quite large plate.

Scriniodinium* cf. *galeatum (Cookson & Eisenack)

(Pl. 6, fig. 2)

Description. The elongate periblast contains a spherical endoblast and is characterized by well-developed apical and antapical pericoels. A small hollow apical horn is present on the periblast. A narrow helicoid cingulum divides the shell into two unequal parts, with the hypotract longer than the epitract. There is no tabulation and no sign of archaeopyle formation. The endophragm is thick, the periphragm thin, both of them have a smooth surface.

Figured specimen. BM(NH) slide V.53967(1). Calcaires de Moulin Wibert, Cap de La Crèche, Boulonnais (CC 448).

Dimensions. Figured specimen : overall length 75 μ, breadth 45 μ ; endoblast diameters 45 × 45 μ. The second specimen was not capable of measurement because of the preservation.

Remarks. *S. galeatum* has been recorded from the Cenomanian of Australia (Cookson & Eisenack, 1960). Two specimens only were observed from the Boulonnais assemblages ; they are closely similar to *S. galeatum*, but their epitract is broader and shorter than that of the Australian holotype. The cingulum, moreover, is helicoid, not circular as described by Cookson and Eisenack. For these reasons, they are compared with, rather than attributed to, *S. galeatum*.

Scriniodinium playfordi Cookson & Eisenack, 1960a

(Pl. 12, fig. 3)

1958 *Gymnodinium crystallinum* Deflandre; Cookson & Eisenack: 22, pl. 1, fig. 2.
1960a *Scriniodinium playfordi* Cookson & Eisenack: 248–249, pl. 37, fig. 6.
1964 *S. playfordi* Cookson & Eisenack; Downie & Sarjeant: 145.
1964 *S. playfordi* Cookson & Eisenack; Eisenack: 771.

1964a *S. playfordi* Cookson & Eisenack; Sarjeant, table 2.
1967a *S. playfordi* Cookson & Eisenack; Sarjeant, table 11.

DESCRIPTION. The periblast is ovate in shape, with an apical horn ; the endoblast slightly terminates in a mamelon form. There is no tabulation ; but a cingulum is present, nearly circular and equatorial. A precingular archaeopyle is developed by the loss of one plate on the dorsal side. The surface of the periphragm and the endophragm are smooth.

FIGURED SPECIMEN. BM(NH) slide V.53955(1). Clay from 15 ft. above the Ringstead Coral Bed, west of Osmington Mills, Dorset (OM 419).

DIMENSIONS. Figured specimen : overall length 80 μ, breadth 60 μ ; endoblast length 65 μ, breadth 52 μ, horn length 8 μ. Range of the French specimens (5 specimens measured) : overall length 55–110 μ, breadth 40–90 μ ; endoblast length 42–90 μ, breadth 40–85 μ.

When compared with the holotype dimensions, as quoted by Cookson and Eisenack (length 166 μ, breadth 147 μ), the European specimens are found to be smaller than the Australian specimens.

REMARKS. *Scriniodinium playfordi* has been recorded from the Oxfordian to the Lower Kimmeridgian of Australia and New Guinea (Cookson & Eisenack, 1958). It is infrequently present in the assemblages from Dorset, Le Havre and the Boulonnais. All the specimens observed, were badly preserved.

Cyst-Family **NETRELYTRACEAE** Sarjeant & Downie, 1966

Genus ***NETRELYTRON*** Sarjeant, 1961

Netrelytron parum sp. nov.

(Pl. 5, fig. 4 ; Pl. 9, fig. 4)

DERIVATION OF THE NAME. Latin, *par*, a pair, named because of the observation of two shells inside the same organic debris mass.

DIAGNOSIS. *Netrelytron* having a broadly ovoidal periblast, tapering to form a strong apical horn at the apex and a blunt, short mamelon at the antapex. Apical and antapical projections are formed by the periphragm only. Endoblast spheroidal, thin-walled and often hard to distinguish. The surfaces of the endophragm and periphragm are smooth or very finely granular.

HOLOTYPE. BM(NH) slide V.52801(2). Shelly clay from the *Liostrea delta* Bed, west of Osmington Mills, Dorset (OM 131).

DIMENSIONS. Holotype : length of the periblast 85 μ, breadth 60 μ ; apical horn length 16 μ, antapical horn length 6 μ. Range of the English specimens (11 specimens measured) : overall length 60–85 μ, breadth 35–60 μ ; apical horn length 10–16 μ, antapical horn length 3–6 μ. French specimens (10 specimens measured) : overall length 62–80 μ, breadth 35–60 μ ; horn length 10–12 μ, antapical horn length 3–5 μ.

DESCRIPTION. The shell is consistently enclosed in a cloak of organic matter. The periblast is ovoidal in shape, with a spherical endoblast. At the apex of the periblast, a strong apical horn is present, but the antapex is only slightly projecting. Both projections are formed by the periphragm only. Neither tabulation nor an archaeopyle was observed in any of the specimens. Although it is usual to find only a single body enclosed in each organic debris mass, two shells, apex to antapex, inside the same organic debris mass were observed in one instance (pl. 5, fig. 4).

REMARKS. This new species is common in the assemblages from Dorset, Normandy and the Boulonnais, but rare in the Le Havre and Stretham material. It is easily distinguishable from the only previously described species of the genus, *N. stegastum*, in its much less-marked antapical horn and more broadly elongate shape.

Netrelytron stegastum Sarjeant, 1961

(Pl. 8, fig. 9 ; Pl. 11, fig. 7)

1961 *Netrelytron stegastum* Sarjeant: 114–115, pl. 15, fig. 15; text-figure 14.
1962b *N. stegastum* Sarjeant; Sarjeant: 494–495, pl. 70, fig. 18, tables 2, 3.
1964 *N. stegastum* Sarjeant; Downie & Sarjeant: 135.
1964a *N. stegastum* Sarjeant; Sarjeant, table 4.
1967a *N. stegastum* Sarjeant; Sarjeant, table 13.

DESCRIPTION. This cavate cyst is spindle-shaped, with apical and antapical horns. There is an endoblast of ovoidal shape. The surface is granular. It was consistently observed with a mass of organic matter surrounding the shell. Neither tabulation nor an archaeopyle was observed.

FIGURED SPECIMENS. BM(NH) slide V.52796(2) and OM 131/14-225. Both from the same locality, shaly clay from the basal Kimmeridge Clay, *Liostrea delta* Bed, Osmington Mills, Dorset (OM 131).

DIMENSIONS. Range of the English specimens (5 specimens measured) : length 89–90 μ, breadth 40–58 μ, horn length 12–16 μ. Range of the French specimens (4 specimens measured) : length 80–88 μ, breadth 57–62 μ, horn length 13–15 μ. Holotype dimensions, as mentioned by Sarjeant (length 125 μ, breadth 55 μ), are larger than the Kimmeridge specimens.

REMARKS. This species has been previously recorded from the Lower Oxfordian of England (Sarjeant, 1961). It is infrequently present in the basal Kimmeridgian assemblages from Dorset, Normandy and Le Havre.

INCERTAE SEDIS

GROUP *ACRITARCHA* Evitt, 1963

SUBGROUP *ACANTHOMORPHITAE* Downie, Evitt & Sarjeant, 1963

Genus ***BALTISPHAERIDIUM*** Eisenack, emend. Downie & Sarjeant, 1963

Baltisphaeridium inusitatum Klement, 1960

(Pl. 13, fig. 5)

1960 *Baltisphaeridium inusitatum* Klement: 60–61, pl. 7, fig. 9.
1964 *B. inusitatum* Klement; Downie & Sarjeant: 91.
1964a *B. inusitatum* Klement; Sarjeant, table 3.

REMARKS. This species has been recorded from the Upper Jurassic (Malm Gamma) of Germany. It is very rare in the basal Kimmeridgian (two specimens from Dorset and one from Normandy were observed).

FIGURED SPECIMEN. BM(NH) slide V.53932(2). Clay from the *Liostrea delta* Bed, Villerville, Normandy (VN 184).

DIMENSIONS. Figured specimen : length 45 μ, breadth 35 μ, process length 28–30 μ. Range of observed English specimens (2 specimens measured) : shell length 40–43 μ, breadth 35–38 μ, process length 23–28 μ.

Genus ***MICRHYSTRIDIUM*** Deflandre, emend. Sarjeant, 1966

Micrhystridium fragile Deflandre, 1947

(Pl. 8, fig. 8 ; Pl. 12, fig. 4)

1947 *Micrhystridium fragile* Deflandre, 8, text-figs. 13–18.
1947 *M. fragile* Deflandre; Valensi, fig. 7.
1953 *M. fragile* Deflandre; Valensi: 41–43, pl. 5, figs. 1–4 & 17–19; pl. 14, figs. 1, 2.
1955 *M. fragile* Deflandre; Valensi, pl. 2, fig. 14.
1959b *M. fragile* Deflandre; Sarjeant: 340, text-figs. 7a–d.
1960 *M. fragile* Deflandre; Sarjeant, pl. 12, fig. 3; pl. 13, figs. 9–14.
1961a *M. fragile* Deflandre; Sarjeant: 105–106, pl. 13, figs. 3, 4; tables 3, 4.
1962a *M. fragile* Deflandre; Sarjeant, tables 2, 3.
1962b *M. fragile* Deflandre; Sarjeant, fig. 8; tables 3, 4.
1963 *M. fragile* Deflandre; Sarjeant, pl. 70, fig. 6.
1963 *M. fragile* Deflandre; Wall & Downie: 774.
1964 *M. fragile* Deflandre; Downie & Sarjeant: 131.
1964 *M. fragile* Deflandre; Takahashi: 205–206, pl. 31, figs. 8–10.
1964a *M. fragile* Deflandre; Sarjeant, table 4.
1965 *M. fragile* Deflandre; Sarjeant: 177, pl. 1, fig. 6.
1965 *M. fragile* Deflandre; Deflandre & Deflandre: fiches 2227–2243.
1966 *M. fragile* Deflandre; Medd: 352, pl. 59, figs. 1, 2.
1967c *M. fragile* Deflandre; Sarjeant, pl. 1, fig. 7; text-fig. 1 h.
1968 *M. fragile* Deflandre; Sarjeant, pl. 1, fig. 5; table 2A.

DESCRIPTION. The spherical to subspherical shell is smooth and thin-walled, bearing 10–18 processes. The processes are strong, straight or curved, hollow, conical and distally closed. In some of the specimens, opening of shell by splitting was observed.

FIGURED SPECIMENS. BM(NH) slide V.53961(2). Clay from Great Ouse River Board Pit, Stretham, Cambridgeshire (SC 444).

BM(NH) slide V.53948(4). Clay from *Rhactorhynchia inconstans* Bed, Ringstead Bay, Dorset (RB 219).

DIMENSIONS. Range of the English specimens : shell diameter 14–18 μ, process length 10–16 μ ; French specimens : shell diameter 12–18 μ, process length 10–15 μ ; Scottish specimens : shell diameter 8–18 μ, process length 7–15 μ. 25 English, 23 French and 5 Scottish specimens were measured. Holotype diameters 10·5 μ, process length 8–10 μ (as quoted by Deflandre). Sarjeant gives the mean diameters of the shells from Normandy as 15, 69 μ (1965). On the basis of these measurements, the Callovian and the basal Kimmeridgian specimens have similar shell diameters.

REMARKS. *M. fragile* has been recorded from the Bajocian and Bathonian of France (Deflandre, 1947 ; Valensi, 1953). Middle Jurassic (Cornbrash) and Upper Jurassic (Oxfordian) of England and France by Sarjeant. Takahashi recorded from Oligocene of Japan (1964) and Medd from Lower Triassic of Western Australia (1966). It is common in English, French and Scottish basal Kimmeridgian materials.

Micrhystridium inconspicuum (Deflandre), Deflandre 1937

(Pl. 1, fig. 8 ; Pl. 8, fig. 11 ; Pl. 11, fig. 6)

1935 *Hystrichosphaera inconspicua* Deflandre: 233, pl. 9, figs. 11–12.
1937 *Micrhystridium inconspicuum* (Deflandre); Deflandre: 32, pl. 12, figs. 11–13.
1947 *M. inconspicuum* (Deflandre); Valensi: 817, text-fig. 8.
1947 *M. inconspicuum* (Deflandre); Deflandre: 6, text-figs. 7–12.
1952 *M. inconspicuum* (Deflandre); Deflandre, text-figs. 26–29.
1953 *M. inconspicuum* (Deflandre); Valensi, pl. 2, fig. 10; pl. 7, figs. 14, 15, 20, 23, 26; pl. 8, figs. 1–5, 7–10, 14, 15, 17–20, 23–29, pl. 14, figs. 8–11.
1959b *M. inconspicuum* (Deflandre); Sarjeant: 340, text-fig. 7b.
1960 *M. inconspicuum* (Deflandre); Sarjeant: 398, pl. 14, fig. 18; text-fig. 1f.
1961 *M. inconspicuum* (Deflandre); Brosius & Bitterli: 40, pl. 2, figs. 17–18; text-fig. 8; table 3.
1961a *M. inconspicuum* (Deflandre); Sarjeant: 105, pl. 13, fig. 5; text-fig. 8f, g; tables 3, 4.
1962a *M. inconspicuum* (Deflandre); Sarjeant, pl. 2, fig. 13; text-fig. 8b.
1963 *M. inconspicuum* (Deflandre); Chornaya: 284, pl. 7, fig. 13.
1963 *M. inconspicuum* (Deflandre); Downie & Sarjeant: 92.
1964 *M. inconspicuum* (Deflandre); Spode: 365, pl. 38, fig. j, text-fig. 2j.
1964 *M. inconspicuum* (Deflandre); Downie & Sarjeant: 131.
1964a *M. inconspicuum* (Deflandre); Sarjeant, table 4.
1964 *M. inconspicuum* (Deflandre); Gocht: 124, text-fig. 44.
1965 *M. inconspicuum* (Deflandre); Sarjeant: 177, pl. 1, fig. 4; table 1.
1965 *M. inconspicuum* (Deflandre); Staplin, Jansonius & Pocock: 180.
1965 *M. inconspicuum* (Deflandre); Deflandre & Deflandre: fiches 2251–2273.
1967c *M. inconspicuum* (Deflandre); Sarjeant: 202–203, pl. 1, fig. 2; text-fig. 1D.
1968 *M. inconspicuum* (Deflandre); Sarjeant, pl. 2, fig. 12; table 2A.

DESCRIPTION. The spherical globular shell has a smooth surface from which arise simple, solid, distally closed processes, about 20–30 in number. There is no regularly formed opening on the surface.

FIGURED SPECIMENS. BM(NH) slide V.53953(1). Clay from 10 ft. above the Ringstead Coral Bed, Osmington Mills, Dorset (OM 418).

BM(NH) slide V.53939(2) and CH 185/10-208, both from Exogyra Marls *c.* 1 m. above the upper Hard Band, Cap de La Hève, Le Havre (CH 185).

DIMENSIONS. French specimens (10 specimens measured) : diameters 10–11 μ, process length 3–5 μ. English specimens (12 specimens measured) : diameters 10–10·5 μ, process length 4·5 μ. Scottish specimens (2 specimens measured) : diameters 8 μ, process length 3 μ.

REMARKS. This species has been recorded from the Middle Jurassic of France (Valensi, 1953 ; Sarjeant, 1962), the Cornbrash of England (Sarjeant, 1959) and the Cretaceous of France (Deflandre, 1935).

Micrhystridium sydus Valensi, 1953

(Pl. 8, fig. 10 ; Pl. 13, figs. 3, 4)

1953 *Micrhystridium sydus* Valensi: 59–60, pl. 8, fig. 40; pl. 9, figs. 3, 5, 11, 17, 23, 24.
1962b *M. sydus* Valensi; Sarjeant, tables 2, 3.
1964 *M. sydus* Valensi; Downie & Sarjeant: 133.
1964a *M. sydus* Valensi; Sarjeant, table 4.
1965 *M. sydus* Valensi; Sarjeant: 178–179, pl. 1, fig. 6.
1965 *M. sydus* Valensi; Deflandre & Deflandre, fiches 2414–2417.
1967c *M. sydus* Valensi; Sarjeant: 201–208.
1968 *M. sydus* Valensi; Sarjeant, table 2A.

DESCRIPTION. The spherical to subpolygonal shell bears 12–14 broad-based, conical processes. These processes are hollow, distally closed ; their cavity connects to the shell cavity. The central body surface is smooth. No opening was observed.

FIGURED SPECIMENS. BM(NH) slide V.53976(1). Shale from 80 ft. above the second dolerite sill, Staffin Bay, Skye (SS 626).

Slide 218/16-324, clay from between Ringstead Waxy Clay and Ringstead Coral Bed, Ringstead Bay, Dorset (RB 218).

DIMENSIONS. English specimens shell diameter 10 μ, process length 7 μ. Range of the Scottish specimens : shell diameters 20–20 μ, process length 7–12 μ ; French specimens : shell diameters 10–12 μ, process length 5–7 μ. 1 English, 3 Scottish and 4 French specimens were measured.

REMARKS. This species was first recorded from the Bathonian of France (Valensi, 1953) ; subsequently Sarjeant observed it in the Upper Jurassic material of England (1962, 1965) and France (1967). It is rare in the basal Kimmeridgian assemblages of France and Scotland, but abundant in English assemblages.

Sarjeant discussed whether *M. sydus* should be placed in the genus *Veryhachium*, since its spine cavity is connected to the shell interior (Sarjeant, 1965) ; however, *M. sydus* has processes in greater number than is typical for *Veryhachium* and also the processes are shorter than is usual for *Veryhachium*.

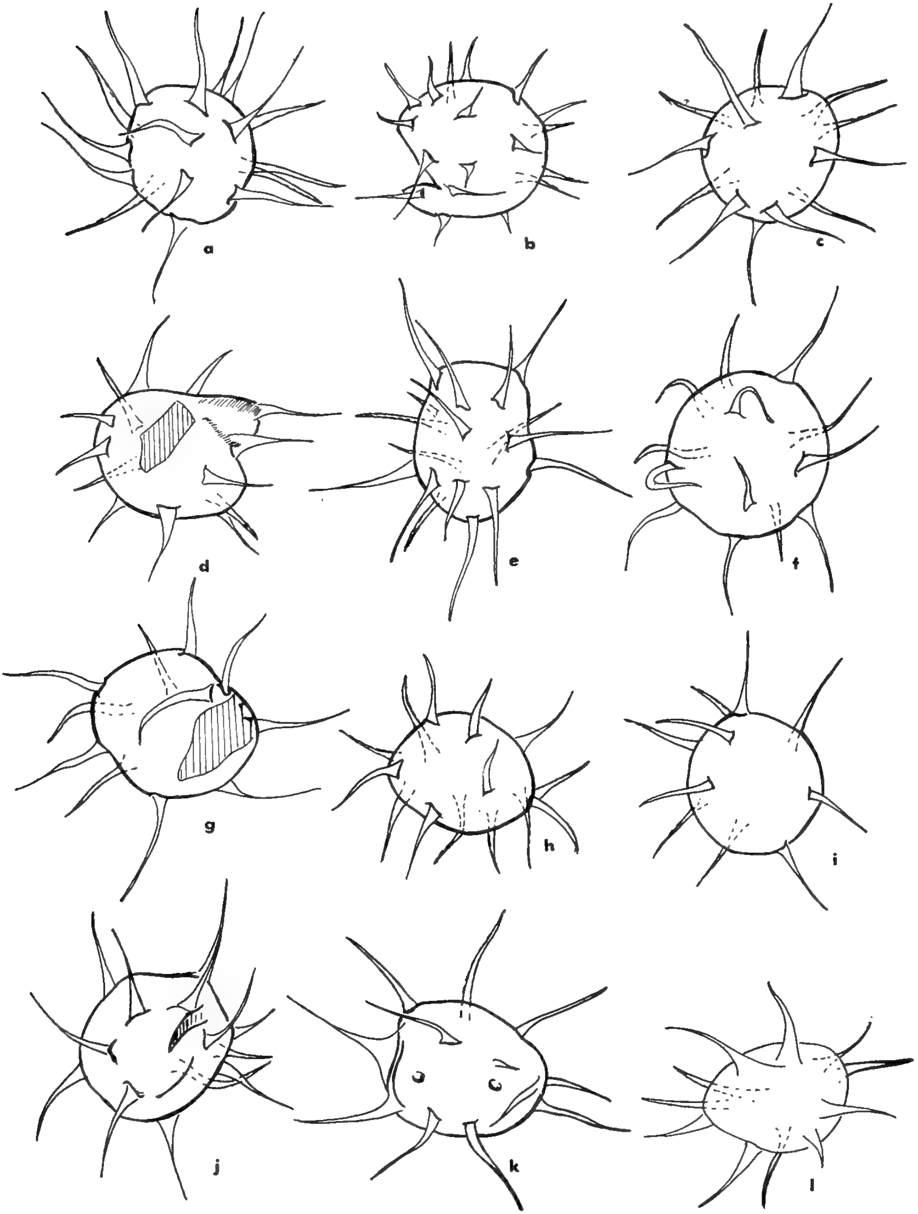

FIG. 34 a–l. *Solisphaeridium stimuliferum* (Deflandre). Specimens from Ringstead Bay Kimmeridge Clay. ×*c.* 1280.

Genus *SOLISPHAERIDIUM* Staplin Jansonius & Pocock, emend. Sarjeant, 1968

Solisphaeridium brevispinosum (Sarjeant) emend. Sarjeant, 1968

(Pl. 2, fig. 7)

1961a *Baltisphaeridium ehrenbergi* var. *brevispinosum* Sarjeant: 103, pl. 15, fig. 18; text-fig. 8a.
1964 *B. ehrenbergi* var. *brevispinosum* Sarjeant; Downie & Sarjeant: 90.
1964a *B. ehrenbergi* var. *brevispinosum* Sarjeant; Sarjeant, table 3.
1968 *Solisphaeridium brevispinosum* (Sarjeant); Sarjeant: 223–224, pl. 1, figs. 3–9.

DESCRIPTION. The spherical shell bears simple processes. The shell surface is smooth and thin-walled. The processes are conical with sharply-pointed tips, hollow, straight or curved ; fifty or more in number. The spine cavity is directly connected with the shell interior. No regularly formed opening was observed ; but an opening by splitting was observed in some of the shells.

FIGURED SPECIMEN. BM(NH) slide V.53957(1). Clay from 20 ft. above the Ringstead Coral bed, west of Osmington Mills, Dorset (OM 420).

DIMENSIONS. Figured specimen : diameters 35 μ, length of the processes 15 μ. Other English specimens : diameters 25–30 μ, process length 8–12 μ. 3 English specimens were measured. The French specimen was not capable of measurement, because of poor preservation.

REMARKS. *S. brevispinosum* has been recorded from the Oxfordian of England and the Upper Callovian-Lower Oxfordian of Normandy. It is rare in the basal Kimmeridgian.

Solisphaeridium stimuliferum (Deflandre) emend. Staplin, Jansonius & Pocock, 1965

(Pl. 13, fig. 6 ; Text-fig. 34 a–l)

1938a *Hystrichosphaeridium stimuliferum* Deflandre: 162, pl. 1, fig. 10.
1947 *H. stimuliferum* Deflandre; Deflandre, fig. 4.
1952 *H. stimuliferum* Deflandre; Deflandre, fig. 8.
1953 *H. stimuliferum* Deflandre; Valensi, pl. 4, figs. 13, 15, 16.
1960 *Baltisphaeridium stimuliferum* (Deflandre); Sarjeant: 397, pl. 12, fig. 9, text-fig 1j.
1961a *B. stimuliferum* (Deflandre); Sarjeant: 100.
1962 *B. stimuliferum* (Deflandre); Sarjeant, pl. 15, fig. 5, text-fig. 8g.
1963 *B. stimuliferum* (Deflandre); Sarjeant, pl. 70, fig. 17, text-fig. 8e.
1964 *B. stimuliferum* (Deflandre); Downie & Sarjeant: 97.
1964a *B. stimuliferum* (Deflandre); Sarjeant, table 3.
1965 *Solisphaeridium stimuliferum* (Deflandre); Staplin, Jansonius & Pocock: 183–184, pl. 18, figs. 1–2, text-figs. 3, 10.
1966 ?*B.* (*Micrhystridium*) *stimuliferum* (Deflandre); W. Wetzel, pl. 17, figs. 10a, 10b.
1968a *Solisphaeridium stimuliferum* (Deflandre); Sarjeant: 223, pl. 3, fig. 6, text-fig. 1.

DESCRIPTION. The shell is subspherical to ovate in shape, with a smooth surface and a thin wall. The processes are hollow, conical, straight or curved, and variable in length. The spine cavities are connected with the shell interior. An irregular break opens the shell.

FIGURED SPECIMENS. BM(NH) slide V.53949(3). From sample RB 219. Clay, immediately base of Kimmeridge Clay, *Rhactorhynchia inconstans* Bed, Ringstead Bay, Dorset.

DIMENSIONS. English specimens (50 specimens measured) : shell length 20–30 μ, breadth 18–28 μ, process length 15–30 μ. Scottish specimens (3 specimens measured): shell diameters 20–25 μ, process length 10–15 μ. French specimens (70 specimens measured) : shell length 21–33 μ, breadth 20–30 μ, process length 16–28 μ.

REMARKS. This Upper Jurassic species was found to be abundant in the base of the Kimmeridgian of Dorset and France ; the specimens are generally well preserved. *S. Stimuliferum* is closely similar to *M. fragile* ; it is, however, consistently larger than *M. fragile*. *S. stimuliferum* is also similar to *Veryhachium irregulare* and *V. rhomboidium* ; differences are that *S. stimuliferum* has diameters consistently above 20 μ, whereas the species of *Veryhachium* may be smaller than 20 μ ; the number of processes is 12–22 in *S. stimuliferum*, but these two species of *Veryhachium* have 3–8 processes. The bases of the processes can clearly be recognized in *S. stimuliferum*, whereas they merge progressively into the shell wall and the point of junction is difficult to place precisely in the species of *Veryhachium*.

SUBGROUP *NETROMORPHITAE* Downie, Evitt & Sarjeant, 1963

Organism ***A***

(Pl. 11, fig. 9)

DESCRIPTION. The shell is elongate, thin-walled, without ornamentation processes or division into fields. The shell surface is smooth. One pole is rounded, but the other is flattened with an opening on it.

FIGURED SPECIMEN. BM(NH) slide V.53948(2). Clay from immediately base of Kimmeridge Clay (*Rhactorhynchia inconstans* bed), Ringstead Bay, Dorset (RB 219).

DIMENSIONS. Figured specimens : length 77 μ, breadth 28 μ. The range of the English specimens (9 specimens measured) : length 58–78 μ, breadth 25–48 μ. Only one French specimen was measured : length 65 μ, breadth 30 μ.

REMARKS. This new form was observed in the assemblages from Dorset and Le Havre. Specimens are generally severely damaged or folded. This form is similar to the members of the subgroup Netromorphitae ; however, the details of its shape and position of the opening afford differences from all described species. Further study may necessitate the erection of a new taxon to accommodate these forms, but information about the range in morphology is, at present, insufficient to justify this.

SUBGROUP *POLYGONOMORPHITAE* Downie, Evitt & Sarjeant, 1963

Genus ***VERYHACHIUM*** Deunff, emend. Downie & Sarjeant, 1963

Veryhachium hyalodermum (Cookson) Downie & Sarjeant, 1963

(Pl. 4, fig. 9 ; Pl. 12, fig. 11)

1956 *Palaeotetradinium hyalodermum* Cookson: 188–189, pl. 1, figs. 12–16.
1961 *P. hyalodermum* Cookson; Alberti, pl. 7, figs. 14, 15, ?18.
1963 *Veryhachium hyalodermum* (Cookson); Downie & Sarjeant: 94.
1963 *V. hyalodermum* (Cookson); Schaarschmidt: 62–63, pl. 17, figs. 1–7, text-fig. 12.
1964 *V. hyalodermum* (Cookson); Downie & Sarjeant: 151.
1964a *V. hyalodermum* (Cookson); Sarjeant, table 3.

REMARKS. This species was originally recorded from Cretaceous (Albian-Cenomanian and ? Turonian) of Australia by Cookson (1956), and named as *Palaeotetradinium hyalodermum.* Alberti observed similar specimens from the Middle Jurassic of Germany and from the Cretaceous of Germany and Poland (1961). When Downie and Sarjeant emended the diagnosis of *Veryhachium*, the species was transferred to this genus by them (1963) on the basis of its general shape and of the structure of its processes. It is infrequently present in the basal Kimmeridgian assemblages.

FIGURED SPECIMENS. BM(NH) slide V.53961(1). Clay from Great Ouse River Board Pit, Stretham, Cambridgeshire (SC 444).

BM(NH) slide V.53620(3). Shale from 100 ft. above the second dolerite sill, Staffin Bay, Skye (SS 627).

DIMENSIONS. Range of the English specimens (7 specimens measured) : overall cross-measurement 12 × 12 μ, process length 3–10 μ. The dimensions of the French specimen : overall cross-measurement 48 × 48 μ, process length 25 μ. Scottish specimen's cross-measurements 25 × 25 μ.

SUBGROUP *PRISMATOMORPHITAE* Downie, Evitt & Sarjeant, 1963

Genus ***STAPLINIUM*** Jansonius, 1962

EMENDED DIAGNOSIS. Unicellular microfossils, cubic to prismatic in shape with sharp edges, but without projections at the angles. The shell is thin-walled and encloses a central cavity. The surface of the test is smooth or granular. Some forms have a large opening on one side of the shell, which is typically the long side.

TYPE SPECIES. *Staplinium hexaeder* Jansonius, 1962, Lower Triassic western Canada.

Staplinium cistum sp. nov.

(Pl. 12, fig. 5 ; Pl. 14, figs. 4, 7)

DERIVATION OF THE NAME. Latin, *cista* box, chest, with reference to the shape of the microfossil.

DIAGNOSIS. A *Staplinium* with polyhedral—roughly coffin-shaped test, thin-walled without any ornamentation or processes. The surface is smooth ; a large opening (pylome) is sometimes present on one side of the test.

HOLOTYPE. BM(NH) slide V.53950(2). Clay from the base of Kimmeridge Clay, *Rhactorhynchia inconstans* Bed, Ringstead Bay, Dorset (RB 219).

DIMENSIONS. Holotype : length 55 μ, breadth 30 μ. Range of English specimens (20 specimens measured) : length 23–73 μ, breadth 18–64 μ. Scottish specimens (2 specimens measured) : length 30–60 μ, breadth 15–35 μ.

DESCRIPTION. This form is a unicellular microfossil, cubic to prismatic in shape. It is thin-walled with a central cavity, without any processes. In some forms, a large opening, formed by the loss of one side of the test, was observed.

REMARKS. Hitherto only one species of *Staplinium* has been recorded : *Staplinium hexaeder* (Jansonius, 1962) from the Lower Triassic of Canada. The specimens of this new species were observed from the Dorset and Scottish assemblages only. These are similar to *S. hexaeder*, but whereas *S. hexaeder* has a granular surface, *S. cistum* has a smooth surface and is longer than *S. hexaeder* (as quoted by Jansonius : length 10–50 μ). Openings have not been recorded in the latter species.

SUBGROUP *PTEROMORPHITAE* Downie, Evitt & Sarjeant, 1963

Genus ***PTEROSPERMOPSIS*** W. Wetzel, 1952

Pterospermopsis australiensis Deflandre & Cookson, 1955

(Pl. 12, fig. 6)

1955 *Pterospermopsis australiensis* Deflandre & Cookson, 286–288, pl. 3, fig. 4, text-figs. 52–53.
1964 *P. australiensis* Deflandre & Cookson; Downie & Sarjeant: 143.

REMARKS. This species has previously been recorded from the Lower Cretaceous of Australia. Specimens were observed, in a moderate number, in the assemblages from Dorset, Stretham and the Boulonnais. Their preservation was, generally, not good. With this observation, the stratigraphic and geographic range of this species are extended from the Lower Cretaceous to the Upper Jurassic and from Australia to France and England.

FIGURED SPECIMEN. BM(NH) slide V.53941(1). Clay from 6 ft. below top of the Black Clay, Holworth, Dorset (HD 191).

DIMENSIONS. Figured specimen : overall diameters 23 × 23 μ, shell diameters 14 × 14 μ. Range of the English specimens (2 specimens measured) : overall diameters 23–50 μ, shell diameters 14–40 μ. Scottish specimens (5 specimens measured) : overall diameters 25–30 μ, shell diameters 8–11 μ. The French specimen could not be measured because of poor preservation.

Pterospermopsis helios Sarjeant, 1959

(Pl. 4, fig. 8)

1959b *Pterospermopsis helios* Sarjeant: 342, pl. 13, fig. 9.
1964 *P. helios* Sarjeant; Downie & Sarjeant: 143.
1964a *P. helios* Sarjeant; Sarjeant, table 3.
1966 *P. helios* Sarjeant; Schulz & Mai, table 1.

REMARKS. This species has previously been recorded from the Upper Jurassic (Upper Cornbrash) of England (Yorkshire) by Sarjeant, 1959. A single well-preserved specimen was observed from the Stretham material only.

FIGURED SPECIMEN. BM(NH) slide V.53963(1). Clay from Great Ouse River Board Pit, Stretham, Cambridgeshire (SC 444).

DIMENSIONS. Overall diameters 20 μ, shell diameters 11 μ. Holotype dimensions (as quoted by Sarjeant) : overall diameters 25 μ, shell diameters 10 μ.

V. CONCLUSIONS

In the assemblages described here, 82 species of Dinoflagellate cysts and 11 species of Acritarcha are present ; their distribution by horizon is shown in Tables 4 A and B. The Kimmeridge Clay assemblages are remarkably rich and varied. It is clear that a number of the species, which have a relatively limited stratigraphic range, will prove of considerable value as stratigraphic indices.

Proximate cysts are dominant at all horizons ; chorate and cavate cysts are present in variable quantity. There is a greater variety of chorate cysts present in the Dorset assemblages than in the French assemblages. 16 species of chorate dinoflagellate cysts were recorded, 5 of these not being observed in the French and 6 not being present in the Scottish assemblages. The chorate cysts are thus less varied in the French assemblages, but they are represented in greater number than in the Dorset assemblages, as seen below.

	Dorset assemblages	Scottish assemblages	French assemblages
Number of species of chorate cysts	16	10	11
Total number of chorate cysts	343	76	381

Generally the chorate cysts are dominant over the cavate cysts in number, in both the Dorset and the French assemblages :

	Dorset assemblages	Scottish assemblages	French assemblages
Total number of chorate cysts	343	76	381
Total number of cavate cysts	139	39	221

Acritarchs are represented by a few species ; *Solisphaeridium stimuliferum* (Deflandre) Staplin, Jansonius & Pocock and *Micrhystridium fragile* Deflandre are dominant :

	Dorset assemblages	Scottish assemblages	French assemblages
Number of *M. fragile*	91	2	17
Number of *S. stimuliferum*	92	3	152
Total number of acritarchs	360	23	228

TABLE 4A

The numerical distribution of Proximate Dinoflagellate cysts in the base of Kimmeridgian assemblages from England, Scotland and France, compared with their previously known stratigraphic range.

