





VOLUME 11

Palaeontology

1968

PUBLISHED BY THE
PALAEOLOGICAL ASSOCIATION
LONDON

Dates of publication of parts in Volume 11

Part 1, pp. 1-162, pls. 1-30	4 March 1968
Part 2, pp. 163-328, pls. 31-64	28 March 1968
Part 3, pp. 329-490, pls. 65-92	2 July 1968
Part 4, pp. 491-642, pls. 93-123	28 November 1968
Part 5, pp. 643-817, pls. 124-54	20 December 1968

THIS VOLUME EDITED BY N. F. HUGHES, GWYN THOMAS, ISLES STRACHAN, R. GOLDRING,
AND M. R. HOUSE

© *The Palaeontological Association, 1968*

PRINTED IN GREAT BRITAIN

CONTENTS

	Part	Page
ARCHANGELSKY, S. Studies on Triassic fossil plants from Argentina. IV. The leaf genus <i>Dicroidium</i> and its possible relation to Rhexoxylon stems	4	500
ARMSTRONG, J. The unusual brachial skeleton of <i>Attenuella convexa</i> sp. nov. (Brachiopoda)	5	783
BATES, D. E. On ' <i>Dendrocrinus</i> ' <i>camabriense</i> Hicks, the earliest known crinoid	3	406
BATTEN, D. J. Probable dispersed spores of Cretaceous <i>Equisetites</i>	4	633
BLACK, M. Taxonomic problems in the study of coccoliths	5	793
BLAKE, D. B. Pedicellariae of two Silurian echinoids from western England	4	576
BOULTER, M. C. A species of compressed sporophyll from the Upper Coal Measures of Somerset	3	445
BRETT, D. W. Studies on Triassic fossil plants from Argentina. III. The trunk of Rhexoxylon	2	236
BULMAN, O. M. B., and RICKARDS, R. B. Some new diplograptids from the Llandovery of Britain and Scandinavia	1	1
CARTER, R. M. Functional studies on the Cretaceous oyster <i>Arctostrea</i>	3	458
CONKIN, J. E., and CONKIN, B. M. A revision of some Devonian Foraminifera from Western Australia	4	601
COPE, J. C. W. <i>Propectinatites</i> , a new Lower Kimmeridgian ammonite genus	1	16
— Epizoic oysters on Kimmeridgian ammonites	1	19
CORDEY, W. G. A new Eocene <i>Cassigerinella</i> from Florida	3	368
— Morphology and phylogeny of <i>Orbinuloides beckmanni</i> (Saito 1962)	3	371
COWEN, R. A new type of delthyrial cover in the Devonian brachiopod <i>Mucrospirifer</i>	2	317
EAMES, F. E. <i>Sindulites</i> , a new genus of the Nummulitidae (Foraminiferidae)	3	435
— CLARKE, W. J., BANNER, F. T., SMOUT, A. H., and BLOW, W. H. Some larger foraminifera from the Tertiary of Central America	2	283
EDWARDS, D. A new plant from the Lower Devonian of New South Wales	5	683
ELLIOTT, G. F. Three new Tethyan Dasycladaceae (calcareous algae)	4	491
ESKER III, G. C. Colour markings in <i>Phacops</i> and <i>Greenops</i> from the Devonian of New York	4	498
FIGGE, K. A goniatite fauna from the Viséan/Namurian boundary	2	264
FRITZ, W. H. Lower and early Middle Cambrian trilobites from the Pioche Shale, east-central Nevada, U.S.A.	2	183
HOLWILL, F. J. W. Tabulate corals from the Ilfracombe Beds (Middle-Upper Devonian) of North Devon	1	44
HUDSON, J. D. The microstructure and mineralogy of the shell of a Jurassic mytilid (Bivalvia)	2	163
JENKINS, T. B. H. Famennian ammonoids from New South Wales	4	535
KEMP, E. M. Probable angiosperm pollen from the British Barremian to Albian strata	3	421
KILENYI, T. I., and ALLEN, N. W. Marine brackish bands and their microfauna from the lower part of the Weald Clay of Surrey and Sussex	1	141
KRÖMMELBEIN, K. The first non-marine Lower Cretaceous ostracods from Ghana, West Africa	2	259
MARTIN, A. R. H. <i>Aquilapollenites</i> in the British Isles	4	549
NEWMAN, B. H. The Jurassic dinosaur <i>Scelidosaurus</i> , Owen	1	40
PANT, D. D., and SINGH, R. S. The structure of <i>Vertebraria indica</i> Royle	5	643
PAUL, C. R. C. <i>Macrocystella</i> Callaway, the earliest glyptocystid cystoid	4	580
— Morphology and function of dichoporate pore-structures in cystoids	5	697

	<i>Part</i>	<i>Page</i>
PHILLIPS, T. L., and ANDREWS, H. N. <i>Biscalitheca</i> (Coenopteridales) from the Upper Pennsylvanian of Illinois	1	104
PIENAAR, R. N. Upper Cretaceous coccolithophorids from Zululand, South Africa	3	361
POCOCK, Y. P. Carboniferous schizophoriid brachiopods from western Europe	1	64
POLLARD, J. E. The gastric contents of an ichthyosaur from the Lower Lias of Lyme Regis, Dorset	3	376
RITCHIE, A. New evidence on <i>Jaymotius kerwoodi</i> White an important ostracoderm from the Silurian of Lanarkshire, Scotland	1	21
ROBERTS, J. Mantle canal patterns in <i>Schizophoria</i> (Brachiopoda) from the Lower Carboniferous of New South Wales	3	389
ROBINSON, E. <i>Chubbina</i> , a new Cretaceous alveolinid genus from Jamaica and Mexico	4	526
ROLLINS, H. B., and BATTEN, R. L. A sinus-bearing monoplacophoran and its role in the classification of primitive molluscs	1	132
RUNWICK, M. J. S. The feeding mechanisms and affinities of the Triassic brachiopods <i>Thecospira</i> Zugmayer and <i>Bactrynum</i> Emmrich	3	329
RUNNEGAR, B. Preserved ligaments in Australian Permian bivalves	1	94
RUSHTON, A. W. A. Revision of two Upper Cambrian trilobites	3	410
SAMANTA, B. K. Nummulites (Foraminifera) from the Upper Eocene Kopili Formation of Assam, India	5	669
SAVAGE, N. M. <i>Planicardinia</i> , a new septate dalmanellid brachiopod from the Lower Devonian of New South Wales	4	627
— Australirhynchia, a new Lower Devonian rhynchonelloid brachiopod from New South Wales	5	731
SEILACHER, A., DROZDZEWSKI, G., and HAUDE, R. Form and function of the stem in a pseudoplanktonic crinoid (<i>Scirocrinus</i>)	2	275
SHERWIN, L. <i>Denckmannites</i> (Trilobita) from the Silurian of New South Wales	5	691
STINTON, F. C., and TORRENS, H. S. Fish otoliths from the Bathonian of southern England	2	246
STRACHAN, I. A new medusoid (?) from the Silurian of England	4	610
SULLIVAN, H. J. A Tournaisian spore flora from the Cemenstone Group of Ayrshire, Scotland	1	116
THOMAS, B. A. A revision of the Carboniferous lycopod genus <i>Eskdalia</i> Kidston	3	439
TOGHILL, P. The graptolite assemblages and zones of the Birkhill Shales (Lower Silurian) at Dobb's Linn	5	654
TUCKER, E. V. The atrypidine brachiopod <i>Dayia navicula</i> (J. de C. Sowerby)	4	612
WALMSLEY, V. G., BOUCOT, A. J., HARPER, C. W., and SAVAGE, N. M. <i>Visbyella</i> —a new genus of resserellid brachiopod	2	306
WEBBY, B. D. <i>Astrocystites distans</i> sp. nov., an edrioblastoid from the Ordovician of Eastern Australia	4	513
WENDT, J. <i>Discohelix</i> (Archaeogastropoda, Euomphalacea) as an index fossil in the Tethyan Jurassic	4	554
WILLIAMS, A. Shell structure of the billingsellacean brachiopods	3	486
ZIEGLER, A. M., COCKS, L. R. M., and MCKERROW, W. S. The Llandovery transgression of the Welsh borderland	5	736

77A.

VOLUME 11 · PART 1

Palaeontology

FEBRUARY 1968

PUBLISHED BY THE
PALAEOLOGICAL ASSOCIATION
LONDON

Price £3

THE PALAEOONTOLOGICAL ASSOCIATION

The Association was founded in 1957 to further the study of palaeontology. It holds meetings and demonstrations, and publishes the quarterly journal *Palaeontology*. Membership is open to individuals, institutions, libraries, etc., on payment of the appropriate annual subscription:

Institute membership	£7. 0s. (U.S. \$16.00)
Ordinary membership	£5. 0s. (U.S. \$13.00)
Student membership	£3. 0s. (U.S. \$8.00)

There is no admission fee. Student members are persons receiving full-time instruction at educational institutions recognized by the Council; on first applying for membership, they should obtain an application form from the Secretary or the Treasurer. All subscriptions are due each January, and should be sent to the Membership Treasurer, Dr. A. J. Lloyd, Department of Geology, University College, Gower Street, London, W.C. 1, England.

Palaeontology is devoted to the publication of papers (preferably illustrated) on all aspects of palaeontology and stratigraphical palaeontology. Four parts at least are published each year and are sent free to all members of the Association. Members who join for 1968 will receive Volume 11, Parts 1 to 5.

All back numbers are still in print and may be ordered from B. H. Blackwell, Broad Street, Oxford, England, at £3 per part (post free). A complete set, Volumes 1-10, consists of 38 parts and costs £114.

Special Papers in Palaeontology is a series of substantial separate works published by the Association. The subscription rate is £6 (U.S. \$16.00) for Institute Members and £3 (U.S. \$8.00) for Ordinary and Student Members. Subscriptions and orders by members of the Association should be placed through the Membership Treasurer.

The following *Special Papers* are available. Members may obtain them at reduced rates through the Membership Treasurer. Non-members may obtain them from B. H. Blackwell, Broad Street, Oxford, England, at the prices indicated.

Special Paper Number One (for 1967): MIOSPORES IN THE COAL SEAMS OF THE CARBONIFEROUS OF GREAT BRITAIN, by A. H. V. Smith and M. A. Butterworth. 324 pp., 72 text-figs., 27 collotype plates. Price £8 (U.S. \$21.00), post free.

Special Paper Number Two (for 1968): EVOLUTION OF THE SHELL STRUCTURE OF ARTICULATE BRACHIOPODS, by Alwyn Williams. 55 pp., 27 text-figs., 24 collotype plates. Price £5 (U.S. \$13.00).

Special Paper Number Three (for 1968): UPPER MAESTRICHTIAN RADIOLARIA OF CALIFORNIA, by Helen P. Foreman. Text with 8 collotype plates. Price £3 (U.S. \$8.00).

Typescripts on all aspects of palaeontology and stratigraphical palaeontology are invited. They should conform in style to those already published in this journal, and should be sent to Mr. N. F. Hughes, Department of Geology, Sedgwick Museum, Downing Street, Cambridge, England, who will supply detailed instructions for authors on request (these are published in *Palaeontology*, 10, p. 707-12).

SOME NEW DIPLOGRAPTIDS FROM THE LLANDOVERY OF BRITAIN AND SCANDINAVIA

by O. M. B. BULMAN and R. B. RICKARDS

ABSTRACT. *Pseudoclimacograptus hughesi* (Nicholson) and *P. undulatus* (Kurck) are placed in the new subgenus *P. (Metaclimacograptus)* with the former species as type. The following new subgenera and species are described: *Pseudoclimacograptus (Clinoclimacograptus) retroversus* subgen. et sp. nov. and *Glyptograptus (Pseudoglyptograptus) vas* subgen. et sp. nov.

JAANUSSON (1960, p. 326) drew attention to some of the differences between the Ordovician and Silurian representatives of the genus *Pseudoclimacograptus sensu* Přibyl 1947. Whilst our examination of *Climacograptus hughesi* (Nicholson) and *C. undulatus* Kurck (the latter = *internexus* Törnquist and *extremus* H. Lapworth) largely confirms Jaanusson's remarks (op. cit., p. 327) concerning the nature of the supragenicular wall and median septum, an additional important difference is the presence, in the Silurian species, of a hood composed of microfusellar tissue (fig. 3e, *sensu* Urbanek 1966). This grows from the geniculum of each thecal tube and tends to further restrict an already narrow aperture. It is considered that the characters distinguishing the younger from the older species of *Pseudoclimacograptus* are sufficient to warrant their separation as a subgenus. The subgenus *P. (Metaclimacograptus)* is defined below, with *C. hughesi* (Nicholson) as type species.

The identification of a genicular hood in late climacograptids affords a remarkable parallel with closely similar hoods described by Urbanek (1958) in what he considers to be late representatives of the genus *Monoclimacis* Frech. It is of interest also that the tendency of these late climacograptids to form structures simulative of thecal hooks takes place at the same horizons as the first developments of thecal hooks in monograptids. Whereas in *P. (Metaclimacograptus)* the 'hook' is formed by growth of a hood from the geniculum of the succeeding theca, in *P. (Clinoclimacograptus) retroversus* subgen. et sp. nov. there is a certain amount of eversion of the aperture coupled with an indentation of the most distal part of the free ventral wall (text-fig. 5).

A similar feature is seen in *Glyptograptus (Pseudoglyptograptus) vas* subgen. et sp. nov. which closely resembles *G. (Glyptograptus)* in the nature of the geniculum, but which exhibits some eversion of the thecal aperture and has a pronounced indentation of the distal part of the free ventral wall (text-fig. 6).

The three new subgenera are late, and relatively short-lived modifications of the respective long-ranging genera.

G. (Pseudoglyptograptus) has only been recorded from the *magnus* Zone and is best regarded as a direct offshoot of *G. (Glyptograptus)* resulting from changes similar to those which led to the formation of *P. (Clinoclimacograptus)*, namely the development of an everted apertural margin and a distal indentation of the supragenicular wall.

SYSTEMATIC DESCRIPTION

Suborder DIPLOGRAPTINA Lapworth 1880 emend. Bulman 1963

Family DIPLOGRAPTIDAE Lapworth 1873

Genus PSEUDOCLIMACOGRAPTUS Přibyl 1947

Type species. Climacograptus Scharenbergi Lapworth 1876.

Amended diagnosis. Diplograptid with supragenicular walls which are usually distinctly convex, occasionally slightly convex, and rarely almost straight or concavo-convex. Median septum zigzag, angular or undulating in proximal region, sometimes becoming straighter distally. Apertural excavations short and deep, often introverted. A genicular hood present in some late representatives.

Remarks. We agree with Jaanusson in setting apart the Silurian representatives of the genus (the presence of a genicular hood is a newly recorded distinguishing feature). However, the genera exhibiting the characteristics described herein are possibly late derivatives of *Pseudoclimacograptus* and they do not in our view merit more than sub-generic distinction. Thus *C. hughesi* (Nicholson) and *C. undulatus* Kurck (= *C. extremus* H. Lapworth and *C. internexus* Törnquist) are included in a new subgenus *P. (Metaclimacograptus)*. Whilst the supragenicular wall of *P. (M.) hughesi* is almost straight (text-figs. 1a–c), that of *P. (M.) undulatus* is as convex as some Ordovician species included by Jaanusson in *Pseudoclimacograptus* s.s. (e.g. *P. a. angulatus*). The median septum of *P. (M.) undulatus* is angular, a feature noted by Jaanusson, but that of *P. (M.) hughesi* is more undulating. In *P. (Clinoclimacograptus) retroversus* the median septum is undulating in the proximal region, but distally can be almost straight. In this species the supragenicular wall retains proximally the pronounced convexity typical of *P. (Pseudoclimacograptus)*, but the apertural margin is strongly everted, tending to become almost hook-like (text-fig. 5), and the distal extremity of the supragenicular wall is concave.

The distinctive features in the thecal morphology of these late pseudoclimacograptids appear to reflect a general tendency in graptoloids at this horizon to form thecal 'hooks', whether this is by growth of a genicular hood, or by pronounced eversion of the apertural margin. The growth of a hood does not necessitate any other structural alterations, and the basic pseudoclimacograptid pattern is broadly retained and easily recognizable. It is quite possible, therefore, that *P. (Metaclimacograptus)* evolved directly from *P. (Pseudoclimacograptus)*. The angular or strongly undulating median septum may simply be a modification related to reduced size of the rhabdosome and closely packed, alternating thecae.

The second way in which a hook may be formed, namely by eversion of the aperture and indentation of the distal portion of the supragenicular wall, naturally involves more fundamental changes of thecal shape, and affinities with the type subgenus are less easily recognizable, and probably further removed, than in *P. (Metaclimacograptus)*. It is reasonable, however, to retain all these forms under *Pseudoclimacograptus*, since they possess essentially convex supragenicular walls, a climacograptid geniculum, and a median septum which can be zigzag, angular, or undulating. The following classification is, therefore, proposed:

P. (*Pseudoclimacograptus*) Přibyl 1947, type species *C. Scharenbergi* Lapworth.

P. (*Metaclimacograptus*) subgen. nov., type species *Diplograpsus Hughesi* Nicholson.

P. (*Climoclimacograptus*) subgen. nov., type species *P. (C.) retroversus* sp. nov.

It is worthy of note that in the late monoclimalacids described by Urbanek (1958) the same two tendencies can be recognized. Thus for example *Monoclimacis micropoma* (Jaekel) shows both genicular hoods and eversion of the apertural margin (see Urbanek, 1958, fig. 67A). Eversion of the apertural margin can also be seen in some early Wenlock monoclimalacids, though in these species it has not yet been established whether the genicular 'spine' is in fact a hood of microfusellar tissue.

Subgenus *P.* (PSEUDOCLIMACOGRAPTUS) Přibyl 1947

Type species. *C. Scharenbergi* Lapworth 1876.

Diagnosis. Climacograptids with convex supragenicular wall; apertural excavations short, deep, and introverted; median septum mostly zigzag.

Subgenus *P.* (METACLIMACOGRAPTUS) subgen. nov.

Type species *Diplograpsus Hughesi* Nicholson 1869.

Diagnosis. Climacograptids with gently convex or almost straight supragenicular walls; apertural excavations short, deep, introverted, and partly covered by a hood growing from the geniculum of the succeeding theca; median septum angular to undulating.

P. (Metaclimacograptus) hughesi (Nicholson)

Text-figs. 1a-c

1869 *Diplograpsus Hughesi* (Nicholson), p. 235, pl. 11, figs. 9, 10.

1906 *Climacograptus Hughesi* (Nicholson); Elles and Wood, pp. 208-10, text-figs. 140a-d, pl. 27, figs. 11a-e.

? 1924 *Climacograptus hughesi* (Nicholson); Hundt, pl. 1, figs. 8-10.

? 1934 *Climacograptus hughesi* (Nicholson); Hsü, p. 67, pl. 5, figs. 7a-c.

? 1937 *Climacograptus hughesi* (Nicholson); Harris and Thomas, pp. 69-70, pl. 1, fig. 1.

1945 *Climacograptus hughesi* (Nicholson); Waterlot, pl. 8, fig. 130.

? 1947 *Climacograptus hughesi* (Nicholson); Ruedemann, p. 428, pl. 73, figs. 30, 31.