No. of samples examined

Species	England								Scotland			France										Previously known range
	OM 131	OM 418	OM 419	OM 420	HD 191	RB 218	RB 219	SC 444	SS 625	SS 626	SS 627	VN 184	CH 185	CH 186	CC 447	CC 448	CC 449	CC 450	CC 451	CC 452	CC 455	
DINOFLAGELLATE CYSTS PROXIMATE																						
Chytroeisphaeridia chytroeides	21	17	14	16	—	—	—	18	18	11	8	—	42	29	—	4	2	—	—	—	—	L.–M. Oxfordian
C. pococki	10	3	1	1	—	—	—	4	5	7	6	—	1	1	—	—	1	—	—	1	—	L.–U. Callovian
Tenua cf. *capitata*	—	—	1	—	—	1	6	1	—	—	—	—	1	—	—	1	1	—	—	—	—	—
T. hystrix	15	3	1	1	—	1	9	12	5	1	3	5	6	3	—	1	5	1	—	2	1	Aptian
T. pilosa	10	1	3	—	—	—	7	9	4	2	1	—	1	—	—	—	—	—	—	—	—	U. Callovian–Oxfordian
T. sp.	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Acanthaulax venusta	—	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	Malm Alpha-Beta
Cryptarchaeodinium calcaratum	—	—	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	L. Kimmeridgian
C. sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Gonyaulacysta aculeata	—	—	—	—	—	—	—	1	—	—	—	1	1	—	2	—	—	—	—	—	—	Malm Gamma
G. angulosa	—	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	1	—	1	—	—	—
G. cladophora	—	—	—	—	—	—	—	1	4	4	1	—	—	—	1	—	—	—	—	—	—	Bajocian–Albian
G. ehrenbergii	—	—	—	—	—	—	—	—	—	—	—	2	—	—	2	1	—	—	—	—	—	—
G. eisenacki	4	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	M. Jurassic–U. Oxfordian
G. cf. *eisenacki*	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—
G. granulata	1	1	—	—	—	—	—	—	—	—	—	—	—	1	2	4	—	8	—	—	1	L. Oxfordian–U. Kimmeridgian
G. granuligera	—	3	2	2	2	7	—	—	—	—	—	2	—	—	3	4	3	15	1	6	1	L. Kimmeridgian
G. cf. *helicoidea*	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
G. hyaloderma	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	M.-U. Kimmeridgian–Eocene
G. jurassica	3	3	6	20	1	50	63	1	10	8	20	9	22	6	2	4	—	5	1	—	—	Bathonian–Kimmeridgian
G. jurassica var. *longicornis*	—	—	1	—	—	—	—	—	1	—	—	—	2	—	—	—	—	3	—	—	—	Oxfordian
G. longicornis	—	—	—	—	—	—	—	—	—	—	—	—	2	—	6	—	3	2	—	—	—	Kimmeridgian
G. cf. *mamillifera*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
G. nuciformis	2	3	2	1	1	—	7	4	1	6	1	1	—	1	1	—	—	9	1	7	1	U. Jurassic
G. pachyderma	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Oxfordian
G. serrata	2	—	2	3	—	—	2	—	1	—	—	6	—	—	—	1	—	2	—	—	—	Tithonian–Neocomian
G. sp. A	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—
G. sp. B	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
G. sp. C	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—	—	—
Occisucysta balios	—	—	—	—	—	—	1	—	—	—	—	2	—	—	1	—	—	1	—	—	—	—
O. sp.	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Leptodinium amabilis	—	—	1	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	L. Kimmeridgian
L. arcuatum	2	—	—	1	—	—	2	—	—	—	—	1	—	—	—	1	—	—	—	1	—	U. Oxfordian
L. clathratum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	Oxfordian–Tithonian
L. egemenii	9	6	1	—	2	1	1	—	—	—	1	—	11	3	—	—	—	—	—	—	—	—
L. cf. *subtile*	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Belodinium dysculum	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Tithonian
Dictyopyxis areolata	—	—	—	—	—	—	—	—	1	—	1	—	1	—	—	—	1	—	—	—	—	M. Callovian–Kimmeridgian
D. sp.	2	—	—	2	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Histiophora cf. *ornata*	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	1	—	—	—	—	—
Meiourogonyaulax staffinensis	3	—	—	—	1	—	5	—	3	—	2	1	—	—	1	—	—	3	—	—	1	—
M. sp.	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
Apteodinium granulatum	—	—	—	—	—	—	5	1	—	—	—	1	—	—	—	—	—	5	1	—	—	Volgian--Cenomanian
A. cf. *maculatum*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Pareodinia ceratophora	8	5	4	5	—	5	14	10	3	1	1	3	14	1	2	12	2	5	—	1	—	Bajocian–U. Oxfordian
Trichodinium sp.	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Imbatodinium sp.	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Nannoceratopsis pellucida	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	U. Oxfordian -L. Kimmeridgian
Indetermined Proximate cysts	46	25	32	24	4	32	149	58	30	19	25	60	54	26	66	64	57	113	10	90	6	—

TABLE 4B

The numerical distribution of Chorate, Proximochorate and Cavate Dinoflagellate cysts and Acritarchs in the basal Kimmeridgian assemblages from England, Scotland and France, compared with their previously known stratigraphic range.

Species	No. of samples examined																		Previously known range
	England								Scotland			France							
	OM	OM	OM	OM	HD	RB	RB	SC	SS	SS	SS	VN	CH	CH	CC	CC	CC	CC	CC	CC	

TABLE 4B

[illegible] cysts and Acritarchs in the basal Kimmeridgian assemblages from England, Scotland and France, compared with their previously known stratigraphic range

Species	No. of samples examined England								Scotland			France										Previously known range
	OM 131	OM 418	OM 419	OM 420	HD 191	RB 218	RB 219	SC 444	SS 625	SS 626	SS 627	VN 184	CH 185	CH 186	CC 447	CC 448	CC 449	CC 450	CC 451	CC 452	CC 455	
CHORATE																						
Cleistosphaeridium ehrenbergii	6	1	—		—	5	2	—	—	—	1	—	2	—	2	—	—	—	—	—	—	L. Oxfordian
C. polyacanthum	1	1		—	—	5	4	—		-	-	-	5	2	3							
C. polytrichum	2	—	1	1	—	1	—		—		—	—	—	—	—		—	—	—	—	—	Bathonian–Kimmeridgian
C. tribuliferum	4	1	3	—	—	11	8	—	—	1	—	—			-	—	—				—	Callovian–Oxfordian
C. sp.				1				-	1			1	1	—	1	1		—		—		—
Hystrichosphaeridium petilum	2	—	2			26	2	—	2	6	3	6	—	—	—	—	—	—	—	—	—	
Oligosphaeridium pulcherrimum		-					2	—	—	—	—	—	—				3	-		—		Cretaceous
Polystephanephorus sarjeantii	7	1	—	—	—	2	-	—				—		1	—		2	—	2			
Prolixosphaeridium cf. *deirense*						—	2	-			—	—	—	—	—	—	—					
P. granulosum	7	1	3		1	19	1	3	2	6	4	1	4		1				-	—	-	Oxfordian–Eocene
P. parvispinum				2	—	-	1	—	2	—	-			—	—		—	—	—	—	—	Oxfordian–Eocene
Systematophora areolata	1	6	[illegible]	5		2	4	4	5	2	9	51	6	6	7	5	6	14	11	15		Malm Delta
S. orbifera	1	13	3	2	—	21	-	—	4	1	1	3	—		32	3	5	4	3	13	—	U. Oxfordian–L. Kimmeridgian
S. sp.								1														
Taeniophora iunctispina	2	—	2	—	—	2	3	—	3		—	3	2	1	4	—	1		3	1		Malm Alpha
Stephanelytron cf. *scarburghense*	5	2	—	—	-		3	—	—	—	3	-	1				—	—	—	—	1	
Indeterminate Chorate cysts	16	7	5	4	1	32	32	6	8	2	12	24	8	4	12	6	11	11	10	11		—
PROXIMOCHORATE																						
Heslertonia pellucida	-							1	—	—	1											
Epiplosphaera reticulospinosa	2	1	1	1	—	—	—	2	-		—	2	—	-				—	—	—	-	Malm Delta
Indeterminate proximochorate cysts				3	—			—	—	1												
CAVATE																						
Endoscrinium cf. *campanula*	3	2		1	—		-	—	—	1		—	—		7	4	1	3	—		—	—
E. galeritum	3	-		—	—	—	1	-	—	—	—				2	—	-		—	—	—	Callovian–Kimmeridgian
E. luridum	2	—	1	—	—	—		—	5	2	1	2	—	—	-		—	—	—		1	Callovian–Kimmeridgian
E. oxfordianum	1	—	-	—		—	—	-	3	—	1	3	1	—	—	—	—		—	—	—	Oxfordian
Psaligonyaulax apaleta	1	—	5	5	—	—	-	2	—	—		2	2	1	3	1	—	3	—			U. Oxfordian–L. Kimmeridgian
P. sp.				1	-		—	—		—	—	-			—	—						
Hexagonifera sp.	1	-		1	—	—	—	—	—	—	1		2	—	—		1					
Parvocavatus tuberosus		1	—	2			—	3	1	—	—	21		24	1	22	1	5	1	—		
Scriniodinium bicuneatum		1	2	—	—	—		—	—	-			—	1		—	—			—	—	U. Oxfordian–L. Kimmeridgian
S. crystallinum	3	3		3	—	8	—	—	1	2	2	1	2	—		1	—	—	1	—	3	Oxfordian–Kimmeridgian
S. dictyotum subsp. *osmingtonensis*	3	—	3	3	-			—			—	—		—	—	2		-				
S. dictyotum subsp. *papillatum*				2	—	—	-	—	—	—	—	—	—	1		-						
S. dictyotum subsp. *pyrum*		1	2	—	—	-	1	—	—	—	—	—	1	1								
S. cf. *galeatum*	—	—	—	—	-		-	—	-	—	—	—		—	—	2						—
S. playfordii			1		—	—	—	—	—				1		4		—		-	—	-	U. Oxfordian–L. Kimmeridgian
Netrelytron parum	14	6	4	8	1	—	—	1	—	—		6	2	2	—	1	1	12	4	1	—	—
N. stegastum	12	—		—	—	-		—		—	—	1	3		—	—	-		—	—	-	Oxfordian
Odontochitina sp.						1																
Indeterminate cavate cysts	6	1	5	4	1	2	7	6	7	4	8	10	4	8	7	15	2	9			8	
Dinoflagellate sp. indet.	35	14	23	8	30	17	106	15	8	7	16	26	38	13	22	32	21	50	29	25	18	—
ACRITARCHA																						
Baltisphaeridium inusitatum	-	-		1		—	—	—	—	-		1	—	—	—		—	—		—	—	Malm Gamma
Micrhystridium fragile	1	7	2	6	1	11	9	25	—	1	5	8	5	2	4	5	1	4	—			Bajocian–Oxfordian
M. inconspicuum	—	4	1	4	1	1	—	80	2			2	12	2	1	—	—		—	—	—	Bajocian–Cretaceous
M. sydus				1	—	1	-	18	—	3		-	4	—	-		—	-		—	—	Bathonian–Oxfordian
Solisphaeridium brevispinosum	3	—		1	—	—	—	—	—	—	—	—	3	—	—	-	—	—	-			U. Callovian–Oxfordian
S. stimuliferum	11	6	4	9	—	36	22	7	1	1	1	24	15	1	33	17	4	4	54	—	-	Bajocian–Oxfordian
Organism A		1	—	1	—	-	11	—	—	—		-	2			—	—		—			
Veryhachium hyalodermum		-						10	—	—	1	1	—	—	-		—			—	—	Albian ?Turonian
Pterospermopsis australiensis		-			1	—	—	1	6	—	—	—		—	-	-	—	—	-		—	Lower Cretaceous
P. helios					-			1	—		—	—	.	—	—	-	—	—	—			Upper Jurassic
Staplinium cystum	5	—	—	—	—	—	17	—	1	—	1	—	—	—	—							
Indeterminate acritarchs	3	1	1	3	3	6	17	5	—	—	—	3	13	-	3							
Pollen and Spores	39	13	27	6	18	41	213	45	40	76	56	10	28	20	8	18	4	32	12	22	73	—
Foraminiferal shell linings	—	—	5	1	—	—		9	13	3	4	-	—	—		1	3					—
Wood fragments	3	—	—	—	—	—	5	—	4	4	1	—		—	-	3	—					—
Total	342	167	185	166	70	345	756	371	206	176	202	311	328	163	322	235	141	329	145	196	115	

On the basis of previous published records, the following species here described were known only from the Lower Kimmeridgian : *Cryptarchaeodinium calcaratum* Deflandre, *Gonyaulacysta granuligera* (Klement) Sarjeant, *Leptodinium amabilis* (Deflandre) Sarjeant, *Systematophora areolata* Klement, *Epiplosphaera reticulospinosa* Klement and *Baltisphaeridium inusitatum* Klement. *Gonyaulacysta hyaloderma* (Deflandre) Sarjeant and *G. longicornis* (Downie) Sarjeant have both been previously reported from Kimmeridgian, *G. hyaloderma* having been observed in the Middle Kimmeridgian and *G. longicornis* having a stratigraphic range including Upper Kimmeridgian ; both these species are represented in the basal Kimmeridgian.

Seven species previously known from U. Oxfordian and L. Kimmeridgian are also present in the basal Kimmeridgian assemblages of England, Scotland and France. These are : *Acanthaulax venusta* (Klement) Sarjeant, *Nannoceratopsis pellucida* Deflandre, *Systematophora orbifera* Klement, *Taeniophora iunctispina* Klement, *Psaligonyaulax apaleta* (Cookson & Eisenack) Sarjeant, *Scriniodinium bicuneatum* (Deflandre) Sarjeant and *S. playfordi* Cookson & Eisenack.

Fourteen species were previously known only from lower horizons and were observed in the basal Kimmeridgian assemblages for the first time : *Chytroesphaeridia chytroeides* Sarjeant (L.–M. Oxfordian), *C. pococki* Sarjeant (L.–U. Callovian), *Tenua pilosa* (Ehrenberg) Sarjeant (U. Callovian–Oxfordian), *Gonyaulacysta eisenacki* (Deflandre) Sarjeant (M. Callovian–U. Oxfordian), *G. nuciformis* (Deflandre) Sarjeant (U. Callovian–Oxfordian), *G. pachyderma* (Deflandre) Sarjeant (Oxfordian), *Leptodinium arcuatum* Klement (U. Oxfordian), *Pareodinia ceratophora* Deflandre (M. Callovian–U. Oxfordian), *Cleistophaeridium ehrenbergi* Deflandre (L. Oxfordian), *C. tribuliferum* Sarjeant (Oxfordian), *Endoscrinium oxfordianum* Sarjeant (Oxfordian), *Netrelytron stegastum* Sarjeant (Oxfordian), *Solisphaeridium brevispinosum* Sarjeant (Oxfordian) and *S. stimuliferum* (Deflandre) Staplin, Jansonius & Pocock (Bajocian–Oxfordian). Assemblages of the basal Kimmeridgian are very close to the Callovian and Oxfordian assemblages.

Seven species previously recorded from higher horizons were observed for the first time in the basal Kimmeridgian : *Tenua hystrix* Eisenack (Aptian), *Gonyaulacysta serrata* (Cookson & Eisenack) Sarjeant (Tithonian–Neocomian), *Belodinium dysculum* Cookson & Eisenack (Tithonian), *Apteodinium granulatum* Eisenack Volgian–Cenomanian), *Oligosphaeridium pulcherrimum* (Deflandre & Cookson) Davey & Williams (Cretaceous) and *Pterospermopsis australiensis* Deflandre & Cookson (L. Cretaceous).

The other 21 previously observed species are long-ranging forms whose known range includes the Kimmeridgian : 14 of them were also known from the Oxfordian. These observations indicate that these species have more affinities with Oxfordian deposits. No detailed work on Portlandian assemblages is available, but it may be noted that some basal Kimmeridgian species suggest relationships with the Lower Cretaceous (Barremian–Cenomanian) assemblages.

Representatives of 7 species were observed in the basal Kimmeridgian assemblages for the first time in Western Europe, having been previously recorded only from Australian and New Guinea assemblages. These are *Gonyaulacysta serrata* Cookson & Eisenack, *Leptodinium clathratum* (Cookson & Eisenack) Sarjeant, *Belodinium dyscu-*

lum Cookson and Eisenack, *Oligosphaeridium pulcherrimum* Deflandre & Cookson, *Psaligonyaulax apaleta* (Cookson & Eisenack) Sarjeant, *Scrinidinium playfordi* Cookson & Eisenack and *Pterospermopsis australiensis* Cookson & Eisenack. 4 of these 7 species were observed in both English and French assemblages : *Gonyaulacysta serrata, Psaligonyaulax apaleta, Scriniodinium playfordi* and *Pterospermopsis australiensis* ; one, *Belodinium dysculum*, only in the Dorset assemblage, and the remaining 3 were observed only from the French assemblages.

Eleven species previously recorded from Germany were observed in the English and French assemblages for the first time : *Tenua hystrix* Eisenack, *Acanthaulax venusta* (Klement) Sarjeant, *Gonyaulacysta aculeata* (Klement) Sarjeant, *G. eisenacki* (Deflandre) Sarjeant, *G. granulata* (Klement) Sarjeant, *G. granuligera* (Klement) Sarjeant, *Leptodinium arcuatum* Klement, *Systematophora areolata* Klement, *S. orbifera* Klement, *Taeniophora iunctispina* Klement, and *Epiplosphaera reticulospinosa* Klement.

The previous studies and this study indicate that 8 species are present in assemblages both from England and France : *Pareodinia ceratophora* Deflandre, *Cleistophaerdium ehrenbergi* Deflandre, *C. polytrichum* (Valensi) Davey, Downie, Sarjeant & Williams, *Prolixosphaeridium granulosum* (Deflandre) Sarjeant, *Scriniodinium bicuneatum* (Deflandre) Sarjeant, *Micrhystridium inconspicuum* Deflandre, *Solisphaeridium brevispinosum* (Sarjeant) Sarjeant, and *S. stimuliferum* (Deflandre) Sarjeant. 4 of these species were formerly represented only in French assemblages : *Chytroeisphaeridia pococki* Sarjeant, *Cryptarchaeodinium calcaratum* Deflandre, *Gonyaulacysta pachyderma* (Deflandre) Sarjeant, and *Leptodinium amabilis* (Deflandre) Sarjeant. 4 species hitherto known only from England are also present in the basal Kimmeridgian assemblages of France : *Chytroeisphaeridia chytroeides* Sarjeant, *Gonyaulacysta longicornis* (Downie) Sarjeant, *E. oxfordianum* Sarjeant, and *Netrelytron stegastum* Sarjeant.

A comparison of the Australian and Western European assemblages, as described by Cookson & Eisenack (1958, 1960 a, b, 1962 a, b), shows some differences between the size ranges of the Australian specimens and those of European : Australian specimens are, generally, considerably larger. When the European assemblages are compared, the English specimens are found to be slightly larger than the French and German specimens. This is, probably, the result of a palaeoecological control, i.e. food supply, climate, salinity, etc. No differences are observed within the species of Britain, that is, between the Scottish, Dorset and Stretham species. This might not be considered to be established by present evidence, however, for relatively small numbers of horizons have been examined in Scotland and from Stretham, Cambridgeshire.

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PLATE 1

Cryptarchaeodinium calcaratum (Deflandre)

FIG. 1. Ventral surface of specimen, V.53959(1) × 1000.
FIG. 2. Dorsal surface of same, viewed by transparency, × 1000.

Scriniodinium dictyotum subsp. ***osmingtonensis*** nov.

FIG. 3. Specimen V.52798(2) × 400.

Epiplosphaera reticulospinosa Klement

FIG. 4. Specimen V.53932(2) × 470.

Gonyaulacysta aculeata (Klement)

FIG. 5. Ventral surface of specimen, V.53965(3) × 473.
FIG. 6. Dorsal surface of same, viewed by transparency, × 473.

Cleistosphaeridium sp.

FIG. 7. Specimen V.53958(1) × 413.

Micrhystridium inconspicuum (Deflandre)

FIG. 8. Specimen V.53953(1) × 1000.

Dictyopyxis areolata Cookson & Eisenack

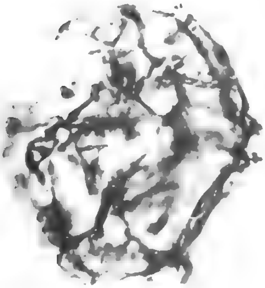
FIG. 9. Specimen V.53974(1) × 1000.

Gonyaulacysta granuligera (Klement)

FIG. 10. Ventral surface of specimen, V.53972(1) × 470.
FIG. 11. Dorsal surface of same, viewed by transparency, × 470.

Hexagonifera sp.

FIG. 12. Specimen V.53621(1) × 560.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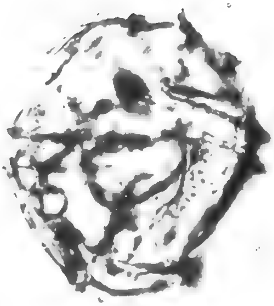
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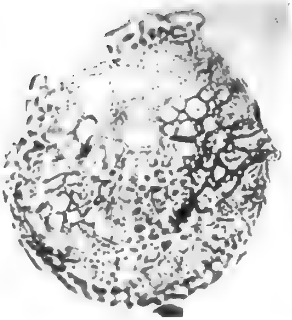
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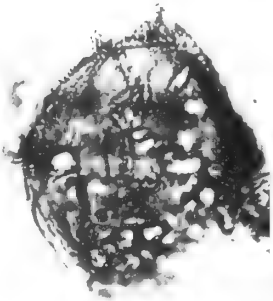
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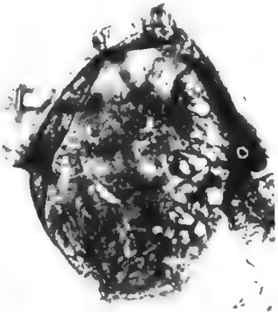
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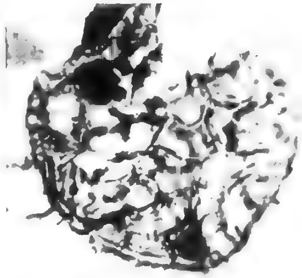
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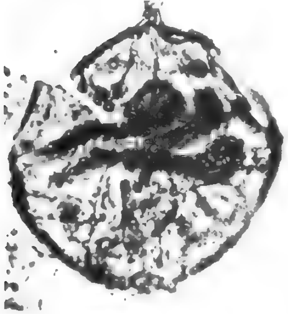
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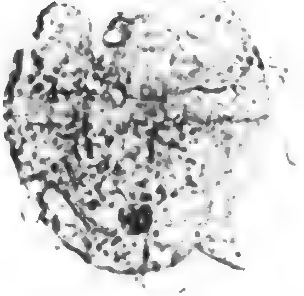
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PLATE 2

Gonyaulacysta cf. ***helicoidea*** (Eisenack & Cookson)

FIG. 1. Ventral surface of specimen, V.53931(1) ×1200.
FIG. 2. Dorsal surface of same, viewed by transparency, ×1200.

Prolixosphaeridium parvispinum (Deflandre)

FIG. 3. Specimen V.53956(2) ×768.

Gonyaulacysta angulosa sp. nov.

FIG. 4. Holotype, ventral surface, V.53934(1) ×820.
FIG. 5. Dorsal surface of same, viewed by transparency, ×820.

Prolixosphaeridium granulosum (Deflandre)

FIG. 6. Specimen V.52799(4) ×665.

Solisphaeridium brevispinosum (Sarjeant)

FIG. 7. Specimen V.53957(1) ×768.

Gonyaulacysta ehrenbergii sp. nov.

FIG. 8. Ventral surface of the holotype, V.53968(1) ×768.
FIG. 9. Dorsal surface of same, viewed by transparency, ×768.

Gonyaulacysta cf. ***eisenacki*** (Deflandre)

FIG. 10. Specimen V.52792(1) ×768.


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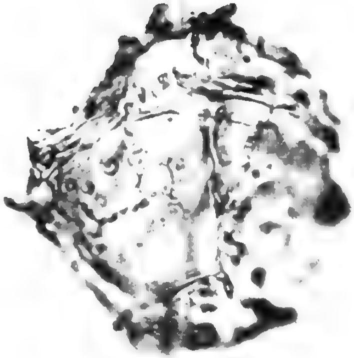
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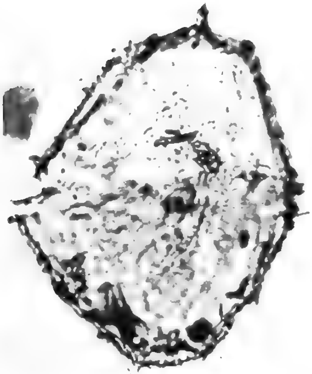
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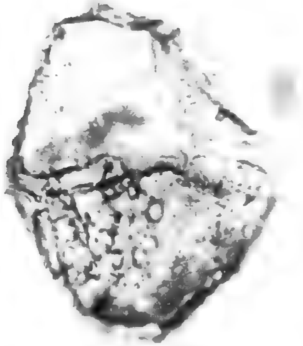
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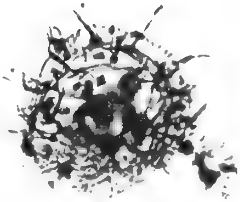
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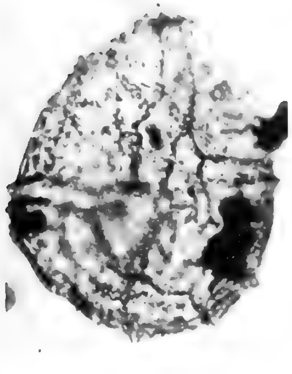
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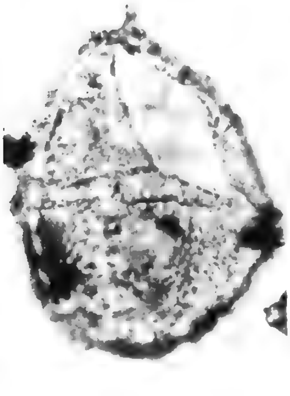
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PLATE 3

Meiourogonyaulax staffinensis sp. nov.

FIG. 1. Specimen V.53620(1) ×768.

Endoscrinium luridum (Deflandre)

FIG. 2. Dorsal view and archaeopyle formation, V.53934(3) ×400.

Gonyaulacysta sp. A

FIG. 3. Ventral surface of specimen, V.53930(1) ×640.

Gonyaulacysta cf. **mamillifera** (Deflandre)

FIG. 4. Dorsal surface of specimen, V.53965(1) ×768.

Gonyaulacysta jurassica (Deflandre)

FIG. 5. Ventral surface specimen, V.53619(3) ×615.

Psaligonyaulax sp.

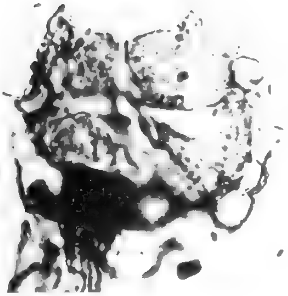
FIG. 6. Specimen V.53956(3) ×765.

Endoscrinium galeritum (Deflandre)

FIG. 7. Ventral surface of specimen, V.52800(4) ×615.
FIG. 8. Dorsal view of same, viewed by transparency. ×615.

Gonyaulacysta eisenacki (Deflandre)

FIG. 9. Ventral surface of specimen, V.52800(1) ×315.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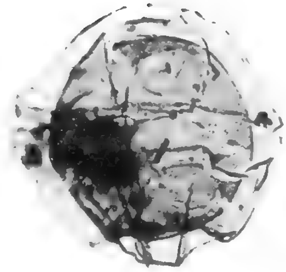
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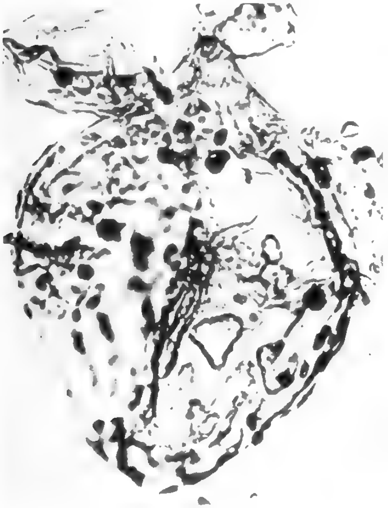
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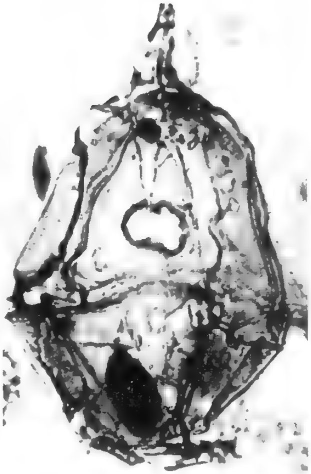
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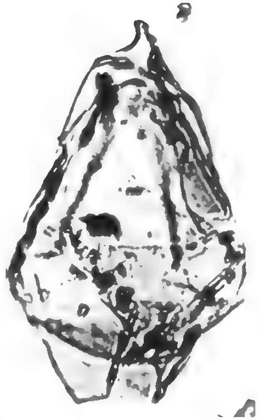
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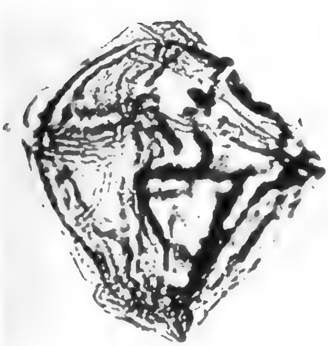
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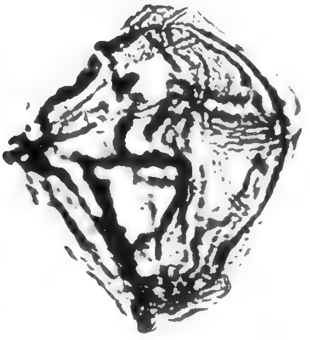
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PLATE 4

Dictyopyxis sp.
Fig. 1. Specimen V.53956(1) ×640.

Trichodinium sp.
Fig. 2. Specimen V.53960(1) ×768.

Systematophora orbifera Klement
Fig. 3. Specimen V.53936(1) ×500.

Cleistosphaeridium polytrichum (Valensi)
Fig. 4. Specimen V. 52799(3) ×640.

Tenua pilosa (Ehrenberg)
Fig. 5. Specimen V.52793(1) ×1000.

Apteodinium granulatum Eisenack
Fig. 6. Dorsal view of specimen V.53949(1) ×600.

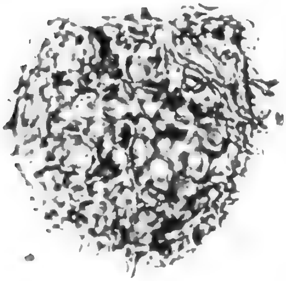
Cleistosphaeridium ehrenbergi (Deflandre)
Fig. 7. Specimen V.52801(1) ×768.

Pterospermopsis helios Sarjeant
Fig. 8. Specimen V.53963(1) ×1600.

Veryhachium hyalodermum (Cookson)
Fig. 9. Specimen V.53961(1) ×1200.

Gonyaulacysta sp. C.
Fig. 10. Ventral surface of specimen, V.53966(1) ×560.
Fig. 11. Dorsal surface of same, viewed by transparency, ×560.

Heslertonia pellucida sp. nov.
Fig. 12. Specimen SC 444/4-216 ×1200.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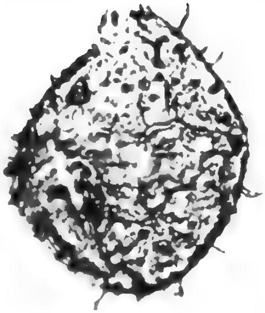
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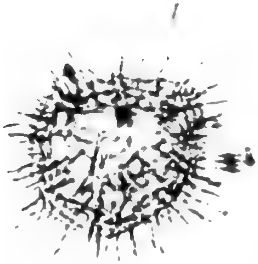
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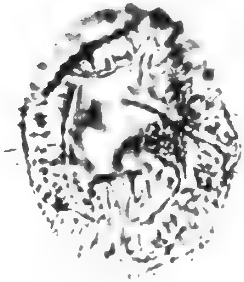
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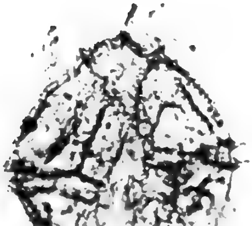
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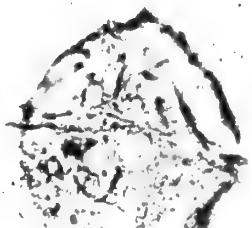
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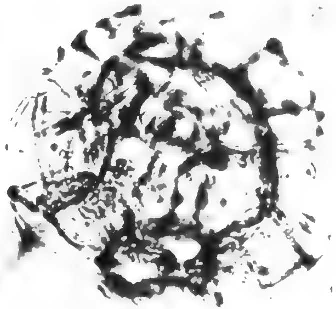
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PLATE 5

Occisucysta balios sp. nov.
Fig. 1. Ventral surface of the holotype, V.53934(2) ×700.
Fig. 2. Dorsal view of same, viewed by transparency, ×700.

Prolixosphaeridium granulosum (Deflandre)
Fig. 3. Specimen V.53960(2) ×400.

Netrelytron parum sp. nov.
Fig. 4. Specimen V.52799(5) ×600.

Scriniodinium bicuneatum (Deflandre)
Fig. 5. Specimen V.53952(1) ×400.

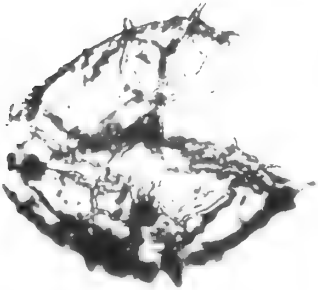
Endoscrinium oxfordianum Sarjeant
Fig. 6. Dorsal view of specimen V.53933(1) ×512.

Gonyaulacysta serrata (Cookson & Eisenack)
Fig. 7. Specimen V.53935(1) ×896.

Tenua hystrix Eisenack
Fig. 8. Specimen V.53947(2) ×768.

Endoscrinium cf. ***campanula*** (Gocht)
Fig. 9. Dorsal view of specimen V.52795(1) ×480.
Fig. 10. Ventral surface of same, viewed by transparency, ×480.

Gonyaulacysta jurassica var. ***longicornis*** Deflandre
Fig. 11. Ventral view of specimen, V.53939(1) ×400.