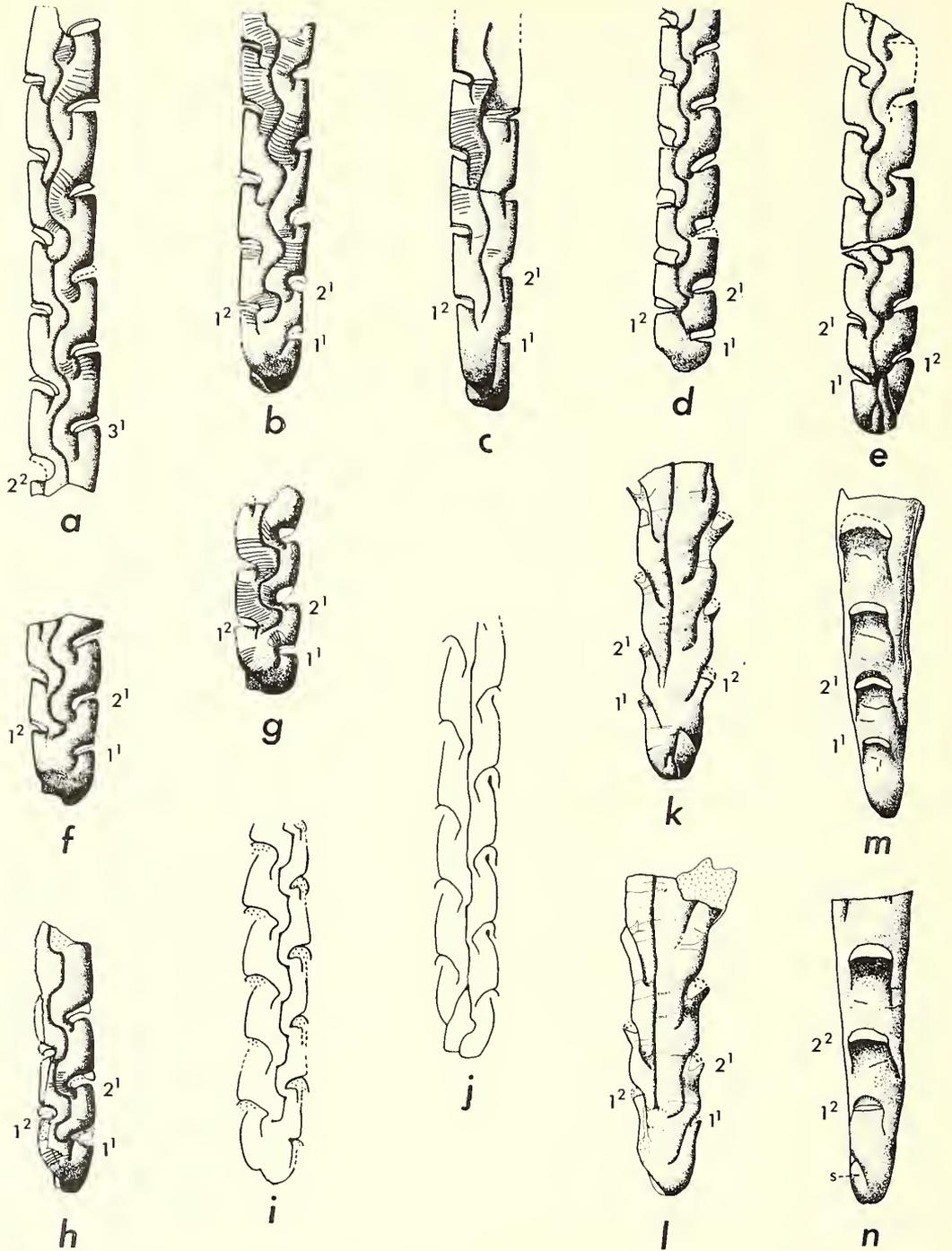
? 1965 *Climacograptus hughesi* (Nicholson, 1869); Stein, pp. 167-8 (pars), fig. 14i.

Neotype. The specimen figured by Elles and Wood 1906, pl. 27, fig. 11a. (Přibyl 1948). B.M. (N.H.) P1890.

Material. Several hundred specimens, mostly preserved in relief in pyrites, from England (Lake District, Cross Fell, Howgill Fells), Wales (Montgomeryshire, Cardiganshire), Scotland (Moffat), Ireland (Tyrone), Sweden (Tommarp), and Denmark (Bornholm).

Horizons. Llandovery Series Silurian, *acinaces-magnus* Zones of Wales, and equivalents.

Description. The tiny rhabdosome is circular in cross-section and parallel-sided after the first three or four thecae, reaching a maximum length of about 1 cm., and a width of less than 1 mm. Most specimens preserved in relief have a width of 0.5-0.6 mm. at the level of th I¹ and quickly reach a maximum of 0.6-0.7 mm. A few specimens have been seen in which the maximum width is 0.8 mm. Flattened specimens are about 1 mm. wide.



TEXT-FIG. 1a-c. *Pseudoclimacograptus* (*Metaclimacograptus*) *hughesi* (Nicholson): a, S.M. A23911, specimen in relief from *acinaces* Zone, Rheidol Gorge; b, S.M. A23912, specimen in relief from

(The theoretical width, πr , of a flattened specimen is 0.95–1.10 mm.) The proximal end is rounded and the sicula visible in obverse view for up to 0.65 mm. The total length of the sicula can be estimated from flattened specimens (in which it can sometimes be detected 'pressed through') at approximately 1 mm. The visible part of th 1^1 grows downwards for 0.2–0.3 mm. before turning upwards for a distance 0.5–0.8 mm. Th 2^1 is the dicalycal theca.

The median septum is complete. On the obverse side it extends proximally as far as the exposed portion of the sicula, whilst on the reverse side the proximal extremity of the median septum is seen curving towards th 1^2 a short distance above the proximal extremity of the $1^2/2^2$ interthecal septum (text-figs. 1*b*, *c*). In the proximal part of the rhabdosome the median septum usually undulates rather more strongly than distally, and in some of the earlier specimens (e.g. text-figs. 1*a*, *b*, of specimens from the *acinaces* Zone) there are traces of the angularity characteristic of the whole length of median septum in *P. (M.) undulatus* (Kurck) (described below). The later *hughesi* specimens, however, have a more gently undulating median septum (text-fig. 1*c*, a specimen from the *triangulatus* Zone).

The nema is only rarely prolonged beyond the distal end of the rhabdosome. Within the rhabdosome it is centrally positioned and is embedded in the median septum. In this position the median septum is straight for a short distance each side of the nema.

The thecal tubes are uniform, strongly sigmoidal, and have a short, deep excavation, whilst the supragenicular wall is almost straight, and the thecal aperture distinctly introverted. At the extreme proximal end the thecae tend to be more tightly packed and are commonly spaced as closely as 16 in 10 mm. The over-all thecal spacing is 16–12 in 10 mm. Each thecal tube exhibits a slight transverse narrowing visible in ventral view, as the aperture is approached. The thecal overlap is not more than one quarter.

A small number of specimens have been found in which a delicate genicular hood is still preserved (text-fig. 1*a*, *b*). The structure appears identical with that observed in *P. (M.) undulatus* (described below), where the hood can be shown to consist of microfussellar tissue with closely spaced growth bands and no visible zigzag suture. In both species the genicular hood is totally unconnected with the preceding thecal tube and should not be regarded as a dorsal extension of the latter. The effect of the genicular hood is to further restrict an already narrow and slit-like aperture. In general form the hood resembles the apertural lappets described in *Dicellograptus* sp. (James 1965), though of course the lappets are composed of normal fussellar tissue (compare for example text-fig. 3*e* herein with text-fig. 7 of James 1965). Like the lappets in *Dicello-*

acinaces Zone, Rheidol Gorge; *c*, S.M. A24965, specimen in relief from *triangulatus* Zone, Rheidol Gorge, listed Sudbury 1958, p. 487. *d–j*. *Pseudoclimacograptus (Metaclimacograptus) undulatus* (Kurck): *d*, S.M. A23090 specimen in relief from Upper Graptolite Shales, Tommarp, Sweden; *e, f*, respectively obverse and reverse views of S.M. A20218, specimen in moderate relief from Skelgill, Lake District; *g*, S.M. A23550, specimen in relief from *convolutus* Zone, listed Jones 1945, p. 320; *h*, S.M. A23561 specimen in relief, listed Jones 1945, p. 321; *i*, Lund, LO1111t, approximate longitudinal section prepared by Törnquist from pyritized specimen, originally figured by him 1893, fig. 27; *j*, Lund LO1110t, approximate longitudinal section of pyritized specimen prepared and figured by Törnquist 1893, fig. 26. *k–n*. *Glyptograptus (Pseudoglyptograptus) vas* subgen. et sp. nov., holotype, Geol. Surv. WEG 4058, *magnus* Zone, Cross Fell, specimen in full relief, apertures slightly damaged: *k*, obverse view; *l*, reverse view; *m*, apertural view of first series of thecae; *n*, apertural view of second series of thecae.

All figures $\times 15$.

graptus sp., each genicular hood achieves its greatest development in the lateral, not the ventral, position (text-fig. 3e).

Remarks. The distinctions of *P. (M.) hughesi* from *P. (M.) undulatus* (Kurck) are dealt with under the description of the latter species. Elles and Wood (1906) included *Climacograptus undulatus* Kurck and *C. internexus* Törnquist in their synonymy of *C. hughesi* (Nicholson). However, examination of Törnquist's (1893) specimens of *internexus* (the 1890 specimens are lost) shows that it is conspecific with *C. extremus* H. Lapworth, whilst Törnquist himself later (1897) considered that his *internexus* was conspecific with, and junior to, *C. undulatus* Kurck.

P. (Metaclimacograptus) undulatus (Kurck)

Text-figs. 1d-j, 3e

- ? 1853 *Diplograptus teretiusculus* (Hisinger); Richter, p. 456, pl. 12, figs. 11–13.
- ? 1871 *Diplograptus teretiusculus* (Hisinger); Richter, pl. 5, figs. 5–7.
- 1882 *Climacograptus undulatus* Kurck, p. 303, pl. 14, fig. 11.
- 1890 *Climacograptus internexus* Törnquist, p. 25, pl. 2, figs. 8, 9.
- 1893 *Climacograptus internexus* Törnquist; Törnquist, p. 6, figs. 23–27.
- 1897 *Climacograptus undulatus* Kurck; Törnquist, pp. 9–10, pl. 1, figs. 22–44.
- 1900 *Climacograptus extremus* H. Lapworth, pp. 134–5, figs. 22A–B.
- 1906 *Climacograptus extremus* H. Lapworth; Elles and Wood, pp. 210–11, text-figs. 141a–c, pl. 27, figs. 13a–b.
- ? 1947 *Climacograptus* cf. *extremus* H. Lapworth; Ruedemann, pp. 426–7, pl. 72, figs. 20, 21.

Holotype. Kurck's original figure (pl. 14, fig. 11) would seem to be a somewhat idealized drawing of a specimen upon what is known to be his type slab (LO479T). There are numerous specimens of *undulatus* on this slab but only one specimen is a reverse view with ten thecal pairs developed.

Horizon of Holotype. *Cyphus* Zone, Bollerup, Sweden.

Material. Many specimens in relief, infilled with pyrites, from England (the Lake District, Cross Fell, Howgill Fells), Wales (Montgomeryshire, Cardiganshire), and Sweden (Tommarp and Bollerup).

Horizons. Llandovery Series, *cyphus-sedgwickii* Zones, ? *turriculatus* Zone.

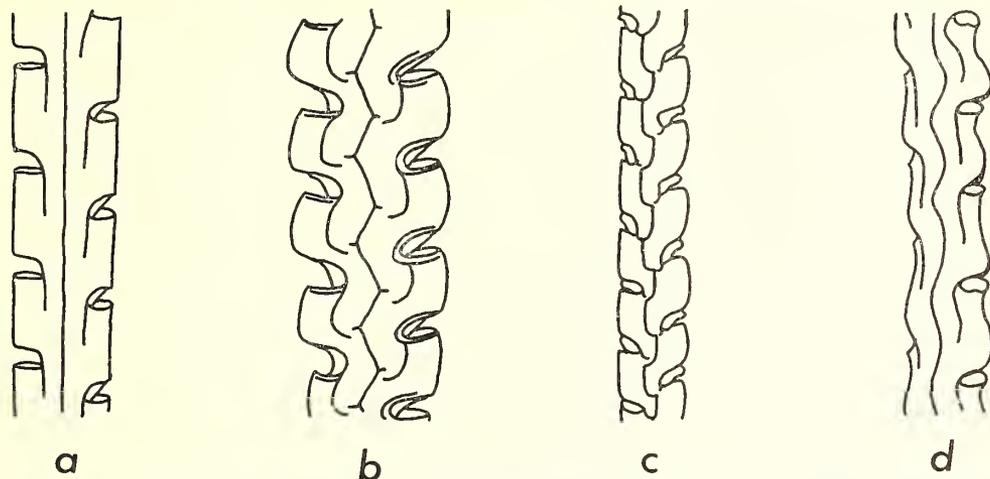
Description. *P. (M.) undulatus* is one of the smallest known climacograptids, having a length usually less than 7 mm. and a maximum width, in relief, of 0.5–0.6 mm. At the level of the th 1¹ the width is 0.4–0.5 mm. The rhabdosome is circular in cross-section. Both H. Lapworth (1900) and Elles and Wood (1906) considered the sicula to be completely enveloped by the early thecae, but it would seem that they were familiar only with the reverse aspect of the species, for in obverse view the sicula is visible for fully half a millimetre (text-fig. 1e). The total length of the sicula is unknown. The visible portion of th 1¹ grows downwards for a distance of approximately 0.3 mm. before turning upwards just below the level of the sicular aperture. The thecae are small, closely packed, and exhibit strong sigmoidal curvature with a typically climacograptid geniculum. The excavation is short and deep and the thecal apertures are introverted. Each thecal tube shows a slight transverse narrowing, visible in ventral view, as the aperture is approached (text-fig. 3e). The thecal overlap does not exceed $\frac{1}{5}$ – $\frac{1}{6}$.

Well preserved specimens show the presence of a genicular hood. Text-fig. 3e illustrates a particularly good specimen in which the form of the hood can be seen. The hood which grows from the geniculum of th 8² (i.e. overhanging the aperture of th 7²)

exhibits closely spaced growth-lines. These are much closer together than the growth-lines of normal fusellar tissue, and the hood is almost certainly composed of micro-fusellar tissue.

At the proximal end the thecae are slightly more closely spaced at about 18–20 in 10 mm. whilst the over-all thecal spacing is 15–20 in 10 mm.

The median septum is complete and angular throughout the length of the rhabdosome. On the obverse side of the rhabdosome it originates at the distal end of the exposed portion of the sicula (text-fig. 1e), whilst in reverse aspect it first appears slightly above the proximal



TEXT-FIG. 2. Diagrammatic comparison of some climacograptid thecal types: a, *Climacograptus* s.str.; b, *Pseudoclimacograptus* (*Pseudoclimacograptus*); c, *P.* (*Metaclimacograptus*) subgen. nov.; d, *P.* (*Climoclimacograptus*) subgen. nov. Approximately $\times 15$.

extremity of the $1^2/2^2$ interthecal septum (text-fig. 1f, g) and, as in *hughesi*, the 2^1 is the dicalycal theca. In one recorded instance (text-fig. 1h) it seems to originate closer to the first series of thecae at about the level of the aperture of th 1^1 . Even in the absence of growth-line evidence it would seem that this specimen is abnormal and that th 1^2 must be the dicalycal theca.

The angularity of the median septum is quite unlike the zigzag septum of earlier pseudoclimacograptids. If the median septum is considered, for example, in relation to th 8^2 of text-fig. 3e it will be seen that the median septum is *concave towards* the early part of th 8^2 and *convex towards* the later part of th 8^2 .

Remarks. It is possible that *P.* (*M.*) *undulatus* is a direct descendant of *P.* (*M.*) *hughesi*. An incipient angular median septum is detectable in some earlier (*acinaces* Zone) specimens of the latter species (text-figs. 1a, b). *P.* (*M.*) *undulatus* may have separated from *P.* (*M.*) *hughesi* at about this level, for the first specimens with a completely angular median septum are recorded at the base of the *triangulatus* Zone.

It may be possible to interpret the evolution of the median septum in terms of the general climacograptid evolution. Silurian climacograptids are mostly smaller and narrower than the Ordovician representatives of the genus, whilst the latest climacograptids in each group are very tiny (e.g. *P.* *undulatus*, *Climacograptus miserabilis*,

C. innotatus). The angular median septum exhibited by *P. (M.) undulatus* is more efficient in terms of close packing of tiny, alternating thecal tubes than either the undulating or zigzag types of earlier pseudoclimacograptids. *P. (M.) undulatus* is the smallest (and last) pseudoclimacograptid known at present. (The last of the climacograptids, an aseptate form as yet undescribed, is of similar dimensions to *P. (M.) undulatus* and occurs towards the top of the Llandovery Series in the Lake District.)

The main distinguishing features between *undulatus* and *hughesi* may be summarized as follows:

- a. *undulatus* is shorter and narrower than *hughesi*;
- b. the thecae are more closely spaced and have less overlap than in *hughesi*;
- c. the supragenicular wall in *hughesi* is usually almost straight;
- d. the median septum of *undulatus* is angular, not undulating.

Subgenus *P. (CLINOCLIMACOGRAPTUS)* subgen. nov.

Type species. P. (C.) retroversus sp. nov.

Diagnosis. Climacograptid with proximally convex and distally concave supragenicular walls; apertures strongly everted so that they face ventrally; median septum gently undulating in the proximal region, often almost straight distally.

P. (Clinoclimacograptus) retroversus subgen. et sp. nov.

Text-figs. 3a-c, 4a-c, 5.

1893 *Climacograptus scalaris* (Hisinger); Törnquist, pp. 2-6, figs. 1-3, 5-8, 11-15, ? 4, 9, 10, 16-22.

non 1890 *Climacograptus scalaris* (Hisinger); Törnquist, p. 23, pl. 11, figs. 12-15.

Holotype. A specimen in the Elles collection (Sedgwick Museum, A52951), text-fig. 4b.

Horizon and locality of holotype. Upper Graptolite Shales, Tommarp, Sweden. The assemblage on the slab suggests *sedgwickii* Zone.

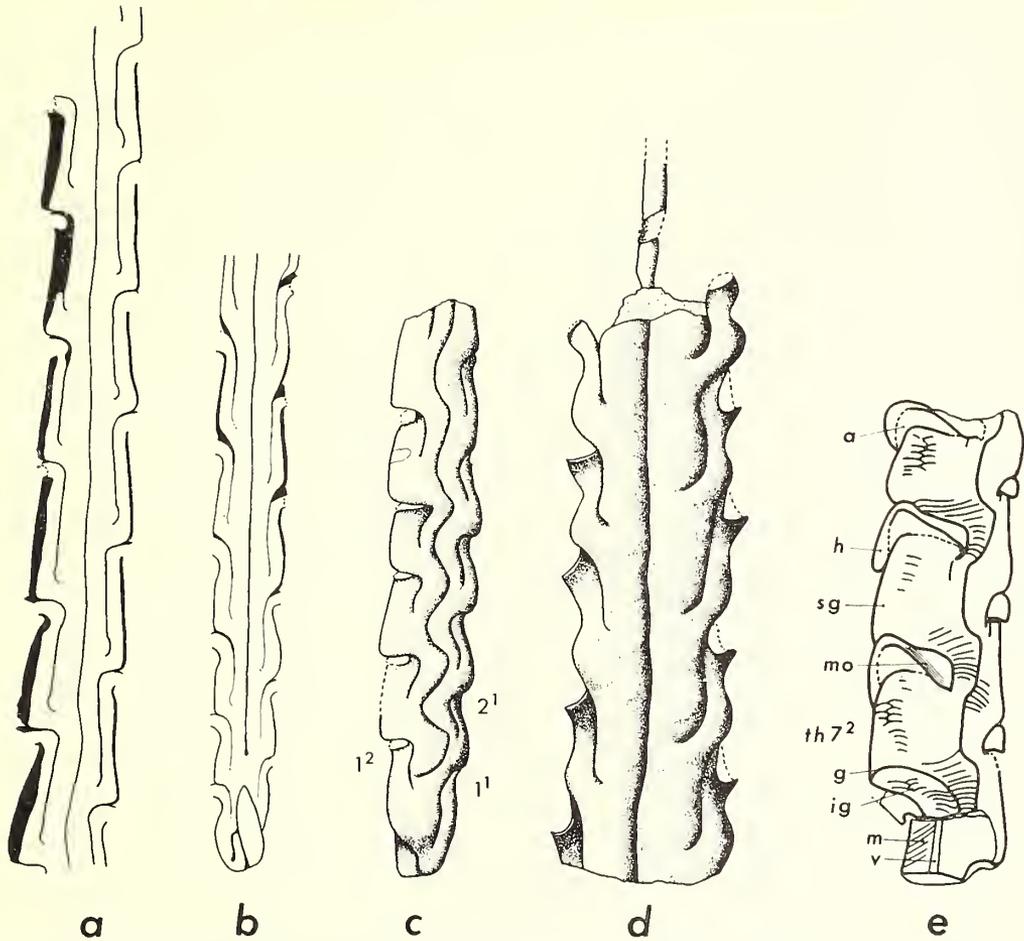
Material. Several hundred specimens in relief, flattened, or both (text-fig. 4b).

Derivation of name. Refers to the almost hook-like thecal apertures.

Horizons and localities. *Triangulatus* Zone, Rheidol Gorge (horizon F of Sudbury 1958); *magnus* Zone, Cross Fell; *convolutus* Zone, Cross Fell and Coalpit Bay, Ireland; *sedgwickii* Zone, Howgill Fells (Lake District) and Tommarp (Sweden).

Description. The rhabdosome is circular in cross section, up to 2.5 cm. in length and reaches a maximum width (in relief) of 1.0 mm. Some specimens exhibit a distal reduction in width, whilst the majority of specimens are about 0.8 mm. wide throughout most of their length. The proximal end is rounded and possesses a short virgella. In obverse aspect (text-fig. 4c) the sicula is visible for up to 0.8 mm. of its total length, which is approximately 1.3 mm. The sicula is visible in reverse view for about 0.3 mm. Th 1¹ is first seen 0.3 mm. above the sicular base and grows down to the level of the sicular aperture before turning upwards.

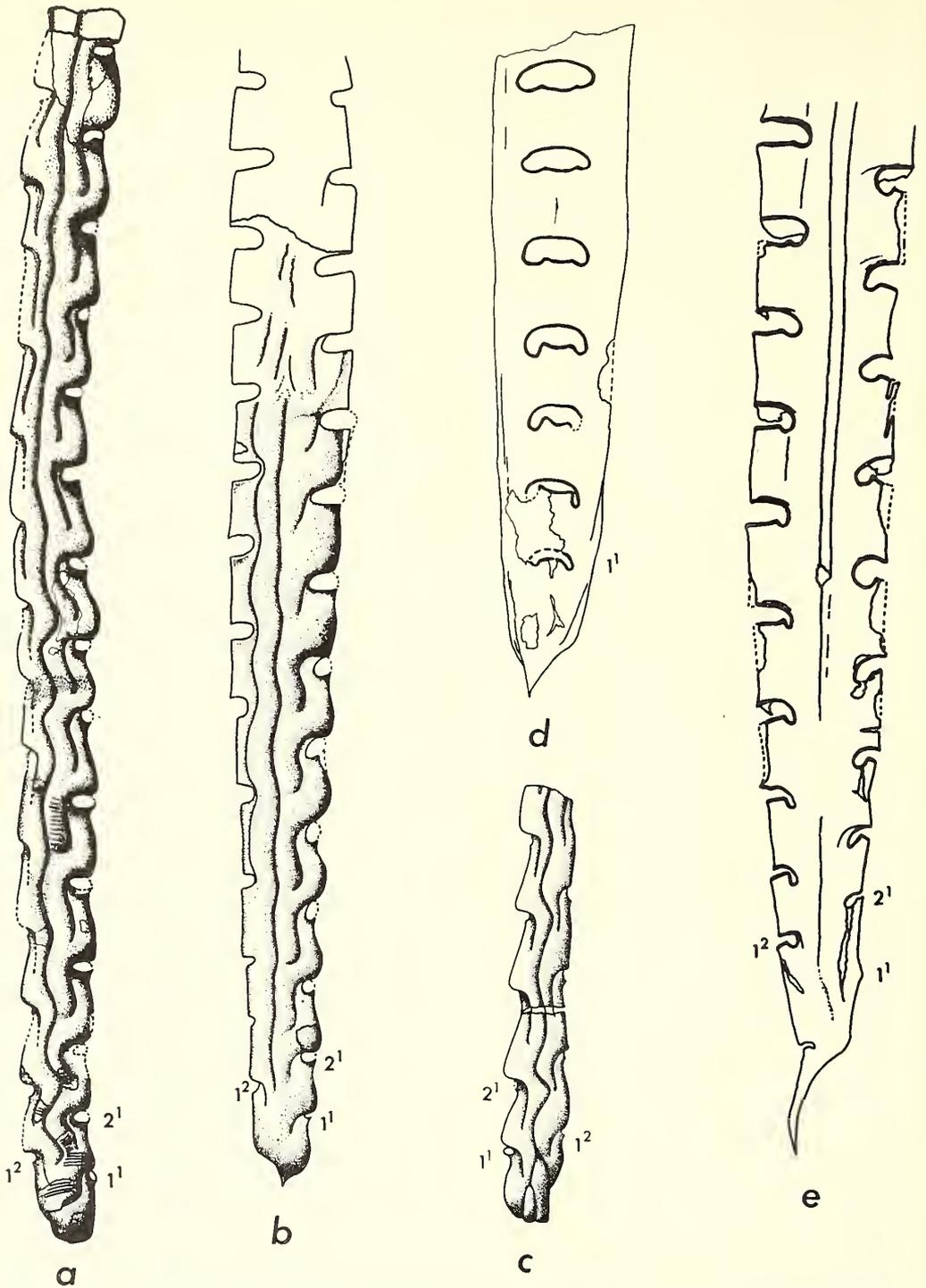
The median septum is complete. On the obverse side it extends proximally as far as the exposed portion of sicula (text-fig. 4c), whilst on the reverse side the proximal



TEXT-FIG. 3a-c. *Pseudoclimacograptus* (*Climoclimacograptus*) *retroversus* subgen. et sp. nov. $\times 15$: a, Lund LO1096t, approximate longitudinal section prepared and figured by Törnquist 1893, fig. 6; b, Lund LO1097t, longitudinal section close to nema prepared and figured by Törnquist 1893, figs. 7 and 8; c, S.M. A24939 internal mould somewhat compressed along its length, *triangulatus* Zone (horizon F), Rheidol Gorge, listed Sudbury 1958 as *Climacograptus lughesi*. d. *Glyptograptus* (*Pseudoglyptograptus*) *vas* subgen. et sp. nov., distal end of holotype, Geol. Surv. no. WEG 4058, *magnus* Zone, Cross Fell. $\times 15$. e. *Pseudoclimacograptus* (*Metaclimacograptus*) *undulatus* (Kurck), subapertural view of part of S.M. A52953, from Upper Graptolite Shales, Tommarp, Sweden; a, apertural region; h, hood; sg, supragenicular wall; mo, microfusellar tissue; g, geniculum; ig, infragenicular wall; m, median septum; v, virgula. $\times 30$.

extremity curves towards the second thecal series just below the level of the aperture of $th\ 2^2$, but above the level of the proximal end of the $1^2/2^2$ interthecal septum (text-figs. 3c, 4a, b). It is probable, therefore, that $th\ 2^1$ is the dicalycal theca. The median septum is more or less straight distally, but in the proximal region varies from strongly to gently undulating (compare text-figs. 3a and b).

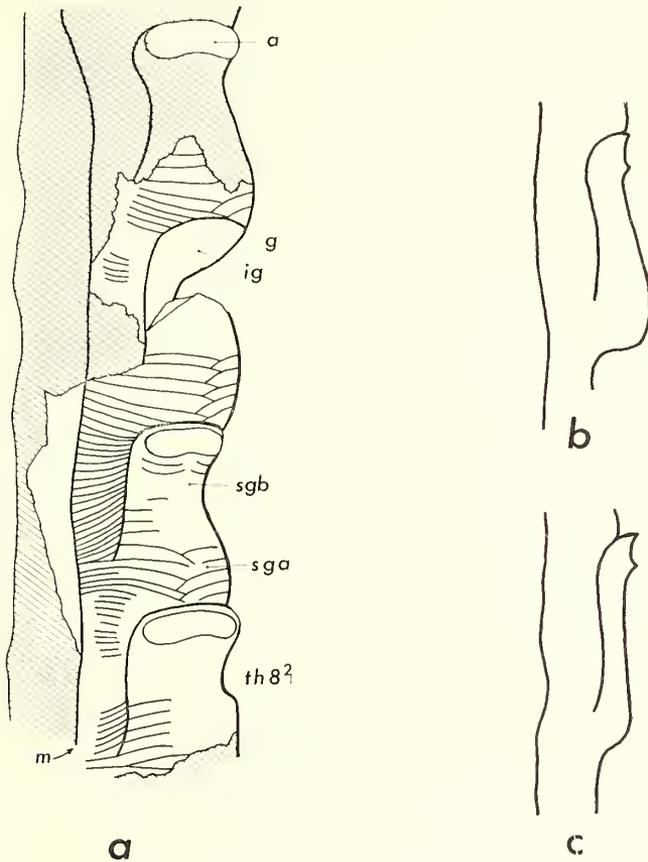
The thecae are uniform, strongly sigmoidal, and have a climacograptid geniculum. The supragenicular wall is at first convex and, as the thecal aperture is approached,



TEXT-FIG. 4a-c. *Pseudoclimacograptus* (*Clinoclimacograptus*) *retroversus* subgen. et sp. nov.: a, S.M. A23951 from *sedgwickii* Zone, Spengill, Westmorland, subapertural view; b, holotype, S.M. A52951, specimen preserved in relief proximally, and distally flattened, Elles Colln., Tommarp, Sweden, probably *sedgwickii* Zone; c, Geol. Surv. no. WEG 4052, *magnus* Zone, Cross Fell, specimen in full relief. d-e. *Climacograptus scalaris*, sensu Törnquist 1890. d, apertural view of flattened specimen on same slab as 'e'; e, Lund, LO935t proximal end of flattened specimen originally figured by Törnquist 1890, pl. 2, fig. 12.

All figures $\times 15$.

becomes concave (text-fig. 5). The thecal apertures are strongly everted. Thecal overlap is about one-half. In the proximal region the thecae are more closely spaced (12–13 in 10 mm.) than distally, where they number 10 in 10 mm.

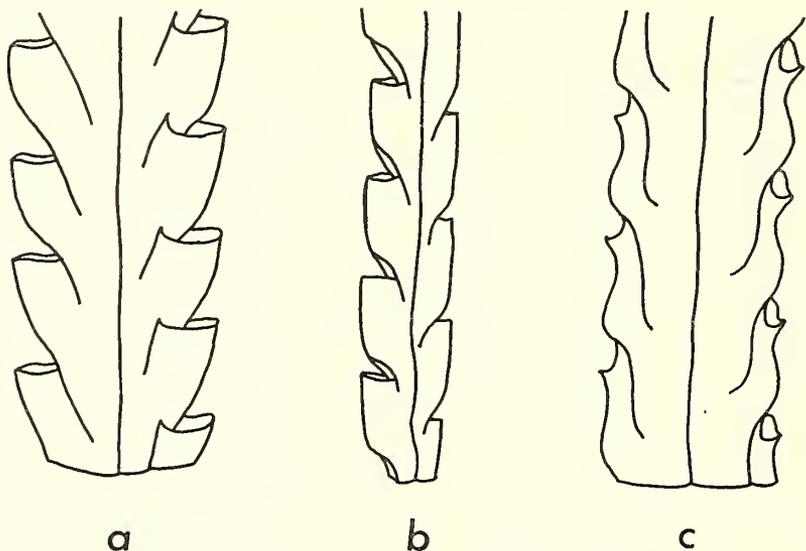


TEXT-FIG. 5. *Pseudoclimacograptus* (*Clinoclimacograptus*) *retroversus* subgen. et sp. nov., S.M. A52952, Elles Colln. *a*, subapertural view of part of specimen preserved in relief infilled with pyrites. Periderm (oblique ruling) has been removed to reveal growth-lines on the pyrite internal mould. Thecal aperture of th 10² has been removed to reveal infragenicular wall of th 11² (ig); m, median septum; sga, supragenicular wall, convex part; sgb, supragenicular wall, concave part; g, geniculum; a, thecal aperture. $\times 30$; *b*, *c*, longitudinal sketch sections, respectively at the level of the zigzag suture and close to the lateral margin of the rhabdosome, to show the form of the 'hooks'.

Remarks. The above description deals with specimens preserved in relief, where thecal details can be ascertained with relative ease. A disconcerting feature of this species, however, is that upon flattening the peculiar and characteristic features (concavo-convex supragenicular wall, and ventrally facing apertures) become unrecognizable. The holotype (text-fig. 4*b*) is a specimen preserved in relief proximally and flattened distally. The distal end is quite indistinguishable from a flattened rhabdosome of an ordinary climacograptid, and were it not for these relatively rare specimens preserved both flattened and in relief, the flattened forms might easily be referred to '*Climacograptus*'.

scalaris' *sensu lato*. It will be noted also that the holotype is preserved as a subapertural view of the first thecal series: since the rhabdosome is almost circular in cross-section the preservation of a specimen flattened in true profile must be subject to a large element of chance. It is possible that a true-profile, flattened specimen might show the concavo-convex supragenicular wall.

Examination of Törnquist's (1893) specimens of *C. scalaris* shows them to be referable to *P. (C.) retroversus* and to be quite distinct from his 1890 specimens of *C. scalaris* (text-figs. 4*d, e* herein). These latter forms have an Ordovician aspect, and it is uncertain if these are conspecific with the true *C. scalaris* (Hisinger).



TEXT-FIG. 6. Diagrammatic comparison of *Glyptograptus (Pseudoglyptograptus)*, *c*, with *G. (Glyptograptus)*, *a* and *b*, approximately $\times 15$.

P. (C.) retroversus is a common fossil in the *convolutus* and *sedgwickii* Zones, and it seems probable that some of the recordings of *C. scalaris* from these levels really indicate the presence of flattened specimens of *retroversus*. *C. scalaris* was regarded by Elles and Wood as a relatively uncommon species.

P. (C.) retroversus is a long-ranging species and it is possible when further material is available from the *triangulatus* and *magnus* Zones that the species may be subdivisible into several stratigraphically useful forms.

Genus GLYPTOGRAPTUS Lapworth 1873

Type species. Diplograptus tamariscus Nicholson 1868.

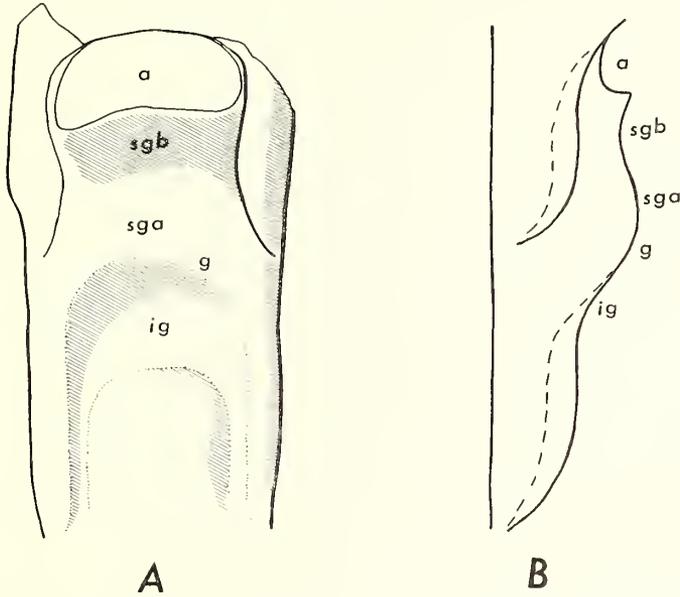
Amended diagnosis. Thecae with gentle sigmoidal curvature; supragenicular wall almost straight, sloping outwards, or rarely with gentle double (concavo-convex) curvature; apertural margins horizontal, undulate, or rarely everted; rhabdosome cross-section ovoid or nearly circular.

Remarks. The generic diagnosis is amended to include the form *Glyptograptus (Pseudoglyptograptus) vas* subgen. et sp. nov.

Subgenus G. (GLYPTOGRAPTUS) Lapworth 1873

Type species. *Diplograpsus tanuariscus* Nicholson 1868.

Diagnosis. Thecae with gently sigmoidal curvature, apertural margins commonly undulate; cross-section ovoid or nearly circular.



TEXT-FIG. 7A, B. Apertural and lateral views of a manually isolated thecal tube of *Glyptograptus (Pseudoglyptograptus) vas* subgen. et sp. nov., partially diagrammatic, S.M. A52958. a, thecal aperture; sga, supragenicular wall, convex portion; sgb, supragenicular wall, concave portion; g, geniculum; ig, infragenicular wall; dashed lines indicate course of thecal tube in the prothecal groove, full explanation in text. $\times 30$.

Subgenus G. (PSEUDOGLYPTOGRAPTUS) subgen. nov.

Type species. *G. (P.) vas* sp. nov.

Diagnosis. A glyptograptid distinguished by its concavo-convex supragenicular wall, strongly everted aperture, and a sub-apertural, transverse constriction.

G. (Pseudoglyptograptus) vas sp. nov.

Text-figs. 1k-n, 3d, 7a, b

Holotype. WEG4058, a specimen preserved in the Geological Survey Museum (Leeds), fig. 1k-u, 3d.

Horizon of holotype. *Magnus* Zone, Llandovery Series.

Derivation of name. (L.) *vas*, vase-shaped, referring to the ventral thecal aspect.

Horizon and localities. *Magnus* Zone, Howgill Fells and Cross Fell.

Material. Four well-preserved specimens in full relief (WEG4058; A52956-8); and other fragmentary or poorly preserved specimens.

Description. The maximum observed rhabdosome length is 3.5 cm., which includes a distally projecting nema of at least 1 cm. The rhabdosome has a circular cross-section. At a distance of 5 mm. from the rounded proximal end the rhabdosome attains a width of 1.0 mm. and thereafter widens steadily to 1.8 mm. at 2.5 cm. The thecae number 11-12 in 10 mm. at the proximal end, and about 9-10 in 10 mm. distally. In the obverse view of the holotype (text-fig. 1*k*) the sicula is visible for 0.6 mm. of its total length, which is unknown. The visible part of the 1¹ grows down from 0.3 mm. to the level of the sicular aperture (text-fig. 1*k*) before turning upwards.

The proximal extremity of the median septum, in obverse view (text-fig. 1*k*), extends close to the 2¹/3¹ interthecal septum. In reverse aspect it reaches to just below the level of the 1² thecal aperture (text-fig. 1*l*). This suggests that th 2¹ is the dicalycal theca: th 2² and 3¹ appear to originate almost simultaneously from th 2¹. There is no growth-line evidence available. The median septum is almost straight.

The thecae are strongly sigmoidal, with a glyptograptid genicular angle. In apertural view the width of the metathecal portion is somewhat narrower than the rhabdosome width (text-fig. 7*A*), whilst the whole metatheca fits into a pronounced hollow in the succeeding protheca (text-fig. 7*A*, *B*). The thecal tubes, therefore, have a somewhat greater volume than is apparent in lateral view. The supragenicular wall is convex immediately above the geniculum, but as the apertural lip is approached becomes strongly concave. Moreover, immediately below the thecal aperture the metathecal tube exhibits a pronounced transverse narrowing, so that the thecal tube in ventral view has a vasiform appearance (text-fig. 7*A*). The aperture is strongly everted.

Remarks. A comparison of text-figs. 5 and 7 emphasizes that a similar stage has been reached in both late pseudoclimacograptids and late glyptograptids. The pseudoclimacograptid lacks the flowing geniculum and ventral, prothecal groove of *G. (P.) vas*.

Acknowledgements. We are indebted to Dr. I. Strachan for his valuable suggestions, and to Dr. A. Rushton for information on Irish graptolites. Dr. H. W. Ball (British Museum), Mr. A. G. Brighton (Sedgwick Museum), Mr. R. V. Melville (Geological Survey), and Professor C. Régnell (Lund University) kindly loaned us specimens in their care. Specimens from the above museums have their catalogue numbers prefixed as follows: B.M. (N.H.), British Museum (Natural History); S.M., Sedgwick Museum; WEG, Geological Survey; LO, Lund. Dr. Adam Urbanek has kindly given us permission to use his term *microfusellar tissue*, which will be fully defined by him in the near future.

REFERENCES

- ELLES, G. L., and WOOD, E. M. R. 1906. A monograph of British graptolites. *Palaeontogr. Soc. [Monogr.]*. Part 5, 181-216, pls. 26-27.
- HARRIS, W. J., and THOMAS, D. E. 1937. Victorian Graptolites (New Series), Pt. 4. *Min. Geol. J.* **1**, 68-79.
- HSÜ, S. C. 1934. The graptolites of the Lower Yangtze Valley. *Monogr. Nat. Research Inst. Geol. A.* **4**, 1-106.
- HUNDT, R. 1924. *Die Graptolithen des deutschen Silurs*. Leipzig.
- JAANUSSON, V. 1960. Graptoloids from the Ontikan and Viruan (Ordov.) limestones of Estonia and Sweden. *Bull. geol. Instn. Univ. Uppsala*, **38**, 290-366.
- JAMES, J. 1965. The development of a dicellograptid from the Balclatchie Shales of Laggan Burn. *Palaeontology*, **8**, 41-53.