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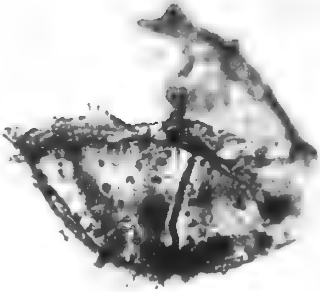

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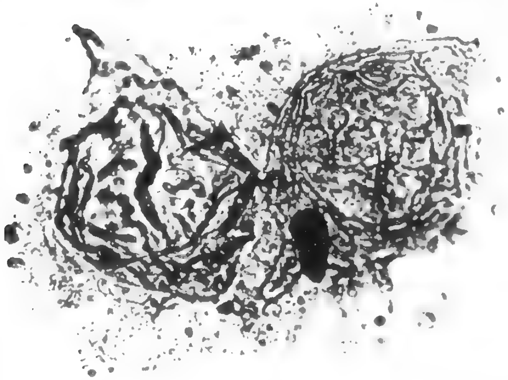

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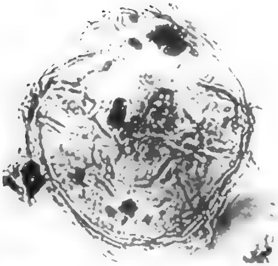

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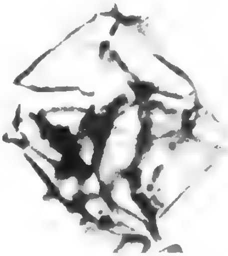

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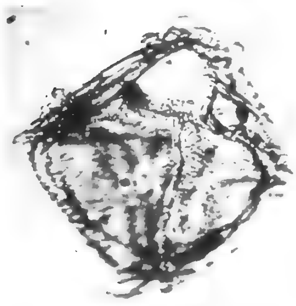

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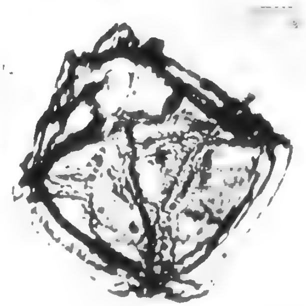

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PLATE 6

Gonyaulacysta nuciformis (Deflandre)

FIG. 1. Dorsal view of specimen V.52793(2) × 1020.

Scriniodinium cf. ***galeatum*** (Cookson & Eisenack)

FIG. 2. Specimen V.53967(1) × 800.

Gonyaulacysta sp. B.

FIG. 3. Ventral view of specimen V.53965(2) × 947.

Cryptarchaeodinium sp.

FIG. 4. Ventral surface of specimen, V.53972(2) × 1300.
FIG. 7. Dorsal surface of same, viewed by transparency, × 1300.

Pareodinia ceratophora Deflandre

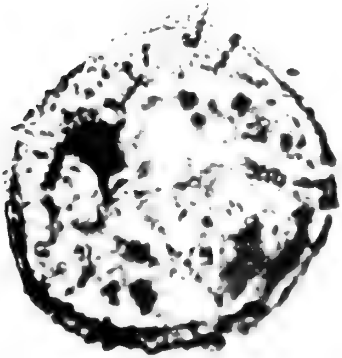
FIG. 5. Specimen V.52802(1) × 794.
FIG. 6. Specimen V.53938(1) × 900.

Psaligonyaulax apaleta (Cookson & Eisenack)

FIG. 8. Specimen V.52804(1) × 480.

Parvocavatus tuberosus sp. nov.

FIG. 9. Holotype, V.53956(4) × 1000.



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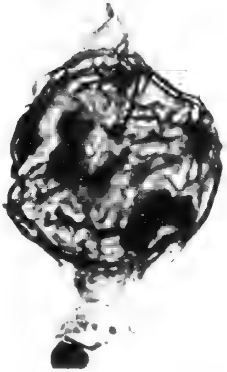

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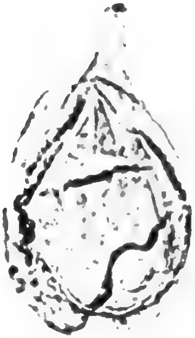

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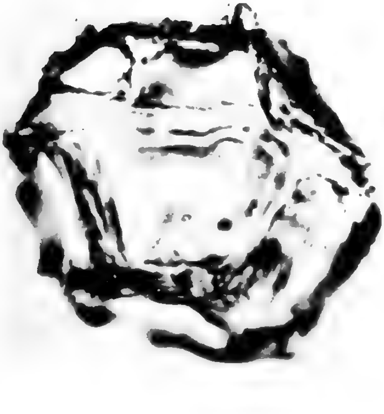

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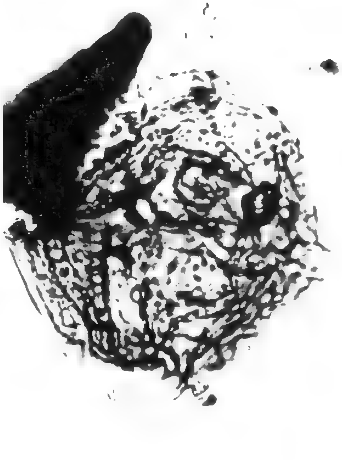

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PLATE 7

Leptodinium arcuatum (Klement)

FIG. 1. Ventral view of specimen V.52799(1) × 615.

FIG. 2. Dorsal view of same, × 615.

Belodinium dysculum Cookson & Eisenack

FIG. 3. Specimen V.52798(1) × 271.

Nannoceratopsis pellucida Deflandre

FIG. 4. Specimen V.52800(2) × 603.

Imbatodinium sp.

FIG. 5. Specimen showing archaeopyle formation, V.52799(2) × 692.

Scriniodinium crystallinum (Deflandre)

FIG. 6. Dorsal view of specimen V.53942(1) × 400.

Oligosphaeridium pulcherrimum (Deflandre & Cookson)

FIG. 7. Specimen V. 53946(1) × 615.

Occisucysta sp.

FIG. 8. Specimen showing archaeopyle formation, V.53945(1) × 845.

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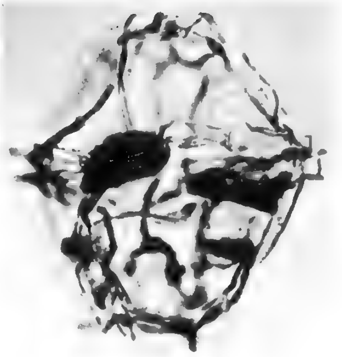

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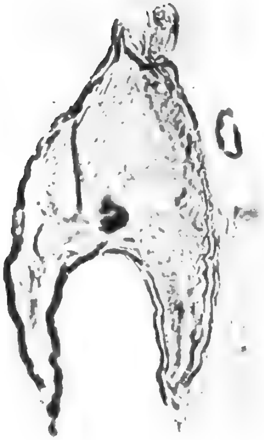

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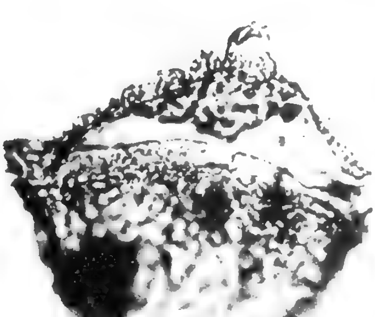

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PLATE 8

Gonyaulacysta granulata (Klement)

FIG. 1. Ventral view of specimen V.53969(1) × 590.

FIG. 2. Dorsal surface of same by transparency, × 590.

Endoscrinium galeritum (Deflandre)

FIG. 3. Specimen RB 219/1-7 × 400.

Gonyaulacysta pachyderma (Deflandre)

FIG. 4. Dorsal view of specimen, V.53950(3) × 532.

Systematophora sp.

FIG. 5. Specimen V.53962(1) × 1000.

Systematophora areolata Klement

FIG. 6. Specimen V.53937(1) × 432.

Odontochitina sp.

FIG. 7. Specimen RB218/12-214 × 600.

Micrhystridium fragile Deflandre

FIG. 8. Specimen V.53961(2) × 1600.

Netrelytron stegastum Sarjeant

FIG. 9. Specimen V.52796(2) × 635.

Micrhystridium sydus Valensi

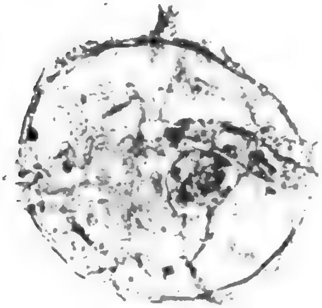
FIG. 10. Specimen RB 218/16-324 × 1600.

Micrhystridium inconspicuum (Deflandre)

FIG. 11. Specimen CH 185/10-208 × 1900.

Scriniodinium dictyotum subsp. ***osmingtonensis*** nov.

FIG. 12. Dorsal view of the holotype, V.52797(1) × 512.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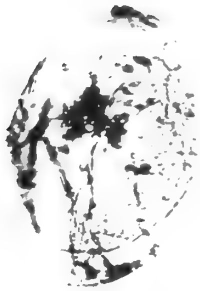
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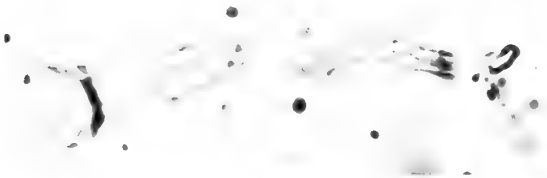
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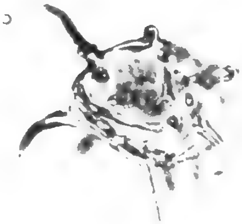
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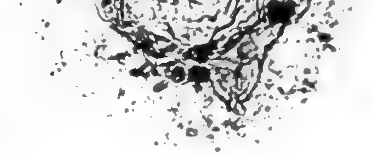
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PLATE 9

Hystrichosphaeridium petilum sp. nov.

FIG. 1. Holotype, V.53944(1) × 768.
FIG. 6. Specimen SS 626/19-171 × 640.

Cleistosphaeridium tribuliferum (Sarjeant)

FIG. 2. Specimen V.53951(1) × 430.

Tenua sp.

FIG. 3. Specimen showing the archaeopyle formation, V.52796(1) × 665.

Netrelytron parum sp. nov.

FIG. 4. Holotype, V.52801(2) × 420.

Teniophora iunctispina Klement

FIG. 5. Specimen V.52800(3) × 512.

Chytroeisphaeridia pococki Sarjeant

FIG. 7. Specimen V.53958(2) × 480.
FIG. 8. Specimen V.53619(1) × 640.

Gonyaulacysta hyaloderma (Deflandre)

FIG. 9. Ventral view of specimen V.53932(1) × 1280.
FIG. 10. Dorsal surface of same, viewed by transparency, × 1280.

Scriniodinium dictyotum subsp. ***papillatum*** nov.

FIG. 11. Dorsal view of holotype, V.53940(1) × 432.


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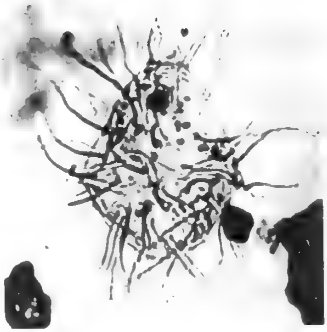
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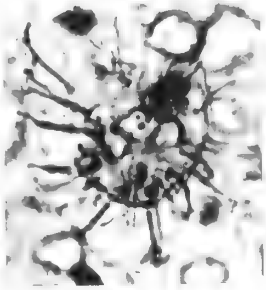
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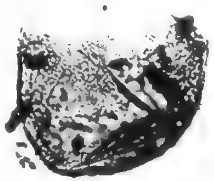
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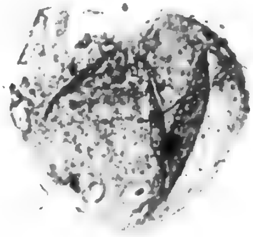
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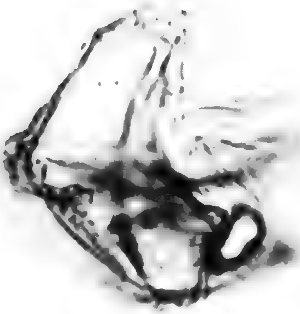
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PLATE 10

Scriniodinium dictyotum subsp. **pyrum** nov.

FIG. 1. Specimen OM 418/9-142 × 2280.

Stephanelytron cf. **scarburghense** (Sarjeant)

FIG. 2. Specimen OM 131/1-267 × 640.

Chytroeisphaeridia pococki Sarjeant

FIG. 3. Specimen V.53954(1) × 600.

Tenua cf. **capitata** (Cookson & Eisenack)

FIG. 4. Specimen V.53947(1) × 768.

Leptodinium egemenii sp. nov.

FIG. 5. Ventral surface of the holotype, V.52794(1) × 850.
FIG. 6. Dorsal surface of same, viewed by transparency, × 850.

Tenua hystrix Eisenack

FIG. 7. Specimen V.52794(2) × 640.

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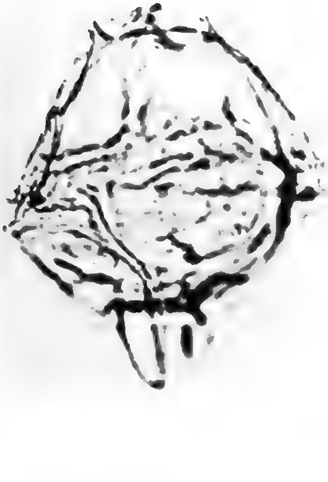

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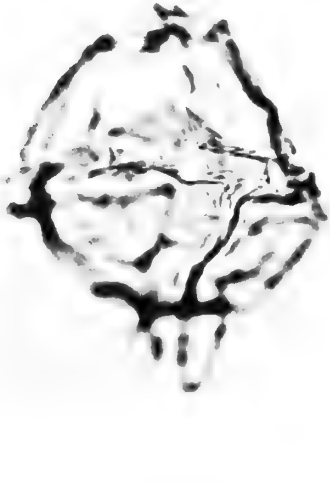

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PLATE 11

Leptodinium cf. ***subtile*** (Klement)

FIG. 1. Ventral view of specimen V.52803(1) ×480

FIG. 2. Dorsal surface of same, viewed by transparency, ×480

Histiophora cf. ***ornata*** (Klement)

FIG. 3. Specimen V. 52964 (1) ×480.

Polystephanephorus sarjeantii sp. nov.

FIG. 4. Holotype, V.52792(2) ×615.

Gonyaulacysta jurassica (Deflandre)

FIG. 5. Dorsal view of specimen V.53951(2) ×768.

Micrhystridium inconspicuum (Deflandre)

FIG. 6. Specimen V.53939(2) ×1900

Netrelytron stegastum Sarjeant

FIG. 7. Specimen OM131/14-225 ×768.

Leptodinium clathratum (Cookson & Eisenack)

FIG. 8. Dorsal view of specimen, V.53971(1) ×468.

Organism A

FIG. 9. Specimen V.53948(2) ×670.

Systematophora areolata Klement

FIG. 10. Specimen SS 625/7-160 ×615.


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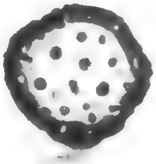
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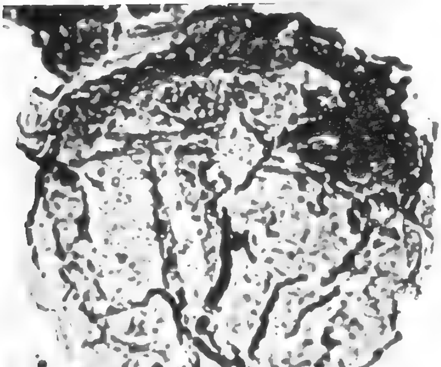
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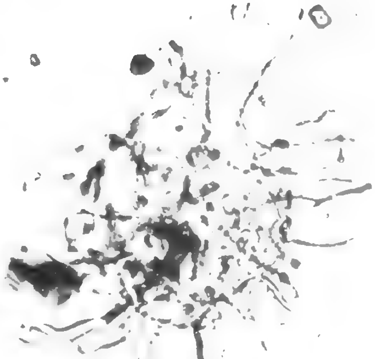
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PLATE 12

Leptodinium amabilis (Deflandre)
FIG. 1. Ventral surface of specimen, V.52805(1) × 1200.
FIG. 2. Dorsal surface of same, viewed by transparency, × 1200.

Scriniodinium playfordi Cookson & Eisenack
FIG. 3. Dorsal view of specimen V.53955(1) × 480.

Micrhystridium fragile Deflandre
FIG. 4. Specimen V.53948(3) × 1200.

Staplinium cistum sp. nov.
FIG. 5. Specimen SS 625/5-36 × 768.

Pterospermopsis australiensis Deflandre & Cookson
FIG. 6. Specimen V.53941(1) × 1920.

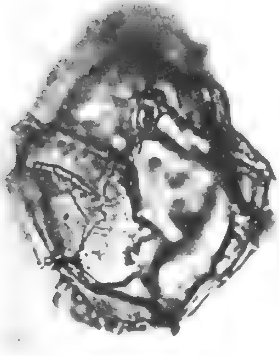
Cleistosphaeridium ehrenbergi (Deflandre)
FIG. 7. Specimen V.53619(2) × 640.

Apteodinium cf. ***maculatum*** (Cookson & Eisenack)
FIG. 8. Specimen V.53970(1) × 416.

Cleistosphaeridium tribuliferum (Sarjeant)
FIG. 9. Specimen V.53978(1) × 768.

Cleistosphaeridium polyacanthum sp. nov.
FIG. 10. Holotype, V.53943(1) × 465.

Veryhachium hyalodermum (Cookson)
FIG. 11. Specimen 53620(3) × 1450.



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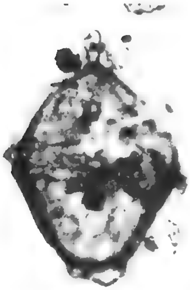

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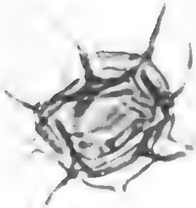

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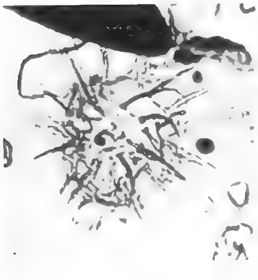

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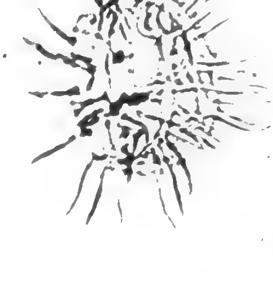

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PLATE 13

Scriniodinium dictyotum subsp. **pyrum** nov.

FIG. 1. Ventral surface of the holotype, V.53949(2) × 510.
FIG. 2. Dorsal surface of same, viewed by transparency, × 510.

Micrhystridium sydus Valensi

FIG. 3. Specimen V.53976(1) × 1000.
FIG. 4. Specimen RB 218/16-324 × 1600.

Baltisphaeridium inusitatum Klement

FIG. 5. Specimen V.53932(2) × 510.

Solisphaeridium stimuliferum (Deflandre)

FIG. 6. Specimen V.53949(3) × 1200.

Prolixosphaeridium granulosum (Deflandre)

FIG. 7. Specimen RB 218/12-215 × 768.

Stephanelytron cf. **scarburghense** (Sarjeant)

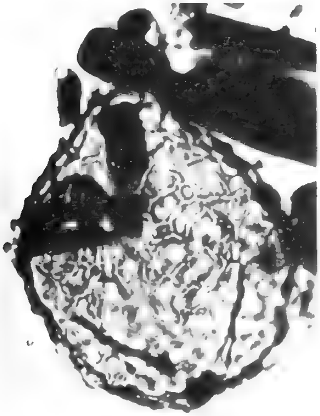
FIG. 8. Specimen V.52792(3) × 1000.

Prolixosphaeridium cf. **deirense** (Davey, Downie, Sarjeant & Williams)

FIG. 9. Specimen V.53950(1) × 768.

Meiourogonyaulax sp.

FIG. 10. Specimen V.53973(1) × 690.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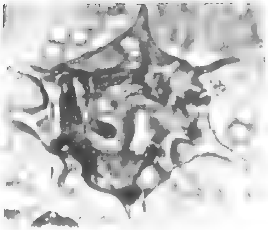
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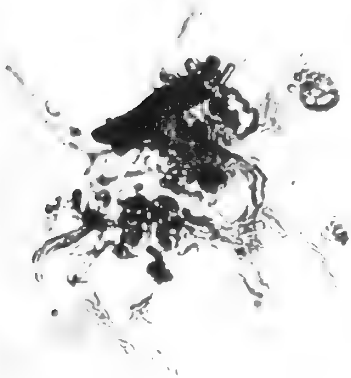
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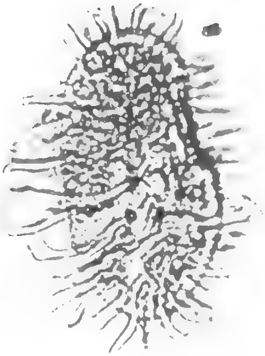
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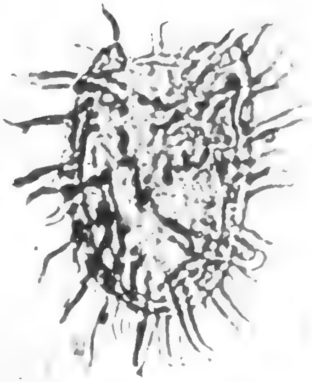
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PLATE 14

Gonyaulacysta jurassica (Deflandre)

FIG. 1. Ventral surface of specimen V.53977(1) × 768.

FIG. 3. Dorsal surface of same, viewed by transparency, × 768.

Heslertonia pellucida sp. nov.

FIG. 2. Ventral surface of holotype, V.53620(2) × 1270.

Staplinium cistum sp. nov.

FIG. 4. Specimen V.53946(2) × 768.

FIG. 7. Holotype, V.53950(2) × 768.

Chytroeisphaeridia chytroeides Sarjeant

FIG. 5. Specimen V.53975(1) × 1000.

Pareodinia ceratophora Deflandre

FIG. 6. Specimen V.53948(1) × 768.


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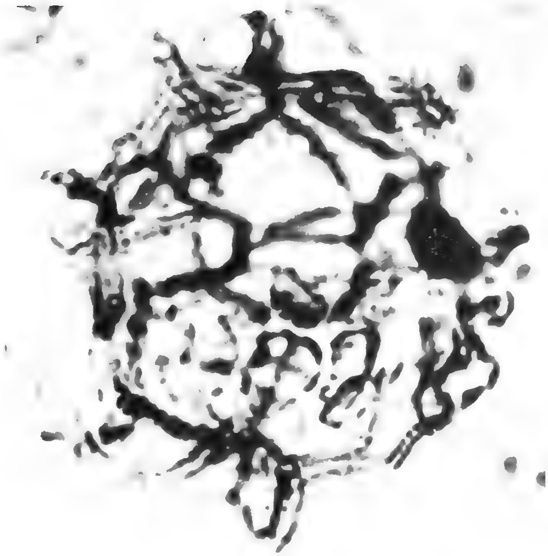
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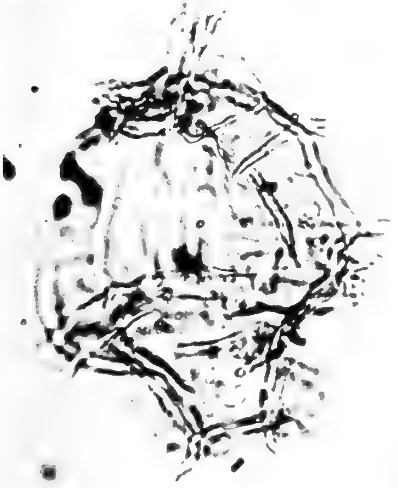
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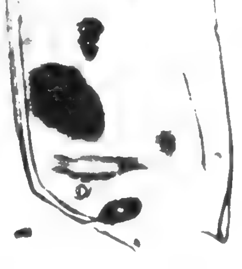
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NON-CALCAREOUS MICROPLANKTON FROM THE CENOMANIAN OF ENGLAND, NORTHERN FRANCE AND NORTH AMERICA. PART II

R. J. DAVEY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 18 No. 8
LONDON : 1970

NON-CALCAREOUS MICROPLANKTON FROM THE CENOMANIAN OF ENGLAND, NORTHERN FRANCE AND NORTH AMERICA

PART II

BY

ROGER JACK DAVEY

Pp. 333–397; 10 *Plates*, 9 *Text-figures*

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THE BRITISH MUSEUM (NATURAL HISTORY)
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LONDON 1970

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NON-CALCAREOUS MICROPLANKTON FROM THE CENOMANIAN OF ENGLAND, NORTHERN FRANCE AND NORTH AMERICA
PART II

By ROGER JACK DAVEY

Manuscript accepted May, 1969

CONTENTS

INTRODUCTION

In Part I of "Non-calcareous Microplankton from the Cenomanian of England, northern France and North America", I described the location of the samples analysed and proceeded to discuss in detail the various genera and species of dinoflagellate cysts encountered in this study. Part II continues the systematics of the dinoflagellate cysts and also deals with the acritarchs—a group of relatively simple marine organisms of unknown affinities. To conclude this Part, and the paper, an appraisal is made of the use of microplankton in stratigraphy. The assemblages obtained from a number of samples from each of three localities, Fetcham Mill, Compton Bay and Escalles, were examined both qualitatively and quantitatively and assessment is made of their stratigraphic value. These results are compared with earlier stratigraphic work performed on stratigraphically comparable sediments from the same geographical region. The samples from Speeton, Hunstanton and Devon were devoid of microplankton or yielded extremely meagre assemblages, and the reasons for this are discussed.

Although the study deals mainly with Cenomanian succession in England and northern France, an attempt has been made to formulate a wider picture by the qualitative analysis of samples from Texas, the United States of America, and Saskatchewan, Canada. Comparisons between these assemblages and the results of other workers show that, although some species are long-ranging, dinoflagellate cysts may be used for both intra- and inter-regional stratigraphic correlation. Finally an attempt is made to draw some tentative palaeogeographical and palaeoecological conclusions from the data available.

I. SYSTEMATIC DESCRIPTIONS

Cyst-Family **XIPHOPHORIDIACEAE** Sarjeant & Downie 1966

Genus ***XIPHOPHORIDIUM*** Sarjeant 1966

Remarks. The diagnosis of the genus *Pyramidium* Clarke & Verdier (1967) shows that it is a synonym of *Xiphophoridium* Sarjeant (1966).

Xiphophoridium alatum (Cookson & Eisenack)

(Pl. 1, figs. 1, 2)

1962 *Hystrichodinium alatum* Cookson & Eisenack: 487, pl. 2, figs. 1–4.
1964 *Hystrichodinium alatum* Cookson & Eisenack; Cookson & Hughes: 43, pl. 5, figs. 12, 13.
1966 *Xiphophoridium alatum* (Cookson & Eisenack) Sarjeant: pl. 16, fig. 11.
1967 *Pyramidium alatum* (Cookson & Eisenack) Clarke & Verdier: 40, pl. 6, figs. 5, 6.

Description. The shell is ovoidal to subpolygonal in shape with a smooth wall commonly bearing a small number of cuspidate tubercles approximately $2\,\mu$ in height (Pl. 1, fig. 2). The periphragm also forms sutural crests, which are particularly well developed in the cingular region (8–12 μ high) and from which arise long, simple, ribbon-like processes. Although the crests are clearly sutural, the tabulation is very difficult to determine because of their height. A relatively small apical archaeopyle, with an angular margin, is occasionally seen.

DIMENSIONS. Range of observed specimens : diameter of central body 32 (47·9) 65 μ, length of processes 16 (26·5) 45 μ. Number of specimens measured, 11.

OCCURENCE. *X. alatum* has been recorded from the Upper Aptian to Cenomanian of Australia (Cookson & Eisenack) and from the Upper Albian to Lower Cenomanian of England (Cookson & Hughes). The specimens described by Sarjeant were obtained from the Cenomanian of Fetcham Mill. It is a rare to fairly common species found at most horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It was not observed in the North American material.

Cyst-Family **DEFLANDREACEAE** Eisenack emend. Sarjeant & Downie 1966

Genus ***DEFLANDREA*** Eisenack emend. Williams & Downie 1966

REMARKS. Nine species, five of them new, are described from the Albian and Cenomanian of Saskatchewan and one from Fetcham Mill. Only one specimen attributable to *Deflandrea* was found in the Lower Chalk of Britain and France. Four specimens were obtained from the Upper Greensand (Albian) of Fetcham Mill. However, in the Albian-Cenomanian sediments (shallow water carbonaceous shales) from Saskatchewan it is very common.

Deflandrea pirnaensis Alberti

(Pl. 1, figs. 3, 4)

1959 *Deflandrea pirnaensis* Alberti: 100, pl. 8, figs. 1–5.

DESCRIPTION. This is a variable species having a broadly ovoidal shell with a fairly well developed apical horn and typically one antapical horn. Rarely a second, much reduced, antapical horn is present. The periphragm is smooth or lightly granular. The cingulum is marked by two low ledges, sometimes having knobbly margins, and is occasionally crossed by low ridges delimiting the plate boundaries. The sulcus is rarely visible. The intercalary archaeopyle, when discernible, possesses a rounded polygonal outline. The operculum is usually in position and opened as a flap. The inner body is oval, slightly thicker than the periphragm, and is occasionally concave posteriorly. It is usually separated for most of its circumference from the outer membrane by a narrow space.

DIMENSIONS. Range of observed specimens : overall length 46 (62·7) 87 μ, overall width 34 (45·5) 63 μ, length of inner body 33 (43·9) 57 μ, width of inner body 31 (38·2) 45 μ. Number of specimens measured, 15.

REMARKS. The above specimens from Saskatchewan are very similar to the type material described by Alberti from the Middle Turonian of Germany, except for their smaller size—the type material measures 80–106 μ in length and 58–64 μ in width. *D. pirnaensis* differs from *D. minor* Alberti (1959) in the possession of a well developed cingulum.

Alberti comments that an archaeopyle was not observed in any of the specimens. In most of the Saskatchewan specimens this structure is difficult to observe, but is usually present. The reason for this difficulty is that the operculum does not become completely detached, but apparently acts as a flap. Thus, after excystment, the operculum seems to have returned to its original position.

OCCURRENCE. *D. pirnaensis* is fairly common in the Cenomanian samples Sas805 and 835, but is rare in sample Sas890 (Lower Cenomanian) and also in samples Sas 967 and 1084 from the Albian. One specimen attributable to this species was located in sample FM520 from the Turonian of Fetcham Mill.

Deflandrea echinoidea Cookson & Eisenack

(Pl. 1, fig. 5)

1960 *Deflandrea echinoidea* Cookson & Eisenack: 2, pl. 1, figs. 5, 6.
1967 *Deflandrea echinoidea* Cookson & Eisenack; Clarke & Verdier: 26, pl. 3, figs. 4, 5.

DESCRIPTION. Three specimens from the Albian of Saskatchewan (sample Sas1084) are similar to the Australian species from the Upper Turonian and Senonian. The outer membrane is elongate-oval in shape with a stout apical horn and two antapical horns. A number of stout, curved spines (1–2 μ in length) arise from this membrane. The spines may be pointed, blunted distally, or reduced to granules ; they are often aligned along reflected plate boundaries. The cingulum (5–7 μ in width) and sulcus are well developed and are delimited by these spines. The archaeopyle is subpolygonal. The inner body is large, subspherical to ovoidal, and abuts against the shell membrane laterally.

DIMENSIONS. Range of observed specimens : overall length 54–67 μ, overall width 41–46 μ, length of inner body 38–45 μ, width of inner body 41–46 μ. Number of specimens measured, 3.

OCCURRENCE. The Saskatchewan specimens extend the range of this species into the Lower Cretaceous (Albian). It is also present in the Turonian and Lower Senonian of England (Clarke & Verdier 1967).

Deflandrea* cf. *echinoidea Cookson & Eisenack

(Pl. 1, fig. 6 ; Pl. 2, fig. 2)

DESCRIPTION. The specimens here compared with *D. echinoidea* possess an ovoidal shell membrane with a small apical horn and are truncated abruptly at the posterior. Arising from the outer membrane are stout, slightly curved, hollow spines (up to 3 μ in length), which tend to be aligned along reflected plate boundaries. The cingulum is well defined (5–7 μ in width), being delimited by strongly developed spines. The sulcus is deeply hollowed and extends from the antapex just onto the epitract. A subpolygonal intercalary archaeopyle is always present. The inner body is ovoidal, its longer axis lying across the cyst and sometimes touching the outer shell membrane.

DIMENSIONS. Range of observed specimens : overall length 50–62 μ, overall width 35–49 μ, length of inner body 31–35 μ, width of inner body 34–41 μ. Number of specimens measured, 5.

REMARKS. The above specimens resemble *D. echinoidea* in most respects, but differ in their smaller size and absence of antapical horns.

OCCURRENCE. Five specimens of *D.* cf. *echinoidea* have been recorded, all from Fetcham Mill ; four from sample FM886 (Albian) and one from sample FM840 (basal Cenomanian).

Deflandrea granulifera Manum var. ***tenuis*** nov.

(Pl. 2, fig. 1)

1962 *Deflandrea granulifera* Manum: 61, pl. 3, fig. 7 only.
1964 *Deflandrea granulifera* Manum; Manum & Cookson: 8.

DERIVATION OF NAME. Latin, *tenuis*, thin—with reference to the nature of the shell wall.

DIAGNOSIS. A variety of *D. granulifera* Manum possessing smooth to lightly granular outer membrane surrounding relatively small, thin-walled inner body.

HOLOTYPE. B.M.(N.H.) V.51990(1), (Pl. 2, fig. 1). Upper Lower Colorado (top of Fish Scale Zone?), International Yarbo Borehole No. 17, Saskatchewan at 967 feet depth. Lower Cretaceous (Albian).

DIMENSIONS. Holotype : shell diameter 85 by 60 μ, inner body diameter 39 by 60 μ. Range : overall length 85–114 μ, overall width 52–63 μ, diameter of inner body 39–60 μ. Number of specimens measured, 8.

DESCRIPTION. *D. granulifera* var. *tenuis* has only been obtained from the Saskatchewan samples and appears to be quite variable. The shell is elongate, typically widest in the cingular region and narrowing slightly anteriorly before broadening to form rounded " shoulders ". The epitract terminates with a conical apical horn, blunted distally. The posterior end of the shell is flat to concave, bearing one pointed conical horn and sometimes a second rudimentary one. The slightly spiral cingulum is always well developed and bordered by fairly high ridges possessing knobbly margins. At regular intervals the bordering ridges of the cingulum are absent, thus it is discontinuous. The sulcus is wide and extends anteriorly from the antapical horns. A rounded, hexagonal intercalary archaeopyle is typically present. The outer membrane is thin and may be smooth or densely granular. The inner body is subspherical, has a slightly thicker wall and is usually more heavily granular than the outer membrane. Occasionally the inner body is in contact with the lateral walls of the shell but more often its small size does not permit this.