- JONES, W. D. V. 1945. Valentian succession around Llanidloes, Montgomeryshire. *Q. Jl. geol. Soc. Lond.* **100**, 309–32.
- KURCK, C. 1882. Några nya Graptolitarter från Skåne. *Geol. För. Stockh. Förh.* **6**, 294–304.
- LAPWORTH, H. 1900. The Silurian Sequence of Rhayader. *Q. Jl. geol. Soc. Lond.* **56**, 67–137.
- NICHOLSON, H. A. 1869. On some new species of graptolites. *Ann. Mag. nat. Hist.* (4), **4**, 231–42.
- PŘIBYL, A. 1947. Classification of the Genus *Climacograptus* Hall, 1865. *Bull. intern. Acad. ichèque Sci.* **58**, 1–12.
- RICHTER, R. 1853. Thüringische Graptolithen. *Z. dt. geol. Ges.* **5**, 439–64.
- 1871. Aus dem thüringischen Schiefergebirge. *Ibid.* **23**, 231–56.
- RUEDEMANN, R. 1947. Graptolites of North America. *Mem. geol. Soc. Amer.* **19**, 652 pp. Baltimore.
- STEIN, V. 1965. Stratigraphische und paläontologische Untersuchungen im Silur des Frankenwaldes. *Nenes. Jb. Geol. Paläont. Abh.* **121**, 111–200.
- SUDBURY, E. 1958. Triangulate Monograptids from the *Monograptus gregarins* zone of the Rheidol Gorge. *Phil. Trans.*, B. **241**, 485–555.
- TÖRNQUIST, S. L. 1890. Undersökningar öfver Siljansområdets graptoliter. 1. *Acta Univ. lund.* **26**, 1–33.
- 1893. Observations on the structure of some Diprionidae. *Ibid.* **29**, 1–14.
- 1897. On the Diplograptidae and Heteroprionidae of the Scanian Rastrites Beds. *Ibid.* **33**, 1–24.
- URBANEK, A. 1958. Monograptidae from erratic boulders of Poland. *Palaeont. pol.* **9**, 104 pp. Warszawa.
- 1966. On the morphology and evolution of the Cucullograptinae (Monograptidae, Graptolithina). *Acta palaeont. pol.* **11**, 291–544.
- WATERLOT, G. 1945. Les Graptolithes du Maroc; Première partie: généralités sur les Graptolithes. *Notes Mém. Serv. Mines Carte géol. Maroc*, **63**.

O. M. B. BULMAN
Sedgwick Museum,
Cambridge

R. B. RICKARDS
Trinity College,
Dublin

Typescript received 15 September 1966

PROPECTINATITES, A NEW LOWER KIMMERIDGIAN AMMONITE GENUS

by JOHN C. W. COPE

ABSTRACT. *Propectinatites websteri* gen. et sp. nov., sub-family Virgatosphinctinae, from the Autissiodorensis Zone of the Lower Kimmeridge Clay of Dorset, is described and figured. Dimorphism is recognized in this genus.

SYSTEMATIC collecting of the perisphinctid ammonites from the type section of the Kimmeridge Clay in Dorset has shown that the lower part of the Upper Kimmeridge Clay is characterized by an evolutionary sequence of species of the genus *Pectinatites*. The earliest specimens of this genus appear to occur at the base of the Elegans Zone, above the highest recorded *Aulacostephanus* (Cope 1967). A search for earlier forms was made in the underlying Autissiodorensis Zone (Ziegler 1962), where perisphinctid ammonites are rare and generally very poorly preserved. One horizon yielded well preserved (though crushed) forms, apparently belonging to a new genus named here *Propectinatites*.

SYSTEMATIC DESCRIPTIONS

Order AMMONITIDA

Family PERISPINCTIDAE

Sub-family VIRGATOSPINCTINAE Spath 1923

Genus PROPECTINATITES gen. nov.

Type species. Propectinatites websteri sp. nov.

Diagnosis. Evolute dimorphic coarse-ribbed ammonites of the sub-family Virgatosphinctinae. Macroconch diameter approximately 150 mm., microconch diameter approximately 90–100 mm. Microconch peristome bears a short pair of lappets. Ribs mainly bifurcate, having a rather ‘untidy’ appearance, with occasional simple and polygyrate ribs.

Remarks. The genus bears some resemblance to the genus *Pectinatites* Buckman, and in particular to species of the subgenus *Arkeillites* Cope. The differences between the latter subgenus and *Propectinatites* are that *Propectinatites* is more coarsely ribbed throughout development; and that the microconchs of *Propectinatites* bear lappets, whereas the microconchs of *Arkeillites* are horned. However, in *Pectinatites (Arkeillites) primitivus* Cope the peristome of the microconch is only feebly inflated ventrally. As this latter species occurs in the lower and middle parts of the Elegans Zone (i.e. is only a little younger geologically than *Propectinatites*) it seems possible that *Propectinatites* evolved into *Pectinatites* by the base of the Elegans Zone, by development of somewhat finer ribbing and loss of the lappets, these being replaced by a ventral peristomal inflation leading to the development of a true ‘horn’ by the end of the Elegans Zone.

There are few published records of any reliability on the ammonite fauna of the Autissiodorensis Zone of Dorset. Among the more recent, Arkell (1947, pp. 66, 73) recorded *Lithacoceras* from these beds, and Ziegler (1962, p. 13) recorded *Subplanites rueppellianus* (Quenst.). The author has been unable to find any evidence for the existence of either of these genera. As shown elsewhere (Cope 1967), the genera *Subplanites* Spath and *Lithacoceras* Hyatt do not occur in the Upper Kimmeridge Clay of Britain. The ammonites there are species of *Pectinatites*, to a large extent homeomorphic with the former Tithonian genera. The author believes that *Propectinatites* is the ammonite genus which Ziegler and Arkell identified with the Tithonian genera. There is certainly a resemblance between the macroconch of *Propectinatites websteri* and *Subplanites rueppellianus*. This latter species, however, is based on lappeted (therefore microconch) specimens. The resemblances are thus between Tithonian microconchs and Kimmeridgian macroconchs, and the similarity must be regarded as homeomorphy.

Propectinatites websteri gen. et sp. nov.

Plate 1, figs. 1, 2

Material. Four specimens (one macroconch, three microconchs). The type specimens are deposited in the British Museum (Natural History).

Holotype. Macroconch BM C. 73731.

Paratypes. Microconch BM C. 73732 and two other microconchs.

Horizon. All the specimens were obtained from shales 30 ft. above the Washing Ledge Stone Band; *Aulacostephanus autissiodorensis* Zone, Lower Kimmeridgian.

Locality. Brandy Bay, Kimmeridge, Dorset.

Description

Macroconch. Moderately evolute shell with a diameter of about 150 mm. The holotype has a diameter of 152 mm., but part of the outer whorl, half a whorl back from the peristome, has broken and the complete diameter was probably about 158 mm. All the specimens of this species are crushed and so the diameter is larger than would be the case if the ammonites had been preserved solid. The umbilical diameter of the holotype (probably unaffected by the crushing) is 75 mm. At 15 mm. diameter there are 26 ribs; at 20, 26; 25, 27; 30, 28; 35, 28; 40, 29; 45, 30; 50, 31; 55, 32; 60, 33; 65, 34. The outer whorl has 37 primary and 77 secondary ribs.

The ribs on the inner whorls are rectiradiate at the umbilical shoulder, they then swing forwards to become slightly prorsiradiate and more or less straight for the remainder of their length. The point of bifurcation of the ribs is fairly high on the whorl-side and for the most part is not visible on the innermost whorls. The umbilical seam uncoils over the last half-whorl and the point of bifurcation of the ribs is thus readily visible on the penultimate whorl.

The ribs on the outer whorl are rather irregular and have an 'untidy' appearance. They become coarser and have a wide angle of furcation. Occasional simple and polygyrate ribs are developed.

The peristome, though slightly damaged, is seen to be simple. The suture line is unknown.

Microconch. Moderately evolute shell having a diameter of 90–100 mm. Diameter of the umbilicus 37–47 mm. The last whorl of the paratype, which is 92 mm. in diameter and has an umbilical diameter of 42 mm., has 37 primary and an estimated 67 secondary ribs. At 15 mm. diameter the paratype has 26 ribs; at 20, 27; 25, 27; 30, 28; 35, 29; 40, 31.

The ribs of the inner whorls are similar in style to those of the macroconch. On the outer whorl the forward inclination is not so pronounced, and the ribs approach the rectiradiate condition. The point of bifurcation of the ribs is not visible on the innermost whorls, but the uncoiling of the umbilical seam over the last half to five-eighths of a whorl renders it visible on the penultimate whorl.

On the outer whorl the ribs become more coarse than those of the inner whorls, and occasional simple ribs are developed. The peristome bears lateral lappets which on one of the paratypes project forwards by some 9 mm.

Remarks. The general similarity of the two forms, their very similar rib density, and their occurrence at the same horizon leave no doubt that the macroconch and microconch figured belong to the same species.

REFERENCES

- ARKELL, W. J. 1947. The geology of the country around Weymouth, Swanage, Corfe, and Lulworth. *Mem. geol. Surv. U.K.*
- COPE, J. C. W. 1967. The palaeontology and stratigraphy of the lower part of the Upper Kimmeridge Clay. *Bull. Br. Mus. Nat. Hist. (Geol.)* **15**, 1–79, pl. 1–33.
- ZIEGLER, B. 1962. Die Ammoniten-Gattung *Aulacostephanus* im Oberjura. *Palaeontographica*, **119A**, 1–172, pls. 1–22.

JOHN C. W. COPE
Department of Geology,
University College,
Swansea,
Wales

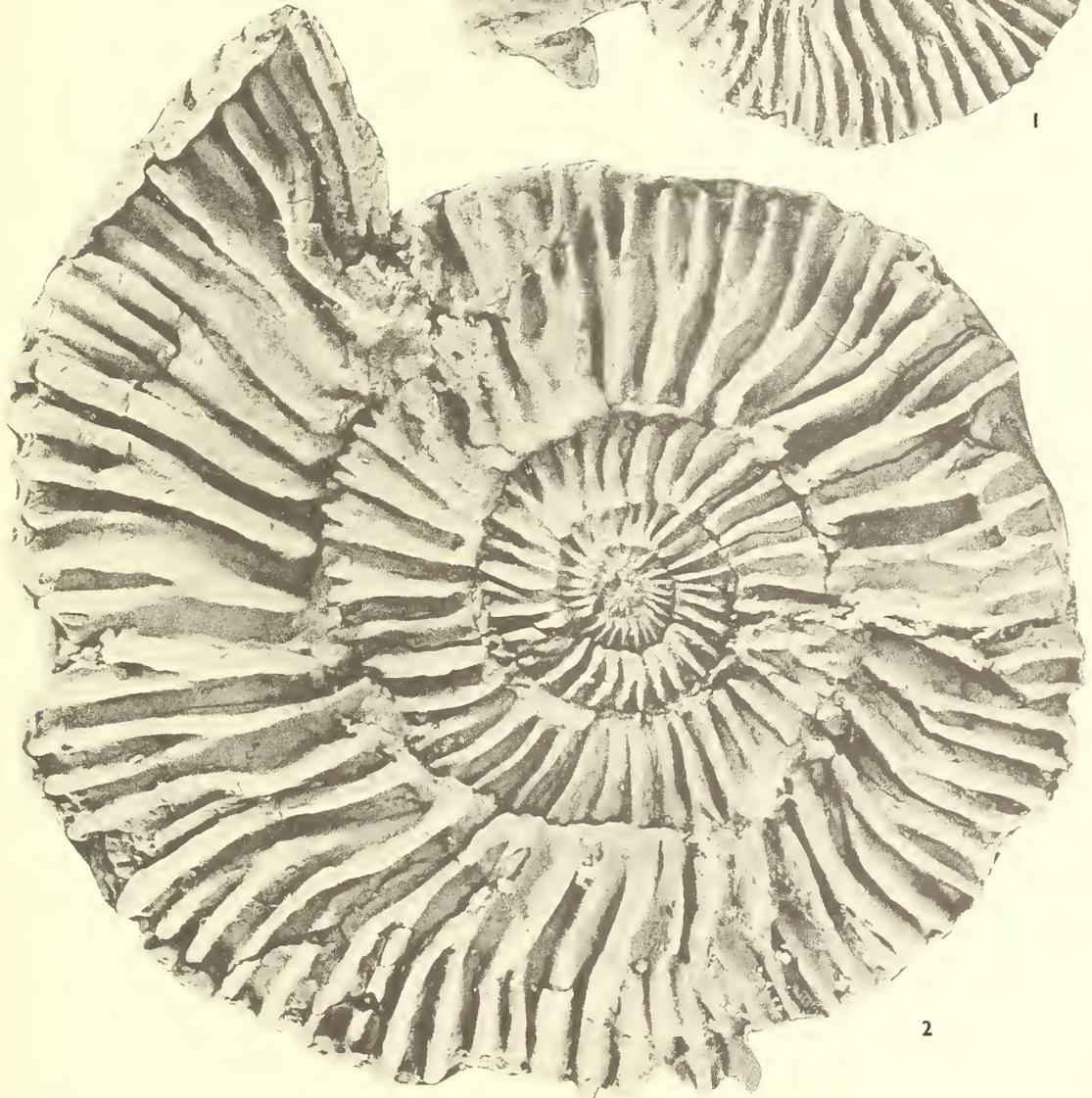
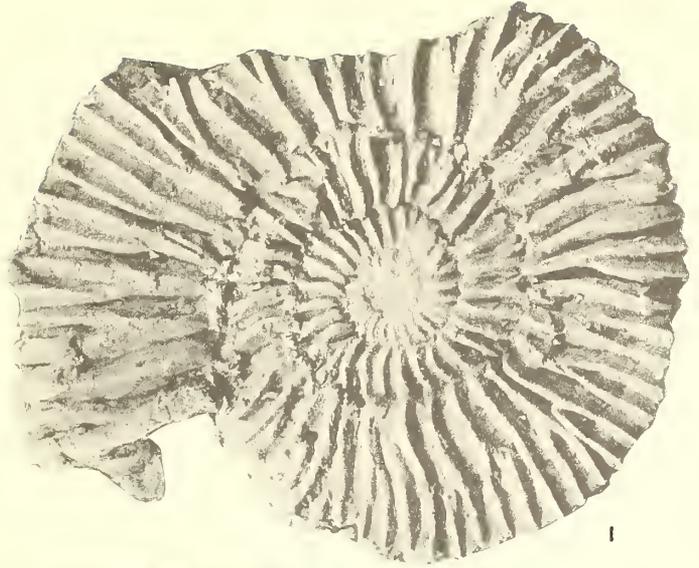
Typescript received 8 October 1966

EXPLANATION OF PLATE I

Fig. 1. *Propectinatites websteri* gen. et sp. nov., paratype, microconch, BM C. 73732.

Fig. 2. *Propectinatites websteri* gen. et sp. nov., holotype, macroconch, BM C. 73731.

Both specimens are from 30 ft. above the Washing Ledge Stone Band, Autissiodorensis Zone, Brandy Bay, Kimmeridge, Dorset. Both figures natural size.



COPE, New Kimmeridgian ammonite *Propectinatites*

EPIZOIC OYSTERS ON KIMMERIDGIAN AMMONITES

by JOHN C. W. COPE

ABSTRACT. Oyster distribution on certain Kimmeridgian ammonites is consistent with attachment occurring after the death of the ammonites.

WHILE collecting ammonites from the Upper Kimmeridge Clay at Kimmeridge in Dorset (Cope 1967), it has been observed that the ammonites are often encrusted with oyster shells. This incrustation has been noted on ammonites from almost all horizons throughout the 500 ft. of shales examined, though it rarely occurs on specimens smaller in diameter than 120 mm. Apart from one case in the collection of approximately 500 ammonites, the incrustation of oysters is confined to the underside of the ammonite shells as they lie in the shales.

If the attachment of oyster spat to the ammonite shell occurred during the life of the ammonite (when presumably it was oriented with its sagittal plane in a vertical position as in the living *Nautilus*), the oysters could be expected to be distributed equally on both sides of the shell. In an instance recorded by Seilacher (1960), attachment of oysters to both flanks (and also to the tabulate venter) of the Upper Cretaceous genus *Buchiceras* is described in which the oysters show a marked slope orientation which confirms that, in this case, attachment and growth occurred on the living ammonite.

In the case of the Kimmeridge Clay ammonites examined, however, the absence of oyster growth on the one side of the shell can best be explained on the assumption that the oyster spat became attached to the ammonite after the death of the latter, when the ammonite shell had settled on the sea-floor (where ammonite conchs would be, in fact, the only objects available for attachment).

Medcof (1955) has shown that Recent oyster larvae prefer to settle on under-surfaces of objects, and the form of the Kimmeridgian ammonite conchs would seem to have allowed spat to seek out such surfaces.

Practically all the ammonites in the section at Kimmeridge are crushed, but if an uncrushed shell of similar original whorl shape and similar strong primary ribbing on the body-chamber is placed on a plane surface, it is seen that there are only two areas in actual contact with that surface. These are (i) adjacent to the peristome, and (ii) opposite this, half a whorl back from the peristome. The other parts of the last whorl, and also the whole umbilical area, do not rest in contact with the surface. In the case of an ammonite shell of this shape lying on the sea-bed, oyster spat would have been able to attach themselves to the under-surface except at the two areas where the shell actually rested in contact with the sea-bed.

The distribution of the oyster shells on the ammonite shells from the Kimmeridge section is generally in agreement with such an hypothesis (see Pl. 2). The area of the peristome and that diametrically opposite to it are usually free from incrustation by oysters. Where incrustation does occur at the supposed areas of contact, it is clear that the

umbonal areas (i.e. the areas of original attachment) of the oysters are not within the areas of contact. It can be supposed that growth by the oyster into the area of contact would not be impossible, since at the time of deposition the Kimmeridgian sea-floor would have been soft.

This fact in itself might appear likely to have inhibited the entry of oyster spat below the shell, as the ammonite shells might have been expected to sink into the sea-bed on first settling on it. Considering, however, that after the death of the free-swimming ammonite the empty shell would only gradually become sufficiently waterlogged to sink to the sea-floor, its ultimate 'touch-down' might be very light indeed, so that it need not necessarily sink in. Once established, the oysters themselves presumably set up enough current action to keep the umbilical space beneath the ammonite free of sediment for an appreciable time. Certainly many of the oysters appear to have reached maturity before burial, so deposition must have been slow. There appears to be some tendency for immature oysters to be conspicuous around the ventral margins of the ammonites, and these may have attached themselves later and been killed by encroaching sediment.

The ammonites and oysters are often both heavily pyritized. However, the apparently normal growth of the benthonic oysters precludes the possibility that anaerobic conditions existed on the sea-floor itself, and the pyritization must have occurred at a later time.

Apart from their existence as epizoans on the ammonite shells, these oysters do not appear in the Kimmeridge Clay and it seems that their development was dependent entirely on the presence of vacated ammonite shells on the sea-floor for the provision of sheltered sites for attachment and growth.

REFERENCES

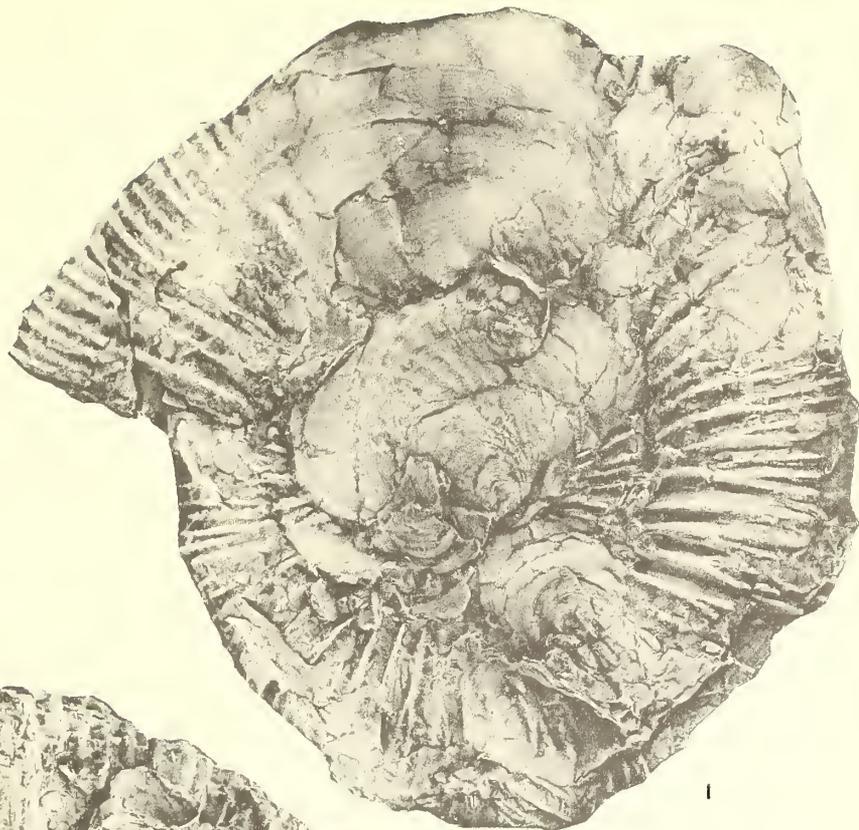
- COPE, J. C. W. 1967. The palaeontology and stratigraphy of the lower part of the Upper Kimmeridge Clay. *Bull. Br. Mus. Nat. Hist. (Geol.)* **15**, 1-79, pls. 1-33.
- MEDCOF, J. C. 1955. Day and night characteristics of spatfall and of behaviour of oyster larvae. *J. Fish. Res. Bd Can.* **12**, 270-86.
- SEILACHER, A. 1960. Epizoans as a key to ammonoid ecology. *J. Paleont.* **34**, 189-93.

JOHN C. W. COPE
Department of Geology,
University College,
Swansea,
Wales

Typescript received 8 October 1966

EXPLANATION OF PLATE 2

- Fig. 1. *Pectinatites (Virgatosphinctoides) elegans* Cope, BM C. 73729, showing attached specimens of *Ostrea bononiae* Sauvage and *O. multiformis* Koch and Dunker. Note the absence of epizic growth in the peristomal region and that diametrically opposite it. $\times 0.65$.
- Fig. 2a. *P. (V.) reisiformis densicostatus* Cope, BM C. 73730, showing incrustation of *O. multiformis*. In this case although the peristomal region is clear, the area diametrically opposite it has been covered by the oyster growth. Note, however, that no oyster was primarily attached within this latter area. $\times 0.7$.
- Fig. 2b. Reverse side of the specimen depicted in Fig. 2a, to show the upper side of the ammonite as it lay in the rock. Note the complete lack of oysters. The obscured areas of the shell are where it is heavily encrusted with pyrite aggregates. $\times 0.35$.
- Both the figured specimens are deposited in the British Museum (Natural History).



1



2a



2b

COPE, Epizoic oysters on Kimmeridgian ammonites



NEW EVIDENCE ON *JAMOYTIUS KERWOODI* WHITE, AN IMPORTANT OSTRACODERM FROM THE SILURIAN OF LANARKSHIRE, SCOTLAND

by ALEXANDER RITCHIE

ABSTRACT. *Jamoytius kerwoodi* White, based on two specimens from the Silurian of Lanarkshire, Scotland is reviewed in the light of many new specimens from the original locality. The associated fauna and probable habitat are discussed. *Jamoytius* is shown to be a cephalaspidomorph agnathan closely related to the anaspids and to the living cyclostomes. The presence is established of an annular cartilage, of sclerotic cartilages and of a cyclostome-like branchial basket. Lateral trunk scales of unusual structure and composition are present. Some further evidence is presented concerning the interpretation of continuous dorsal and lateral finfolds and the caudal fin is shown to be heterocercal (probably hypocercal). *Jamoytius* is thus a marine anaspid-like ostracoderm unspecialized enough to be on or near the line leading to the living cyclostomes, and could not, as was previously suggested, have represented the ancestral condition from which either the Cephalochordata or the Gnathostomata have arisen.

THE original material of *Jamoytius kerwoodi* White consisted of two specimens (BM P11284-5) discovered amongst some ostracoderm material purchased in 1914 by the British Museum (Natural History) from a local collector, William McPherson. The material came from the Silurian inlier near Lesmahagow, Lanarkshire, Scotland and the locality was given as 'the Logan Water, 1 mile below the watershed with Dippal'. The specimens were tentatively labelled 'allied to *Lasanius*', an anaspid which is common in a much younger horizon in the same inlier—the 'Downtonian' fish bed of Peach and Horne (1899), now thought to be of U. Wenlock-L. Ludlow age (Rolfe and Fritz 1966). Although mentioned by Smith Woodward (1921, p. 26) in his first Linnaean address, they lay undescribed for more than twenty years until White (1946) published the first account of the material. In his interesting and detailed interpretation he pictured *Jamoytius* as a primitive, naked, fish-like chordate which, although geologically late was 'probably a conservative element of the main stock from which the various groups of craniate chordates arose'.

The order Euphanerida and family Jamoytiidae were erected on the following diagnosis (White 1946, p. 96): 'Fossil Agnatha without armour or endoskeletal calcification; notochord persistent; simple lateral finfolds present; median fin-folds represented by elongated dorsal and anal fins. Eyes probably simple, very large and anteriorly placed. Muscle-segments simple and numerous with single flexure and undivided by horizontal septum. Mouth ? terminal; intestine short and straight.'

This interpretation placed *Jamoytius* in a very important position in relation to the early evolution of the vertebrates and White (1946, p. 93) said that in his opinion, *Jamoytius* was 'undoubtedly the most primitive of the 'vertebrate' series of which we have knowledge' and that it may perhaps be considered 'a more likely ancestor for *Amphioxus* than any of the other, specialized Agnatha . . .'. *Jamoytius* in many ways appeared to fit closely the role of an 'ancestral agnathan' postulated by White (1935) in a suggested phylogeny of the Agnatha.

White's interpretation has not, however, been accepted by all vertebrate palaeontologists and alternative suggestions have been put forward which may be summarized as follows. Gregory (1951) accepted White's interpretation, adding that 'taken altogether this very ancient type tends to connect *Amphioxus* with the anaspid ostracoderms', and 'quite conceivably, however, the boneless *Jamoytius* may well have been on the way toward *Amphioxus* while the bony *Cephalaspis* may have been on or near the line leading to the lampreys'. Wängsjö (1952, p. 566) suggested that *Jamoytius* was a naked or larval thelodont and Robertson (1953, p. 734) that it was a euphaneropid anaspid. Berrill (1955), in a general review of the form with especial emphasis on the nature of the eyes, remarked on the absence of branchial structures and suggested the presence of a pharynx and atrium comparable with that in *Amphioxus*. Denison (1956) and Robertson (1957) in comprehensive reviews on the habitats of the early vertebrates, discussed the Scottish Silurian inliers and their faunas. Robertson accepted White's interpretation but Denison considered *Jamoytius* to be 'for its time, an advanced though not necessarily highly specialized vertebrate. The absence of dermal armour, the fusiform body, the presence of long lateral and dorsal fin-folds (if they really do exist), the highly developed metamerism and large eyes are all characters of a very active, fast-swimming vertebrate, functionally more progressive than most of his contemporaries'. Denison and Robertson both concluded, from the associated fauna, that *Jamoytius* lived in a marine environment.

White (1958, p. 229) summarized several of the above views and reiterated that *Jamoytius* was, as had been originally suggested, 'the conservative derivative of the ancestors of them all'. In the same volume Westoll (1958, p. 196) reinterpreted the 'lateral fin-folds' as remains of the dorsal and anal fins. Stensiö (1958) suggested for the first time that the 'carbonized remains of the body muscles' of *Jamoytius* were, in fact, exoskeletal structures; he compared them with the scales of the Anaspida and included the family Jamoytiidae in the Anaspida. Smith (1957) agreed with Stensiö and further suggested that the 'myocommata' of White were actually the thickened, basal, dorsoventral ridges of the scales. Tarlo (1960, fig. 5) re-examined the holotype, confirmed Stensiö's interpretation and suggested that dorsal ridge scales were also present near the midline of the body in the holotype.

The writer (Ritchie, 1960) published a preliminary account of *Jamoytius* based on new material and the light it threw on the type specimens. It was shown that *Jamoytius* possessed a terminal, subcircular mouth, lateral eyes and a heterocercal (probably hypocercal) caudal fin. The presence of scales was confirmed and evidence of a branchial apparatus resembling that of the Anaspida and the living petromyzontids was observed in the holotype. One specimen (P.U. 12865 in counterpart) which was referred to as a small *Jamoytius* (1960, p. 648) has since been borrowed for examination and found to be wrongly identified. It is a new and rather problematical organism which, with a second similar specimen found during the present research, will be described elsewhere.

Jamoytius has also been described as a possible ammocoete of an ostracoderm (Newth, in Young 1962, p. 128) and, more recently Dechaseaux (1963) and Lehman (1964) have again reviewed its relationships with *Amphioxus* and the fossil and living agnathans. The conflicting interpretations underline the importance of new and well-preserved material of this important agnathan.

STRATIGRAPHY

The Lesmahagow Silurian inlier and the smaller Hagshaw Hills inlier to the south were first described in detail by Peach and Horne (1899) and the stratigraphy has recently been revised by Jennings (1961) and Rolfe (1961)—accounts which have been summarized by Walton (1965, pp. 194–9, figs. 5.15, 5.16).

Peach and Horne (1899, pp. 572–5) described the *Ceratiocaris* beds (Bed 3) in detail, mentioning that they included the so-called Ludlow fish-band. From their description of the various localities where *Ceratiocaris* and the coelolepid *Thelodus scoticus* Traquair occurred it is apparent that Peach and Horne considered the horizon exposed below Logan Water Dam (Shanks Castle) as the equivalent of another horizon exposed along Logan Water some 700 yd. SSW. of Logan House. The latter bed, which during the present research has yielded abundant ceratiocarids and numerous specimens of *Thelodus scoticus* Traquair, *Jamoytius kerwoodi* White and the problematical *Ainiktozoon loganense* Scourfield (1937), will be referred to below as the '*Jamoytius* horizon'. It became apparent to both Jennings and the writer that the *Jamoytius* horizon and the *Ceratiocaris* beds of Shanks Castle differed significantly in lithology and fauna. Jennings located *Ceratiocaris* beds of the Shanks Castle type in tributaries to the west of Logan Water, some distance upstream from the exposures of the *Jamoytius* horizon and at a stratigraphic level estimated to be about 700 ft. above the latter horizon.

In Jennings's Lesmahagow succession (Walton, 1965, fig. 5.16) the *Jamoytius* horizon is within the Patrick Burn Formation and the *Ceratiocaris* beds are near the base of the Kip Burn Formation.

Remains of thelodonts have been discovered at many different levels within the Patrick Burn Formation but the majority consist of pockets of disarticulated denticles, probably of coprolitic origin, enclosed in small calcareous nodules. A similar thelodont-bearing nodule has been recorded from the Hagshaw Hills in the Ree Burn Formation which may be roughly equivalent in age (Rolfe, 1961, p. 254). In only one horizon of the Patrick Burn Formation have articulated thelodonts been discovered and here—in the *Jamoytius* horizon—they are associated with a rich and varied fauna.

The *Jamoytius* horizon is exposed along both banks of the Logan Water some 700 yd. SSW. of Logan House (NGR 737346—738347). The beds dip 12–15°/290° and as the result of two small NNW.–SSE. faults which downthrow to the west the full thickness of the horizon is accessible in three separate outcrops within 60–80 yd. The central exposure is a cliff face some 30–40 ft. high with massive greywackes forming the top. At least one of the famous 'Camp Siluria' sites was at this locality (Macnair, 1905, Pl. VI, figs. 1, 2) and it seems probable that the bulk of the original material discovered by Macnair and the various amateur collectors came from this cliff face, but during the present research the face was worked back until it became difficult to obtain further material due to the steepness and danger of falling rock. The exposure to the east of the cliff consists of rock which is either very weathered and fragmentary or extremely fresh and difficult to work.

A third outcrop of the fish-bearing horizon was located and exposed by the writer immediately upstream from the main cliff on the opposite (south) bank of the stream. Originally covered by scree, it proved possible without great difficulty to uncover the fossiliferous section diagonally across the slope to expose an almost complete section

from which suitably weathered material could be obtained with relative ease. The present investigations have, therefore, been largely concentrated on this outcrop.

The *Jamoytius* horizon, 30–35 ft. in thickness, consists of alternating grey-black, carbonaceous siltstones which are finely laminated (40–60 laminae per inch) and of non-laminated, olive to greyish-green mudstones. The siltstone:mudstone ratio changes very rapidly vertically through the bed but so far as could be observed the units maintained remarkably constant thickness areally. The individual siltstone/mudstone units vary considerably in thickness ($\frac{1}{4}$ –4 in.) with the siltstones more frequently the thicker members. The siltstone laminae in thin section are seen to be rich in organic debris; the carbonaceous content of the mudstones appears to be low and macroscopic remains are almost entirely confined to the laminated siltstones. These remains occur throughout the *Jamoytius* horizon but are noticeably more abundant and best-preserved in the middle 20 ft. or so.

Calcareous nodules occur throughout but are especially common in certain horizons when they may be spaced less than 2 ft. apart. Generally the concretions lie within the siltstone units but several instances were noted where a nodule layer occurred either partly or wholly within the mudstone layer, in which case organic remains were extremely rare in the concretions. In the siltstone units the concretions almost always enclose, and appear to have formed around, organic remains. The siltstone laminae continue undisturbed through the nodules but the degree of compaction within the nodules is considerably less than in the surrounding sediment. Jennings (1961, p. 122) has shown that 'manganese is often enriched and both potassium and phosphorus deficient in the concretions when compared to the shales in which they occur'.

The majority of the nodules are small (90–95% < 2 in. in diameter) and enclose the carapace or the abdomen and telson of *Ceratiocaris papilio* Salter. A considerable number contain thelodont remains, either articulated individuals, patches of skin or more commonly thick layers of disarticulated denticles, probably of coprolitic origin. Approximately half of the articulated thelodonts discovered here were in normal siltstone and the rest were partly or almost completely enclosed in nodules which reached 7–8 in. in length and were of an elongate, oval shape tapering from the anterior to the posterior end of the fish. The lateral and caudal fins almost always lay outside the margins of the nodule. A small number of nodules (< 1%) partly enclosed *Aiiriktozoon* individuals; four of these were discovered *in situ* and four in museum collections from the same locality. No specimen of *Jamoytius* has, as yet, been discovered in a nodule.

The fauna of the *Jamoytius* horizon and relative abundance of the various members is as follows:

Chordata

<i>Thelodus scoticus</i> Traquair	moderately common
<i>Jamoytius kerwoodi</i> White	rare

Protochordata?

<i>Aiiriktozoon loganense</i> Scourfield	moderately common
--	-------------------

Arthropoda

<i>Ceratiocaris papilio</i> Salter (small form)	very common
<i>Ceratiocaris papilio</i> Salter (giant form)	very rare

<i>Beyrichia</i> sp.	very rare
<i>Cyamocephalus loganensis</i> Currie	very rare
<i>Slimonia acuminata</i> Salter	rare
<i>Pterygotus (Erettopterus) bilobus</i> Woodward	very rare
<i>Hughmilleria</i> sp.	very rare
Mollusca	
<i>Pteronitella?</i> sp.	rare
<i>Platyschisma</i> cf. <i>helicites</i> Sowerby	rare
small orthocone cephalopods	rare
Problematica	
<i>Dictyocaris ramsayi</i> Salter	common
<i>Taitia catena</i> Crookall	very rare
'stem' and 'disc-shaped' structures	common
Gen. et sp. nov.	very rare

The last named is a striated hook-like object of uncertain affinities which will be described elsewhere with a similar specimen from the Lower Palaeozoic of Norway. Traquair recorded a second species of *Thelodus*, *T. planus* Traquair, from this horizon, but the writer has been unable, despite the large number of *Thelodus* individuals now available from the same locality, to assign any, with certainty, to *T. planus*. Pending a full review of the thelodonts, which is under preparation, *T. planus* is regarded as a species of doubtful validity.

Apart from one nodule layer which yielded several well-preserved *Thelodus* individuals there was little evidence that either *Ainiktozoon* or the fish were more common in certain layers. The ceratiocarids occasionally appeared to be more abundant in some siltstone units than in others but the extremes of weathering and varying degrees of fissility encountered at different levels throughout the *Jamoytius* horizon had the effect of making sparsely fossiliferous units appear quite prolific and vice versa.

A noticeable feature of the weathered zones is the abundance of black carbonized remains around 1-2 in. across, many of which appear to show organized structures composed of fibrous material; no regular shape could, however, be discerned. These organic remains, possibly of an algal nature, on occasion almost cover the bedding planes but when they are traced laterally into the unweathered zone they become indistinguishable against the grey-black siltstone.

PRESERVATION

The state of preservation in the *Jamoytius* horizon varies greatly in different layers of apparently identical lithology; *Jamoytius* and *Ceratiocaris* (cf. Rolfe, 1962) are the two forms which are most affected. The exoskeleton of *Jamoytius* may be preserved in considerable detail along with the softer tissues of the scale-free cephalo-branchial region (Pl. 3, 4, 6) but the preservation may also be such (Pl. 5, fig. 3) that there is little trace of the scales and the outline of the body remains only as a faint carbon stain.

The ceratiocarids show similar variation ranging from specimens with considerable detail preserved to those where even the thickened margins of the carapace are barely

visible. These diagenetic effects are possibly related to the varying lengths of time the organisms lay exposed before being covered with sediment. *Thelodus* is not affected to the same extent.

There would appear to have been a complete absence of burrowing organisms and no evidence of tracks or trails was detected on bedding plane surfaces. The relative rarity of molluscan remains is probably an original feature and not the result of selective diagenesis—the few lamellibranchs, gastropods, and cephalopods which did turn up were quite well-preserved. The association of small colonies of lamellibranchs (*Pteronitella*?) with patches of carbonized material suggests that the former may have floated into the area attached to pieces of seaweed. Pockets of thelodont denticles, most often enclosed in small calcareous nodules, are probably of coprolitic origin; only two specimens showed these denticles strung out in something resembling a worm casting.

AGE

Although many horizons of the Lesmahagow and Hagshaw Hills successions have yielded a wealth of ostracoderm and arthropod remains few of the forms encountered are of any stratigraphic value and most are peculiar to the inliers. The other invertebrates present suggest an U. Valentian–L. Wenlock age for the Patrick Burn Formation (containing *Jamoytius*, *Thelodus scoticus*, *Ainiktozoon*, etc.), and various ages between U. Wenlock and M. Ludlow (Rolfe and Fritz 1966) have been proposed in recent years for the later fish beds which yield *Birkenia*, *Lasanius*, *Thelodus taiti*, *Lanarkia* (3 spp.), *Ateleaspis* and eurypterids (Downtonian fish bed of Peach and Horne, 1899). Unless, or until, better material for dating becomes available these dates must be regarded as provisional. There can be little doubt, however, that *Jamoytius kerwoodi* White and *Thelodus scoticus* Traquair are the oldest complete vertebrates known to date in Europe.

Preparation and Photography. Since very few specimens of *Jamoytius* were completely exposed during discovery, mechanical preparation often proved necessary. This was carried out by means of a Burgess Vibrotool adapted to take steel gramophone needles and small chisels. With only a thin carbon stain present even the better preserved specimens proved difficult to expose satisfactorily and the much fainter specimens were virtually impossible. During experiments on isolated fragments with acid preparation it was discovered that exposure to 15% HF for several minutes (with subsequent neutralization and extensive washing) had the effect of whitening the rock surface without noticeably affecting the carbonized body stain. The increased contrast which resulted made it possible to obtain good photographic results from even the faintest individuals. The specimens were photographed under alcohol and none of the prints have been retouched.

SYSTEMATIC DESCRIPTION

Family JAMOYTIIDAE White 1946

Genus JAMOYTIUS White 1946

Jamoytius kerwoodi White 1946

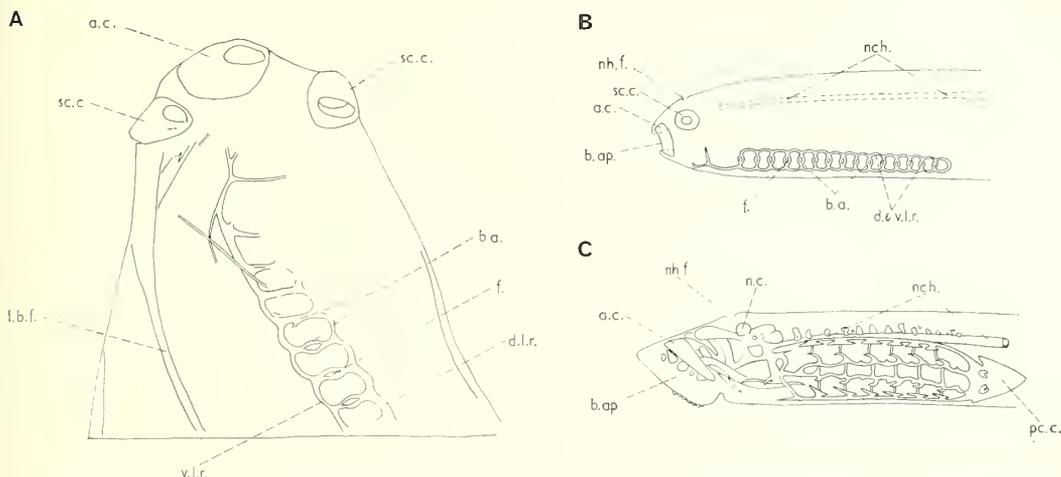
Plates 3–6

Material. Holotype, in counterpart, BM P.11284 a, b (White 1946, text-fig. 1) and BM P. 11285 (1946, text-fig. 2). Scottish Geological Survey, in counterpart, GSE 1182, 1183 (Ritchie 1960, p. 647). Professor F. H. Stewart, Grant Institute of Geology, University of Edinburgh possesses several specimens

of which the best preserved are F.R. 1393 a,b (Ritchie 1960, p. 647) and F.R. 1601 (Pl. 4, fig. 2, Pl. 6, fig. 1). Other specimens collected by the writer and figured herein have been presented to the British Museum (Natural History) and to the Royal Scottish Museum. The Royal Scottish Museum has recently purchased another specimen, RSM 1965. 59.1 a and b, collected by E. Stollery. The writer still possesses several rather poor specimens. The total number available to date, including incomplete specimens (but not counterparts) is around twenty.