REMARKS. Manum (1962) gave a detailed analysis of *D. granulifera* from the Upper Cretaceous of Arctic Canada and noted that two forms appeared to be present. These forms differed in the density of the granulation and also in the thickness of the inner body wall. Since some intergradation between the two forms existed, Manum considered that both forms should be placed in the single species *D. granulifera*. The more typical form possesses a dense granulation with an inner body wall of approximately 2 μ in thickness. The other, rarer form, which is the only one represented in the Saskatchewan material, possesses a smooth to lightly granular outer membrane, and an inner body with a thin wall only slightly thicker than the outer membrane. Another differentiating feature is that the inner body is smaller in this form and is not in contact with the lateral walls of the shell. This form because of these distinguishing features is here created a variety of *D. granulifera*. *D. granulifera* var. *tenuis* nov. is rather similar to *D. spectabilis* Alberti (1959), especially in some specimens when the shoulders are not particularly pronounced. The inner body of *D. spectabilis*, from the Senonian of Germany, is extremely delicate and difficult to discern. Thus *D. granulifera* var. *tenuis*, which possesses a light granulation and a thin-walled inner body, appears to occupy an intermediate position between the typical form of *D. granulifera* and *D. spectabilis* and warrants its distinction as a variety.

Moderately, well preserved specimens are extremely rare due to the thinness of the shell wall.

OCCURRENCE. *D. granulifera* var. *tenuis* is a rare species, found in the following Albian and Cenomanian samples from Saskatchewan—Sas1084, 967, 890, 835 and 805.

Deflandrea pontis-mariae (Deflandre)

(Pl. 1, figs. 10, 11)

1936 *Gymnodinium pontis-mariae* Deflandre: 9, pl. 2, figs. 7–9.
1965 *Deflandrea pontis-maria* (Deflandre) Vozzhennikova; pl. 49, fig. 5.

DESCRIPTION. The shell is elongate-ovoidal, with a large, sub-conical apical horn and a similar antapical horn placed asymmetrically. The outer membrane is thin, smooth or lightly granular. The cingulum is well defined being delimited by two low ridges, and is only slightly spiral. The sulcus is weakly defined and an archaeopyle has not been observed. The inner body is subspherical, its wall being slightly thicker than that of the outer membrane.

DIMENSIONS. Range of observed specimens : overall length 50 (65·1) 74 μ, overall width 33 (38·3) 46 μ, length of inner body 34 (35·4) 38 μ, width of inner body 31 (34·3) 39 μ. Number of specimens measured, 7.

REMARKS. The present specimens resemble the type material described by Deflandre (1936), from the Upper Cretaceous, in particular the specimen illustrated in his pl. 2, fig. 8. The single specimen illustrated by Vozzhennikova is also very similar.

The species is easily distinguishable by its overall form, in particular by the presence of a single, well developed antapical horn. Although an intercalary archaeopyle has not been observed, all the other features exhibited by this species confirm Vozzhennikova's view that it should be attributed to the genus *Deflandrea*.

OCCURRENCE. *D. pontis-mariae* occurs in two Saskatchewan samples. It is common in sample Sas805 (Cenomanian) and very rare in sample Sas1084 (Albian).

Deflandrea suspecta (Manum & Cookson) comb. nov.

(Pl. 2, fig. 5)

1964 *Hexagonifera suspecta* Manum & Cookson: 9, pl. 1, figs. 9–13.

DESCRIPTION. The periphragm membrane is very thin and closely surrounds the inner body, except at the apex where there is a short, blunt apical horn. The inner body is subspherical to ovoidal and possesses a thick wall (1·5–2 μ thick). The wall is densely granular and sometimes, in addition, bears small tubercles. The inner body opens by the loss of three plates beneath the apex on one surface. The central plate, of the three, is hexagonal in shape and the two side plates are pentagonal.

DIMENSIONS. Range of observed specimens : shell length 61–68 μ, width 56–59 μ. Number of specimens measured, 5.

REMARKS. The specimens are very similar in all respects to the type material from the Upper Cretaceous of Arctic Canada. The loss of three plates to form an opening just beneath the apex of the inner body is a characteristic feature. These three plates are reflections of the three anterior intercalary plates in the tabulation of the Peridinoid dinoflagellate theca and are thus situated on the dorsal surface. The hexagonal plate is the reflected plate 2a and the two pentagonal plates reflect plates 1a and 3a. The apex of the inner body and the anterior central surface of the epitract do not help to form the opening and are equivalent to the four apical plates (plate 1′–4′). Thus a Peridinoid tabulation is present as seen in a number of species of *Deflandrea* described by Manum (1962). This species is, therefore, transferred from *Hexagonifera* Cookson & Eisenack to *Deflandrea*. As yet an anterior intercalary archaeopyle has not been observed in the outer membrane, probably because of the extremely fine and transparent nature of this membrane. The genus *Hexagonifera*, by contrast, is characterised by the formation of an apical archaeopyle developed by the removal of a six-sided apical plate.

OCCURRENCE. *D. suspecta* is a common species found at only one horizon in Saskatchewan (sample Sas835) of Cenomanian age.

Deflandrea magna sp. nov.

(Pl. 2, figs. 6–8)

DERIVATION OF NAME. Latin, *magnus*, large—with reference to the size of this species.

DIAGNOSIS. Shell elongate—ovoidal, truncated posteriorly with single, pointed antapical horn. Epitract subconical, apical horn not differentiated. Outer membrane smooth or slightly granular, enclosing subspherical inner body. Inner body and outer membrane sometimes in contact laterally but more often separated by narrow space. Cingulum, on outer membrane, well defined, weakly spiral, marked by low ledges having knobbly margin. Sulcus broad. Archaeopyle subpolygonal, operculum typically in place.

HOLOTYPE. B.M.(N.H.) V.51988(1). Second White Speckled Shale, International Yarbo Borehole No. 17, Saskatchewan at 835 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : overall length 102 μ, overall width 67 μ, length of inner body 55 μ, width of inner body 57 μ. Range : overall length 69 (95·9) 118 μ, overall width 49 (64·7) 85 μ, length of inner body 36 (51·0) 61 μ, width of inner body 43 (51·6) 57 μ. Number of specimens measured, 12.

DESCRIPTION. Due to the fineness of the outer membrane, it is always folded to some extent. The cingulum (7 to 10 μ in width) is slightly concave and is sometimes crossed by low ridges marking the cingular plate boundaries. The lower boundary of the cingulum is occasionally interrupted. The archaeopyle is elongate—ovoidal anteriorly and polygonal posteriorly ; the operculum typically remains in position. The inner body possesses a slightly thicker wall, is subspherical rarely with a posterior concavity, and usually has an apical region composed of disarranged plates. Sometimes the three anterior intercalary plates are obvious. Rarely the latter plates, together with the apical plates, are absent.

REMARKS. *D. magna* sp. nov. most closely resembles *D. accuminata* Cookson & Eisenack (1958) from the Cenomanian to Lower Turonian of Australia. *D. accuminata* differs in that the inner body is relatively small, it possesses an apical horn, and the cingulum is poorly defined. The forms illustrated by Manum & Cookson (1964) from Arctic Canada are more similar, but again the cingulum is very reduced. *D. pirnaensis* Alberti (1959) resembles *D. magna* but has a more pronounced apical horn and does not usually possess an obvious archaeopyle.

OCCURRENCE. *D. magna* has only been recorded from the Cenomanian of Saskatchewan. It is a common species in sample Sas835 and rare to fairly common in samples Sas805 and 890.

Deflandrea glomerata sp. nov.

(Pl. 1, figs. 7–9)

DERIVATION OF NAME. Latin, *glomeratus*, ball—with reference to the overall circular shape of the shell.

DIAGNOSIS. Cyst smooth-walled, circular in outline with single pointed antapical horn asymmetrically placed. Apical horn absent. Inner body circular in outline and in contact with outer membrane except in apical and antapical regions. Cingulum and sulcus typically absent. Archaeopyle angular, six-sided, with similar shaped opening on inner body.

HOLOTYPE. B.M.(N.H.) V.51988(2). Second White Speckled Shale, International Yarbo Borehole No. 17, Saskatchewan at 835 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : overall length 97 μ, overall width 70 μ, length of inner body 72 μ, width of inner body 69 μ. Range : overall length 71 (82·9) 97 μ, overall width 55 (65·9) 75 μ, length of inner body 57 (67·3) 79 μ, width of inner body approximately equals overall width. Number of specimens measured, 14.

Description. These cysts are relatively simple and show little variation. At the apical region of the outer membrane there is typically a small number of concentric wrinkles—perhaps a very rudimentary apical horn. In one specimen a part of the cingulum is indicated by a few aligned granules. It is significant that the inner body possesses a six-sided opening directly beneath the archeopyle in the outer membrane. Both are a reflection of plate 2a in the original dinoflagellate theca.

Remarks. The circular outline with a simple antapical horn easily differentiates *D. glomerata* sp. nov. from all previously described species.

Occurrence. *D. glomerata*, a Saskatchewan species, is common in sample Sas835 (Cenomanian), only two specimens being recorded outside this horizon : in samples Sas805 (Cenomanian) and Sas967 (Albian).

Deflandrea globosa sp. nov.

(Pl. 2, fig. 3)

Derivation of name. Latin, *globosus*, round as a ball—with reference to the circular outline of this species.

Diagnosis. Shell subspherical to subpolygonal, with small number of concentric folds at apex, and very reduced single antapical horn placed asymmetrically. Apical horn, cingulum and sulcus absent. Inner body entirely in contact with outer membrane. Wall smooth to slightly granular. Intercalary archaeopyle, angular, six-sided.

Holotype. B.M.(N.H.) V.51988 (3). Second White Speckled Shale, International Yarbo Borehole No. 17, Saskatchewan at 835 feet depth. Upper Cretaceous (Cenomanian).

Dimensions. Holotype : shell length 69 μ, shell width 66 μ. Range : shell length 62 (67·5) 78 μ, shell width 48 (58·8) 66 μ. Number of specimens measured, 6.

Description. This species is extremely simple in form, possessing only a very rudimentary antapical horn to mar its smooth outline. The operculum is typically in place and the archaeopyle outline is only discerned with some difficulty.

Remarks. In overall appearance *D. globosa* sp. nov. strongly resembles *D. glomerata*. They differ in that *D. globosa* possesses a very rudimentary antapical horn and that the inner body is entirely in contact with the outer membrane. The lack of an apical horn (apical wrinkles being present), any tabulation and the spherical form indicate that these two species are closely related. Because of this and the presence of an intercalary archaeopyle, *D. globosa* is placed in the genus *Deflandrea*.

Occurrence. This species has only been recorded from a single sample (Sas835) Saskatchewan in which it is fairly common.

Deflandrea sp. A

(Pl. 3, fig. 1)

Description. The shell is elongate—ovoidal in shape. Posteriorly there are two small antapical horns, one being slightly longer than the other. An apical horn is absent, there being present in this region a small number of concentric folds. The outer membrane is smooth, of moderate thickness (c. 1 μ), and possesses a very faintly defined cingulum. A six-sided intercalary archaeopyle is present. The inner body is subspherical and is in contact with the shell wall laterally. The wall of the inner body is of similar thickness to that of the outer membrane and is lightly granular.

FIGURED SPECIMEN. B.M.(N.H.) V.51991(2). Upper Lower Colorado (just above the top of Viking Formation), International Yarbo Borehole No. 17, Saskatchewan at 1084 feet depth. Lower Cretaceous (Albian).

DIMENSIONS. Figured specimen : overall length 93 μ, overall width 64 μ, length of inner body 59 μ, width of inner body 63 μ.

REMARKS. Although only one specimen of *Deflandrea* sp. A. was located, its distinctive nature warranted careful description. The lack of an apical horn and the presence of apical folds indicates that it is related to *Deflandrea glomerata*. However, the overall shape of the latter is different. *Deflandrea* sp.A. most closely resembles *D. pellucida* Deflandre & Cookson (1958) from the Eocene of Australia, the latter differing in the possession of an apical horn.

Cyst-Family **ENDOSCRINIACEAE** Vozzhennikova emend. Sarjeant & Downie, 1966

Genus ***PSALIGONYAULAX*** Sarjeant 1966

Psaligonyaulax deflandrei Sarjeant

(Pl. 3, figs. 4, 5)

1964 *Gonyaulax cassidata* Eisenack & Cookson; Cookson & Hughes: 42, pl. 5, fig. 11 only.
1966 *Psaligonyaulax deflandrei* Sarjeant: 137, pl. 14, figs. 7, 8; text-fig. 35.
1967 *Gonyaulacysta extensa* Clarke & Verdier: 30, pl. 4, figs. 7–9; text fig. 11.

DIMENSIONS. Range of type material : overall length 67 (76·9) 87 μ, overall width 39 (47·6) 59 μ. Number of specimens measured, 16.

REMARKS. This species was first figured by Cookson & Hughes (1964) from the Cambridge Greensand (?Albian-basal Cenomanian) as *Gonyaulax cassidata*. *P. deflandrei* is similar to the latter species except that it possesses a well defined posterior pericoel. The two species are undoubtedly closely related and it is sometimes very difficult to distinguish them when the posterior region of the shell is damaged or obscured.

OCCURRENCE. *P. deflandrei* is a rare species found throughout the Cenomanian of Fetcham Mill and Escalles. It is very rare at Compton Bay and was not observed in the North American material.

Genus ***PALAEOHYSTRICHOPHORA*** Deflandre emend. Deflandre & Cookson 1955

DIAGNOSIS. Dinoflagellate cysts with a generally thin theca furnished with a cingulum ; sulcus clear or indistinct, plates absent, membrane covered with irregularly disposed, stiff or soft spines or hairs. Archaeopyle precingular.

REMARKS. The presence of a precingular archaeopyle has been added to the diagnosis.

One species attributed to this genus, *P. infusorioides*, has been recorded from the Cenomanian of England, France, Texas and Saskatchewan. It has also been recorded from material of Upper Cretaceous age in Australia (Cookson & Eisenack 1958), Germany (Alberti 1961) and Arctic Canada (Manum & Cookson 1964). It therefore has a wide geographical distribution. Detailed study of the Cenomanian in a restricted area has shown that the occurrence of this species coincides with the base of this stage, as defined by its macrofauna, and it is therefore an important index fossil. This conclusion has also been arrived at by Clarke & Verdier (1967 ; 82).

Palaeohystrichophora infusorioides Deflandre

(Pl. 3, figs. 2, 6)

1934 *Palaeohystrichophora infusorioides* Deflandre: fig. 8.

1965 *Palaeohystrichophora infusorioides* Deflandre; Vozzhennikova: pl. 9, fig. Л; pl. 21, fig. **3**; pl. 43, fig. Б.

1967 *Palaeohystrichophora infusorioides* Deflandre; Clarke & Verdier: 28, pl. 4, fig. 10. (See also for earlier references).

DESCRIPTION. This cyst is of ovoidal to spindle-like shape, composed of a thin outer membrane surrounding a slightly thicker inner body. The outer membrane and inner body are only in contact in the cingular region, there being anterior and posterior pericoels. The cingulum is clearly marked by two ridges. The epitract is conical and usually larger than the hypotract, which may be rounded or truncated posteriorly. The outer membrane is smooth or slightly granular and usually bears a moderate number of hairlike spines ; these tend to be concentrated along the boundaries of the cingulum and sulcus and also at the apex. Occasionally the spines are very few in number and are restricted to the apex or cingular region. Very rarely the spines may be seen to be aligned along plate boundaries, demarcating the precingular and postcingular plates. The inner body is subspherical, usually slightly thicker than the outer membrane and smooth, but may sometimes be considerably thicker (up to about $1{\cdot}5\,\mu$) and densely granular. The thickening of the central body wall is usually accompanied by a decrease in the number of spines, some specimens being almost bald. Typically the shell appears to be entire but very rarely the presence of a precingular archaeopyle has been observed.

DIMENSIONS. Range of observed specimens : shell length 33 (44·1) 63 μ, inner body length 27 (35·1) 42 μ, shell width (= width of inner body) 27 (35·7) 47 μ, maximum length of spines 4 (6·1) 10 μ. Number of specimens measures, 29.

REMARKS. Most specimens of *P. infusorioides* from the Cenomanian in all respects resemble the type material from Upper Cretaceous (Senonian) as described by Deflandre. Occasionally the inner body is thicker than normal and the spines less numerous; however, there seems to be a complete gradation between the normal representatives of this species and these forms. The reduced number of spines is reminiscent of *P. paucisetosa* Deflandre (1943), but in this latter species the spines are stiff and the inner body is not in contact with the outer membrane.

The distribution of this species is fully discussed in the stratigraphic conclusions (p. 384).

Genus *STEPHODINIUM* Deflandre

EMENDED DIAGNOSIS. Cavate cysts possessing an ovoidal inner body and surrounding periphragm membrane. Inner body and outer membrane in contact on ventral surface, and at apex and antapex of shell. Maximum separation in cingular region. Apical horn usually present. Tabulation present on outer membrane, sutures marked by low ridges. Archaeopyle precingular.

TYPE SPECIES. *Stephodinium coronatum* Deflandre 1936. Upper Cretaceous; France.

REMARKS. The presence of a tabulation on the holotype of *S. coronatum*, although not described by Deflandre, has been verified by Clarke & Verdier (1967 ; 67).

Stephodinium coronatum Deflandre

(Pl. 6, figs. 1, 2, 4)

1963a *Stephodinium coronatum* Deflandre; 58, text-fig. 104.
1967 *Stephodinium coronatum* Deflandre; Clarke & Verdier: 67, pl. 12, figs. 10, 11. (See also for earlier references).

DESCRIPTION. An ovoidal inner body is surrounded by a large, smooth, tabulate, periphragm membrane. A blunt apical horn (about 8 μ in height) is present. The plate boundaries are marked by low thickenings of the periphragm membrane and typically give rise to a small spine (2–3 μ in height) when joining one another. The thickenings demarcating the cingulum are sometimes denticulate. Although the full tabulation has not been determined, there appear to be five large precingular plates of an elongate pentagonal shape. The third precingular plate is typically lost in archaeopyle formation. There are five postcingular plates and a single, more or less pentagonal antapical plate. The ventral surface is devoid of tabulation. Rarely the periphragm membrane possesses large, subcircular perforations.

DIMENSIONS. Range of observed specimens : maximum diameter of outer membrane 65 (71·2) 82 μ, minimum diameter of outer membrane 52 (61·9) 69 μ, diameter of central body 36 (45·1) 54 μ. Number of specimens measured, 12.

REMARKS. The specimens studied are identical with the type material from the Upper Albian-Lower Cenomanian of England.

OCCURRENCE. In addition to the type material, *S. coronatum* has also been recorded from the Upper Cretaceous (probably Cenomanian) of Arctic Canada by Manum & Cookson and from the Middle and Upper Albian of Roumania by Baltes (personal communication). In the material examined it is a rare to very rare species at most horizons at Fetcham Mill and Compton Bay, but only occurs in three samples from Escalles. It was also recorded from the Albian sample FM886, but was absent from the Turonian sample FM520, and from the North American material.

Cyst-Family **NELSONIELLACEAE** Eisenack emend. Sarjeant & Downie 1966

Genus ***SCRINIODINIUM*** Klement 1957

DIAGNOSIS. Ovoid, dorso-ventrally slightly compressed shell with darker spherical to ovoid inner body. A spiral cingulum often only marginally visible. Occasionally clear tabulation with sulcus. Archaeopyle precingular.

REMARKS. The presence of a precingular archaeopyle has been included in the diagnosis of this genus.

Scriniodinium campanula Gocht

(Pl. 3, figs. 7, 8)

1959 *Scriniodinium campanula* Gocht: 61, pl. 4, fig. 6; pl. 5, fig. 1.

1967 *Scriniodinium campanula* Gocht; Clarke & Verdier: 28, pl. 3, figs. 6, 7. (See also for earlier references).

DESCRIPTION. The shell is rhomboidal in outline ; the dorsal surface is strongly convex or pyramidal and the ventral surface practically flat. A small, stout apical horn is present, commonly truncated distally. The shell surface is smooth or slightly granular. An inner body, of similar shape to the outer shell wall, appears to be present. The cingulum, approximately 6 μ in width, is well developed on the dorsal surface and only extends onto the ventral surface for a short distance. It is delimited by two parallel folds in the shell wall, the folds occasionally bearing a few small spines. The ventral surface is almost devoid of any tabulation.

A well developed fold, reflecting a plate boundary, is present on the dorsal hypotract running from the cingulum to the antapex. The dorsal surface is pyramidal, the apex of the pyramid being where the dorsal hypotractal fold abuts against the cingulum. The dorsal surface of the epitract bears an elongate, pentagonal, precingular archaeopyle. Rarely two small folds beneath the apex are present, probably delimiting apical plates. On the ventral surface, just anterior to the antapex there is consistently a moderate sized, subcircular hole in the shell wall.

DIMENSIONS. Range of observed specimens : length of shell 72 (90·2) 108 μ, width 62 (73·5) 86 μ. Number of specimens measured, 22.

REMARKS. Sections of the cyst walls, illustrated by Cookson & Hughes, indicate that an inner body is absent and that the shell wall is only one layer thick. Cookson & Hughes argue that the inner body appearance is due to " the steepness of the gradient of the dorsal convexity ". However, in the Cenomanian specimens, if the margin of the archaeopyle is examined carefully, there appears to be an outer, very lightly granular layer and an inner smooth layer. This is as would be expected since practically all the dinoflagellate cysts examined so far are two-layered. As Cookson & Hughes points out it is possible that the two layers typically adhere closely together.

The hole in the ventral surface was first remarked upon by Cookson & Hughes and is a consistent feature of all specimens examined. Its existence possibly helps to govern the buoyancy of the cyst in some way.

OCCURRENCE. *S. campanula* is a rare to common species of all horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It has also been recorded from the Albian sample FM886 and the Turonian sample FM540, both from Fetcham Mill. It has not been observed in the Saskatchewan material, and only a single specimen has been recorded from Texas (Upper Woodbine). The recorded stratigraphic range of this species is Valanginian to Middle Turonian.

Cyst-Family **HEXAGONIFERACEAE** Sarjeant & Downie 1966

Genus ***HEXAGONIFERA*** Cookson & Eisenack 1961

REMARKS. This genus appears to be restricted in stratigraphic range, being recorded only from the Albian and Upper Cretaceous; it is, therefore, of stratigraphic importance.

Hexagonifera chlamydata Cookson & Eisenack

(Pl. 3, figs. 3, 9, 10)

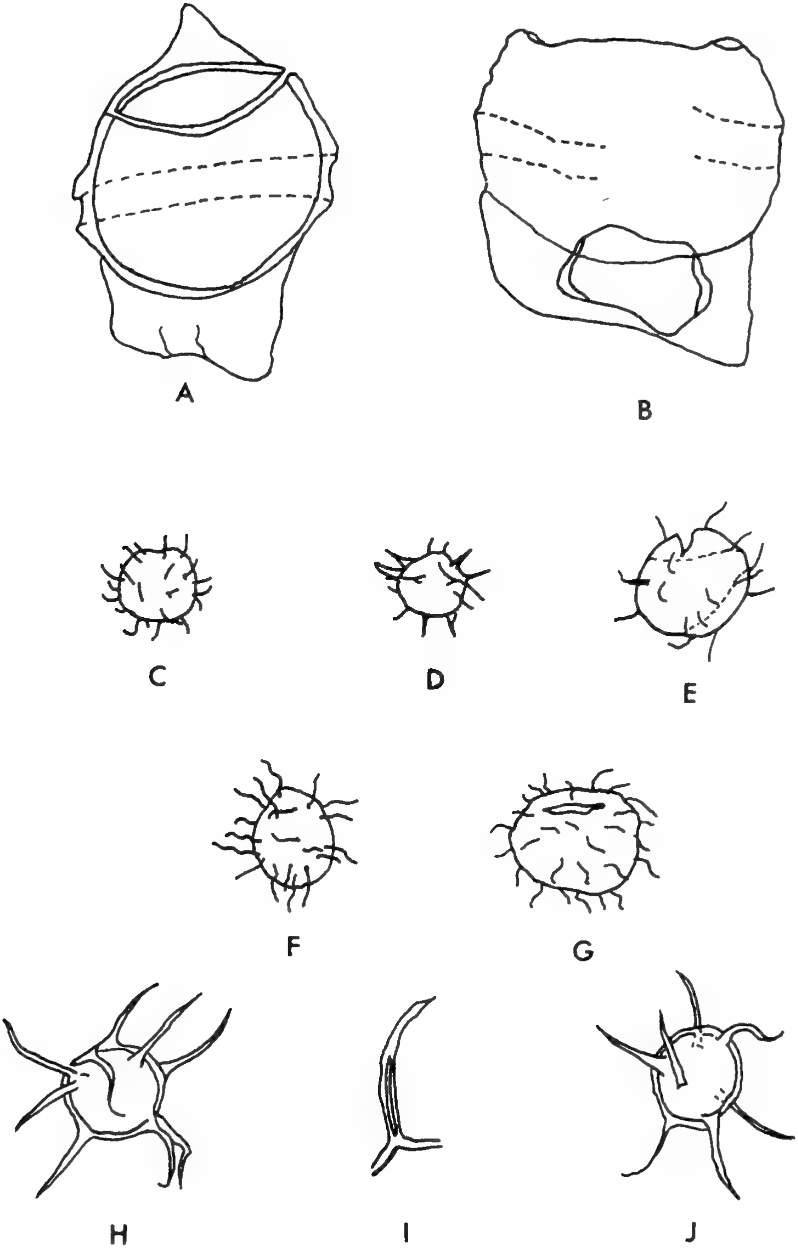
1962 *Hexagonifera chlamydata* Cookson & Eisenack: 496, pl. 7, figs. 1–3, 5–8.
1964 *Hexagonifera chlamydata* Cookson & Eisenack; Cookson & Hughes: 53, pl. 10, figs. 7–9.
1967 *Hexagonifera chlamydata* Cookson & Eisenack, Clarke & Verdier: 69, pl. 11, figs. 6–8.

DESCRIPTION. The inner body is ovoidal and is completely enclosed by a large, thin membrane of variable size. The inner body is thick walled (1–2 μ in thickness) and may be very lightly or densely granular, verrucose or slightly reticulate. The outer membrane is thin, may be finely granular, and is typically folded. A small apical prominence has been observed on this membrane (pl. 3, fig. 3). The apical region is usually detached in archaeopyle formation, the archaeopyle appearing to be only slightly angular sometimes with a sulcal notch. The detached operculum is six-sided.

DIMENSIONS. Range of observed specimens: overall diameter 40–99 μ, central body length 38 (49·4) 62 μ, width 30 (44·8) 58 μ. Number of specimens measured, 17.

REMARKS. The Cenomanian specimens here described strongly resemble the type material from Australia, of Albian and probably Cenomanian age. Identical specimens have been described from the basal Cenomanian of England by Cookson & Hughes. Baltes (personal communication) has also recorded this species from the Lower Cenomanian of Roumania, and Clarke & Verdier from the Turonian and Senonian of England.

OCCURRENCE. *H. chlamydata* is infrequent at most horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It occurs in the Lower Cenomanian material from Saskatchewan (samples Sas890, 835), but not in the Texas material.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Genus *OVOIDINIUM* nov.

DERIVATION OF NAME. Latin, *ovum*, egg—with reference to the egg-shaped inner body.

DIAGNOSIS. Bicavate dinoflagellate cysts, possessing one or two antapical horns and typically an apical horn. Periphragm and endophragm only in contact medially. Inner body subspherical, smooth or granular, commonly possessing a cingulum. Periphragm smooth or granular, forming sulcus. Tabulation absent. Archaeopyle apical with slightly angular margin.

TYPE SPECIES. *Ascodinium verrucosum* Cookson & Hughes 1964. Cambridge Greensand (probably basal Upper Cretaceous, Cenomanian), England.

REMARKS. Two species, *Ascodinium verrucosum* Cookson & Hughes and *A. scabrosum* Cookson & Hughes, have been transferred to *Ovoidinium*. *Ascodinium* Cookson & Eisenack (1960) differs from *Ovoidinium* in that the archaeopyle is not strictly apical and that the inner body of the former is not in contact laterally with the periphragm membrane. The archaeopyle in *Ascodinium* is more or less circular, mainly situated on the dorsal surface and only just includes the apex and a small part of the ventral surface. *Deflandrea cinctum* Cookson & Eisenack (1958) from the Upper Neocomian or Lower Aptian of Australia is also transferred to *Ovoidinium*. This species is bicavate, possesses an apical archaeopyle and a well defined cingulum.

Species belonging to *Ovoidinium* have a very restricted occurrence in the samples examined. In Europe they occur only in sample FM840 (Fetcham Mill) and CB1 (Compton Bay) from the basal Cenomanian, and therefore appear to be of stratigraphic value in marking the base of the Cenomanian. In Saskatchewan this genus has been recorded from samples Sas1084, 1023 and 890. The stratigraphical significance of this genus is fully discussed in a later section (see p. 390).

Ovoidinium verrucosum (Cookson & Hughes)

(Pl. 4, figs. 1, 2; Fig. 1A)

1964 *Ascodinium verrucosum* Cookson & Hughes: 41, pl. 5, figs. 4–7.

DESCRIPTION. The specimens examined strongly resemble the type material from the basal Cenomanian of England. The inner body is thick-walled (c. 2 μ), finely granular and possesses a distinct cingulum. The periphragm membrane bears numerous large tubercles and forms a distinct sulcus confined mainly to the

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FIG. 1. *Ovoidinium verrucosum* (Cookson & Hughes). A. Complete specimen—operculum partially detached (×900). *Ovoidinium ostium* sp. nov., B. Paratype illustrating subrectangular opening in the posterior pericoel (×900). *Micrhystridium inconspicuum* (Deflandre). C. Specimen with opening towards the north (×1500). D. Specimen with longer spines than usual (×1800). E. Specimen having a crescentic opening (×1500). *Micrhystridium piliferum* Deflandre. F. Entire specimen (×1500). G. Specimen with slit-like opening (×1500). *Micrhystridium alveospinum* sp. nov. H. Specimen illustrating crescentic opening (×900). I. Enlargement of a spine illustrating spinal cavity (×900). J. Holotype (×900).

hypotract. At the antapex this membrane is typically extended into a single horn, asymmetrically placed, and at the apex gives rise to a small horn. The operculum occasionally remains attached. The specimens from Compton Bay are more symmetrical antapically, have a less well defined cingulum and fewer tubercles than the Fetcham Mills examples. The tubercles are sometimes in the form of small truncated processes.

DIMENSIONS. Range : overall length 60–61 μ (2 complete specimens) ; shell length (operculum missing) 43 (47·8) 58 μ, length of inner body 32 (36·6) 42 μ, width of inner body 34 (43·4) 53 μ. Number of specimens measured, 10.

REMARKS. *O. verrucosum* may be distinguished from *O. scabrosum* (Cookson & Hughes 1964) by the surface ornamentation, shape of hypotract and distinct cingulum.

OCCURRENCE. In the Cenomanian material examined this species was recorded in the lowermost samples from Fetcham Mill (FM840) and from Compton Bay (CB1).

Ovoidinium scabrosum (Cookson & Hughes)

(Pl. 4, figs. 3, 4)

1964 *Ascodinium scabrosum* Cookson & Hughes: 40, pl. 5, figs. 1–3.

DESCRIPTION. *O. scabrosum* was only recorded from a single sample in the Cenomanian, sample CB1 from Compton Bay, where it is fairly common. In all respects these specimens are extremely similar to the type material described by Cookson & Hughes (1964) from the Upper Gault and Cambridge Greensand of England. The inner body is minutely, but densely, granular and is surrounded by a thin, hyaline outer membrane. The latter is in contact with the inner body only in the cingular region, thus there is an anterior and a posterior pericoel. The outer membrane forms a short apical horn and usually two small antapical horns of approximately the same size. The cingulum is extremely faint, if visible at all. An apical archaeopyle is always present, the operculum sometimes remaining attached to the main body of the cyst. The archeopyle margin is only very slightly angular, there being no sharp indentations indicating the positions of the precingular plates.

DIMENSIONS. Range of observed specimens : overall length 63–65 μ (2 complete specimens) ; shell length (operculum missing) 42 (47·1) 52 μ, length of inner body (operculum missing) 30 (35·2) 41 μ, width of inner body 34 (40·3) 50 μ. Number of specimens measured, 9.

REMARKS. *O. scabrosum* may be distinguished from other species in this genus by the inner body ornamentation, the hyaline outer membrane and the presence of two antapical horns of approximately equal size.

OCCURRENCE. It is noteworthy that *O. scabrosum* was only recorded from sample CB1 and not from sample FM840, the lowest sample from Fetcham Mill. This probably indicates that sample CB1 was obtained from a slightly lower horizon than sample FM840 since *O. scabrosum* was not obtained from the Chalk Marl by Cookson & Hughes (1964) whereas *O. verrucosum* was.

Ovoidinium ostium sp. nov.

(Pl. 4, figs. 5, 6 ; Fig. 1B)

Derivation of name. Latin, *ostium*, entrance or opening—with reference to the opening in the wall of the posterior pericoel.

Diagnosis. Inner body subspherical, lightly but densely granular, with moderately thick wall. Periphragm slightly granular, sometimes bearing tubercles. Apical pericoel small, with poorly developed horn ; posterior pericoel asymmetrical, possessing sub-rectangular opening on ventral surface. Cingulum and sulcus moderately well defined. Apical region generally lost in archaeopyle formation.

Holotype. B.M.(N.H.) V.51987(1). Upper Lower Colorado (Fish Scale Zone?), International Yarbo Borehole No. 17, Saskatchewan at 1023 feet depth. Lower Cretaceous (Albian).

Paratype. B.M.(N.H.) V.51991(1). Upper Lower Colorado (just above top of Viking Formation), International Yarbo Borehole No. 17, Saskatchewan at 1084 feet depth. Lower Cretaceous (Albian).

Dimensions. Holotype : overall length 59 μ, length of inner body 39 μ, width of inner body 40 μ. Paratype : length (operculum missing) 50 μ, length of inner body 35 μ, width of inner body 48 μ. Range : length (operculum missing) 37 (46·2) 63 μ, length of inner body 28 (34·4) 45 μ, width of inner body 37 (43·1) 54 μ. Number of specimens measured, 9.

Description. The inner body wall (1–1·5 μ thick) is surrounded by an outer membrane (approximately 0·5 μ thick), the two being in contact only in the cingular region. A characteristic sub-rectangular shaped opening is always developed on the ventral surface of the posterior pericoel membrane (text-fig. 1B). The opening lies towards the posterior end of the sulcus and is typically closed by an operculum. The operculum of the apical archaeopyle is usually detached and the archaeopyle margin is only sightly angular.

Remarks. *O. ostium* sp. nov. is similar to *O. scabrosum* and *O. verrucosum* and tends to grade into the one or the other depending on the form of ornamentation. The opening is the posterior pericoel membrane, however, is distinctive and quite characteristic. The operculum closing this opening is always attached and, therefore, acted as a lid. The purpose of this structure can only be surmised. The most probable explanation is perhaps that this opening allowed sea water into the posterior pericoal so regulating the bouyancy of the cyst in some manner.

Occurrence. *O. ostium* has only been recorded from Saskatchewan, in samples Sas1084 and 1023 (Albian), and sample Sas890 (Lower Cenomanian). It is fairly common in the lower two samples but rare in the Cenomanian sample.

Other Species

The following species is here attributed to the genus *Ovoidinium* on the basis of the apical archaeopyle, and anterior and posterior pericoels:

Ovoidinium cinctum (Cookson & Eisenack 1958) comb. nov. = *Deflandrea cincta* Cookson & Eisenack : 1958 Proc. R. Soc. Vict. **70**(1), 26 ; pl. IV, figs. 1–3.

Cyst-Family **PSEUDOCERATIACEAE** Eisenack emend.
Sarjeant & Downie 1966.

Genus ***PSEUDOCERATIUM*** Gocht 1957
Subgenus ***PSEUDOCERATIUM*** Gocht

Pseudoceratium dettmannae Cookson & Hughes
(Pl. 5, fig. 1)

1964 *Pseudoceratium dettmannae* Cookson & Hughes: 51, pl. 7, figs. 1–4.

DESCRIPTION. One specimen attributable to this species was observed in the lowest Cenomanian sample from Fetcham Mill (sample FM840). The specimen possesses an apical archaeopyle with a slightly angular margin. The operculum is still attached and is conical in shape with a well developed apical horn. The main part of the shell has four sides of approximately equal length and bears an apical and two lateral horns. Two membranes of similar height (15–20 μ) are situated around the circumference of the shell. They are densely pitted and sometimes possess large circular perforations. The shell wall is very lightly granular. The cingulum is extremely faintly marked by an aligned concentration of granules.

DIMENSIONS. Overall length 101 μ, width 92 μ.

REMARKS. The specimen described is very similar to the type material from the Upper Gault and Cambridge Greensand (Upper Albian—? Lower Cenomanian) of England.

OCCURRENCE. *P. dettmannae* has only been recorded from the Upper Albian and basal Cenomanian of England.

Genus ***ODONTOCHITINA*** Deflandre emend.

EMENDED DIAGNOSIS. Cavate cysts consisting of spherical inner body and outer membrane. Outer membrane extended into long tapering apical horn and two shorter tapering antapical horns. Very rarely, short, branching precingular and postcingular processes are present. Archaeopyle apical.

TYPE SPECIES. *Ceratium operculatum* O. Wetzel 1933. Upper Cretaceous ; Germany.

REMARKS. The overall shape of these cysts strongly resembles that of species in the modern genus *Ceratium* Shrank. This was first noticed by O. Wetzel (1932), who originally placed the type species in the genus *Ceratium*. Thus it appears probable that *Odontochitina* is the cyst-genus of *Ceratium*, but this is unlikely to be proved since *Odontochitina* is purely Mesozoic and *Ceratium* is present-day. No intermediate cyst types are obvious. One species, *O. blastema* sp. nov., possesses small precingular and postcingular processes but unfortunately the tabulation formula could not be determined. The thecal tabulation of *Ceratium* is characteristic (4′, 0a, 5″, 5‴, 2⁗) and if obtained would verify a relationship.

Odontochitina operculata (O. Wetzel)

(Pl. 4, figs. 7 ; Pl. 5, fig. 2)

1933 *Ceratium* (*Euceratium*) *operculatum* O. Wetzel: 170, pl. 11, figs. 21, 22.
1966 *Odontochitina operculata* (O. Wetzel); Sarjeant: 208, pl. 21, fig. 2. (See also for earlier references).
1967 *Odontochitina operculata* (O. Wetzel); Clarke & Verdier: 59, pl. 13, figs. 1, 7.

DESCRIPTION. The endophragm and periphragm of these cysts are thin and smooth. The antapical horns may be of almost equal size but typically one is appreciably longer than the other. Usually the longer process is situated just to one side of the antapex, while the other arises from approximately half way along the opposite side, in specimens possessing an anchaeopyle. An apical archaeopyle is commonly present, the margin being only slightly angular.

DIMENSIONS. Range of observed specimens : length of apical region (operculum) 188–275 μ (2 specimens) ; length of antapical horns 51 (84·7) 130 μ, width of central body 39 (51·2) 67 μ. Number of specimens measured, 9.

REMARKS. *O. operculata* is an easily recognisable species and appears to be widespread geographically. The earliest record is by Pocock (1962) from the Upper Jurassic of Canada. Many authors, such as Gocht 1959, Alberti 1961 and Górka 1963, have described it from the Cretaceous System (Upper Hauterivian—Senonian).

OCCURRENCE. *O. operculata* is a common species at all horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It has also been recorded in two samples from Saskatchewan (Sas1084 and 805) and in the Upper Woodbine of Texas.

Odontochitina costata Alberti

(Pl. 4, figs. 8, 9 ; Pl. 5, fig. 3)

1961 *Odontochitina costata* Alberti: 31, pl. 6, figs. 10–13.
1967 *Odontochitina costata* Alberti: Clarke & Verdier: 58, pl. 13, figs. 4–6. (See also for earlier references).

DESCRIPTION. The shape of the shell is very similar to that of *O. operculata*. The shell surface may be smooth or very lightly punctate. The central body commonly possesses a small apical protruberance and more rarely a small protruberance opposite each of the antapical horns. Both apical and antapical horns possess 2 to 4 striations along their entire length and typically have a small number of large circular to elongate perforations. The striations are low ridges formed by a slight thickening of the horn periphragm. On one specimen, a small process is situated at the proximal end of the small antapical horn. The apical region is typically removed in archaeopyle formation.

DIMENSIONS. Range of observed specimens : length of apical region (operculum) 88 (227·7) 290 μ, length of antapical horns 69 (90·5) 118 μ, width of central body 38 (57·7) 76 μ. Number of specimens measured, 12.

OCCURRENCE. *O. costata* is rare to common at most horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It was also recorded in three samples from Saskatchewan—samples Sas1084 and 1023 (Albian) and Sas890 (Lower Cenomanian). The specimens studied, resemble the type material from the Cenomanian–Turonian of Germany in all respects.

Odontochitina blastema sp. nov.

(Pl. 5, figs. 4, 5)

DERIVATION OF NAME. Greek, *blastema*, offshoot or sucker—with reference to the subsidiary processes.

DIAGNOSIS. Central body ovoidal ; outer membrane forming long tapering apical horn and two shorter tapering antapical horns. Periphragm smooth or slightly punctate ; in region of central body gives rise to small number of branched precingular and postcingular processes. Apical region commonly lost in archaeopyle formation.

HOLOTYPE. B.M.(N.H.) V.51989(1). Chalk, Bureau de Recherches Géologiques et Minières Borehole, Escalles, Pas de Calais at 159 metres depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : width of central body 48 μ, length of antapical horns 54 and 61 μ, length of subsidiary processes 8–20 μ. Range : length of apical horn 78 μ (one specimen) ; length of antapical horns 50 (55·7) 61 μ, width of central body 41 (44·4) 51 μ, length of subsidiary processes 4–23 μ. Number of specimens measured, 5.

DESCRIPTION. *O. blastema* sp. nov. is of the typical *Odontochitina* shape but possesses a number of subsidiary processes. These processes vary considerably in size and shape. They may be finely acuminate or more usually they branch, either distally or proximally, and terminate with a small bifurcation. When well developed they are seen to be in two series encircling the central body. One series (precingular) lies just posterior to the archeopyle margin, while the other series (postcingular) is situated towards the posterior end of the central body. Between the two series, corresponding approximately to the widest part of the central body, there is an area devoid of processes marking the position of the cingulum. In one specimen (pl. 5, fig. 5) two processes are present also on the proximal part of the larger antipical horn.

REMARKS. The presence of well developed subsidiary processes easily differentiates *O. blastema* from all previous described species in this genus. Since the overall form of the shell is identical to that of other members of *Odontochitina*, it was considered proper that this species should be placed in this genus. *Hystrichosphaera ceratioides* Deflandre (1937) is similar in size, overall form and posesses precingular and postcingular processes. However, this species possesses a distinct tabulation and, therefore, is easily distinguished from *O. blastema*.

OCCURRENCE. Only five specimens of *O. blastema* have been recorded. These occur in the following samples : FM730 (2 specimens) and FM690 from Fetcham Mill, and E165 and E159 from Escalles. Thus this species has not been observed in the Lower Cenomanian.

Cyst-Family **MEMBRANILARNACIACEAE** Sarjeant & Downie 1966

Genus ***CHLAMYDOPHORELLA*** Cookson & Eisenack 1958

DIAGNOSIS. Shell enclosed in delicate membrane supported by closely arranged, slender, bifurcating spines of approximately equal length. Archaeopyle apical.

REMARKS. The presence of an apical archaeopyle has been added to the original diagnosis as given by Cookson & Eisenack (1958).

This genus appears to be very similar to *Gardodinium* Albert (1961), both possessing an outer membrane supported by fine processes, an apical archaeopyle and an apical horn. *Gardodinium* however, possesses a definite subpolygonal outline, and precingular and postcingular plate boundaries are lightly defined. *Chlamydophorella nyei* as figured by Cookson & Eisenack (1958) sometimes has a subpolygonal outline but a tabulation has never been observed.

Chlamydophorella nyei Cookson & Eisenack

(Pl. 6, figs. 5, 7, 8)

1958 *Chlamydophorella nyei* Cookson & Eisenack: 56, pl. 11, figs. 1–3.
1962 *Chlamydophorella nyei* Cookson & Eisenack; Cookson & Eisenack: 496, pl. 7, figs. 14–16.
1964 *Chlamydophorella nyei* Cookson & Eisenack; Manum & Cookson; 10, pl. 5, fig. 3.

DESCRIPTION. The shell is subspherical, with a rounded apical horn. Processes numerous, delicate (less than 0·5 μ wide), widening slightly proximally and bifurcating distally to give two small spines. These spines support a very fine membrane which completely surrounds the shell. Apical archaeopyle occasionally visible.

DIMENSIONS. Range of observed specimens : shell diameter 32 (40·0) 52 μ, maximum length of processes 3 (6·0) 8 μ. Number of specimens measured, 13.

REMARKS AND OCCURRENCE. *C. nyei* is common in the Albian and Cenomanian samples from Saskatchewan—samples Sas1084, 967, 890, 835 and 805—and strongly resembles the type material from Australia, of Aptian to Lower Turonian age. However, the angular outline clearly shown in the photographs of the type material was not observed. This species has previously also been recorded from the ? Cenomanian of Arctic Canada by Manum & Cookson. *C. nyei* as described by Cookson & Hughes (1964) has been discussed earlier under *Cleistophaeridium huguonioti*, to which species their forms have been reattributed.

Cyst-Family UNCERTAIN

Genus ***DOROCYSTA*** nov.

DERIVATION OF NAME. Greek, *doros*, leather bag or purse ; *kystis*, bladder or sac—with reference to the purse-like shape of this dinoflagellate cyst.

DIAGNOSIS. Shell small, broad-based with sides converging anteriorly to small apical face. Cingulum typically present and occasionally precingular and postcingular plate boundaries. Small number of processes, simple or branched, usually 4 at anterior and 5 at posterior of shell. Angular archaeopyle commonly present in centre of anterior face.

TYPE SPECIES. *Dorocysta litotes* sp. nov. Upper Cretaceous (Cenomanian) ; France.

REMARKS. The size, shape of the shell and the presence of a cingulum differentiates this genus from all previously described genera.

Dorocysta litotes sp. nov.

(Pl. 5, figs. 6, 7 ; Fig. 2A)

DERIVATION OF NAME. Greek, *litotes*, simple—with reference to the simple nature of the cyst.

DIAGNOSIS. Shell wall smooth or lightly granular. Four anterior and four or five posterior processes, forked medially, occasionally terminating in small bifurcation. Cingulum commonly present and occasionally one or two precingular and postcingular plate boundaries. Angular apical archaeopyle typically present.

HOLOTYPE. B.M.(N.H.) V.51982(4). Chalk, Bureau de Recherches Géologiques at Minières Borehole, Escalles, Pas de Calais at 159 metres depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : shell length 25 μ, width 23 μ, length of processes 9–11 μ, number of processes 9. Range : shell length 19 (22·7) 26 μ, width 13 (18·2) 23 μ. maximum length of processes 8 (13·0) 17 μ. Number of specimens measured, 9.

DESCRIPTION. The anterior face of the shell is rectangular, with a process arising from each corner. In the centre of this face there is a small angular archaeopyle, perhaps formed by the loss of a single apical plate. At the posterior end of the shell there are 4, or more usually 5, processes arranged around the broad base. The cingular and plate boundaries are delimited by low thickenings of the periphragm. The cingulum usually possesses a normal circular perforation (1–2 μ wide) in the centre of one surface.

REMARKS. This distinctive species is entirely different from all previously described forms of dinoflagellate cysts.

OCCURRENCE. Two specimens were recorded from the Lower Cenomanian of Compton Bay (samples CB1 and CB5). The other specimens occurred in the Escalles material—one in sample E159, 2 in sample E201 and 5 in sample E183.

Thus this species, although occurring only very spasmodically, is distributed throughout the Cenomanian of Escalles.

Genus ***ASTROCYSTA*** nov.

DERIVATION OF NAME. Greek, *astron*, star ; *kystis*, sac or cell—with reference to the pentagonal shape of the cyst.

DIAGNOSIS. Proximate cyst of pentagonal shape, composed of two layers, typically in contact. One apical and two antapical horns. Tabulation lightly marked, peridinoid. Cingulum circular and archaeopyle, when seen, intercalary.

TYPE SPECIES. *Palaeoperidinium cretaceum* Pocock 1962. Lower Cretaceous (Barremian) ; Canada.

REMARKS. This genus differs from *Deflandrea* in that the endophragm is, for the most part, in contact with the periphragm. The two membranes may diverge slightly in the extremities of the antapical horns. In contrast, the endophragm in *Deflandrea* typically forms a well defined central body which is in contact with the outer membrane mainly in the cingular region.

Astrocysta cretacea (Pocock)

(Pl. 2, fig. 4)

?1936 *Palaeoperidinium* sp. Deflandre: 31, pl. 4, fig. 7.
1962 *Palaeoperidinium cretaceum* Pocock: 80, pl. 14, figs. 219–221.

EMENDED DIAGNOSIS. Shell pentagonal ; epitract triangular, with broadly conical apical horn ; hypotract bearing two conical antapical horns of unequal length. Outer membranes thin, enclosing inner body of similar shape. Cingulum marked by low ridges. Weak tabulation sometimes developed, marked by low thickenings of periphragm. Outline of anterior intercalary plate 2a usually present, but plate typically in place.

HOLOTYPE. Slide No. 3382–10 (44·8–119·8), Imperial Oil Ltd., Calgary, Alberta. Lower Cretaceous (Barremian) ; Imperial McMurray Test Hole No. 6, at 640 feet depth.

DIMENSIONS. Range of type material 81 (88) 95 μ, breadth 50 (59) 69 μ, length of longer hypotractal horn 12 (19) 25 μ, length of shorter hypotractal horn 4 (8) 10 μ. Range of Saskatchewan specimens : overall length 86 (102·5) 118 μ, overall width 57 (73·0) 82 μ. Number of specimens measured, 8.

DESCRIPTION. The apical and two antapical horns are well developed, the latter differing in size from one another. The outer membrane is extremely thin, wrinkled and often possesses slight thickenings which occasionally bear small pointed spines. These thickenings partially outline a tabulation which resembles the *Peridinium*-type tabulation described by Manum (1963). The cingulum is bordered to two low ridges and is only slightly laevo-rotatory. An archaeopyle has never been observed but the outline of plate 2a is usually present.

REMARKS. Manum & Cookson (1964) describe a similar species, *Palaeoperidinium* cf. *cretaceum*, from the Upper Cretaceous of Arctic Canada. This form differs from *Astrocysta cretacea* by being more circular in outline, possessing a reduced apical horn and two rather small antapical horns of similar size. *A. cretacea* is also rather similar to *Lejeunia tricuspis* O. Wetzel but the latter possesses a more pronounced cingulum.

OCCURRENCE. This species was originally described from the Upper Jurassic of Western Canada by Pocock as *Palaeoperidinium cretaceum.* The specimens here described from Saskatchewan are identical with the type material and occur at only one horizon (Sas 1023) where they are common. This sample is of Lower Cretaceous (Albian) age. *Palaeoperidinium* spec., figured by Deflandre (1936 ; pl. 4, fig. 7) is very similar and may be conspecific.

OTHER SPECIES

The following species are here included in *Astrocysta* on the basis of similarity in structure:

Astrocysta kozlowskii (Górka 1963) comb. nov.

= *Lejeunia kozlowskii* Górka, 1933 Acta palaeont. polon., **8** (1), 41: pl. V, fig. 4.

Astrocysta tricuspis (O. Wetzel 1933) comb. nov.,

= *Peridinium tricuspis* O. Wetzel, 1933 Palaeontographica, **77,** 166: pl. 2, fig. 14.

Cyst-Family **GYMNODINIACEAE** Bergh

Genus ***DINOGYMNIUM*** Evitt, Clarke & Verdier 1967

Dinogymnium sp. A

(Pl. 6, fig. 6)

DESCRIPTION. The shell is more or less fusiform, the hypotract being considerably longer than the epitract. The epitract is conical, with a rounded apex ; the hypotract narrows gradually towards the posterior and terminates abruptly at the truncated apex. The cingulum forms the widest region of the shell and is up to 9 μ wide. The shell bears a moderate number of crests which run longitudinally along the shell and terminate against the cingulum. The crests (up to 3 μ in height) have an undulating outer margin.

FIGURED SPECIMEN. B.M.(N.H.) V.51985(1). Upper Lower Colorado (just above the top of the Viking Formation), International Yarbo Borehole No. 17, Saskatchewan at 1084 feet depth. Lower Cretaceous (Albian).

DIMENSIONS. Single specimen : overall length 68 μ, length of epitract 25 μ, length of hypotract 43 μ, overall width 40 μ.

REMARKS. *Dinogymnium* sp. A. closely resembles *D. nelsonense* Cookson (1956), in particular the specimen figured by Cookson & Eisenack (1958 ; pl. 1, fig. 8). It differs in the possession of well defined crests, having an undulatory outer margin, instead of a longitudinal folding of the shell wall. The specimen figured by Vozzhennikova (1965 ; pl. 49, fig. A) is also similar but possesses folds in place of crests.

Dinogymnium sp. B

(Pl. 6, fig. 3)

DESCRIPTION. The shell is biconical, epitract and hypotract being of similar size, with a pronounced medial cingulum demarcated by two transverse folds of the shell wall. The shell apex is bluntly pointed and the apex rounded. The shell surface is puckered into a small number of ridges which run from the cingulum to the apex or antapex of the shell. These ridges are better developed on the epitract than on the hypotract.

FIGURED SPECIMEN. B.M.(N.H.) V.51979(4). Second White Speckled Shale, International Yarbo Borehole No. 17, Saskatchewan at 835 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Single specimen : overall length 16 μ, overall width 11 μ.

REMARKS. This extremely small form of *Dinogymnium* most closely resembles *D. cretaceum* Deflandre (1934), from the Upper Cretaceous of France, in general appearance. However, the shell length in the type material of the latter ranges from 33 to 42 μ.

Group *ACRITARCHA* Evitt 1963

Subgroup *ACANTHOMORPHITAE* Downie, Evitt & Sarjeant, 1963

Genus ***MICRHYSTRIDIUM*** Deflandre emend. Sarjeant 1966

G. & M. Deflandre (1965) first commented on the shell openings in *Micrhystridium.* Examples possessing openings have been observed in the Cenomanian but are not common—most specimens apparently being entire. There appear to be two principle types of opening, one being slit-like and the other being an irregularly shaped hole. In the former type the slit is generally crescentic (Test-fig. 1H), commonly extending to the centre of the shell. In this case it is probable that the encysted organism forced its way out, the cyst splitting and the two halves gaping apart. It is possible that a crescentic sliver of shell is lost but this is thought to be unlikely. Similar but smaller crescentic or horseshoe shaped slits have been described by Sarjeant (1966), the organism in this case escaping by pushing aside a flap-like portion of the shell wall. In these types of opening the shell is apparently complete, so that after the organism has made its exit the two parts of the shell may spring together again, cellulose being semi-elastic, and the shell would then appear to be unbroken. This is probably the reason why so many specimens appear to be without an opening. It is possible that some or all of these slit-like openings are due to rupture of the cyst during compaction of the sediment.

The second type of opening is an irregular hole, a portion of the shell being definitely missing, as in *M. parvispinum* Deflandre (1946; text-fig. 6). The margin of the opening may be smooth or partially ragged but is never angular, as in dinoflagellate cysts, or circular, as in *Baltisphaeridium.* The formation of such a hole may be by the liberation of a cellulose solvent, but this is purely conjectural. At present it is impossible to say whether or not the opening always occupies the same position on the shell, due to the difficulty in orienting specimens.

Wall (1965) after a thorough study of the Lower Jurassic of England concluded that representatives of the genus *Micrhystridium* appear to favour an inshore and possibly a partly enclosed environment. The inshore environment of these organisms seems to be substantiated by their abundance in the Lower Cenomanian of Fetcham Mill and especially Compton Bay, whereas they decrease in the higher horizons.

Micrhystridium minutispinum Wall

(Pl. 6, fig. 14)

1965 *Micrhystridium minutispinum* Wall: 158, pl. 3, figs. 8–10; pl. 7, fig. 12.

DESCRIPTION. This species possesses a thin-walled, spherical to subpolygonal shell which bears a small number of minute conical spines. An opening, represented as a curved split, was well developed in one specimen.

DIMENSIONS. Range of Cenomanian forms : diameter of shell 6–8 μ, length of spines 0·5–1 μ. Number of specimens measured, 4.

REMARKS. The Cenomanian representatives of this species appear to be identical with the specimens described by Wall from the Lower Jurassic of England. Since this species had not been recorded from the Upper Jurassic or Lower Cretaceous, the Cenomanian specimens may be reworked, may simply have been overlooked in these horizons or may only be morphologically similar and not genetically related.

OCCURRENCE. *M. minutispinum* is a very rare species, only four specimens being located in samples FM770 and FM650 from Fetcham Mill.

Micrhystridium deflandrei Valensi

(Pl. 6; figs 10, 11; Figs. 2J, K)

1948 *Micrhystridium deflandrei* Valensi: 545, text-fig. 5, Nos. 3, 5.
1953 *Micrhystridium deflandrei* Valensi; Valensi: 51, pl. 7, figs. 19, 21, 22.
1955 *Micrhystridium deflandrei* Valensi; Valensi: 589, pl. 3, fig. 18.
1960 *Micrhystridium deflandrei* Valensi; Sarjeant: 400, text-fig. 1q.
1962 *Micrhystridium deflandrei* Valensi; Sarjeant: text-fig. 9e.

DESCRIPTION. The shell of this species is spherical to subspherical and bears

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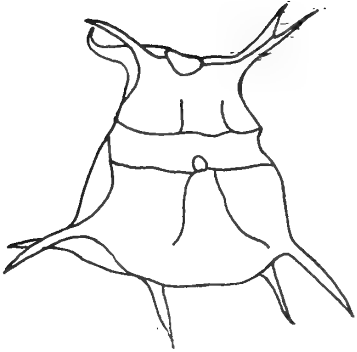
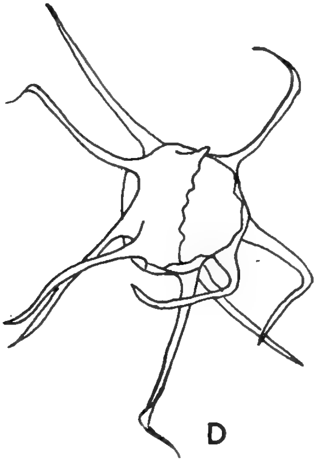
FIG. 2. *Dorocysta litotes* sp. nov. A. Holotype illustrating lightly marked tabulation and cingular perforation (× 1100). *Veryhachium* sp. C. B. Specimen illustrating process arrangement (× 900). *Micrhystridium singulare* Firtion. Specimens C, D and E showing extremes of variation (× 900). *Micrhystridium recurvatum* forma *brevispina* Valensi. F. Specimen with subcircular opening (× 1500). G. Opening to the north (× 1500). *Micrhystridium rigidum* sp. nov. H. Specimen with unusually long spines (× 1500). I. Holotype (× 1500). *Micrhystridium deflandrei* Valensi. Specimens J and K illustrating size variation (× 1500). *Micrhystridium bifidum* sp. nov. L. Holotype (× 1500).



A

B

C



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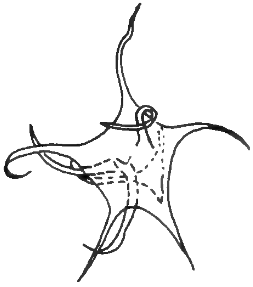

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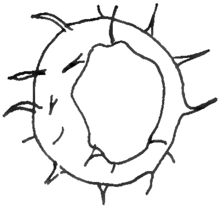

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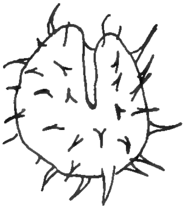

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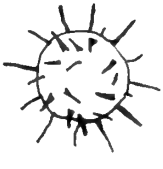

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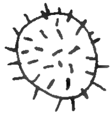

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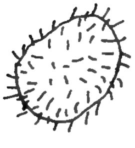

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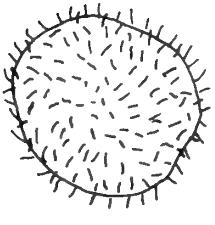

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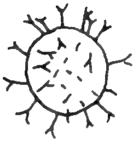


L

a large number of small spines. The spines are very fine but rigid, straight or slightly curved, and are of an equal distance from one another. The length of the spines on a specimen is approximately constant.

DIMENSIONS. Range of Cenomanian forms : diameter of shell 5 (11·6) 16 μ, length of spines 0·75–1 μ. Number of specimens measured, 5.

REMARKS. The Cenomanian examples of *M. deflandrei* are very similar to the type material from the Middle Jurassic (Bathonian) of France. Valensi observed that the spines were arranged in parallel rows so that a lozenge-shaped chequer-work pattern was formed. This alignment is difficult to see in the forms studied and may well be absent. The specimens of *M. deflandrei* illustrated by Sarjeant (1960, 1962) from the Upper Jarassic (Oxfordian) are identical with the observed Cenomanian examples.

OCCURRENCE. *M. deflandrei* was found only in the sample from the Upper Woodbine Formation of Texas and was there fairly common.

Micrhystridium recurvatum forma ***brevispinosa*** Valensi

(Pl. 6, figs. 12, 13; Figs. 2F, G)

1953 *Micrhystridium recurvatum*, forma *brevispinosa* Valensi: 44, pl. 6, figs. 9, 10.

DESCRIPTION. This form possesses a spherical to ovoidal shell, from which arise a moderate number (25–45) of slightly curved, short spines. The length of the spines is between 12 and 25% of the shell diameter. They are rigid and are probably hollow, although this is difficult to tell with any degree of certainty. Most specimens possess a well developed opening. Both forms of opening are present—the subcircular opening and the curved, slit-like opening (Text-figs. 2F, G).

DIMENSIONS. Range of Cenomanian forms : diameter of shell 10·5 (13·7) 21 μ, length of spines 2 (2·7) 3·5 μ. Number of specimens measured, 9.

REMARKS. The Cenomanian specimens cannot be differentiated morphologically from *M. recurvatum* forma *brevispinosa* as described by Valensi from the Middle Jurassic of France.

OCCURRENCE. This is a rare species of all horizons throughout the Cenomanian of England, France and North America.

Micrhystridium cf. ***variabile*** Valensi

(Pl. 7, figs. 1, 2)

DESCRIPTION. This species has an ovoidal to subspherical thin-walled shell, which bears a moderate number of spines (35–50). The spines of *M.* cf. *variabile* are distinctive and characteristic. The proximal one-third to one-half of a spine is columnal ; it widens slightly proximally and to a more marked extent distally. At the distal widening the spine divides into one, two or three fine branches which may occasionally branch again. The spines on a single specimen are extremely variable but the basic bipartite form is always retained.

DIMENSIONS. Range of Cenomanian forms : diameter of shell 6·5–9 μ, length of spines 2–3 μ. Number of specimens measured, 4.

REMARKS. Only four specimens of *M.* cf. *variabile* have been observed, all in the Lower Cenomanian. These appear to be very similar to the type material described by Valensi (1953) from the Middle Jurassic (Bajocian) of France. They are, however, smaller—range for the diameter of the shell given by Valensi is 12 to 18 μ—and the spines are less numerous. As so few specimens were found, the characteristic form of the spines warrants that they should be compared with the species *M. variabile* ; the size difference and stratigraphic separation prevent confident assignation. The scarcity of this species in the Cenomanian and that it only occurs in the lower horizons indicates the possibility that it is a derived form.

OCCURRENCE. *M.* cf. *variabile* has been found in the following lower Cenomanian samples : CB3, E213, and E207. It has not been observed in the North American Cenomanian.

Micrhystridium piliferum Deflandre

(Pl. 7, figs. 3, 4 ; Figs. 1F, G)

1937 *Micrhystridium piliferum* Deflandre: 80, pl. 15, fig. 11.
1947 *Micrhystridium piliferum* Deflandre; Deflandre: text-fig. 1, No. 16.
1952 *Micrhystridium piliferum* Deflandre; Deflandre: text-fig. 20.
1957 *Micrhystridium piliferum* Deflandre; Downie: text-fig. 5e.

DESCRIPTION. The Cenomanian specimens belonging to this species possess smooth, subspherical shells, from which arise fairly numerous, hair-like spines. The latter vary in length between 20 and 50% of the shell diameter. A slit-like opening has been observed in a few specimens (Text-fig. 1G).

DIMENSIONS. Range of Cenomanian forms : diameter of shell 6 (9·6) 16 μ, length of spines 2·5 (3·3) 5 μ. Number of specimens measured, 11.

REMARKS. The observed specimens strongly resemble *M. piliferum* as described by Deflandre from the Upper Cretaceous. This species is based on a single specimen of shell diameter 20 to 22 μ, this being appreciably larger than any of the Cenomanian specimens. The surface of the shell is also finely punctate. It is considered that the Cenomanian specimens would fall into the range of variation of *M. piliferum* and have, therefore, been placed in this species.

M. aff. *fragile*, as described by Brosius & Bitterli (1961) from the Middle Triassic, strongly resembles the Cenomanian specimens of *M. piliferum* and possibly belongs to this species.

OCCURRENCE. *M. piliferum* is a rare species at most horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles.

Micrhystridium inconspicuum (Deflandre)

(Pl. 7, figs. 5–7 ; Figs. 1C, D, E)

1935 *Hystrichosphaera inconspicua* Deflandre : 233, pl. 9, figs. 11, 12.
1937 *Micrhystridium inconspicuum* (Deflandre) Deflandre : 32, pl. 12, figs. 11–13.
1947 *Micrhystridium inconspicuum* (Deflandre) ; Valensi : 817, text-fig. 8.
1947 *Micrhystridium inconspicuum* (Deflandre) ; Deflandre : 6, text-figs. 7, 12.
1952 *Micrhystridium inconspicuum* (Deflandre) ; Deflandre : text-figs. 26–29.
1953 *Micrhystridium inconspicuum* (Deflandre) ; Valensi : pl. 2, fig. 10 ; pl. 7, figs. 14, 15, 20, 23–36 ; pl. 8, figs. 1–5, 7–10, 14, 15, 17–20, 23–29 ; pl. 14, figs. 8–11.
1959 *Micrhystridium inconspicuum* (Deflandre) ; Sarjeant : 340, text-fig. 7b.
1960 *Micrhystridium inconspicuum* (Deflandre) ; Sarjeant 398, pl. 14, fig. 18 ; text-figs. 1f. 1g.
1961 *Micrhystridium inconspicuum* (Deflandre) ; Brosius & Bitterli : 40, pl. 2, figs. 17, 18 ; text-fig. 8.
1961 *Micrhystridium inconspicuum* (Deflandre) ; Sarjeant : 105, pl. 13, fig. 5 ; text-fig. 8f.
1962 *Micrhystridium inconspicuum* (Deflandre) ; Sarjeant : pl. 2, fig. 13, text-fig. 8b.

DESCRIPTION. This species has a spherical to subpolygonal, thin-walled shell from which arise a moderate number of simple, rigid, apparently solid spines (25–45), varying in length from 25 to 50% of the shell diameter. The shell surface is usually smooth; however, in two specimens, a faint reticulation was observed. The spines, apparently arranged haphazardly over the shell surface, may be erect, but are more commonly curved to some extent. Proximally the spines may either arise abruptly or gradually from the shell. In the latter case the spines have wide bases, giving the shell a subpolygonal outline. Distally the spines terminate in a point.

Many of the specimens in the Cenomanian possess a well defined opening which appears as a curved slit extending inwards from the outer margin of the shell (Text-fig. 1E).

DIMENSIONS. Range of Cenomanian specimens : shell diameter 6 (8·1) 13 μ, length of spines 1 (2·9) 5 μ. Number of specimens measured, 18.

REMARKS. Valensi (1953) divided *M. inconspicuum*, as found in the Middle Jurassic of France, into six series based on the relative length and form of the spines and the dimensions of the shell. The Cenomanian specimens appear to belong in the third and fourth series, the remaining variants being absent. It is, however, debatable that all the specimens which Valensi placed in this species actually belong there. The specimens described by Sarjeant (1960, 1961, 1962) of *M. inconspicuum* from the Upper Jurassic (Oxfordian) are extremely similar to the Cenomanian examples.

OCCURRENCE. *M. inconspicuum*, as found in the Cenomanian of England and France, is very similar to the type material described by Deflandre from the Senonian of France. This species is most abundant in the Lower Cenomanian, comprising 65% of the microplankton in one sample (sample CB1), and although it becomes less abundant in the Upper Cenomanian it is always common. It has not been recorded from North America.

Micrhystridium singulare Firtion

(Pl. 6, fig. 9 ; Figs. 2C, D, E)

1952 *Micrhystridium singulare* Firtion : 160, pl. 8, figs. 1, 2.

EMENDED DIAGNOSIS. Shell moderately large, subpolygonal to polygonal, thin-walled. Spines, few in number, hollow with broad bases, the cavity being continuous with that of the shell.

HOLOTYPE. As illustrated by Firtion (1952 ; pl. 8, fig. 1). Place of lodgement unknown. Cenomanian : France.

DIMENSIONS. Holotype : shell diameter 14·5 by 18·5 μ, length of spines 14·6–19·7 μ. Range of Cenomanian specimens : shell diameter 7 (15·4) 21 μ, length of processes 7·5 (17·2) 30 μ. Number of specimens measured, 15.