MORPHOLOGY

Jamoytius kerwoodi is a moderately large agnathan reaching 180–200 mm. in length. The head is bluntly rounded and slightly narrower than the long, tubular trunk. The scale covering which is the major feature of the trunk is absent over the anterior 4 cm. of the head.



TEXT-FIG. 1. *Jamoytius kerwoodi* White. *a*, interpretation of isolated head showing well-preserved branchial remains, BM P47787 (cf. Pl. 5, fig. 1). *b*, attempted reconstruction in lateral view of the cartilaginous structures in the head and branchial region of *Jamoytius*. *c*, Cartilaginous skeleton of *Lampetra fluviatilis* for comparison. a.c. = annular cartilage; b.a. = branchial arch; b.ap. = buccal aperture; d.l.r. = dorsal (epitrematic) longitudinal rod; f. = foramen in the branchial arch; l.b.f. = crushed remains of the left branchial framework; nch. = notochord; nh.f. = naso-hypophysial foramen; pc.c. = pericardial cartilage; sc.c. = sclerotic cartilage; v.l.r. = ventral (hypotrematic) longitudinal rod.

Head and branchial region. The head region is somewhat narrower than the trunk and most specimens show clear evidence of three distinct stains near the anterior end of the bluntly rounded head, one in a subterminal position and two in an extreme anterolateral position. These strongly carbonized structures are interpreted as the remains of the mouth and eyes (Pl. 3, figs. 1, 2, Pl. 4, fig. 1, Pl. 5, figs. 1–3).

Near the anterior end of most individuals in which the head is preserved is a round, oval, or irregular structure, 6–7 mm. across, with fairly distinct margins. In the holotype (White 1946, text-fig. 1, Ritchie 1960, fig. 1*a*) and in other specimens (Ritchie 1960, fig. 1*b*; this paper, Pl. 3, fig. 2, Pl. 4, figs. 1–3) the stain is ring-shaped with a well-defined rim and less deeply carbonized central area. From its position and shape

therefore it appears to be the carbonized remains of an annular structure, presumably cartilaginous in original composition, which might have encircled the buccal aperture (text-fig. 1 *a, b*). Such an annular cartilage is present in the living cyclostomes (text-fig. 1 *c*) although not in a terminal position as a result of the anterior extension of the buccal margins into a broad sucker. If this interpretation is correct the circular shape in *Jamoytius* would seem to indicate that it is equivalent to the adult and not the ammocoete stage of the living cyclostomes since the latter has a vertical, oval slit-like aperture. The fuller implications of the nature of the mouth in *Jamoytius* are covered in the discussion.

In most of the specimens with the annular cartilage preserved two other distinct stains, 4–5 mm. across, are present near the antero-lateral margins of the head (Pl. 3, fig. 2, Pl. 4, fig. 1, Pl. 5, figs. 1–3). These structures, lying about 1 cm. posterior to the terminal or subterminal mouth are almost certainly remains of the eyes. The extreme antero-lateral position rules out any possibility that they could represent other paired cranial structures such as otic capsules. In shape they vary from circular to irregular with margins which may be sharply or poorly defined. That they are not structureless, as White suggested (1946, p. 94), can be readily observed in the new material (Pl. 5, fig. 1). The eye-stain near the right margin gives the impression of a crushed hollow ball with apertures on the upper and lower (or external and internal) surfaces which are superimposed but slightly offset (text-fig. 1 *a*).

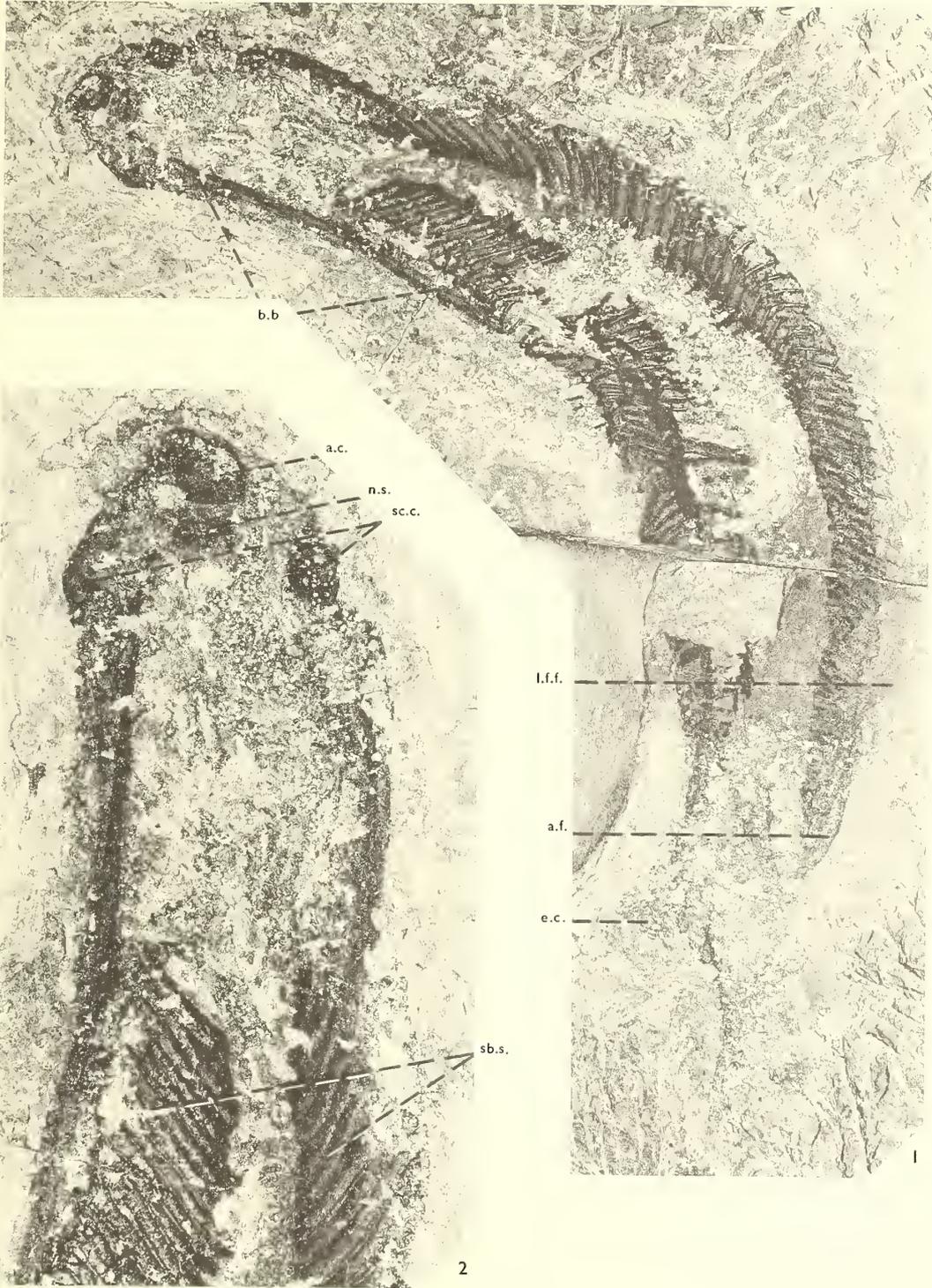
Dark stains representing the remains of eyes are not uncommon in fossil fish, and many specimens of anaspids (*Birkenia* and *Lasanius*) and coelolepids (*Thelodus* and *Lamarkia*) from a much younger horizon in the same inlier show distinct traces of the eyes. It is not even necessary to suggest that the soft tissues of the eye have left the carbon stain. The answer is probably provided by the cephalaspids where the eyeball was almost completely enclosed in a subspherical, sclerotic ossification with a laterally directed slit (cf. *Aceraspis*, Heintz, 1939). The eye-stains of *Jamoytius*—and the other anaspids and coelolepids—may therefore be reasonably interpreted as the remains of unossified, presumably cartilaginous, sclerotic structures surrounding the actual eyeball (text-fig. 1 *a, b*).

Nothing which can be interpreted as the remains of a lens has yet been observed in the *Jamoytius* eyestains, but since *Jamoytius* would appear to have been a fairly large, active swimmer it seems unlikely that it would have possessed simple, light-sensitive, lensless cups as suggested by Berrill (1955, p. 206). Although there is no direct evidence there seems little reason to doubt that a lens of some sort was present. The position of the eyes in relation to the annular cartilage and, as will be shown later, to the branchial framework, is not markedly different from that in *Petromyzou*. The petromyzontid eye has come to occupy a lateral position, not by posterior migration of the eye itself, but through the enlargement of the sucker anterior to the annular cartilage.

The branchial apparatus. As mentioned in an earlier paper (Ritchie 1960) very faint markings which appeared to be remains of branchial structures were observed in the

EXPLANATION OF PLATE 3

Figs. 1, 2. *Jamoytius kerwoodi* White. 1, complete specimen seen from the dorsal surface, BM. P47784 (figured Ritchie 1960, text-fig. 1 *b*), $\times 1$. 2, Anterior end of same specimen, $\times 1.8$. a.c. = annular cartilage; a.f. = anal fin; b.b. = branchial basket; e.c. = epichordal lobe (of caudal fin); l.ff. = lateral fin-fold; n.s. = nasal structure (?); sb.s. = suprabranchial scales; s.c. = sclerotic cartilage. Specimen photographed under alcohol.



RITCHIE, *Jamoytius* from the Scottish Silurian

head region of the holotype (1960, fig. 1*a*) but it was impossible at that time to determine whether these were remains of the actual branchial pouches, of the external apertures or of some related structures. The remains in question extended backwards from just behind the right eye (parallel to the margin of the head) to a position opposite the anterior scales.

The new material includes several specimens with similar branchial remains preserved in even greater detail (Pl. 4, fig. 1, Pl. 5, figs. 1, 3) and a much fuller understanding is now possible. These branchial structures are most clearly preserved in an isolated specimen of a *Jamoytius* head, some 45 mm. in length (Pl. 5, fig. 1, text-fig. 1*a*). The annular and sclerotic cartilages are well preserved and, in addition, running along the midline of the head from about 1 cm. posterior to the mouth to the edge of the specimen is a well-defined ladder-like framework with seven or eight crossbars at regularly spaced intervals. The most likely interpretation is that we have, preserved here for the first time in the fossil record, a simple 'branchial basket' the original material of which was almost certainly cartilage. Only one side of the branchial framework is clearly visible but if the specimen is viewed from the dorsal aspect with the right side of the 'basket' the better preserved, then the left-hand framework is probably represented by a strongly carbonized line which converges to meet the margin behind the left eye. This is the situation also in the holotype (Ritchie 1960, fig. 1*a*) and other specimens (Pl. 4, fig. 1); this peculiarity of preservation, with one half of the branchial basket seen in detail and the other side crushed vertically, is typical of most specimens and suggests the head was rounded in cross-section. That the basket framework was indeed paired is confirmed by the latest faint specimen to be discovered in which both right and left sides are clearly visible.

The branchial basket (Pl. 5, fig. 1, text-fig. 1*a*) appears to have been of a relatively simple construction with two sinuous longitudinal rods linked at regular intervals by vertical crossbars, the branchial arches. In this specimen some seven, possibly eight arches are visible, 5 mm. in length and 3.5 mm. apart. The last three arches are widest in the middle and give the appearance of bifurcating around an oval perforation; the more anterior arches, which are less distinctly preserved, do not show this feature although one has a projecting spur on the posterior margin. The ventral (? hypotrematic) longitudinal rod continues anteriorly, curving in the direction of the mouth and terminating some 5 mm. short of it. Near the anterior end another transverse rod meets the longitudinal rod at right angles, parallel to the branchial arches but separated from the anterior arch by 1.5–2 times the average inter-arch distance. Since this specimen is incomplete posteriorly we have to look elsewhere for evidence concerning the full extent of the branchial framework. In a more complete specimen, (Pl. 5, fig. 3) the branchial remains extend from just behind the left eye for a considerable distance parallel to the margin, becoming narrower posteriorly. Some ten or eleven arches are visible up to a break in the specimen but there is evidence that they continue at least 10–12 mm. beyond the fracture. From this and other specimens it would appear that the total number of branchial arches may reach or even exceed fifteen, which is not unlikely when one recalls that the anaspid *Pharyngolepis oblongus* Kiaer had fifteen branchial apertures and that a similar number of pouches is still present in some of the living myxinoids (e.g. *Bdellostoma*).

The difficulties (and pitfalls) in interpreting such nebulous structures as those in the

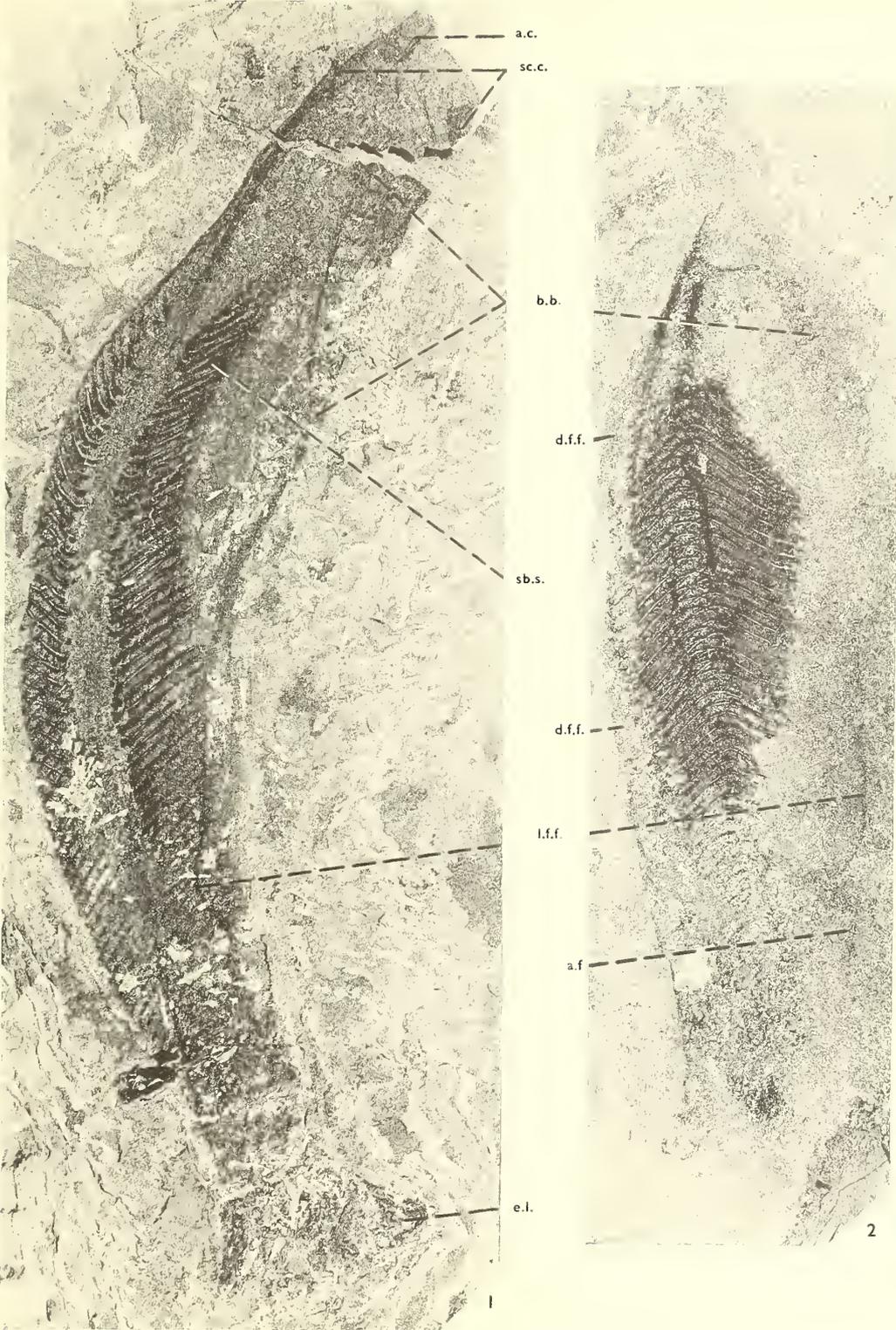
head and branchial region of *Jamoytius* are obvious but text-fig. 1a-c shows a possible interpretation of the best preserved head, an attempted reconstruction of the cartilaginous structures in *Jamoytius* and a sketch of the corresponding features in *Petromyzon*. There is no evidence in *Jamoytius* that the branchial arches continued past the dorsal (epitrematic?) longitudinal rod to connect with the notochord or that they extended ventrally to meet in the midline such as we find in *Petromyzon* and *Lampetra*. In these respects the *Jamoytius* branchial basket is of a basically simpler pattern than the complex framework of the adult lampreys and is closer to that found in the ammocoete. The general similarity of the *Jamoytius* and petromyzontid branchial baskets would seem to indicate that the gill pouches in the former were of normal cyclostome type—oval or sub-spherical chambers with a lining of folded respiratory epithelium. The comparatively large size of *Jamoytius*, the well-developed lateral eyes, and the small, circular buccal aperture must surely imply that the gills were of the adult cyclostome type and not that found in the ammocoete. Watson (1954) reached the same conclusion about the nature of the gills in the Osteostraci, Stensiö (1927) having earlier considered them to be of the ammocoete type. Since it seems unlikely that any ciliary mechanism could have produced sufficient respiratory or feeding current for an active animal the size of *Jamoytius*, it must be assumed that a muscle-pump system had been developed.

The structures described above are all fairly distinct and any attempt to label other features in the head region verges on guesswork; it should be noted, however, that an extremely faint subcircular stain has been observed just behind the annular cartilage in two specimens (Pl. 3, fig. 2, Pl. 5, fig. 3). This is tentatively interpreted here as a nasal structure, perhaps the nasal foramen. There are no signs of the otic capsules, of semi-circular canals nor of a cartilaginous piston which might indicate the presence of a rasping tongue.

The trunk. The trunk of *Jamoytius* appears to have been long, straight, and tubular, perhaps slightly flattened on the ventral surface and tapering only towards the base of the caudal fin. The well-preserved segmental structures present in the trunk of the holotype were interpreted by White (1946, text-fig. 1, p. 91) as the remains of the myomeres (with longitudinal fibres occasionally preserved) 'separated by the clear infillings of the spaces left by the decayed septa, giving the effect of a series of hollow rods or bones'. The myomeres were apparently of a simple type with single forward flexure and no horizontal septum—a feature found only in vertebrates above the cyclostome level. The suggestion that the soft parts of the animal had been preserved in the holotype was apparently supported by the almost complete absence of segmental structures in the second specimen (1956, text-fig. 2), a type of preservation which White, with some justification, considered to be more normal. As described above Smith (1957) and Stensiö (1958, 1964) suggested that the segmental remains in question were, in fact, scales, a view supported by Tarlo (1960) and the writer (Ritchie 1960) after examination of the original and new material respectively.

EXPLANATION OF PLATE 4

Figs. 1, 2. *Jamoytius kerwoodi* White. 1, complete specimen seen from the dorsal surface, RSM 1966. 3.1 (cf. also Pl. 6, fig. 2). 2, specimen seen in lateral view, F.R. 1601 (cf. also Pl. 6, fig. 1). a.c. = annular cartilage; a.f. = anal fin; b.b. = branchial basket; d.ff. = dorsal fin-fold (?); e.l. = epichordal lobe (of caudal fin); l.ff. = lateral fin-fold; sb.s. = suprabranchial scales; sc.c. = sclerotic cartilage. Specimens photographed under alcohol. Both natural size.