DESCRIPTION. The shell, being thin-walled, is often distorted giving specimens the appearance of having bilateral symmetry. In undistorted specimens the diamter of the shell is constant in all directions. The spines are typically longer than the shell diameter and may be curved or, more rarely, flexuous. The number of spines present usually varies from 6 to 9, but one specimen with eleven and two specimens with twelve have been observed. An opening, in the form of a large circular hole with an irregular margin, was only observed in one specimen (Text-fig. 2D).

REMARKS AND OCCURRENCE. Firtion appears to have diagnosed this species by describing a single specimen, figured on his pl. 8, fig. 1. The " equatorial pad " described by Firtion is almost certainly a fold in the wall of the shell and, therefore, cannot be used in the orientation of a specimen. As in most other species of *Micrhystridium* a definite line of bilateral symmetry is absent.

Specimens very similar to the examples illustrated by Firtion have been observed at Fetcham Mill, Compton Bay and Escalles. The Text-figure examples show extremes of variation within this species and also the gradation of some specimens to forms belonging to the genus *Veryhachium* Deunff. *M. singulare* is also comparable to *M. stellatum* Deflandre (1945) from the Silurian. However, the spines of the former are constantly less numerous and usually relatively longer.

Micrhystridium alveospinum sp. nov.

(Pl. 7, figs. 8, 9 ; Figs. 1H, I, J)

DERIVATION OF NAME. Latin, *alveus*, cavity or channel, and *spina*, thorn—with reference to the hollow spines or processes.

DIAGNOSIS. Shell spherical to subspherical ; shell wall moderately thick, smooth, bearing small number of processes varying between 60 and 120% of shell diameter. Processes may be rigid, straight or curved, or flexuous ; commonly possessing tubule not connecting with shell cavity, rarely solid. Opening in form of curved split commonly present.

HOLOTYPE. Geol. Surv. Colln. slide PF.3043(2). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 810 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: shell diameter 16 by 16μ, length of processes 12–13μ, number of processes 8. Range: shell diameter 10 (14·9) 21μ, length of processes 7 (13·3) 25μ, number of processes 6 (9) 12. Number of specimens measured, 23.

DESCRIPTION. The shell wall of *M. alveospinum* is smooth and relatively thick (c. 0·75–1·5 μ). It is possible that the wall is two layered but it is very difficult to be certain of this. The processes taper gradually from a slightly widened base to a fine point distally. Occasionally there is a slight constriction or " neck " just above the base of the process—the process being solid at this point (Text-fig. 1I). Thereafter the process may widen slightly and the central part is occupied by a fine tubule. Intermittently the wall of the process may thicken thus obstructing the lumen of the tubule. Solid processes are occasionally present on a specimen possessing mainly hollow ones.

REMARKS. The distinctive nature of the processes distinguishes *M. alveospinum* sp. nov. from all previous described species. *M. lymensis* var. *lymensis* Wall (1965), from the Lower Jurassic, is very similar but possesses narrower processes which are usually solid.

OCCURRENCE. *M. alveospinum* is a rare species and appears to be restricted to the Lower and Middle Cenomanian at Fetcham Mill, Compton Bay and Escalles. Two specimens have been found in sample Sas 1084 from Saskatchewan.

Micrhystridium bifidum sp. nov.

(Pl. 7, figs. 10, 11 ; Fig. 2L)

DERIVATION OF NAME. Latin, *bifidus*, split into two parts, with reference to the forked processes.

DIAGNOSIS. Shell spherical to subspherical ; shell wall smooth bearing moderate number of forked processes, all of approximately equal length. Process length equivalent to between 20 and 30% of shell diameter : these divide distally into two spinelets perpendicular to each other.

HOLOTYPE. Geol. Surv. Colln. slide PF.3994(1). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 690 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : shell diameter 6 by 7 μ, length of processes c. 1·5 μ. Range : shell diameter 6 (7·5) 10 μ, length of processes 1 (1·8) 3 μ. Number of specimens measured, 9.

DESCRIPTION. The processes usually divide producing spinelets of the same length, but occasionally one is longer and may be recurved. In one specimen observed some of the processes do not fork but are capitate, terminating with a bulbous extremity. A slit-like opening is sometimes present.

REMARKS. The simple form of the forked processes distinguishes *M. bifidum* sp. nov. from all other described species of *Micrhystridium*. *M. ambiguum* Deflandre (1937) from the Upper Cretaceous and ?*M. incertum* Deunff (1958) from the Ordovician both possess forked processes, but the two spinelets lay parallel to the shell surface. The former has a shell diameter 20–22 μ and is thus considerably larger than *M. bifidum*. ?*M. incertum* however, appears to possess an outer membrane and is doubtfully a member of this genus.

Occurrence. *M. bifidum* was present in five samples, all from the Upper Cenomanian—samples FM690, 670, 650 and E171, 165. In sample FM690 it is common but rare in the others.

Micrhystridium rigidum sp. nov.

(Pl. 7, figs. 12, 13 ; Figs. 21H, I)

Derivation of name. Latin, *rigidus*, stiff or inflexible—with reference to the rigid nature of the spines.

Diagnosis. Shell spherical to subspherical ; shell wall thin, smooth bearing moderate number of rigid straight spines. Spines equivalent to less than half shell diameter of length (constant on an individual) and regularly spaced.

Holotype. Geol. Surv. Colln. slide PF.3993(1). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey, at 690 feet depth. Upper Cretaceous (Cenomanian).

Dimensions. Holotype : shell diameter 6 by 7 μ, length of spines c. 1 μ. Range : shell diameter 5 (6·8) 7 μ, length of spines 1 (1·8) 3 μ. Number of specimens measured, 10.

Description. The spines are straight and quite sturdy. Proximally they widen only slightly when joining the shell and thereafter are parallel sided. Distally the spines are blunt. This may be especially well seen in specimens possessing longer than average spines (Tex-fig. 1H).

Remarks. The characteristic rod-like spines differentiate *M. rigidum* sp. nov. from all previously described species contained within the genus with the exception of the Carboniferous *M. bacilliferum* Deflandre (1946), the validity of which is doubtful since a drawing was published without a description. In this species, the spines are somewhat similar but are not equally spaced over the surface of the shell.

Occurrence. *M. rigidum* is a rare species in most horizons throughout the Cenomanian of Fetcham Mill. Only one specimen was found in the Compton Bay material and it was not observed from Escalles and North America.

Subgroup *POLYGONOMORPHITAE* Downie, Evitt & Sarjeant 1963

Genus ***VERYHACHIUM*** Deunff emend. Downie & Sarjeant 1963

Remarks. Sarjeant (1967) described for the first time the presence of slit-like openings in *Veryhachium* which are, within a species, always orientated in the same manner with respect to the spines. Such an opening has only occasionally been observed in the Cenomanian specimens studied.

Examples of *Veryhachium* range throughout this stage and are always relatively rare, although they are slightly more common in the lower horizons of the Cenomanian. Wall (1965) deduced that *Veryhachium* favoured an open-sea environment as opposed to the near-shore one of *Micrhystridium*. Because of the rarity of *Veryhachium* in the Cenomanian the above statement cannot be verified or refuted on the evidence available.

Veryhachium reductum Deunff

(Pl. 7, figs. 14, 15 ; Fig. 3C)

1958 *Veryhachium trisculum* var. *reductum* Deunff : 27, pl. 1, figs. 1, 3, 8, 10–12, 14, 15, 17, 22, 23.
1961 *Veryhachium reductum* Deunff ; Jekhowsky : 210, pl. 2, figs. 33–37.
1961 *Veryhachium reductum* Deunff ; Brosius & Bitterli : 36, pl. 1, figs. 3–6 ; text-figs. 1a–e.
1962 *Veryhachium reductum* Deunff ; Cookson & Eisenack : 492, pl. 4, fig. 17.
1963 *Veryhachium reductum* Deunff ; Stockmans & Willière : 455, pl. 1, fig. 16 ; pl. 3, figs. 3, 4 ; text-fig. 8 ; pl. 1, fig. 11? ; text-fig. 9.
1963 *Veryhachium reductum* Deunff ; Downie & Sarjeant : 94.
1964 *Veryhachium reductum* Deunff ; Cookson & Hughes : 56, pl. 11, fig. 8.
1965 *Veryhachium reductum* Deunff ; Wall : 160, pl. 4, fig. 10, 11.

DESCRIPTION. The Cenomanian examples are very similar to the type material from the Ordovician of France. The central body is triangular, slightly inflated, bearing a process at each corner. The processes blend into the central body and may be hollow or partly solid. In length they measure between 75 and 125% of the diameter of the central body. The central body sometimes possesses an elongate slit (Text-fig. 3C). This may be formed by compaction or may possibly be an opening through which the encysted organism escaped.

DIMENSIONS. Range of Cenomanian specimens : diameter of central body (measured from base of process to side opposite) 12 (16.1) 21 μ, length of processes 10 (14·7) 20 μ. Number of specimens measured, 10.

OCCURRENCE. *V. reductum* has been previously recorded from the Ordovician, Silurian, Permo-Trias, Jurassic and Lower Cretaceous by various authors. It, therefore, appears to be a long-ranging morphospecies of little stratigraphic use. In the Cenomanian of Fetcham Mill, Compton Bay and Escalles it is a rare species, found only in the lower horizons.

Veryhachium cf. ***reductum*** Deunff

(Pl. 6, fig. 16 ; Figs. 3D, E)

DESCRIPTION. Two specimens were closely similar to *V. reductum* Deunff but possessed slightly elongate central bodies, thus imparting a bilateral symmetry to the cyst.

DIMENSIONS. Text-fig. 3D : slide PF3040 : diameter of central body 12 by 16 μ, maximum length of processes 10 μ. Text-fig. 3E : slide PF3040 : diameter of central body 12 by 15 μ, maximum length of processes 18 μ.

REMARKS. *V.* cf. *reductum* differs from *V. reductum* only by the possession of a slightly elongate central body. It appears to be intermediate in morphology between *V. reductum* and *Domasia liassica* Wall (1965 ; pl. 5, figs. 2, 3).

Occurrence. Both specimens of *V.* cf. *reductum* were found in sample FM670 from the Upper Cenomanian of Fetcham Mill.

Veryhachium reductum forma ***breve*** Jekhowsky

(Pl. 7, fig. 17 ; Fig. 3J)

1957 Hystrichospheres, Kara-Murza : 7, pl. 1, figs. 31, 34, 35.
1961 *Veryhachium reductum* forma *breve* Jekhowsky : 212, pl. 2, figs. 38–44.

Description. A form of *V. reductum* possessing reduced processes.

Dimensions. Figured specimen (Pl. 7, fig. 17) : diameter of central body 21 μ, length of processes 2–5 μ.

Remarks. Only one specimen of *V. reductum* forma *breve* was found, this in sample E201 from Escalles. The test is poorly preserved, appearing to have been oxidised, and certainly differs in preservation from other microplankton in the same sample, thus indicating that the specimen is derived.

Veryhachium cf. ***hyalodermum*** Cookson

(Pl. 7, fig. 18 ; Figs. 3A, B)

Description. A form of *Veryhachium* possessing a large, slightly inflated central body, from which radiate five or six hollow, curved processes. The processes are longer than the diameter of the central body, have broad bases and taper distally to a fine point. Although the test wall is of moderate thickness all specimens have been broken or distorted to some extent. One specimen (Text-fig. 3B) is unusual in that it possesses an hour-glass shaped central body from which arise six processes.

Dimensions. Range of observed specimens : diameter of central body c. 20–29 μ, maximum length of processes 23–37 μ.

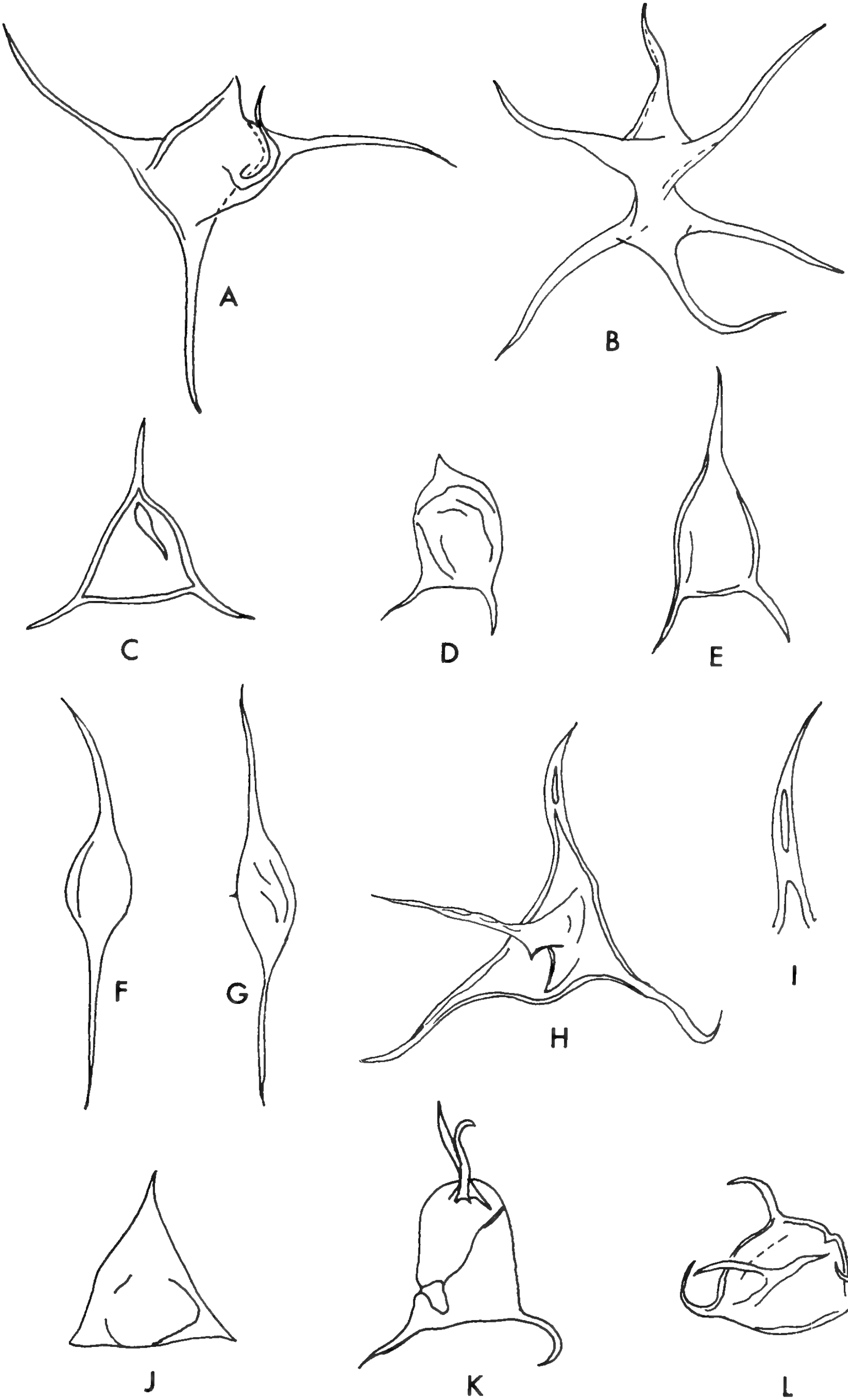
Remarks. *V. eisenacki* Deunff (1961), from the Devonian, is of similar appearance, but the wall is microperforate and the processes are closed proximally. The forms described above are most closely related to *V. hyalodermum* from the Albian–?Turonian of Australia, although this species according to Cookson possesses only four processes, fewer than in the material studied here.

Occurrence. *V.* cf.*hyalodermum* is a rare species found mainly at the base of the Cenomanian at Fetcham Mill and Compton Bay, only one specimen being found at a higher horizon—sample FM730.

Veryhachium irregulare forma ***subtetraedron*** Jekhowsky

(Pl. 8, fig. 1 ; Fig. 3L)

1961 ? *Veryhachium irregulare* forma *subtetraedron* Jekhowsky : 208, pl. 1, figs. 4–9.
1963 *Veryhachium irregulare* forma *subtetraedron* Jekhowsky ; Downie & Sarjeant : 94.



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DESCRIPTION. The form of the central body is tetrahedral and inflated. The corners of the tetrahedron give rise to hollow, rather slender, curved processes.

DIMENSIONS. Figured specimen (Pl. 8, fig. 1) : diameter of central body 16 by 20 μ, length of processes c. 10 μ, width of process at base c. 1·5 μ.

REMARKS. One specimen attributable to this species was found in the Cenomanian of Fetcham Mill. The processes appear to be slightly finer than those seen in the type material from the Permo-Trias of Yugoslavia, but in all other respects it is very similar.

Veryhachium rhomboidium Downie

(Pl. 8, figs. 2, 3)

1959 *Veryhachium rhomboidium* Downie : 62, pl. 12, fig. 10.
1960 *Veryhachium rhomboidium* Downie ; Stockmans & Willière : 2, pl. 1, fig. 9 ; pl. 2, fig. 23.
1963 *Veryhachium rhomboidium* Downie ; Downie & Sarjeant : 94.
1963 *Veryhachium rhomboidium* Downie ; Wall & Downie : 781, pl. 114, figs. 1–3.
1963 *Veryhachium rhomboidium* Downie ; Downie : 636.

DESCRIPTION. Specimens possess a square to rectangular central body which bears six to nine hollow processes. There is always one spine situated at each end of the four corners, the subsidiary processes being arranged fairly symmetrically on the medial region of the central body. The processes are fairly sturdy and measure between 60 and 120% of the smaller central body diameter in length.

DIMENSIONS. Range of observed specimens : diameter of central body 14 (19·4) 25 μ, length of processes 13 (14·6) 19 μ. Number of specimens measured, 7.

REMARKS. The Cenomanian examples of this species appear to be more comparable to the type material from the Silurian than to the Permian specimens described by Downie (1963). This is because the Permian forms possess very slender processes which are usually flexuous.

OCCURRENCE. *V. rhomboidium* has been described from the Silurian, Devonian and Permian, and is here recorded for the first time from the Mesozoic. It is a very sparsely distributed species in the Cenomanian and has been recorded from the following samples : FM730, CB1, E213 and also from sample Sas1084 (Albian).

FIG. 3. *Veryhachium* cf. *hyalodermum* Cookson. A. (×900). B. " Hour-glass " shaped specimen (×900). *Veryhachium reductum* Deunff. C. Specimen possessing an elongate opening (×600). *Veryhachium* cf. *reductum* Deunff. D. Specimen with short " apical " process (×1000). E. (×1000). *Leiofusa* cf. *jurassica* Cookson & Eisenack. F. (×900). G. Specimen with reduced medial process (×900). *Veryhachium metum* sp. nov. H. Holotype (×900). I. Enlargement of spine to show spinal cavity (×1500). *Veryhachium reductum* forma *breva* Jekhowsky. J. (×900). *Veryhachium* sp. A., K. (×900). *Veryhachium irregulare* forma *subtetraedron* Jekhowsky. L. (×900).

Veryhachium metum sp. nov.

(Pl. 8, figs. 5, 6 ; Figs. 3H, I)

Derivation of name. Latin, *meta*, conical column at the end of the Rome circus —with reference to the form of the processes.

Diagnosis. Central body tetrahedral slightly inflated. Four simple processes arise from corners of central body ; these are of moderate length, always partly solid, but hollow proximally.

Holotype. Geol. Surv. Colln. Slide PF. 3045(2). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 840 feet depth. Upper Cretaceous (Cenomanian).

Dimensions. Holotype : diameter of central body 15 μ, length of processes 23–25 μ. Range : diameter of central body 14 (15·9) 18 μ, length of processes 11 (18·3) 25 μ. Number of specimens measured, 9.

Description. All the specimens have been compressed flat, so that three processes now lie in one plane and the fourth is bent over into a slightly higher or lower plane. The processes are solid for the distal one-half to three-quarters of their length, there sometimes being a fine tubule in this region (Text-fig. 3I). The length of the processes is usually greater than the diameter of the central body.

Remarks. The form of the central body and the nature of the processes make *V. metum* sp. nov. an easily identifiable species. *V. hyalodermum* Cookson (1956) and *V. europaeum* Stockmans & Willière (1960) are similar but possess processes that are entirely hollow. At present it is considered unnecessary to erect a new genus to accommodate those forms possessing processes which are partly solid.

Occurrence. *V. metum* is found sparsely throughout the Cenomanian of Fetcham Mill and Compton Bay and is slightly more common in the lower horizons. At Escalles specimens have only been obtained from the lowermost sample (E213).

Veryhachium sp. A

(Pl. 8, fig. 4 ; Fig. 3K)

Description. The central body is elongate—triangular and bears four processes —one arising from each corner of the base of the triangular central body and one on either side of the apex (posterior). The processes are slender with fairly narrow bases and appear to be hollow.

Dimensions. Figured specimen (Pl. 8, fig. 4): diameter of central body 14 by 20 μ, length of processes c. 14 μ.

Remarks. The shape of the central body is very similar to *V. delmeri* and *V. limaciforme* described by Stockmans & Willière (1963) from the Silurian. However, these species only possess one posterior process. *Veryhachium*? sp. Wall (1965) is also similar but possesses processes with broad bases. Wall infers that this form may be a transitional type between *Veryhachium* and *Dormasia liassica* Wall (1965).

One specimen only of this distinctive form was recorded in the material examined and this was from Compton Bay. The test wall is lightly pitted, indicating an unusual amount of oxidation and suggesting the possibility that this specimen is derived.

Veryhachium sp. B

(Pl. 7, fig. 19)

DESCRIPTION. Three specimens have been recorded possessing sub-polygonal central bodies and eight processes. The processes are hollow, usually slightly curved, have wide bases which blend into the central body and are regularly arranged.

DIMENSIONS. Diameter of central body 17–24 μ, length of processes 23–25 μ.

REMARKS. The three specimens described above lie at the transition between two genera, *Micrhystridium* and *Veryhachium*. They fall just within the size limit of *Micrhystridium* and are similar to some forms described as *M. stellatum* Deflandre (1942). However, they are referable to *Veryhachium* because of the broad bases of the processes, which give the central body a subpolygonal outline, and the processes are relatively low in number.

OCCURRENCE. The three specimens are from samples FM690 (Fetcham Mill) and E213 (Escalles).

Veryhachium sp. C

(Pl. 8, fig. 10 ; Fig. 2B)

DESCRIPTION. A single specimen possessing eleven processes was recorded from the lower Cenomanian of Escalles. Five of the processes lie on a medial plane at the corners of a pentagon, the remaining processes being arranged symmetrically three above and three below this plane.

DIMENSIONS. Diameter of central body 17 by 17 μ, length of processes 10–13 μ.

REMARKS. *Veryhachium* sp. C, like *Veryhachium* sp. B, is similar to *Micrhystridium stellatum* Deflandre but is considered to belong to *Veryhachium* because of the broad bases to the processes which give the central body a subpolygonal outline.

OCCURRENCE. The single specimen was obtained from sample E213, from Escalles.

Genus ***TUBULOSPINA*** nov.

DERIVATION OF NAME. Latin, *tubulus*, tubular ; *spina*, thorn, or spine—with reference to the tubular nature of the processes.

DIAGNOSIS. Acritarchs with triangular, tetragonal or polygonal tests, with corners drawn out into tapering processes. Small number of subsidiary processes (usually 1–6) symmetrically arranged on test surface. Spines simple, closed both distally and proximally and typically hollow.

TYPE SPECIES. *Tubulospina oblongata* sp. nov. Upper Cretaceous (Cenomanian); England.

REMARKS. This genus has been erected for forms differing from *Veryhachium* principally in that they possess processes which are closed proximally. The basal portion of the process wall is greatly thickened so forming a " plug " which separates the process cavity from the central body cavity.

Tubulospina oblongata sp. nov.

(Pl. 8, figs. 7–9 ; Fig. 4)

DERIVATION OF NAME. Latin, *oblongus*, longer than broad—with reference to the rectangular shape of the central body.

DIAGNOSIS. Central body rectangular, smooth and thick-walled. Each corner gives rise to one process and there are, in addition, a small number of symmetrically arranged subsidiary processes. Processes simple, stout and usually hollow.

HOLOTYPE. B.M.(N.H.) V.51984(1). Chalk, Compton Bay, Isle of Wight at 44 feet above the base of the Cenomanian. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : diameter of central body 22 by 27 μ, length of processes c. 30 μ, number of processes 7. Range : diameter of central body 13 (20·9) 32 μ, length of processes 14 (26·6) 40 μ, number of processes 5 (7) 10. Number of specimens measured, 17.

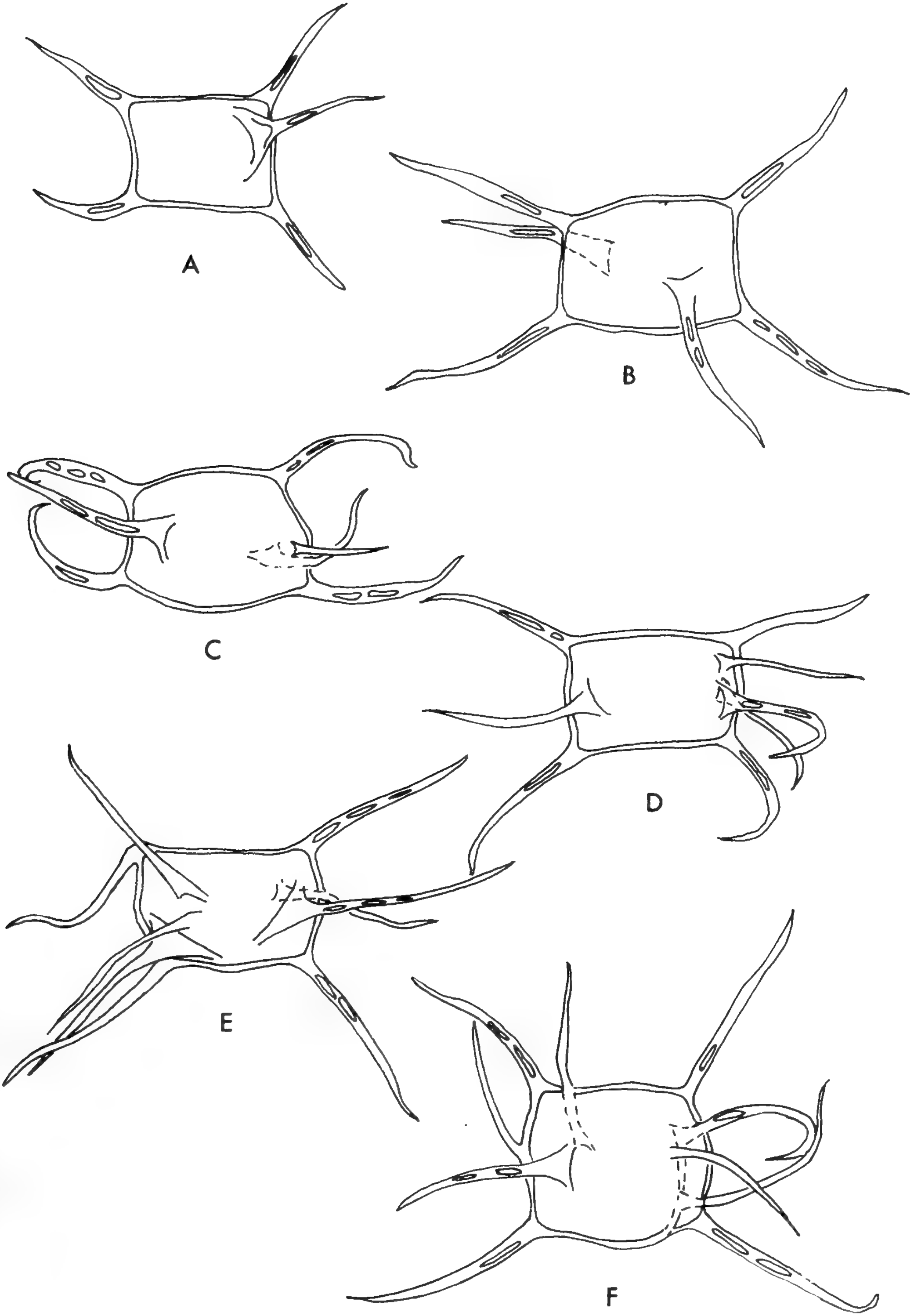
DESCRIPTION. The majority of processes possess a fine tabule which is not in connection with the central body cavity. At the base of a process its wall is greatly thickened, so forming a basal " plug ". The subsidiary processes are symmetrically arranged on the surface of the central body ; that is they are never concentrated on one side or at one end of the central body but are distributed so that they balance one another. The number of subsidiary spines range from one to six and their arrangement has been shown on a series of drawings (Text-figs. 4A–F).

REMARKS. The form of the central body, the thick wall and the structure of the processes easily differentiates *T. oblongata* sp. nov, from all previously described species. The most similar species are *V. rhomboidium* and *Acanthodiacrodium sukatschevi* Timofeyev (1959), both from the Palaeozoic. These species possess a rectangular central body which is, however, thin-walled and gives rise to hollow processes.

Micrhystridium (?) sp. C, illustrated by Balteş (1963) from the Albian, is rather similar, although smaller, and may belong to *T. oblongata.*

OCCURRENCE. *T. oblongata* is a rare species found throughout the Cenomanian of Fetcham Mill, but only in the Lower Cenomanian of Compton Bay and Escalles. It has not been observed in the North American material studied.

FIG. 4. *Tubulospina oblongata* sp. nov. This figure illustrates a series of specimens with a progressive increase in the number of subsidiary spines. A. 1 subsidiary spine (×900). B. 2 subsidiary spines (×900). C. 3 subsidiary spines (×900). D. 4 subsidiary spines (×900). E. 5 subsidiary spines (×900). F. 6 subsidiary spines (×900).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Subgroup *NETROMORPHITAE* Downie, Evitt & Sarjeant 1963

Genus ***LEIOFUSA*** Eisenack 1938

REMARKS. The genus *Leiofusa* was originally diagnosed only for spindle-shaped acritarchs most having a ratio of overall length to central body length of 1–1·5 : 1. In these forms it is difficult to differentiate the central body from the processes accurately. Wall (1965), in a study of *L. jurassica*, found all gradations from the spindle-shaped forms to forms with a distinct central body. These latter forms only are found in the Cenomanian and they appear to be a simple type of *Veryhachium* bearing only two processes. The occasional presence of a third reduced process on the central body concurs with this idea.

Leiofusa cf. ***jurassica*** Cookson & Eisenack

(Pl. 8, fig. 11 ; Pl. 9, fig. 1 ; Figs. 3F, G)

DESCRIPTION. This species possesses a small elongate central body with simple, elongate processes extending from each pole. Ratio of overall length to length of central body is 2–3 : 1. In two specimens a small spine (2–3 μ long) was seen to arise from the middle of the central body (Text-fig. 3F).

DIMENSIONS. Range of observed specimens : overall length 35 (59·2) 76 μ, length of central body 15 (20·3) 25 μ, breadth of central body 10 (11·9) 14 μ. Number of specimens measured, 10.

REMARKS. *L.* cf. *jurassica* possesses a relatively short central body when compared with the type material from the Upper Jurassic of Australia and for this reason it is only comparable with *L. jurassica.*

Wall (1965) figures specimens of *L. juassica* (pl. 5, figs. 10, 11) from the Lower Jurassic of England which appear to be very similar to the Cenomanian forms, the central body being relatively small. He also shows that there is in the Lower Jurassic a complete gradation from this form to the spindle-shaped forms of the type material. However, such a gradation was not observed in the Cenomanian.

OCCURRENCE. *L.* cf. *jurassica* is fairly common in samples FM840 and CB1 from the basal Cenomanian; only two other examples being found and these in samples FM670.

Subgroup *HERKOMORPHITAE* Downie, Evitt & Sarjeant 1963

Genus ***CYMATIOSPHAERA*** O. Wetzel emend. Deflandre 1954

Cymatiosphaera radiata O. Wetzel

(Pl. 8, figs. 12, 13)

1932 *Cymatiosphaera radiata* O. Wetzel : pl. 2, fig. 13.
1933 *Cymatiosphaera radiata* O. Wetzel : 27, pl. 4, fig. 8.
1960 *Cymatiosphaera radiata* O. Wetzel ; Cookson & Eisenack : 9, pl. 2, figs. 21, 22.

DESCRIPTION. The shell is spherical to subspherical, smooth walled and bears a network of fairly high fine membranes which delimit subpolygonal areas. The membranes are supported by radial columns which may bifurcate distally. There appears to be some variation in the density of the membranes and further study may lead to a subdivision using this as a basis. However, as yet, this is not possible.

DIMENSIONS. Range of observed specimens : shell diameter 13 (22·1) 38 μ, height of membranes 3 (8·1) 11 μ. Number of specimens measured, 18.

REMARKS. *C. radiata* was first described from the Upper Chalk of Germany and later from the Albian and Cenomanian of Australia by Cookson & Eisenack. All forms are very similar and of small size.

OCCURRENCE. *C. radiata* is infrequent at most horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles, but has not been recorded in the North American samples.

Cymatiosphaera costata sp. nov.

(Pl. 9, figs. 2, 3)

DERIVATION OF NAME. Latin, *costa*, rib—with reference to the low membranes covering the shell surface.

DIAGNOSIS. Shell spherical with thick smooth wall, its surface divided into number of subpolygonal areas by low membranes supported at corners of polygons by spines not extending beyond membrane. Membranes undulatory or wavy in plan view.

HOLOTYPE. B.M.(N.H.) V.51988(4). Second White Speckled Shale, International Yarbo Borehole No. 17, Saskatchewan at 835 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : shell diameter 17 μ. Range: shell diameter 9 (14·1) 17 μ. Number of specimens measured, 7.

DESCRIPTION. The shell wall is relatively thick, 0·5–1 μ ; its surface being divided by fine membranes into approximately 25 subpolygonal areas, each about 4–5 μ in width. These membranes are weak and only stand perpendicular to the shell surface at the corners of the polygons where they are supported by the small spines. Between the spines they lie at an angle to the surface and in plan view appear to be wavy. The spines are short (about 1 μ in height) and appear to be hollow. Some specimens are split, but a pylome has not been observed.

REMARKS. *C. costata* sp. nov. most closely resembles *C. parva* Sarjeant (1959) from the Middle Jurassic of England. However, the membranes of the latter are straight and never undulatory in plan view. *C. costata* is also very similar to a Canadian Jurassic form, described by Pocock (1964) in an unpublished report under the name of *Dictyotidium eastendense*, but the former possesses fewer delimited areas.

OCCURRENCE. This distinctive species is common in three samples from Saskatchewan, samples Sas890, 835 and 805, of Cenomanian age. It has not been recorded elsewhere.

Cymatiosphaera asarota sp. nov.