RITCHIE, *Jamoytius* from the Scottish Silurian

Although the new interpretation is not so dramatic as the original the trunk scales of *Jamoytius* are nevertheless remarkable structures. The head region lacks any scale covering for some 4 cm. posterior to the mouth; from this point to the caudal pedicel (where they become so faint as to be indistinguishable) the trunk is covered by some 60–65 scales on either side. Each scale, slightly less than 2 mm. in width, is separated from the next by an extremely regular, uncarbonized strip about 0.4 mm. wide (Pl. 3, fig. 1, Pl. 4, fig. 1, Pl. 6, figs. 1, 2). Since most of the available specimens are flattened dorso-ventrally the scales are frequently folded and distorted making it rather difficult to visualize their exact shape during life. Only one individual, F.R. 1601, discovered and prepared by Professor F. H. Stewart, shows the animal in lateral view (Pl. 4, fig. 2, Pl. 6, fig. 1). In this instance the scales over the mid-trunk region are well preserved but anteriorly and posteriorly they were covered with a thin film of matrix which proved extremely difficult to remove. The scales of the right side are almost completely preserved but those of the left side are partly visible along a narrow strip with strongly carbonized margins which follows approximately the line of flexure (Pl. 6, fig. 1). The complete scales, best displayed anteriorly and posteriorly to this strip, show a single forward flexure with an angle of 100–5° which is probably close to the condition in life. The point of flexure is smoothly rounded, not angular as in most of the anaspids, and the scales appear to be continuous from the mid-dorsal line to the ventral terminations, with the portion ventral to the flexure at least one and a half times as long as the shallower dorso-lateral part. Anteriorly, where the scales and branchial structures are both present, the ventral portions of the scales are poorly developed; this corresponds to the supra-branchial region in the anaspids (Stensiö 1958, fig. 127) and the lampreys where the segmental musculature continues forwards over the branchial region.

The continuous nature of the trunk scales suggests (*a*) that they coincided very closely with the external surface of the myomeres and (*b*) that the material of which the *Jamoytius* scales were composed was not heavily mineralized and rigid but possessed considerable flexibility. If this were not the case each scale row would be subdivided into several articulating elements such as we find in *Pharyngolepis*, *Birkenia*, etc. (Kiaer 1924, p. 65, fig. 29). The only transverse fissures observed in the trunk scales of *Jamoytius* lie in the posterior suprabranchial region (Pl. 6, fig. 1).

The individual scales do not appear to have overlapped, as earlier workers suggested, and the uncarbonized, inter-scale strip does not represent either the myocommata (White 1946) or the dorso-ventral ridge present on the inner surface of more typical anaspid scales (cf. Gross 1938, 1958). Certain aspects in the preservation of *Jamoytius* scales suggest a rather unusual composition, quite different from that in *Birkenia* and the Norwegian anaspids. Only occasionally do they display a slight relief; in several instances the scales have been folded almost double without fracturing (Pl. 3, fig. 1, Pl. 6, fig. 2) or the ventral and dorsal portions may be dragged almost into line. These features suggest not only considerable flexibility but firmness and extremely strong connective tissue between the scales since few of the specimens known to date show much evidence of disarticulation. There would appear to have been an almost complete absence of mineralization and there is nothing to indicate the presence of bone or dentine, so the earlier reference (Ritchie 1960) to 'exoskeletal ossification (scales)' in *Jamoytius* is incorrect. The original scale material, now preserved only as a carbonized

stain, may have been a horny, epidermal substance, perhaps akin to keratin which is present in the teeth of lampreys and in small quantities in the scales of living fish and amphibians.

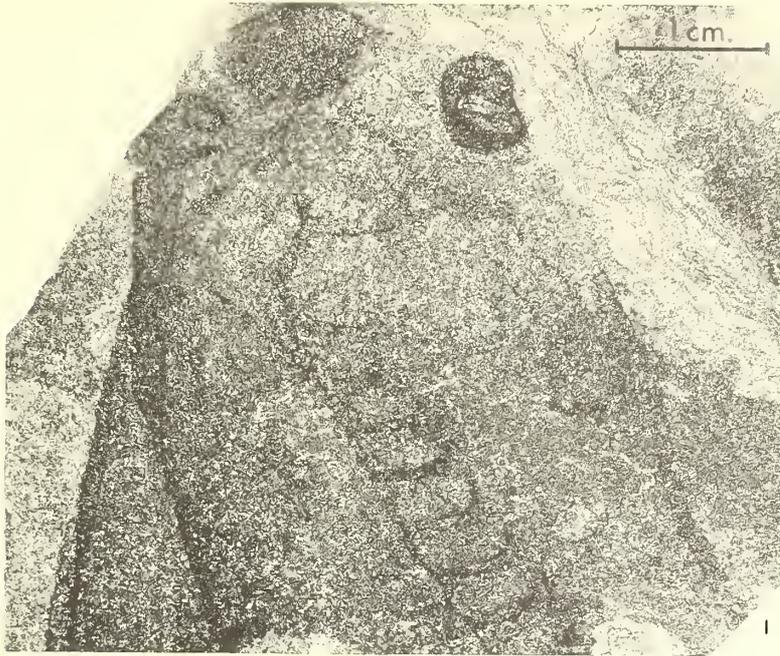
In most *Jamoytius* specimens the scale surface is evenly carbonized with more deeply carbonized margins but occasionally the surface is traversed by an intricate network of minute, branching fissures (Pl. 6, figs. 1, 2). There are several possible explanations; the fissures may represent an original canal system within and between the scales, they may indicate post-mortem fungal invasion or they may simply be the result of posthumous cracking during the processes of burial. This effect may explain the structures taken by White (1946) to be the remains of longitudinal muscle fibres, and by Stensiö (1958) to be a scale ornamentation comparable with that of the Norwegian anaspids. Such an ornamentation is certainly not visible in most of the better preserved specimens of *Jamoytius*. The only features of significance, other than those described above, are to be seen in the interscale strips of a few individuals (Pl. 6, fig. 3); the junction between the scales is marked by a line of minute, regularly spaced, circular 'pores' which in places become elongate and confluent. They may represent the bases of hollow tubercles whose tops have been removed with the counterpart or they may indeed have been pores connecting with the surface. Their position—between the scales—and the fact that they are not visible in many of the better-preserved individuals make interpretation difficult.

In about two-thirds of the *Jamoytius* specimens known to date the scales are extremely faint or almost completely lacking (Pl. 5, fig. 3; White 1946, text-fig. 2), although the same individuals frequently have well-preserved remains of the mouth, eyes, and branchial structures. This absence of scales is almost certainly the result of diagenesis and the individuals in question are usually more shapeless and broader in the head and trunk than are individuals with the scale covering well preserved.

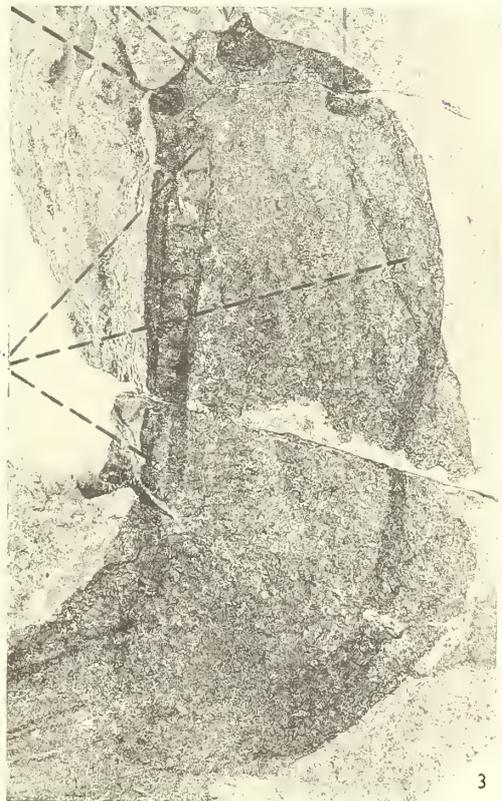
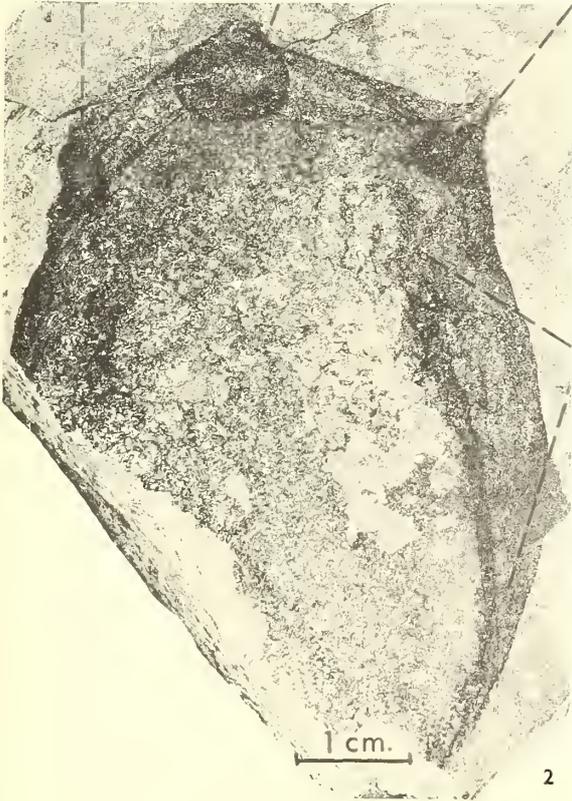
Other structures in the trunk region, similar to those which White interpreted as remains of the notochord and intestine (1946, text-fig. 1), are to be seen in several of the new specimens (Pl. 3, fig. 1, Pl. 4, fig. 2, Pl. 6, fig. 1). In the holotype (White 1946, text-fig. 1) the structure interpreted by White as the notochord is probably one margin of the wide, straight intestine, the other side being correctly labelled (cf. Tarlo 1960, fig. 5). Anteriorly, where the notochord was interpreted as forking, the branch running towards the left margin is more likely to be the remains of the left side of the branchial basket. RSM 1966.3.1 (Pl. 4, fig. 1) which shows a remarkable resemblance to the holotype (Ritchie 1960, fig. 1a), displays an almost identical preservation of the branchial remains. In the laterally compressed individual, F.R. 1601 (Pl. 4, fig. 2, Pl. 6, fig. 1), a similar strip with deeply carbonized margins extends for a considerable distance along the trunk approximately parallel to the body axis, appearing to turn downwards at its posterior end. This must represent either the notochord or the intestine, but is rather wide for the remains of a simple, unstricted notochord and more dorsally placed than one might

EXPLANATION OF PLATE 5

Figs. 1-3. *Jamoytius kerwoodi* White. 1, head with well-preserved mouth, eyes, and branchial structures, BM P47787, $\times 2$ (for interpretation see text-fig. 1a). 2, head with extremely fine annular cartilage, RSM 1966.3.3, $\times 1.5$. 3, anterior end of specimen in which trunk scales are barely visible, RSM 1966.3.2, $\times 1$. a.c. = annular cartilage; b.b. = branchial basket; n.s. = nasal structure (?); sc.c. = sclerotic cartilage. Specimens photographed under alcohol.



sc.c. a.c. sc.c. n.s. a.c. sc.c.



expect to find the intestine preserved (cf. *Endeiolepis*, Stensiö 1939, Pl. 1, figs. 1, 2, text-fig. 7). It is interpreted here as more probably the intestine slightly displaced in the processes of decomposition, but the alternative explanation is by no means impossible.

The attitude and nature of preservation of the *Jamoytius* individuals would appear to indicate that the fish was not, unlike most of the anaspids, markedly laterally compressed. The frequency of dorsally compressed individuals (Pl. 3, Pl. 4, fig. 1, Pl. 5, fig. 3) need not, however, imply that the actual animals, in life, were similarly flattened. If, as seems probable, the head and trunk were long, straight, and subcircular in cross-section, post-mortem muscular contraction would twist the animal, in the horizontal plane, to one side or the other; consequently, it would tend to come to rest either on the dorsal or on the ventral surface and to be preserved in this attitude. Laterally flattened remains of *Jamoytius* would thus be relatively rare, as appears to be the case in the material available to date.

Fins. In the original interpretation of *Jamoytius* (White 1946) certain structures were taken to be the remains of long fin-folds, a long dorsal fin, a shorter anal fin and undivided ventro-lateral fin-folds (cf. text-fig. 2a) which were envisaged as extending 'along the length of the body to the caudal pedicel without interruption'. Ever since the work of Goodrich (1906) provided good morphological evidence for the 'Lateral Fin-fold Theory' of earlier workers, it had been hoped that the fossil record would yield evidence of such fin-folds in geologically early chordates. *Endeiolepis ameri* Stensiö (1939) from the U. Devonian of Canada and *Jamoytius kerwoodi* White from the Silurian of Scotland were the two forms which appeared to provide the best evidence, but several dissenting views have been expressed, especially on the interpretation of *Jamoytius*.

Denison (1956) questioned the existence of fin-folds in *Jamoytius*, and Westoll (1958) reinterpreted White's lateral fin-folds (1946, text-fig. 1) as the remains of the dorsal and anal fins. Ritchie (1960) presented evidence that neither the interpretations of Westoll nor White were correct, and that the structures in question could be better explained as the ventral termination of the body scales with an intervening scale-free strip running the length of the ventral surface. It was suggested that the remains lying outside the main body stain in the holotype—interpreted by White as 'displaced skin' (1946, text-fig. 1)—were in fact those of the lateral fins and that faint but definite lines running postero-laterally were probably the fin rays of these lateral fin-folds (Ritchie 1960, fig. 1a).

The way is thus clear for a reappraisal of the fin-fold interpretation. While the new material of *Jamoytius* does provide additional evidence on this important aspect it is much less definite and conclusive than had been hoped, for several reasons. The lateral fins of *Jamoytius* must have been rather flimsy structures lacking a covering of scales; against a background of well-preserved scales they would be indistinguishable. Even if they lie outside the main body stain (as in the holotype) they are extremely difficult to observe against the grey-black matrix, especially in specimens prepared by Vibrotool or dental mallet. The best hope, not yet realized, is for a completely exposed specimen on a naturally splitting bedding plane.

Meanwhile the best evidence is provided by the one specimen in lateral view, F.R. 1601 (Pl. 4, fig. 2). The head and caudal parts are not preserved but in the posterior trunk region a distinct ventral margin can be distinguished some 10 mm. below the ventral ends of the well-preserved, lateral scales. The remains of the intestine (?), described above, appear to slope down in the direction of a deep, rounded notch

situated at the posterior end of the ventral margin. This probably indicates the position of the anal opening, in which case the ventral margin anterior to the anus may represent the lower edge of a lateral fin-fold while that posterior to the anal notch may be interpreted as the remains of a low, rounded, anal fin.

In the dorsally compressed individuals remains of the fins are even more difficult to recognize. Longitudinal carbon stains are often visible along the trunk (Pl. 4, fig. 1), especially in faint specimens, where they may be the remains of fins or perhaps only the result of folded skin material. A lateral fin is possibly present in BM P47784 (Pl. 3, fig. 1).

Evidence for the dorsal fin is equally inconclusive. Although 'dorsal fin rays' were identified by White (1946, text-fig. 1) and reinterpreted as 'ridge scales' by Tarlo (1960, fig. 5) little trace of similar structures has been seen in other specimens. The dorsal fin-fold is possibly present along the dorsal margin in F.R. 1601 (Pl. 4, fig. 2) as a long, low stain extending over most of the trunk.

The caudal fin is preserved, although rather poorly, in two specimens (Pl. 3, fig. 1, Pl. 4, fig. 1); in both the body axis, or caudal pedicel, is turned to one side while a triangular stain on the other side reveals the presence of a well-developed fin lobe. The caudal fin is thus heterocercal but the nature of preservation makes it impossible to distinguish from the material whether it is normal heterocercal or reversed (hypocercal). From the general similarity of *Jamoytius* to the anaspids and to the living cylostomes it is assumed that the triangular fin represents the dorsal, or epichordal, lobe and that the caudal axis turns downwards to form a hypocercal fin. Several fin rays can be distinguished in the epichordal lobe of RSM 1966.3.1 (Pl. 4, fig. 1). The full extent of the fin is not visible but there can be little doubt that it resembled the general anaspid type (e.g. *Birkenia*).

The fins of *Jamoytius* thus appear to have been developed as follows: the median fin-fold is represented by a long, low, continuous dorsal fin, a hypocercal caudal fin with sub-triangular epichordal lobe and a low, rounded anal fin. The lateral fin-folds probably extended from the posterior end of the branchial row to the anus with a more or less straight outer margin (text-fig. 2*b*). As Westoll pointed out (1958, p. 196) White's original interpretation implied 'that the paired fin-folds extended on either side of the anal fin, which would be unique' (cf. text-fig. 2*a*).

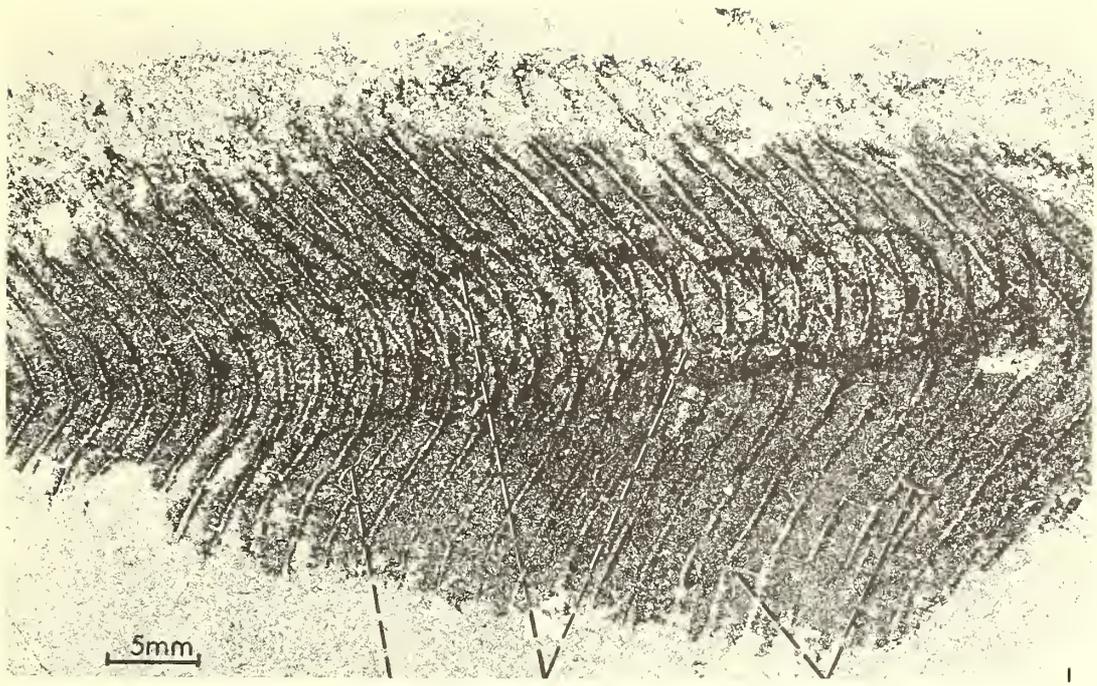
The discovery of well-developed lateral fins in *Endeiolepis aneri* Stensiö (1939), *Pharyngolepis oblongus* Kiaer, *Pharyngolepis heintzi* Ritchie, and an undescribed form from the Downtonian of Stonehaven (Ritchie 1964) indicates that such fin-folds were the rule rather than the exception in the active fusiform anaspids. This provides some support, therefore, for the still rather inconclusive evidence concerning the lateral fin-folds of *Jamoytius*.

DISCUSSION

The new evidence concerning *Jamoytius kerwoodi* White confirms that in most respects it is a cephalaspidomorph agnathan which most closely resembles the known

EXPLANATION OF PLATE 6

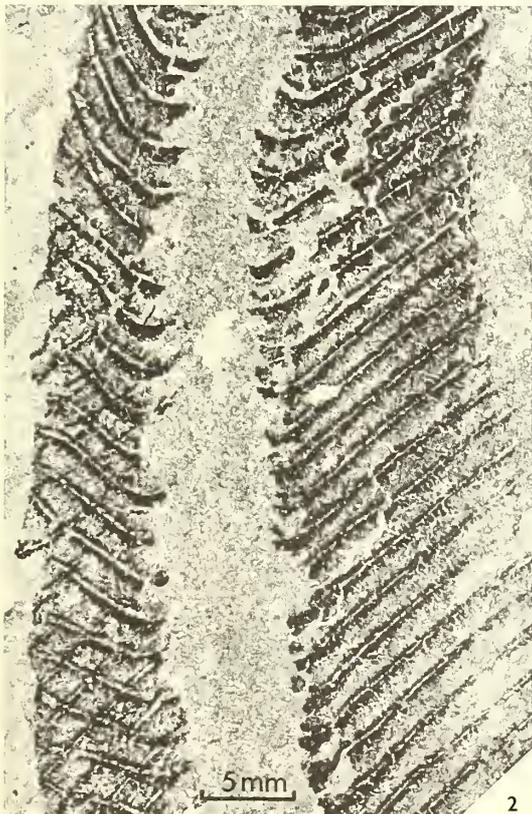
Figs. 1-3. *Jamoytius kerwoodi* White. 1, detail of F.R. 1601 (Pl. 4, fig. 2) $\times 2.4$. 2, detail of RSM 1966.3.1 (Pl. 4, fig. 1) $\times 2.5$. 3, detail of fragment displaying pores (or truncated tubercles) between the scales, BM P47785, $\times 6$. int.? = intestine (or possibly notochord); ir.f. = irregular fractures; t.f. = transverse fissures. Specimens photographed under alcohol.