(Pl. 9, figs. 6, 7)

DERIVATION OF NAME. Latin, *asarotum*, floor laid in mosaic—with reference to the subpolygonal fields covering the shell surface.

DIAGNOSIS. Shell large, spherical to subspherical ; shell wall smooth, thin. Shell surface divided into number of subpolygonal areas by low stout ridges, rarely fine membranes. Ridges undulatory in plan view.

HOLOTYPE. B.M.(N.H.) V.51983(1). Top of Second White Speckled Shale, International Yarbo Borehole No. 17, Saskatchewan at 805 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : shell diameter 46 μ. Range : shell diameter 44 (47·8) 53 μ. Number of specimens measured, 7.

DESCRIPTION. The shell is subdivided into approximately 30–40 areas by stout ridges (c. 1 μ in width and 1·5 μ in height) which undulate over the shell surface. Occasionally fine membranes replace the ridges. The areas delimited are subpolygonal and fit together rather like pieces of a jig-saw puzzle. Shell openings have not been observed.

REMARKS. *C. asarota* sp. nov. is very similar to *C. costata* in general appearance but is considerably larger and ridges, rather than membranes, typically delimit the shell areas. *C. asarota* also resembles *Dictyotidium eastendense* (Pocock 1964, unpublished), but possesses fewer delimited areas.

OCCURRENCE. *C. asarota* is common in two Cenomanian samples (Sas835 and 805) from Saskatchewan.

Cymatiosphaera conopa sp. nov.

(Pl. 9, figs. 4, 5)

DERIVATION OF NAME. Latin, *conopium*, mosquito-net—with reference to the net-like pattern on the shell surface.

DIAGNOSIS. Shell spherical to subspherical ; shell wall smooth, thick. Shell surface subdivided by network of low ridges, rarely membranes, into large number of regular polygonal areas. Short, hollow spines situated at corners of polygons.

HOLOTYPE. B.M.(N.H.) V.51983(2). Top of Second White Speckled Shale, International Yarbo Borehole No. 17, Saskatchewan at 805 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype : shell diameter 26 by 27 μ. Range : shell diameter 26–34 μ. Number of specimens measured, 4.

DESCRIPTION. The shell wall is relatively thick, approximately 1·5 μ. The shell surface bears a polygonal network of low ridges, usually under 0·5 μ in height, with low (c. 1 μ) hollow spines situated at the corners of the polygons. The latter are usually perfectly symmetrical, being 5, 6 or 7 sided, of approximately 3 μ in width and 80–100 in number. Shell openings have not been observed.

REMARKS. *C. conopa* sp. nov. is easily distinguished from all previously described species by its large number of symmetrical polygons and the lack of a papilla in the centre of the polygons.

OCCURRENCE. This is a fairly common species found in only one sample Sas805 from Saskatchewan.

Subgroup *PTEROMORPHITAE* Downie, Evitt & Sarjeant 1963

Genus ***PTEROSPERMOPSIS*** O. Wetzel 1952

REMARKS. Members of this genus have only been recorded from the Saskatchewan material.

Pterospermopsis cf. ***helios*** Sarjeant

(Pl. 9, figs. 8, 9)

DESCRIPTION. The subspherical central body is surrounded by a circular equatorial membrane. Both the central body and the equatorial membrane are smooth. The membrane is traversed radially by a small number of folds and thickenings.

DIMENSIONS. Range of observed specimens : diameter of central body 11 (22·7) 34 μ, overall diameter 24 (39·4) 51 μ. Number of specimens measured, 8.

REMARKS. *P.* cf. *helios* is considerably larger than *P. helios* Sarjeant (1959)—overall diameter 25 μ—and the folds and thickenings in the equatorial membrane are not as regularly positioned. The outer margin of the membrane is generally entire ; it is occasionally seen to be puckered due to folding. This entire margin indicates that the majority of the radial markings are thickenings, and probably to support the membrane.

OCCURRENCE. *P.* cf. *helios* is an infrequent to common species in all the samples from Saskatchewan.

Subgroup *DINETROMORPHITAE* Downie, Evitt & Sarjeant 1963

Genus ***DIPLOTESTA*** Cookson & Eisenack 1960

REMARKS. Definite dinoflagellate features are absent in this genus which is therefore treated as an acritarch until further systematic evidence becomes available.

Diplotesta angelica Cookson & Hughes

(Pl. 9, figs. 10–12)

1964 *Diplotesta angelica* Cookson & Hughes : 56, pl. 11, figs. 1–5.
1964 *Diplotesta angelica* Cookson & Hughes ; Manum & Cookson : 25, pl. 5, fig. 7.

DESCRIPTION. The shell is thin-walled and elongate, one side being strongly convex, the other being usually weakly concave or more rarely straight. The shell narrows towards both ends, terminating with rounded apices. One apex is typically open. The margin of the opening is irregular and the operculum may bear a few small spines (pl. 9, fig. 10). The inner body is ovoidal in shape and stains more easily than the outer shell wall, probably indicating that it is slightly thicker. It appears to be entire.

DIMENSIONS. Range of observed specimens : shell length 50 (68·2) 104 μ, width 31 (36·7) 48 μ. Number of specimens measured, 13.

REMARKS. The Cenomanian specimens are identical with the type material from the Upper Gault, Cambridge Greensand and Chalk Marl (Upper Albian–Lower Cenomanian) of England.

OCCURRENCE. *D. angelica* is a rare species occurring at most horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. Two specimens have also been recorded in the Cenomanian from Saskatchewan (samples Sas835 and 805).

Class *CHLOROPHYCEAE*

Order CHLOROCOCCALES?

Family **UNCERTAIN**

Genus ***PALAMBAGES*** O. Wetzel 1961

REMARKS. O. Wetzel (1933) gave the first description of these organisms under the name of " Morulosae " comparing them with certain colonial algae and with the egg-balls of certain planktonic crustaceans. Manum & Cookson (1964) fully reviewed the *Palambages* and concluded that they represented green algal colonies. They drew attention to the fact that these organisms increased their cell number by factors of 2, there being 2, 4, 8, 16, 32 . . . etc., cells in a colony. They found *Palambages* colonies possessing approximately 16, 32, 64 and 128 cells, thus indicating that increase by a factor of 2 also occurs in this fossil group. Forms possessing 8 and approximately 64 and 128 cells have been observed in the Albian and Cenomanian samples examined. They also suggested, probably correctly, that the number of cells per colony should not be used as a distinction between species. Size of an individual cell also appears to be quite variable. It was considered, in view of this, that the surface ornamentation provided the most useful distinguishing character.

Palambages Form A Manum & Cookson

(Pl. 10, figs. 1–3)

1964 *Palambages* Form A Manum & Cookson : 24, pl. 7, figs. 3–6.

DESCRIPTION. The colonies are always flattened and the individual cells distorted. (The original shape of the colonies and individual cells was probably spherical.) The maximum cell diameter ranges from 15 to 35 μ and the entire colony measuring from 44 to 119 μ in diameter. In the colonies possessing a small number of cells, the latter tend to be larger. The cell wall is typically smooth, only one specimen being slightly granular. Most of the cells are irregularly split.

Remarks. The specimens described here all appear to belong to *Palambages* Form A described by Manum & Cookson. This form is characterized by possessing cells 20–30 μ in diameter and having a smooth to lightly granular shell wall. Only two colonies observed are composed of individual cells of greater diameter than 20 μ, these being approximately 28 and 35 μ in diameter.

Occurrence. *Palambages* Form A is a rare species occurring in four samples from Saskatchewan—Sas1084 and 967 from the Albian, and Sas835 and 805 from the Cenomanian.

Palambages Form D nov.

(Pl. 10, figs. 4, 5)

Description. One specimen has been observed possessing 8 ovoidal cells of diameter 16 to 21 μ. The cell walls are smooth. Three cells in the colony are seen each to possess a single small, hollow, thorn-like spine opposite the larger axis of the cell. All the cells are split irregularly.

Figured specimen. Geol. Surv. Colln. slide PF.3046(3). Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 840 feet depth. Upper Cretaceous (Cenomanian).

Dimensions. Diameter of individual cells 16 to 21 μ ; diameter of colony 39 by 47 μ.

Remarks. The shape of the colony is typical of all *Palambages*. However, the presence of spines has not been observed previously and differentiates this form from all previously described types.

Unidentifiable Algal Remains

(Pl. 10, figs. 8–10)

Description. In a number of samples, from Devon, Hunstanton and Speeton, simple algal cells are the only organic constituent present. They may be rare or exceedingly common as in the highest sample from Hunstanton (H3). In the samples containing abundant dinoflagellate cysts, such as in the normal Cenomanian Chalk, these algal remains are absent.

The algal cells, although typically spherical to subspherical, may be variously shaped. Some have small daughter cells budding from the larger parent cell (Pl. 10, fig. 9), and others seem to be in the act of division (Pl. 10, fig. 10). They possess relatively thick, granular walls and are stained red by safranin.

Dimensions. Examples from the Hunstanton sample H3 : cell diameter 12–46 μ.

II. CONCLUSIONS

1. *Fetcham Mill, Compton Bay and Escalles*

The chalk samples analysed from the above three localities are entirely fine-grained, except for the ones obtained from the very basal horizons of the Cenomanian. All samples were productive and yielded well preserved and varied microfloral assemblages. Thus, during the Cenomanian, the chalk sea environment at these localities was a favourable one for the deposition and for the preservation of organic-shelled microfossils.

At each locality the percentage of microplankton increases at the expense of the miospores, from the basal Cenomanian towards the top of this stage. In the topmost samples the miospore content is below 1% at all three localities, whereas in the lowest sample from Compton Bay it is 20%, 12% at Fetcham Mill and 10% at Escalles. The Upper Greensand sample (FM 886) contains 45% miospores and the Turonian sample (FM 520) less than 1%. This percentage decrease of terrestrially-derived miospores in comparison with the marine microplankton as the succession is ascended, indicates an increase in the distance between the position of sedimentation and the positions of the landmasses during the lower part of the Cenomanian. Other factors possibly involved are changes in terrestrial vegetation, and in direction of prevailing winds and marine currents.

Foraminiferal shell linings (pl. 10, fig. 5–7), biserial and trochoid, are present only in samples from Escalles. They are common in all the samples from this locality except the lower three (E.213, 207 and 201), where they are absent. They have been observed in palynological preparations by a number of authors—for example McKee, Chronic and Leopold (1959) in lagoonal deposits, Muller (1959) in deltaic sediments and Sarjeant (1960, 1961, 1962) from the Upper Jurassic and Lower Cretaceous of England—and appear to be very cosmopolitan in distribution. The reason for their absence from Fetcham Mill, Compton Bay, and also from Texas and Saskatchewan, is not known at present, but it must be related to an environmental factor.

Both quantitative and qualitative analyses were performed on all the assemblages obtained from Fetcham Mill, Compton Bay and Escalles samples.

The percentage abundance of each species in the microplankton assemblage was calculated for each sample from the above three localities. The majority of the assemblages are dominated by a small number of forms—four forms together usually composing 75% or more of the assemblage. Thus, only the percentage abundance of these four forms can be compared and contrasted with any degree of accuracy. The remaining species in each assemblage, sometimes as many as 50, each usually form 1% or less of the assemblage and cannot be compared quantitatively. The four forms that are able to be compared quantitatively are *Palaeohystrichophora infusorioides*, *Cleistosphaeridium huguonioti*, *Micrhystridium* species (predominantly *M. inconspicuum*) and the *Hystrichosphaera ramosa* group.

P. infusorioides is by far the most abundant species at the majority of horizons, as indicated in text-fig. 5. In only two samples is this not so—the lowest Cenomanian samples from Fetcham Mill and Compton Bay (samples FM840 and CB 1)—in which it is very rare. The lowermost sample from Escalles (sample E 213) is not located at the base of the Cenomanian and the assemblage contains 16% of this species. However, in sample E 213 the percentage abundance of *P. infusorioides* appears to be declining towards the base of this stage and it is considered probably that at the base of the Cenomanian at this locality this species would be very rare. Thus at the base of this stage in southern England, and probably northern France, *P. infusorioides* is extremely rare and, thereafter, in higher horizons rapidly becomes very common. The appearance of this distinctive species in this region is therefore considered to coincide with the base of the Upper Cretaceous (Cenomanian).

The samples analysed were taken at 15–20 ft. intervals. Thus the correlation of the peaks and troughs shown on the percentage abundance graphs may not be more accurate than within 10 ft.

With reference of the graph of *P. infusorioides*, there is a prominent peak (peak 1) near the top of the *varians* Zone which is present at each locality. This peak probably marks similar stratigraphic horizons and probably indicates that samples CB 7, FM 750 and E 195 are of similar age. The percentage of *P. infusorioides* in these samples is respectively 56, 58 and 79. Two more peaks (peaks 2 and 3) may also be of stratigraphic value.

Cleistosphaeridium huguonioti is a common species throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles except for the topmost samples from Compton Bay (CB 21), where it is rare, and Escalles (E.153), where it has not been recorded. It is absent from Turonian sample FM 520. The percentage abundance graphs of this species (including its variety *pertusum*) for Compton Bay and Escalles appear to be remarkably similar (text-fig. 6), but correlation with Fetcham Mill is more problematical. Prominent peaks (peak 1) occur in the Compton Bay and Escalles graphs at the *varians/subglobosus* zonal boundary. The samples at these horizons are CB 9 (26% *C. huguonioti*) and E 183 (35·5%). Less obvious markers may be indicated by peak 2 and plateau 3.

The percentage abundance of the varieties of *Hystrichosphaera ramosa* were plotted graphically but correlation between the three localities was not possible.

Dinoflagellate cysts outnumber acritarch remains in all samples except one, the lowest sample from Compton Bay (CB 1), where the latter total 69% of the microplankton assemblage. *Micrhystridium* is by far the most abundant acritarch and the percentage abundance for each sample is shown in text-fig. 7.

In the lowest sample from Compton Bay (CB 1)the *Micrhystridium* percentage is 65 ; in the remainder of the *varians* Zone it varies between 14 and 20%. This genus in the *subglobosus* Zone at Compton Bay undergoes a rapid decline and varies between under 1 and 4%. This distribution may indicate that *Micrhystridium* favour the relatively near shore, and perhaps shallow water environment of the *varians* Zone, or that dinoflagellates were unsuited to this environment and the cysts are therefore scarce compared with *Micrhystridium.* The former conclusion is probably more correct since the dinoflagellate cyst assemblage obtained from sample CB 1 is as rich in species as any other sample. Hence the percentage abundance graphs of this genus are difficult to interpret and perhaps only one peak (peak 1) may possibly be used in correlation.

The above quantitative results are summarized in text-fig. 8, and show that correlation, using the percentage abundance of certain species within a restricted sedimentary area (southern England and northern France), is possible.

Many species of dinoflagellate at the present time have a world-wide distribution (Wood 1953) and it is probable that many fossil species, especially during the relatively uniform climatic conditions of the Cretaceous, were of similar wide-spread

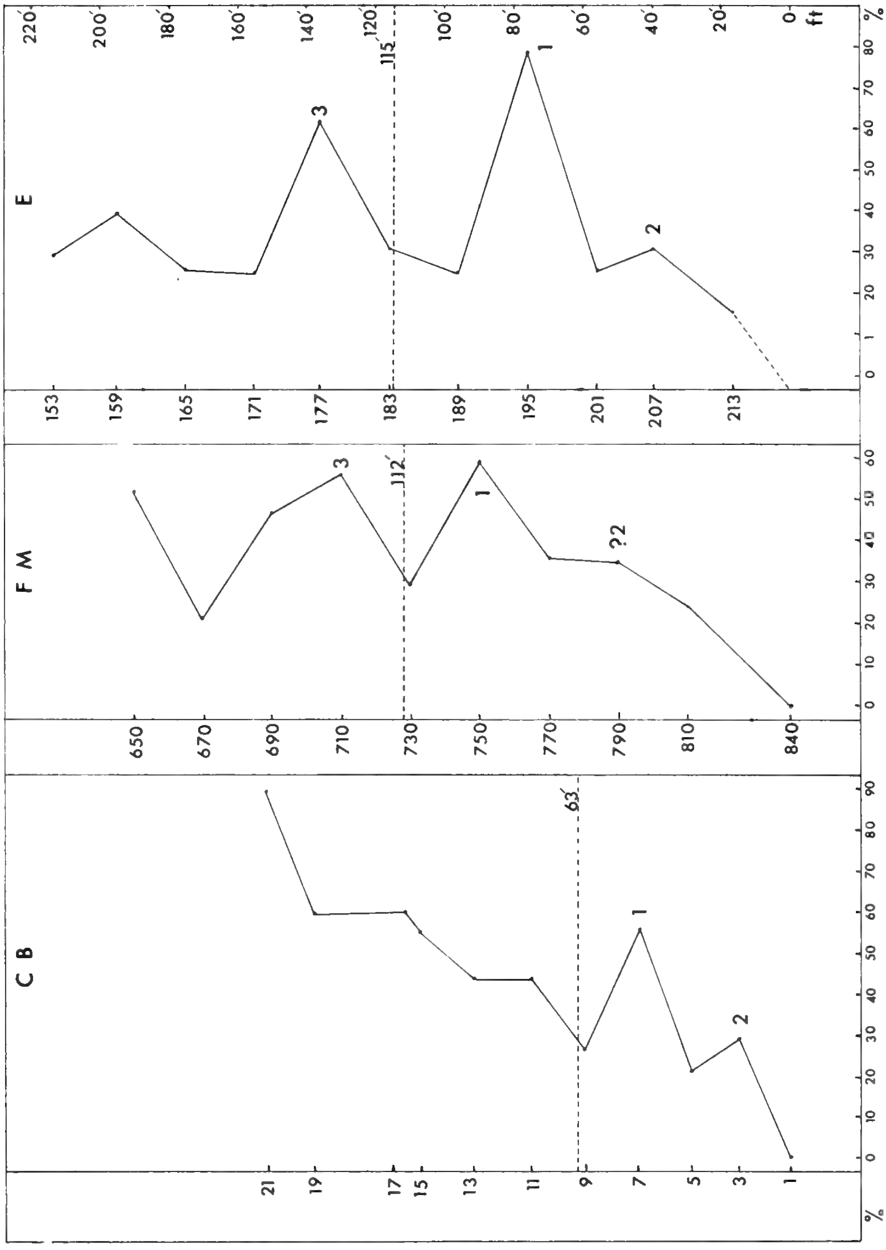

FIG. 5. Percentage abundance graphs for *Palaeohystrichophora infusorioides* at the three localities—Compton Bay, Fetcham Mill and Escalles.

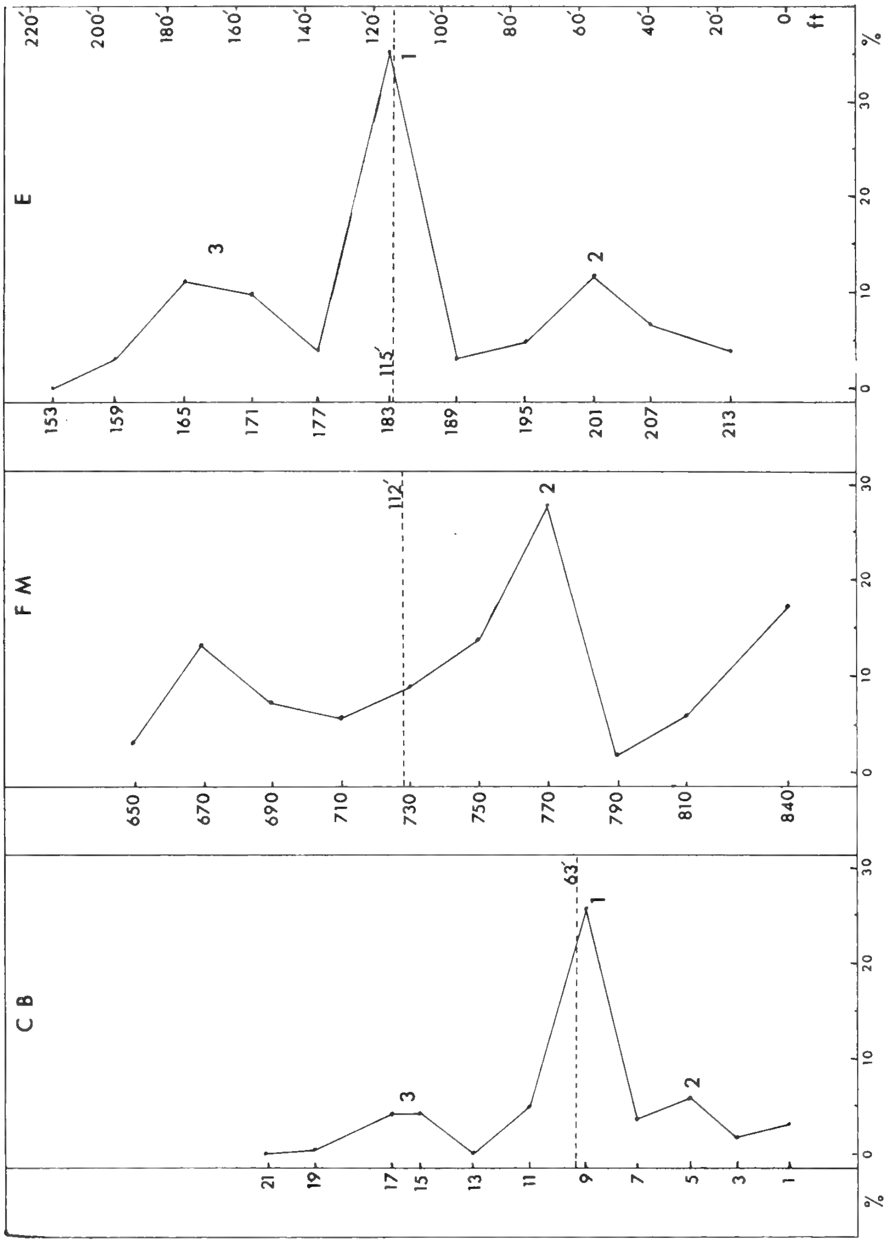

FIG. 6. Percentage abundance graphs for *Cleistosphaeridium huguonioti* at the three localities—Compton Bay, Fetcham Mill and Escalles.

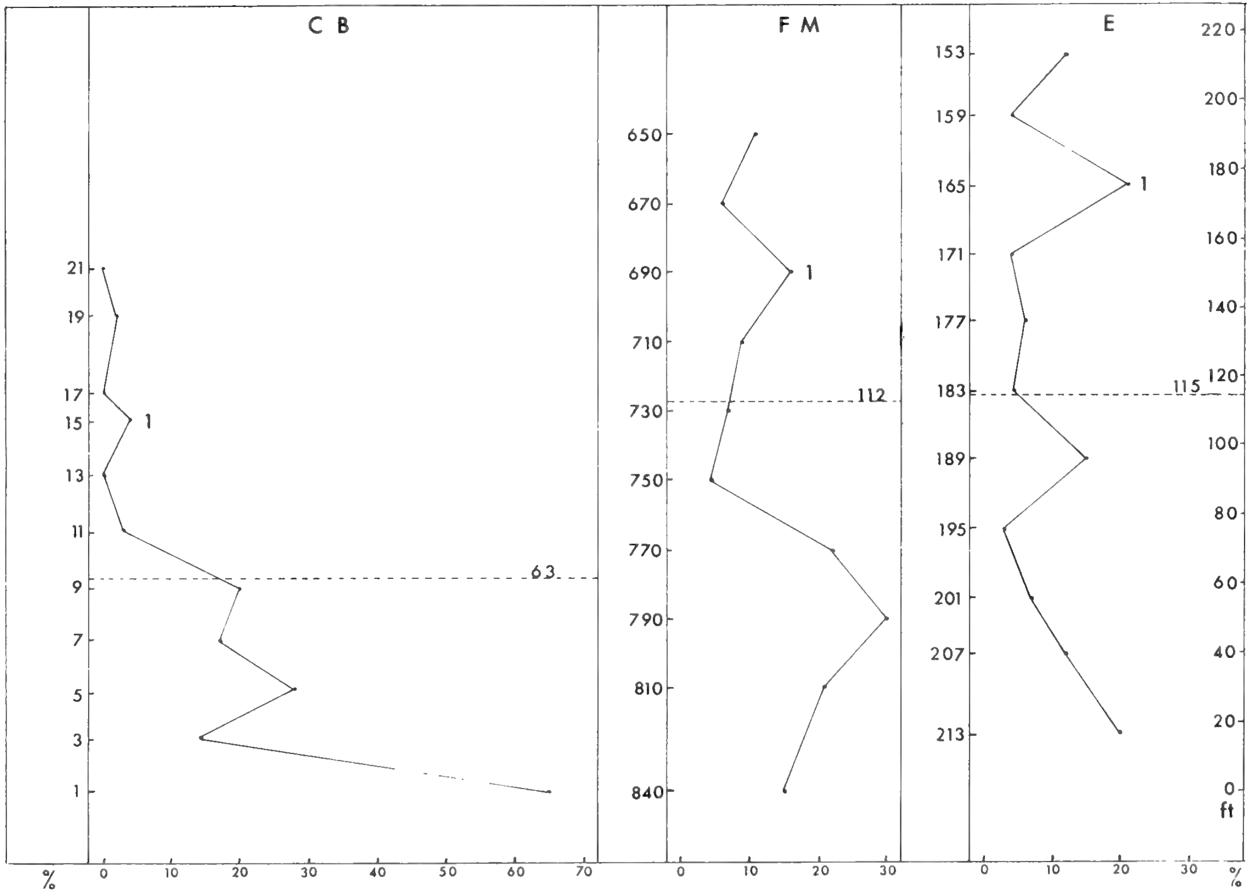

FIG. 7. Percentage abundance graphs for *Micrhystridium* at the three localities—Compton Bay, Fetcham Mill and Escalles.

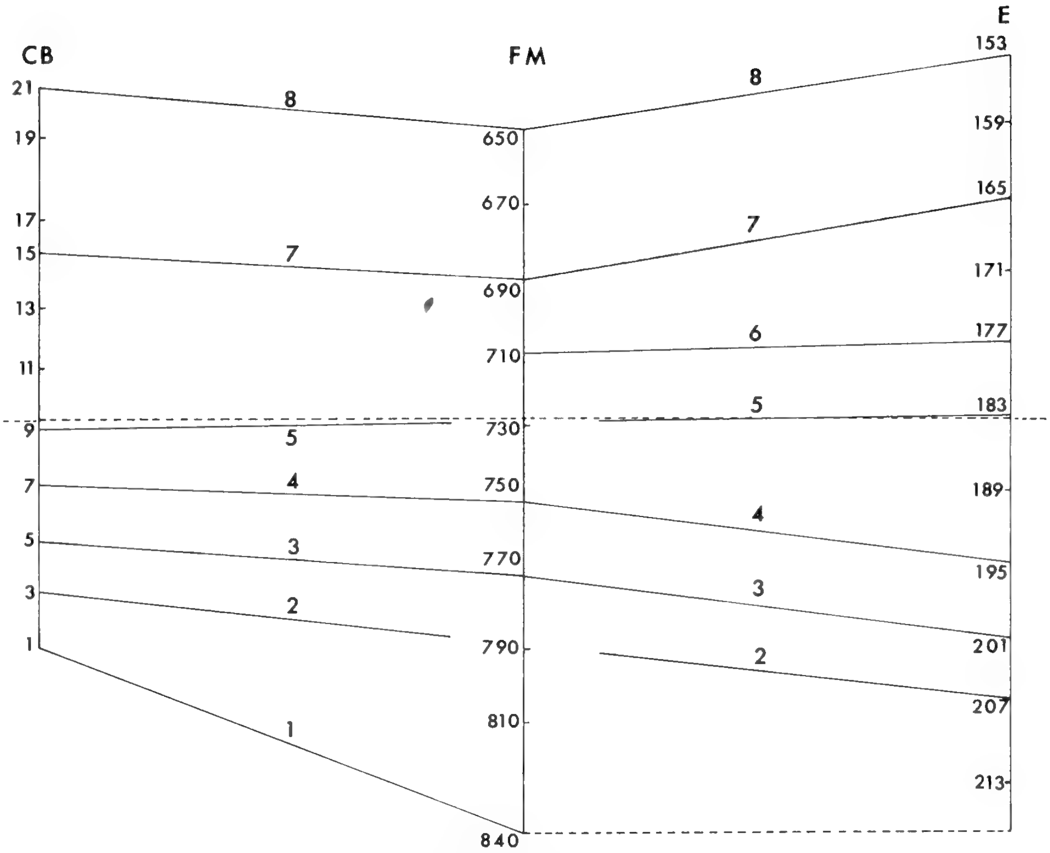

FIG. 8. Correlation between Compton Bay, Fetcham Mill and Escalles based on the quantitative results. 1. Base of Stage marked by first appearance of *P. infusorioides*. 2. *P. infusorioides* peak 2. 3. *C. huguonioti* peak 2. 4. *P. infusorioides* peak 1. 5. *C. huguonioti* peak 1. 6. *P. infusorioides* peak 3. 7. *Micrhystridium* peak 1. 8. Top of the Stage marked by the *Actinocamax plenus* Marls.

distribution and so of use in long distance correlation. The percentage abundance graphs produced indicate certain horizons of maximum abundance and these may be used cautiously in correlating the three localities. The results obtained are reasonably satisfactory and indicate that if samples had been analysed at intervals of 10 ft. or less, correlation would have been correspondingly better.

The stratigraphic distribution of all the less abundant species present in the samples examined has been discussed in the remarks at the end of each specific description in the systematic section. The distribution of the stratigraphically useful microplankton in the Cenomanian is shown for each locality in text-fig. 9A–C. From these distribution charts, using the quantitative analysis results to correlate the samples, an idealised Cenomanian section for this region has been constructed (of equal thickness to that of Fetcham Mill) to show the overall distribution of these species (text-fig. 9D).

The base of the Cenomanian sequence is clearly marked by the presence of four species which are not recorded higher in the succession. Of these species two, *Ovoidinium scabrosum* and *Gonyaulacysta fetchamensis*, have also been recorded in the Albian sample from Fetcham Mill (FM 886). The two species of *Ovoidinium* (*O. scabrosum* and *O. verrucosum*) were first described from the Upper Albian—basal Cenomanian sediments of Cambridgeshire, England (Cookson and Hughes 1964). The fourth species only present in the lowermost Cenomanian is *Cleistosphaeridium polypes* var. *calvulum*. This was also recorded by Cookson and Hughes (as *Hystrichosphaeridium recurvatum* subsp. *polypes*) from the Upper Gault and Cambridge Greensand but not from the Chalk Marl. Thus it appears probable that the matrix of the Cambridge Greensand is the lateral equivalent of the Chlorotic Marl and is of basal Cenomanian age.

Of the remaining species shown in text-fig. 9 many are found in the topmost horizon of the Cenomanian and probably extend into Turonian. However, only five of these were observed in the Turonian sample from Fetcham Mill (FM 520). These were *P. infusorioides*, *Microdinium veligerum*, *Exochosphaeridium pseudohystrichodinium*, *Hystrichodinium dasys* and *Hystrichosphaeridium deanei*.

Clarke and Verdier (1967), after a detailed examination of microplankton of the Upper Cretaceous (Cenomanian–Senonian) from the Isle of Wight, formulated five zones, together with five subzones, and seven palynological " intervals " based on the extinction points of species. The Cenomanian constitutes a single zone which is divided into three subzones. The zonal fossil selected is *Litosphaeridium siphoniphorum*. This is a distinctive microfossil and is present in all Cenomanian samples from the three localities in the present study, but is absent from the Albian and Turonian samples examined. The base of the zone is marked by the first appearance of *Palaeohystrichophora infusorioides*. In the present study it is not possible to define accurately the top of the Cenomanian since sampling did not continue systematically into the Turonian. Clarke and Verdier, however, note the disappearance of six distinctive species at the top of this zone, none of which were recorded from the Turonian sample analysed.

The index fossil of the lower subzone, *Dinopterygium perforatum*, was not located by the author in the present study. Other fossils characteristic of this subzone are

Microdinium veligerum (*M. irregulare* of Clarke and Verdier), found only in the middle and upper Cenomanian by the author : *Canningia reticulata* and *Hystrichosphaera cingulata* var. *granulata* were both absent. The base of the middle subzone is characterised by the first appearance of *Hystrichosphaera crassimurata* and the top by the last appearance of *Epelidosphaeridium spinosum*. The former appears to be an excellent marker (text-fig. 9) and the latter was not recorded from the upper two to five samples from the three localities (p. 42). The base of the upper subzone, that of *Cleistosphaeridium huguonioti*, is taken as being from the last appearance of *E. spinosum* to the disappearance of six distinctive species ; in particular *C. huguoniti*, *L. siphoniphorum*, and *Microdinium setosum*.

The present study verifies many of Clarke and Verdier's stratigraphic results and supports the hypothesis that the Cenomanian may be adequately defined utilising the first appearance of *P. infusorioides* for the base and the last appearance of *C. huguonioti* for the top. Of the subzones the middle one, that of *E. spinosum*, and the upper one, that of *C. huguonioti*, appear to be practical units of subdivision. However, the lower subzone, that of *D. perforatum*, could not be recognised at Fetcham Mill, Compton Bay or at Escalles and does not appear to be of wide application.

A small number of species that may perhaps be derived have been noted in the systematics section ; in particular species belonging to the genus *Michrystridium*. These species suggest a Lower to Middle Jurassic or perhaps a Silurian source, but no obviously derived dinoflagellate cysts are recorded here. Clarke and Verdier (1967), in their extensive study of microplankton from the Upper Cretaceous, similarly did not observe derived forms.

2. *Speeton*

Microplankton and miospores were completely absent from the samples processed from this locality, the only organic constituent being small, thick-walled algal remains (p. 383). These are rare in the lower samples, becoming more common in samples 6 and 7.

This absence of practically all organic matter at Speeton strongly suggests that relatively intensive oxidation has removed these constituents from the sediment. The Speeton chalk does not seem to be unusual in its macro-fauna, although at certain horizons it is relatively abundant ; brachiopods and lamellibranchs in the lower part of the succession, and higher up together with echinoids, are quite common. Thus before any penecontemporaneous and post-depositional oxidation took place, the number of microplankton and miospores that could be incorporated in the sediment was probably greatly depleted by the action of the above scavengers.

3. *Hunstanton*

The two samples from the *varians* Zone at Hunstanton were found to be completely devoid of microplankton and miospores and to contain only a very few of the thick-walled algal remains. Thus these samples are comparable to those of Speeton and the microfossils under study are probably absent for the same reasons.

The third sample (H 3) analysed, from the base of the *subglobosus* Zone, contains a small number of hystrichosphere fragments comprising approximately 2% of the assemblage. The remainder of the assemblage is composed of the thick-walled algal cells. Three forms of microplankton have been identified—*Oligosphaeridium complex*, *Hystrichosphaeridium tubiferum* and *Cymatiosphaera* sp.—and also one disaccate pollen grain.

4. *Devon*

Microplankton were completely absent from the seven samples analysed. One disaccate pollen grain was found (sample D 1), and algal remains were present in two samples (D 3 and D 5).

The sediment from these localities was deposited in shallow water, near land, and is often of quite coarse grains. Thus a combination of shallow water, with current action, and oxidation probably prevented the preservation of microplankton.

5. *Texas*

The two samples analysed consist of relatively near shore, fine-grained sediments containing abundant land plant fragments, approximately 90% miospores and 10% microplankton. The microplankton assemblage consists of 25 species and varieties, all of which have been recorded from the Cenomanian of England and France. Thus it is highly probable that in the Upper Cretaceous there was free communica-

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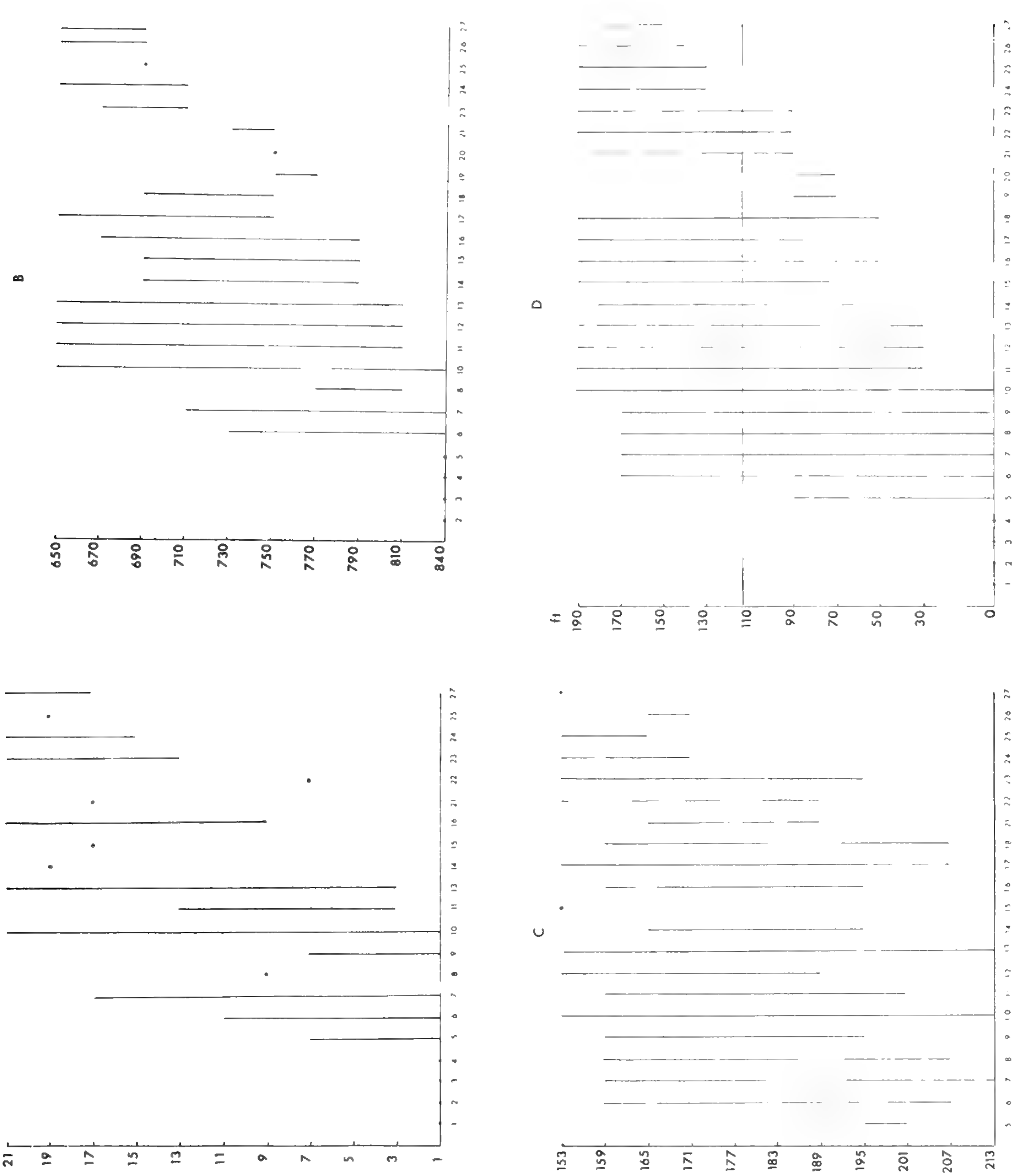
FIG. 9. Chart to show the distribution of the restricted species at the three localities:
A. Compton Bay. B. Fetcham Mill. C. Escalles.
The overall distribution of the restricted species is shown as in D.

1. *Ovoidinium scabrosum* (Cookson & Hughes)
2. *Ovoidinium verrucosum* (Cookson & Hughes)
3. *Gonyaulacysta fetchamensis* Sarjeant
4. *Cleistosphaeridium polypes* var. *clavulum* nov.
5. *Cribroperidinium intricatum* sp. nov.
6. *Gonyaulacysta exilicristata* sp. nov.
7. *Cleistosphaeridium multifurcatum* (Deflandre)
8. *Hystrichosphaeridium readei* Davey & Williams
9. *Microdinium variospinum* sp. nov.
10. *Palaeohystrichiophora infusorioides* Deflandre
11. *Histiocysta palla* sp. nov.
12. *Microdinium* cf. *ornatum* Cookson & Eisenack
13. *Microdinium veligerum* (Deflandre)
14. *Adnatosphaeridium chonetum* (Cookson & Eisenack)
15. *Microdinium distinctum* sp. nov.
16. *Hystrichosphaera crassimurata* Davey & Williams
17. *Cassiculosphaeridia reticulata* sp. nov.
18. *Exochosphaeridium pseudohystrichodinium* (Deflandre)
19. *Gonyaulacysta whitei* Sarjeant
20. *Polysphaeridium pumilum* Davey & Williams
21. *Cleistosphaeridium polypes* (Cookson & Eisenack)
22. *Hystrichodinium dasys* sp. nov.
23. *Hystrichosphaeridium deanei* Davey & Williams
24. *Cleistosphaeridium huguonioti* var. *pertusum* nov.
25. *Prolixosphaeridium coniculum* sp. nov.
26. *Micrhystridium bifidum* sp. nov.
27. *Cleistosphaeridium heteracanthum* (Deflandre & Cookson)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tion of forms between Europe and the Gulf region of the United States by means of sea currents.

Three stratigraphically restricted species of microplankton were identified—*P. infusorioides, Hystrichosphaera crassimurata* and *Cleistosphaeridium polypes*. The last species has only been recorded from the Middle and Upper Cenomanian of Europe (text-fig. 9D) and suggests that these samples are probable of this age. Ammonites collected from these horizons indicate the same age for these samples.

6. *Saskatchewan*

The six samples analysed are cabonaceous mudstones, land plant debris being extremely abundant, and contain approximately 80% miospores and 20% microplankton.

The microplankton flora is well preserved ; acritarchs, in particular *Micrhystridium Cymatiosphaera* and *Pterospermopsis*, are common. The dinoflagellate cyst flora obtained is distinctive and very different from that found in England, France or Texas. *Deflandrea* is by far the most abundant genus in the Saskatchewan assemblages, and is conspicuously absent from the English and French assemblages.

A small number of species are common to this locality and to England and France. *P. infusorioides* is a common species in samples Sas 805 and 835 but rare in sample Sas 890. The genus *Ovoidinium* is represented in Saskatchewan by *O. ostium*, a species rather similar to *O. verrucosum*. *O. ostium* is common in samples Sas 1084, 1023 and 967 but rare in sample Sas 890. Thus the rare occurrence of *P. infusorioides* and the genus *Ovoidinium* in sample Sas 890 appears to be comparable to their distribution in samples FM 840 and CB 1 from the basal Cenomanian of England. For this reason the base of the Cenomanian has been placed just below sample Sas 890 at a depth of 900 ft. at the base of the Second White Speckled Shale (Upper Colorado).

Other species of stratigraphic value common to Saskatchewan, England and France are *Cleistosphaeridium polypes*, found in sample Sas 835 indicating a Middle to Upper Cenomanian age for this sample ; *Cribroperidinium intricatum*, found in samples Sas 1023 and 1084 probably mainly an Albian species but ranging up into the Lower Cenomanian ; and *Microdinium variospinum* found only in sample Sas 1084 and previously recorded throughout the major part of the Cenomanian of England and France, except for the uppermost 20 ft.

The abundance of the genus *Deflandrea* in the Albian–Cenomanian samples from Saskatchewan is an interesting phenomenon. *Deflandrea* occurs in assemblages of similar age in northern Germany, Arctic Canada and eastern Australia. The assemblages from Arctic Canada (Manum and Cookson 1964) and Saskatchewan are similar and in Cretaceous time were brought into direct contact by the Arctic Sea. In northern Germany the Cenomanian was deposited north of the Anglo–Belgium Ridge in the North-Eastern Sea, the latter being connected to the Boreal Ocean. It is possible that the genus *Deflandrea* has a preference for cooler water and that the Arctic Sea of northern Canada and the Boreal Ocean of Europe were connected and contained similar microplankton assemblages during the Cenomanian. The Tethyan assemblages of England, France and Texas are very different and *Deflandrea* is absent. Clarke and Verdier (1967), in their study of assemblages from the Upper Cretaceous of the Isle of Wight, first record *Deflandrea* from the Senonian. This possibly indicates a change in the palaeo-environmental conditions in the Chalk Sea at that time.

Wood (1953) states that in cooler water the total number of species of phytoplankton is less than in warm water. This reiterates the above idea that the Saskatchewan sea was cooler than the sea in the British region, since the number of species present in the Lower Chalk is far greater than that obtained from Saskatchewan. However, the absolute number of specimens (number of specimens per gram of sample) in each region is approximately the same.

An interesting corollary to this question of temperature is that with an increase of temperature, the density of sea water decreases. Hence dinoflagellates inhabiting warm water produce cysts with relatively large surface area so as to retard the rate of sinking, for once the encysted organism enters the aphotic zone (approximately at 300 ft. depth) it has little chance of survival. Thus in warm sea water the cysts are predominantly chorate and as the temperature of the water decreases the proportion of proximate and cavate cysts increases. The Cenomanian assemblages from England and France contain very few proximate and cavate cysts, and chorate cysts are by far the most abundant. Conversely, as would be expected, the cool water Saskatchewan assemblages are composed predominantly of *Deflandrea*, a cavate cyst genus and to a lesser extent of proximate cysts.

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PLATE 1

Xiphophoridium alatum (Cookson & Eisenack)

Lower Chalk, Fetcham Mill Borehole.

FIG. 1. Antapical view, sulcal region to the south. FM690/12 (depth, 690 feet). ×500 (phase contrast).

FIG. 2. Lateral view. PF.3988 (depth, 750 feet). ×500.

Deflandrea pirnaensis Alberti

Upper Colorado, Saskatchewan.

Fig. 3. Cingulum well shown. V.51979 (depth, 835 feet). ×500.

FIG. 4. Operculum present, remaining attached posteriorly. V.51979 (depth, 835 feet). ×500.

Deflandrea echinoidea Cookson & Eisenack

FIG. 5. Lower Colorado, Saskatchewan (depth, 1084 feet). V.51991. ×500.

Deflandrea cf. ***echinoidea*** Cookson & Eisenack

FIG. 6. Upper Greensand, Fetcham Mill Borehole (depth, 886 feet). Archaeopyle present and spines aligned along plate sutures. FM886/2. ×500.

Deflandrea glomerata sp. nov.

FIG. 7. Enlargement of holotype archaeopyle and apical " wrinkles ". V.51988 (2). ×975.

FIG. 8. Holotype. V.51988 (2). ×500.

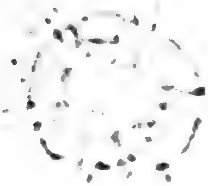
FIG. 9. Upper Colorado, Saskatchewan (depth, 835 feet). Detached operculum. V.51988. ×975.

Deflandrea pontis-mariae (Deflandre)

Upper Colorado, Saskatchewan (depth, 805 feet).

FIG. 10. V.51983. ×500.

FIG. 11. V.51983. ×500.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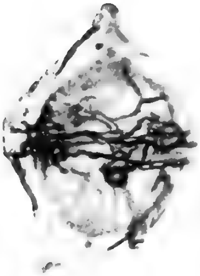
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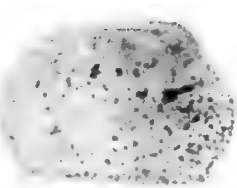
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PLATE 2

***Deflandrea granulifera* var. *tenuis* nov.**

FIG. 1. Type : archaeopyle and interrupted cingulum illustrated. V.51990 (1). ×500.

***Deflandrea* cf, *echinoidea* Cookson & Eisenack**

FIG. 2. Lower Chalk, Fetcham Mill Borehole (depth, 840 feet). Specimen possessing archaeopyle and sulcal depression. Slide FM840/8. ×500.

***Deflandrea globosa* sp. nov.**

FIG. 3. Holotype. V.51988 (3). ×500.

***Astrocysta cretacea* (Pocock)**

FIG. 4. Lower Colorado, Saskatchewan (depth, 1023 feet). V.51980. ×500.

***Deflandrea suspecta* (Manum & Cookson)**

FIG. 5. Upper Colorado, Saskatchewan (depth, 835 feet). Specimen possessing faint apical horn and inner body divided anteriorly to produce three anterior intercalary plates. V.51979. ×500.

***Deflandrea magna* sp. nov.**

FIG. 6. Holotype : operculum in position joined posteriorly. V.51988 (1). ×500.

FIG. 7. Upper Colorado, Saskatchewan (depth, 835 feet). Enlargement to show knobbly margin of cingulum. V.51988. ×975.

FIG. 8. Upper Colorado, Saskatchewan (depth, 835 feet). V.51979. ×500.


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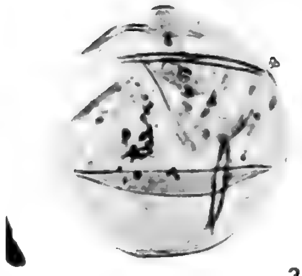
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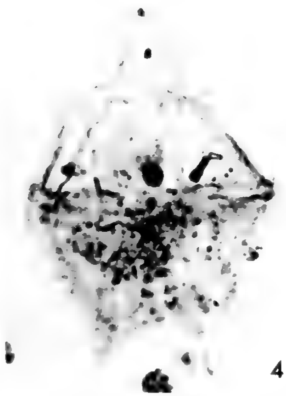
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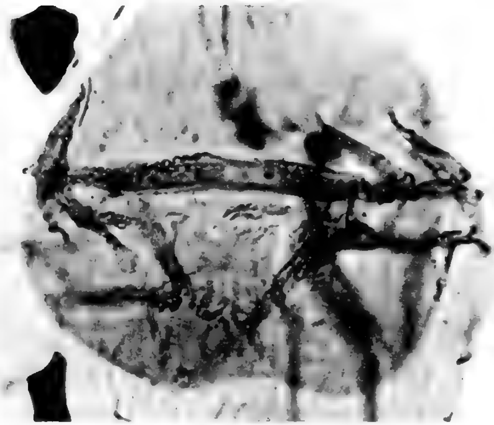
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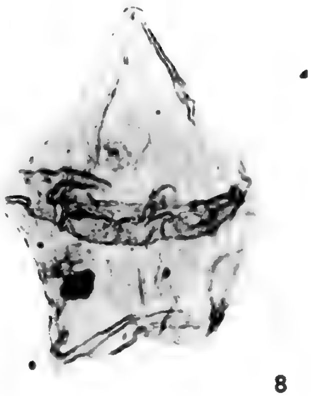
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PLATE 3

Deflandrea Sp. A.

FIG. 1. Lower Colorado, Saskatchewan. V.51991 (2). × 500.

Palaeohystrichophora infusorioides Deflandre

FIG. 2. Upper Colorado, Saskatchewan (depth, 835 feet). V.51979. × 500.

FIG. 6. Lower Chalk, Fetcham Mill Borehole (depth, 750 feet). Central body wall thicker than usual and spines fewer. Slide F.3988. × 500.

Hexagonifera chlamydata Cookson & Eisenack

Lower Chalk, Fetcham Mill Borehole.

FIG. 3. Complete specimen with reticulate central body; operculum partially detached. FM840/9 (depth, 840 feet). × 500.

FIG. 9. Lower Chalk, Escalles (depth, 165 metres). Detached operculum with sulcal prolongation towards the south. V.51981. × 975.

FIG. 10. Specimen with large outer membrane ; apical archaeopyle visible. FM840/10 (depth, 840 feet). × 500.

Psaligonyaulax deflandrei Sarjeant

FIG. 4. Ventral view of holotype. Slide PF.3049 (1). × 500.

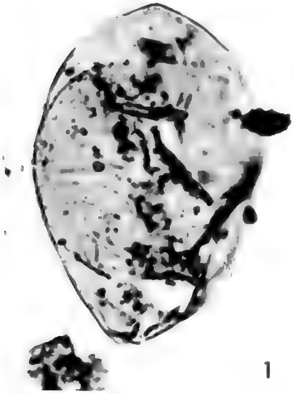
FIG. 5. Lower Chalk, Escalles (depth, 159 metres). Lateral view, archaeopyle to the north-west. V.51982. × 500.

Scriniodinium campanula Gocht

Lower Chalk, Fetcham Mill Borehole.

FIG. 7. Ventral surface illustrating the large posterior perforation. PF.3988 (depth, 750 feet). × 500.

FIG. 8. Dorsal surface with archaeopyle. PF.3988 (depth, 750 feet). × 500.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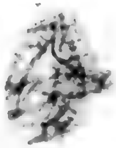
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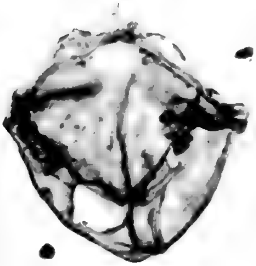
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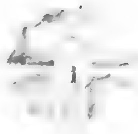
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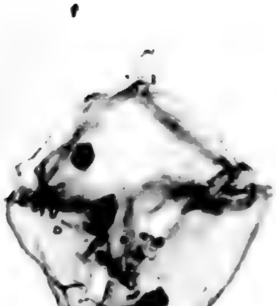
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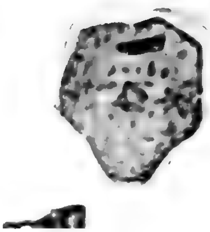
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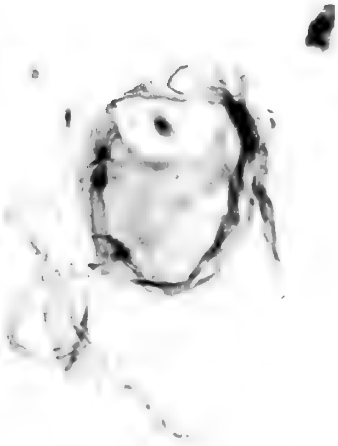
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PLATE 4

Ovoidinium verrucosum (Cookson & Hughes)

Lower Chalk, Fetcham Mill Borehole.

Fig. 1. Complete specimen. FM840/18. (depth, 840 feet). × 500.

Fig. 2. Specimen with archaeopyle developed. PF.3032 (depth, 840 feet). × 500.

Ovoidinium scabrosum (Cookson & Hughes)

Lower Chalk, Compton Bay.

Fig. 3. Complete specimen. CB1/E (at base of Chalk). × 500.

Fig. 4. Specimen with archaeopyle developed. CB1/E (at base of Chalk). × 500.

Ovoidinium ostium sp. nov.

Lower Colorado, Saskatchewan.

Fig. 5. Holotype. V.51987 (1). × 500.

Fig. 6. Paratype showing subrectangular opening in the posterior pericoel wall. V.51991 (1). × 500.

Odontochitina operculata (O. Wetzel)

Fig. 7. Lower Chalk, Compton Bay (151 feet above base of Chalk). Detached operculum. CB21/D. × 390.

Odontochitina costata Alberti

Fig. 8. Lower Chalk, Compton Bay. Detached operculum showing small apical horn on central body. CB21/C (151 feet above base of Chalk). × 500.

Fig. 9. Complete specimen. CB11/15 (76 feet above base of Chalk). × 250.

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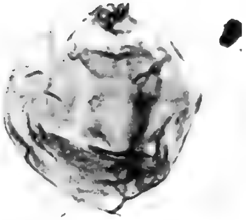

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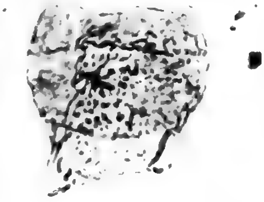

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PLATE 5

Pseudoceratium dettmannae Cookson & Hughes

Fig. 1. Lower Chalk, Fetcham Mill Borehole (depth, 840 feet). Specimen with operculum partially detached. FM840/9. × 500.

Odontochitina operculata (O. Wetzel)

Fig. 2. Lower Chalk, Compton Bay (151 feet above base of Chalk). CB21/D. × 390.

Odontochitina costata Alberti

Fig. 3. Lower Chalk, Compton Bay (151 feet above base of Chalk). Complete specimen. CB21/D. × 250.

Odontochitina blastema sp. nov.

Fig. 4. Holotype. V.51989 (1). × 500.

Fig. 5. Lower Chalk, Fetcham Mill Borehole (depth, 690 feet). Specimen showing precingular and postcingular processes. FM690/12. × 500 (phase contrast).

Dorocysta litotes sp. nov.

Fig. 6. Holotype illustrating lightly marked tabulation and cingular perforation. V.51982 (4). × 975.

Fig. 7. Lower Chalk, Compton Bay (at base of Chalk). Specimen with forked apical processes. CB1/D. × 975.


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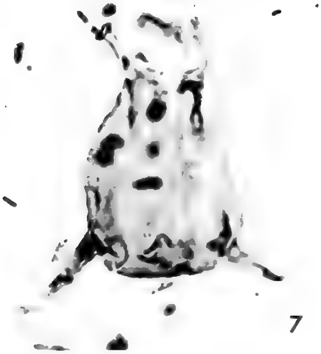
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PLATE 6

Stephodinium coronatum Deflandre

Lower Chalk, Fetcham Mill Borehole.

FIG. 1 Dorsal view showing outer membrane and apical horn. PF.3049 (depth, 730 feet). × 500.

FIG. 2 Apical view showing archaeopyle in outer membrane. PF.3987 (depth, 730 feet). × 500.

FIG. 4. Antapical view showing antapical plate. FM730/8 (depth, 730 feet). × 500.

Dinogyminium Sp. B.

FIG. 3. Upper Colorada, Saskatchewan. V.51979 (4). × 1250.

Chlamydophorella nyei Cookson & Eisenack

FIG. 5. Upper Colorado, Saskatchewan (depth, 835 feet). Enlargement to show fine branched processes. Sas 835/4. × 975 (phase contrast).

FIG. 7. Lower Colorado, Saskatchewan (depth, 1084 feet). V.51991. × 500.

FIG. 8. Lower Colorado, Saskatchewan (depth, 890 feet). Specimen with apical horn and operculum partially detached. Sas890/3. × 500.

Dinogyminium Sp. A

FIG. 6. Lower Colorado, Saskatchewan, V.51985 (1). × 500.

Micrhystridium singulare Firtion

FIG. 9. Lower Chalk, Fetcham Mill Borehole (depth, 690 feet). PF.3030. × 500.

Micrhystridium deflandrei Valensi

Upper Woodbine Formation, Texas.

FIG. 10. T.5/3. × 975.

FIG. 11. T.5/3. × 975.

Micrhystridium recurvatum forma **brevispinosa** Valensi

Lower Chalk, Escalles.

FIG. 12. Specimen possessing large irregular opening. E201/5 (depth, 201 metres). × 975.

FIG. 13. E207/3 (depth, 207 metres). × 975.

Micrhystridium minutispinum Wall

FIG. 14. Lower Chalk, Fetcham Mill Borehole. Specimen possessing a split-like opening FM77016 (2). × 1250.

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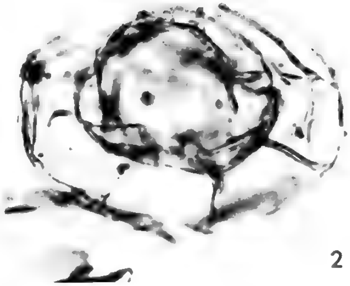

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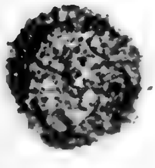

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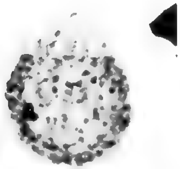

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PLATE 7

Micrhystridium cf. ***variabile*** Valensi

FIG. 1. Lower Chalk, Escalles (depth, 213 metres). E213/4. ×975.
FIG. 2. Lower Chalk, Compton Bay (15 feet above base of Chalk). CB3/B. ×975.

Micrhystridium piliferum Deflandre

Lower Chalk, Escalles.

FIG. 3. E165/1 (depth, 165 metres). ×975.
FIG. 4. E195/3 (depth, 195 metres). ×975.

Micrhystridium inconspicuum Deflandre

FIG. 5. Lower Chalk, Compton Bay (at base of Chalk). CB1/37. ×975.
FIG. 6. Lower Chalk, Compton Bay (137 feet above base of Chalk). CB19/B. ×975.
FIG. 7. Lower Colorado, Saskatchewan (depth, 1023 feet), V.51987. ×975.

Micrhystridium alveospinum sp. nov.

FIG. 8. Lower Chalk, Compton Bay (depth, 59 feet). CB9/D. ×500.
FIG. 9. Holotype PF.3043 (2). ×500.

Micrhystridium bifidum sp. nov.

Lower Chalk, Fetcham Mill Borehole (depth, 690 feet).

FIG. 10. PF.3994. ×975.
FIG. 11. Holotype PF.3994 (1). ×975.

Micrhystridium rigidum sp. nov.

Lower Chalk, Fetcham Mill Borehole.

FIG. 12. FM810/6 (depth, 810 feet). ×975.
FIG. 13. PF.3992 (depth, 840 feet). ×975.

Veryhachium reductum Deunff

FIG. 14. Lower Chalk, Escalles (depth, 159 metres). V.51982. ×500.
FIG. 15. Lower Chalk, Compton Bay (at base of Chalk). CB1/E. ×500.

Veryhachium cf. ***reductum*** Deunff

Lower Chalk, Fetcham Mill Borehole (depth, 670 feet).

FIG. 16. PF.3040. ×975.

Veryhachium reductum forma ***breve*** Jekhowsky

FIG. 17. Lower Chalk, Escalles (depth, 201 metres). E201/5. ×975.

Veryhachium cf. ***hyalodermum*** Cookson

FIG. 18. Lower Chalk, Fetcham Mill Borehole (depth, 730 feet). FM730/8. ×500.

Veryhachium Sp. B.

FIG. 19. Lower Chalk, Escalles (depth, 213 metres). E213/4. ×500.


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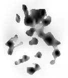
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PLATE 8

Veryhachium irregulare forma ***subtetraedron*** Jekhowsky

FIG. 1. Lower Chalk, Fetcham Mill Borehole (depth, 770 feet). FM770/4. × 500.

Veryhachium rhomboidium Downie

FIG. 2. Lower Chalk, Fetcham Mill Borehole (depth, 730 feet). PF.3987. × 500.

FIG. 3. Lower Colorado, Saskatchewan (depth, 1084 feet). V.51991. × 500.

Veryhachium Sp. A

FIG. 4. Lower Chalk, Compton Bay (144 feet above base of Chalk). V.51984. × 500.

Veryhachium metum sp. nov.

FIG. 5. Holotype. PF.3045 (2). × 500.

FIG. 6. Lower Chalk, Escalles (depth, 201 metres). E201/5. × 500.

Tubulospina oblongata sp. nov.

FIG. 7. Holotype. V.51984 (1). × 500.

FIG. 8. Lower Chalk, Fetcham Mill Borehole. Enlargement to show hollow spines closed proximally. × 975.

FIG. 9. Lower Chalk, Escalles (depth, 213 metres). E213/4. × 500.

Veryhachium Sp. C.

FIG. 10. Lower Chalk, Escalles (depth, 213 metres). E213/4. × 500.

Leiofusa cf. ***jurassica*** Cookson & Eisenack

FIG. 11. Lower Chalk, Fetcham Mill Borehole (depth 840 feet). PF.3035. × 500.

Cymatiosphaera radiata O. Wetzel

Lower Chalk, Fetcham Mill Borehole.

FIG. 12. PF.3030 (depth, 690 feet). × 975.

FIG. 13. PF.3988 (depth, 750 feet). × 975.

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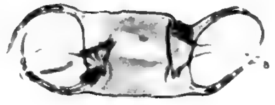

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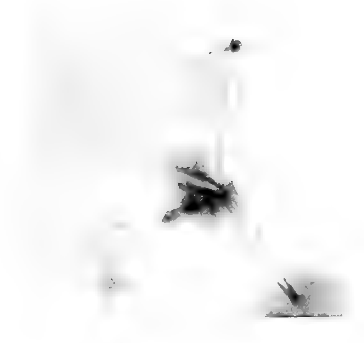

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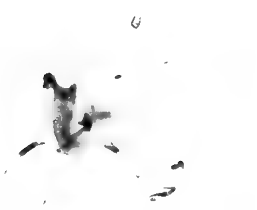

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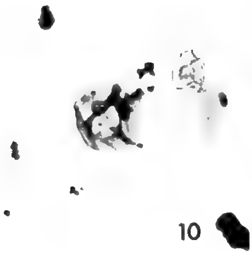

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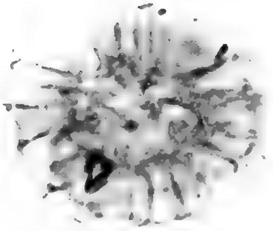

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PLATE 9

Leiofusa* cf. *jurassica Cookson & Eisenack

Fig. 1. Lower Chalk, Compton Bay (at base of Chalk). Slide CB1/D. × 500.

Cymatiosphaera costata sp. nov.

Fig. 2. Holotype. Surface view. V.51988 (4). × 975.
Fig. 3. Medial section. × 975.

Cymatiosphaera conopa sp. nov.

Fig. 4. Holotype. Surface view. V.51983 (2). × 975.
Fig. 5. Holotype. Medial section. × 975.

Cymatiosphaera asarota sp. nov.

Fig. 6. Holotype. V.51983 (1). × 500.
Fig. 7. Holotype. Surface reticulation. × 500.

Pterospermopsis* cf. *helios Sarjeant

Fig. 8. Lower Colorado, Saskatchewan (depth, 1084 feet). Plan view. V.51991. × 975.
Fig. 9. Upper Colorado, Saskatchewan (depth, 835 feet). Lateral view. V.51988. × 975.

Diplotesta angelica Cookson & Hughes
Lower Chalk, Fetcham Mill Borehole.

Fig. 10. Lateral view. FM690/14 (depth, 690 feet). × 500.
Fig. 11. " Top " view. PF.3045 (depth, 840 feet). × 500.
Fig. 12. Enlargement to show apical opening and the presence of a few small spines. PF.3987 (depth, 730 feet). × 975.


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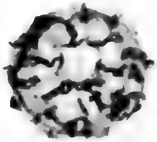
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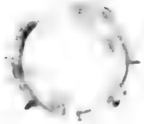
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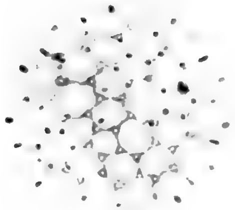
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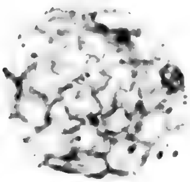
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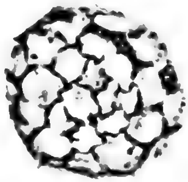
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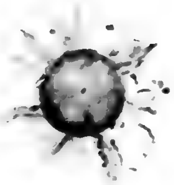
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PLATE 10

Palambages Form A. Manum & Cookson

Fig. 1. Upper Colorado, Saskatchewan (depth, 835 feet). Colony possessing 8 cells. V. 51979. × 500.

Fig. 2. Lower Colorado, Saskatchewan (depth, 967 feet). Colony possessing approximately 128 cells. Sas967/2. × 500.

Fig. 3. Upper Colorado, Saskatchewan (depth, 835 feet). Colony possessing approximately 32 cells. V.51988. × 500.

Fig. 4. PF.3046 (3). × 500 (phase contrast).

Palambages Form D nov. Figured specimen

Fig. 5. Enlargement to show small spines. PF.3046 (3). × 1250 (phase contrast).

Foraminiferal shell lining

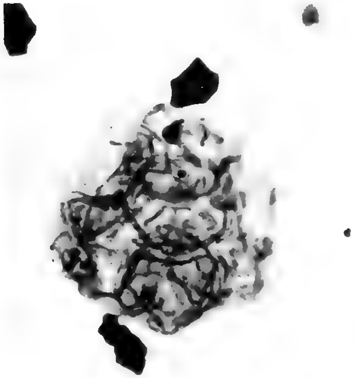
Lower Chalk, Escalles (depth, 195 metres).

Fig. 6. E195/3. × 500.
Fig. 7. E195/3. × 500.

Algal cell(s)

Lower Chalk, Hunstanton.

Fig. 8. H3/2. × 500.
Fig. 9. H3/2. × 500.
Fig. 10. H3/2. × 500.



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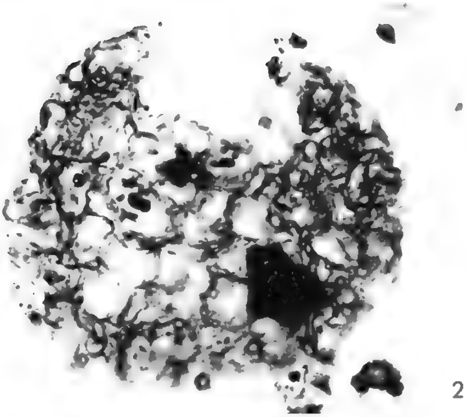

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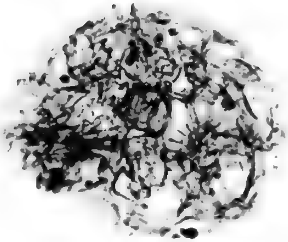

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INDEX TO VOLUME 18

New taxonomic names and the page numbers of the principal references are printed in **Bold** type. An asterisk (*) denotes a figure.

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3. Davey, R. J., Downie, C., Sargeant, W. A. S. & Williams, G. L. Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 248; 28 Plates, 64 Text-figures. 1966. £7.
3. Appendix. Davey, R. J., Downie, C., Sargeant, W. A. S. & Williams, G. L. Appendix to Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 24. 1969. 16*s.*
4. Elliott, G. F. Permian to Palaeocene Calcareous Algae (Dasycladaceae) of the Middle East. Pp. 111; 24 Plates, 17 Text-figures. 1968. £5 2*s.* 6*d.*
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