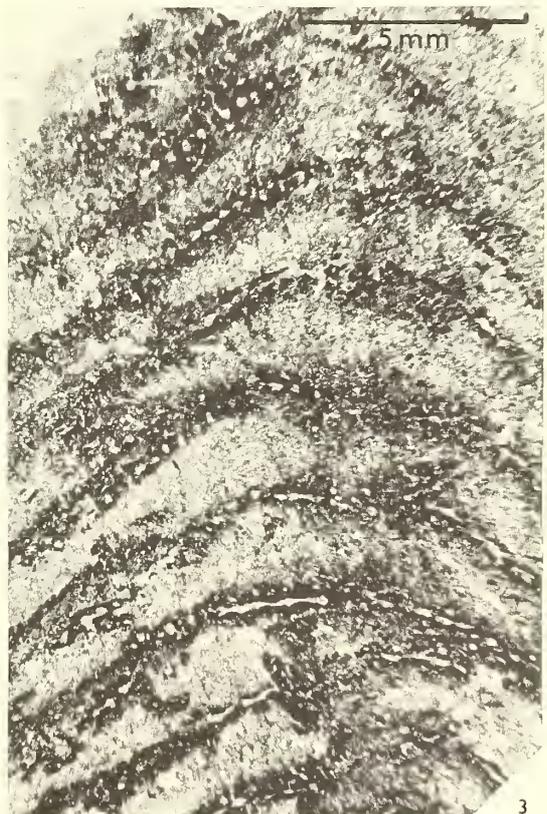
lr.f

int.?

c.f.



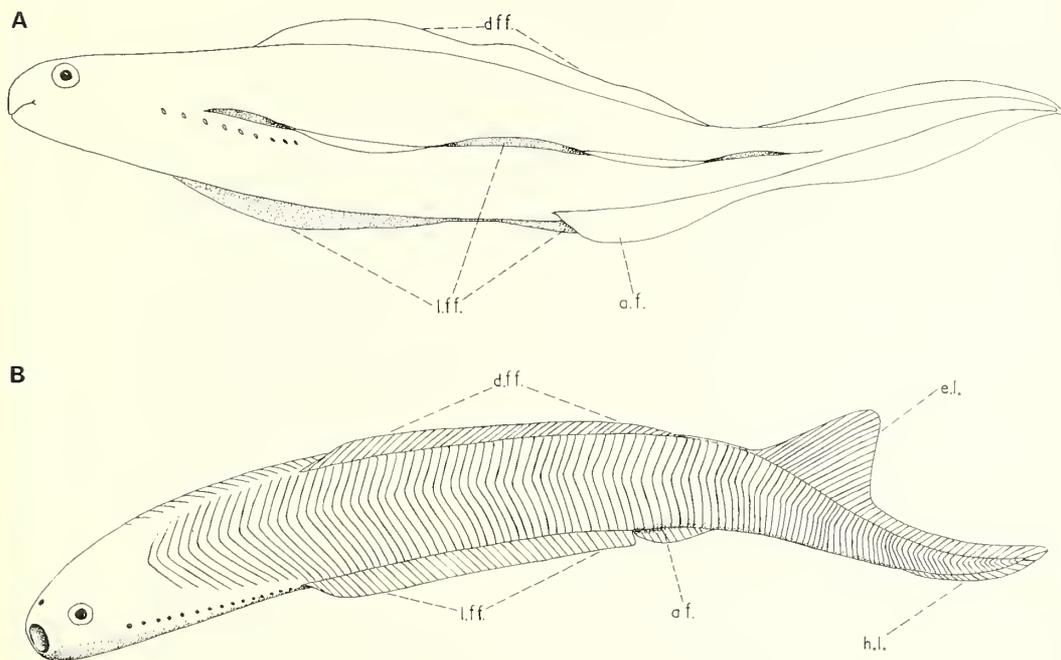
2



3

RITCHIE, *Jamoytius* from the Scottish Silurian

anaspids and the living cyclostomes (especially the petromyzontids). The writer agrees with Denison (1956, pp. 374–5, 424) and Robertson (1957, pp. 166–7) that the associated fauna of abundant phyllocarid crustaceans, occasional lamellibranchs, gastropods, cephalopods, and ostracods suggests that *Jamoytius* lived in a marine environment. The very thin, regular laminations in the enclosing siltstones and the undisturbed



TEXT-FIG. 2. *Jamoytius kerwoodi* White. *a*, reconstruction after Wilson (in Swinton 1961) to show original interpretation of fin-folds (for an earlier reconstruction, without branchial openings, see Lehman, 1964, fig. 4). *b*, new reconstruction of *Jamoytius* based on all available material. a.f. = anal fin; d.f.f. = dorsal fin-fold; e.l. = epichordal lobe; h.l. = hypochochordal lobe; l.f.f. = lateral fin-folds.

nature of many of the remains indicate very quiet conditions of deposition with no evidence of a burrowing fauna and an apparent absence of scavengers. As Robertson pointed out, there is little to indicate that the chordates were swept on death into the sea from rivers or estuaries. The elongate, tubular shape of *Jamoytius* contrasts strongly with the dorso-ventrally flattened thelodonts from the same deposits and it seems unlikely that the former, at least, was a bottom-dwelling animal.

The nature of the buccal opening in anaspids provides a limited amount of evidence on the probable nature of their feeding mechanisms. Heintz (1958, fig. 4) and the writer (Ritchie 1964, fig. 1*a-c*) have both interpreted the buccal aperture, at least in certain anaspids, as a vertically elongate, oval slit and find no evidence to support Stensiö's

interpretations (1964, p. 155, fig. 25 A, B) in which a considerable area of soft tissue is depicted projecting beyond the rostral scales; his *Birkenia* restoration (fig. 25B), modified after Heintz (1958), seems especially unrealistic. The buccal aperture in *Jamoytius*, as indicated by the size and shape of the annular cartilage, was surprisingly small for the size of the animal and was certainly not appropriate for a plankton feeder such as *Pharyngolepis* and *Birkenia* may have been. The feeding mechanism of agnathans has been discussed by Denison (1961, pp. 178–9) who pointed out that ‘if the anaspids did not have mechanisms for biting or nibbling, if they were too large and active to be adequately nourished by ciliary currents and mucus entanglement of small particles, and if they were not adapted for plankton or bottom feeding, about the only possibility left is suctorial feeding of some sort. It is not impossible that their feeding was similar to that of some living cyclostomes, though it is unlikely that they were as highly specialized for parasitism as are lampreys.’

This certainly sums up the position in *Jamoytius*, if not in all other anaspids, and one is led to consider which of his contemporaries *Jamoytius* may have relied on for nourishment by suctorial means. The exoskeletons of the numerous ceratiocarids and less frequent eurypterids show no evidence of such attacks, nor do the well-preserved remains of thelodonts from the same deposits. The only organic remains in the *Jamoytius* horizon which display possible evidence of suctorial attack are the large carbonaceous sheets of *Dictyocaris*, a problematical organism interpreted as a phyllocarid crustacean by Størmø (1935). These sheets, which may be up to 1 ft. across and are often irregular in shape, are frequently found to be perforated by numerous circular or subcircular holes, 3–5 mm. in diameter, apparently randomly distributed over the surface (Størmø 1935, fig. 1f, pp. 275–6). Similar holes are found in specimens of *Dictyocaris* from other localities in Scotland and Norway. The size of the holes compares closely with the internal diameter of the *Jamoytius* annular cartilage. Since sections of perforated *Dictyocaris* show no disturbance of the laminae either above or below by burrowing organisms, and since no other member of the fauna shows similar features the circumstantial evidence supports the identification of *Jamoytius* (and possibly *Thelodus*) as a causal factor. The writer is not convinced by the evidence for interpreting *Dictyocaris* as a phyllocarid crustacean, or even, perhaps, as an animal. If *Jamoytius* did create the holes in *Dictyocaris* this might imply the presence of a rasping device such as Stensiø reconstructed in the Norwegian anaspids (Stensiø 1958, figs. 126–7; cf. also Ritchie 1964, p. 17). Although no trace is visible in the head of *Jamoytius* of a rasping tongue it need not have been a very substantial structure. It seems probable that the petromyzontids initially fed on plant material and scraped algae from rocks and from the skin of other fish and that, almost by accident, they later developed a taste for blood; or as Hendrickson (in Strahan 1963, p. 98) has suggested, ‘the ectoparasitic habit may have arisen in ostracoderms that had developed a suctorial mouth in connexion with a benthic microphagous (or perhaps grazing) habit and were able with this device to feed on the epizootic or epiphytic organisms of other bottom-living animals. Transition from this to an ectoparasitic habit would follow an evolutionary pattern which has been demonstrated in many groups of animals.’

However it fed, the anterior position of the first branchial arches in *Jamoytius* and the apparently horizontal position of the branchial basket must mean that the buccal cavity was quite small, that the external openings were opposite the holobranchs and that the

'conduits branchiaux externes' were not posteriorly directed as they must have been in *Pterygolepis* (Stensiö 1964, fig. 28c). With such indefinite branchial remains and no knowledge of the position of the otic capsules it would be foolhardy to label the individual gill arches but it seems probable that *Jamoytius* and the other anaspids, like the petromyzontids, retained one or more prevagal innervated gills. In its horizontally aligned, uncompressed branchial apparatus, which begins immediately behind the orbit, *Jamoytius* differs from the other known anaspids. It also differs in possessing flexible, unossified scales which run unbroken from the mid-dorsal to ventro-lateral surface, and in the apparent persistence of a long, low, dorsal fin-fold which in most anaspids is represented by a row of median, dorsal, ridge scales; in this respect, probably a primitive feature, *Jamoytius* resembles *Endeiolepis* (Stensiö 1939, text-fig. 7) and there could conceivably be a close relationship between them.

Jamoytius differs from the living cyclostomes in the presence of scales and lateral fin-folds. The scales may easily have been lost but the absence of lateral fins in the petromyzontids and myxinoids is more difficult to explain away. There is still considerable disagreement over the relationships of the various ostracoderms with the cyclostomes. Stensiö's views that the petromyzontids are derived from cephalaspidomorph ancestors and the myxinoids from heterostracans have been strongly criticized by many workers on the grounds that the Heterostraci were probably diplorhinal while the Osteostraci, Anaspida, and Cyclostomata are monorhinal (Tarlo 1961, Heintz 1963). If this latter interpretation is correct then the Heterostraci 'cannot be regarded as more closely related to the Myxinids than to other agnathous groups' (Wängsjö 1952, p. 564).

The living cyclostomes may therefore be reasonably regarded as an offshoot of the basic cephalaspidomorph stock which has split into the petromyzontid and myxinoid groups since Silurian times.

The cephalaspids, despite all their anatomical similarities to the petromyzontids, are surely too specialized even from their first appearance to be possible ancestors. It seems more likely that the anaspid stock, and in particular *Jamoytius* as an unspecialized anaspid, is on or near the line leading to the petromyzontids, and, less certainly, to the myxinoids. Strahan (1958, p. 93) in an interesting study of living and fossil agnathans using D'Arcy Thompson's method of coordinate deformations, comes to similar conclusions regarding the origin of lampreys but expresses strong reservations about deriving myxinoids from the same stock. Robertson (1954, 1957) from his studies on osmotic regulation and the salt content of plasma has demonstrated that the myxinoids may be derived directly from marine chordate ancestors and not secondarily from unknown freshwater ancestors. 'The related lampreys, on the other hand, have acquired osmotic regulation, essential for anadromous habits and permanent life in fresh water, and the persisting anadromous members maintain this regulation even in sea water' (Robertson 1957, pp. 174-5).

Jamoytius kerwoodi White, as a Middle Silurian cyclostome inhabiting a marine environment is well placed to give rise to either, or both, of the surviving lines of agnathans, and the absence of lateral fins in the specialized, and probably degenerate, living forms may be a secondary, and not a primary, feature. The presence, in *Jamoytius*, of a lamprey-like branchial apparatus must remove any lingering suspicion that it might represent the stock which gave rise either to the Cephalochordata (Amphioxus) or to the Gnathostomata.

Acknowledgements. Thanks are extended to Dr. G. Y. Craig, University of Edinburgh, who supervised this research from 1959–63, to Professor F. H. Stewart, University of Edinburgh for invaluable criticism, for the loan of material and for assistance in excavating the *Jamoytius* locality. The author is indebted also to Dr. E. I. White for allowing access to the type material in the British Museum (Natural History) and advice on interpretation; to Mr. H. A. Toombs of the same department for the use of facilities; to Dr. C. D. Waterston, Royal Scottish Museum, Edinburgh, Professor G. L. Jepsen and Dr. D. Baird, University of Princeton, New Jersey, Mr. R. Wilson, H.M. Geological Survey, Edinburgh for the loan of material; to Dr. R. Kille, Dr. R. S. Miles, Dr. G. M. Robertson, Dr. L. B. H. Tarlo, Professor T. S. Westoll, and many others for useful discussions and suggestions. The first year of research was supported by a grant from the Department of Scientific and Industrial Research.

REFERENCES

- BERG, L. 1955. *Classification of Fishes, both Recent and Fossil*. 2nd edition, Leningrad.
- BERRILL, N. J. 1955. *The Origin of Vertebrates*. Oxford University Press.
- DECHASEAUX, C. 1963. *Jamoytius*, Amphioxus et le début de l'histoire des Vertébrés. *Annls Paléont.* **49**, 325–30.
- DENISON, R. H. 1956. A review of the habitat of the earliest Vertebrates. *Fieldiana, Geol.* **11**, 357–457.
- 1961. Feeding mechanisms of Agnatha and early Gnathostomes. *Amer. Zool.* **1**, 177–81.
- GOODRICH, E. S. 1906. Notes on the development, structure and origin of the median and paired fins of fish. *Quart. J. Micr. Sci.* (N.S.), **50**, 333–76.
- GREGORY, W. K. 1951. *Evolution Emerging*. 2 vols., New York.
- GROSS, W. 1938. Der histologische Aufbau der Anaspiden-Schuppen. *Norsk geol. Tidsskr.* **17**, 191–5.
- 1958. Anaspidenschuppen aus dem Ludlow des Ostseegebietes. *Paläont. Z.* **32**.
- HEINTZ, A. 1939. Cephalaspida from the Downtonian of Norway. *Skr. norske Vidensk-Akad.* **5**, 1–119.
- 1958. The head of the Anaspid *Birkenia elegans* Traquair. In *Studies on Fossil Vertebrates*, ed. T. S. Westoll, 71–85, London.
- 1963. Phylogenetic aspects of myxinoids. Pp. 9–21 in *The Biology of Myxine*. xiii+1–588, Oslo.
- JENNINGS, J. S. 1961. The geology of the eastern part of the Lesmahagow Inlier. Ph.D. Thesis, University of Edinburgh.
- KIAER, J. 1924. The Downtonian Fauna of Norway, I, Anaspida. *Skr. norske Vidensk-Akad.* **1**, 5–136.
- LEHMAN, J.-P. 1964. L'origine des Vertébrés. In *Traité de Paléontologie*, **4** (1), 78–91. Paris.
- MACNAIR, P. 1905. Camp Siluria. *Trans. geol. Soc. Glas.* **12**, 203–13.
- PEACH, B. N. and HORNE, J. 1899. The Silurian Rocks of Britain. 1. Scotland, *Mem. Geol. Surv. U.K.*
- RITCHIE, A. 1960. A new interpretation of *Jamoytius kerwoodi* White. *Nature*, **188**, 647–9.
- 1964. New light on the morphology of the Norwegian Anaspida. *Skr. norske Vidensk-Akad.* (N.S.), **14**, 1–35.
- ROBERTSON, G. M. 1953. Some attempts at phylogeny of early vertebrates. *Iowa Acad. Sci.* **60**, 725–37.
- ROBERTSON, J. D. 1954. The chemical composition of the blood of some aquatic chordates, including members of the Tunicata, Cyclostomata and Osteichthyes. *J. exp. Biol.* **31**, 424–42.
- 1957. The habitat of the early vertebrates. *Biol. Rev.* **32**, 156–87.
- ROLFE, W. D. I. 1961. The geology of the Hagshaw Hills Silurian Inlier, Lanarkshire. *Trans. Edin. geol. Soc.* **18**, 240–69.
- 1962. Grosser morphology of the Scottish Silurian phyllocarid crustacean, *Ceratiocaris papilio* Salter in Murchison. *J. Paleont.* **36**, 912–32.
- and FRITZ, M. A. 1966. Recent evidence for the age of the Hagshaw Hills Silurian inlier. *Scott. J. Geol.* **2**, 159–64.
- SCOURFIELD, D. J. 1937. An anomalous fossil organism, possibly a new type of Chordate from the Upper Silurian of Lesmahagow, Lanarkshire, *Ainiktozoon loganense* gen. et sp. nov. *Proc. R. Soc.* **121B**, 533–47.
- SMITH, I. C. 1957. New restorations of the heads of *Pharyngolepis oblongus* Kiaer and *Pharyngolepis kiaeri* sp. nov., with a note on their lateral-line systems. *Norsk geol. Tidsskr.* **37**, 373–402.

- STENSJÖ, E. A. 1927. The Downtonian and Devonian Vertebrates of Spitzbergen. Pt. I, Family Cephalaspida. *Skr. Svalbard Nordishavet*, **12**, xii+391 pp.
- 1939. A new anaspid from the Upper Devonian of Scaumenac Bay in Canada, with remarks on the other anaspids. *K. Svenska Vetensk-Akad. Handl.* (3) **18**, 1–25.
- 1958. Les Cyclostomes fossiles ou ostracodermes. In *Traité de Zoologie*, **13**, *Agnathes et Poissons*, 173–425, Paris.
- 1964. Les Cyclostomes fossiles ou ostracodermes. In *ibid.* **4** (1), 96–382, Paris.
- STORMER, L. 1935. *Dictyocaris* Salter, a large crustacean from the Upper Silurian and Downtonian. *Norsk geol. Tidsskr.* **15**, 265–98.
- STRAHAN, R. 1958. Speculations on the evolution of the Agnathan head. In *Proc. Cent. and Bicent. Congr. Biol.*, Singapore, 83–94.
- 1963. The Behaviour of Myxinoids. *Acta zool. Stockh.* **44**, 73–102.
- SWINTON, W. E. 1961. *The Story of Prehistoric Animals*. Rathbone Books, London.
- TARLO, L. B. H. 1960. The invertebrate origins of the vertebrates. *Rep. int. geol. Congr.* 21, (*Norden*) **22**, 113–23.
- 1961. *Rhinopteraspis cornubica* (McCoy) with notes on the classification and evolution of the pteraspids. *Acta palaeont. polonica*, **6**, 367–400.
- TRAQUAIR, R. H. 1899. Report on fossil fishes collected by the Geological Survey of Scotland in the Silurian rocks of the south of Scotland. *Trans. R. Soc. Edinb.* **39**, 827–64.
- 1905. Supplementary report on fossil fishes collected by the Geological Survey of Scotland. *Trans. R. Soc. Edinb.* **40**, 879–88.
- WALTON, E. K. 1965. In *The Geology of Scotland*. Ed. G. Y. Craig, 194–200. Edinburgh.
- WÄNGSJÖ, G. 1952. The Downtonian and Devonian Vertebrates of Spitsbergen. IX, Morphologic and systematic studies of the Spitsbergen Cephalaspids. *Skr. norsk. Polarinst.* **97**, 1–611+addendum.
- WATSON, D. M. S. 1954. A consideration of Ostracodermes. *Phil. Trans. R. Soc.* **B238**, 1–25.
- WESTOLL, T. S. 1958. The lateral fin-fold theory and the pectoral fins of Ostracoderms and early fishes. In *Studies on Fossil Vertebrates*. Ed. T. S. Westoll, 181–211, London.
- WHITE, E. I. 1935. The Ostracoderm *Pteraspis* Kner and the relationships of the agnathous vertebrates. *Phil. Trans. R. Soc.* **B225**, 381–457.
- 1946. *Jamoytius kerwoodi*, a new chordate from the Silurian of Lanarkshire. *Geol. Mag.* **83**, 89–97.
- 1958. Original environment of the Craniates. In *Studies on Fossil Vertebrates*. Ed. T. S. Westoll, 212–33, London.
- WOODWARD, A. S. 1921. Presidential Address, 1920. *Proc. Linn. Soc.* **132**, 25–34.
- YOUNG, J. Z. 1962. *The Life of Vertebrates* (2nd ed.) Oxford.

A. RITCHIE
Department of Geology,
St. George's Square,
Sheffield 1

Present address,
The Australian Museum,
Sydney, N.S.W.,
Australia

THE JURASSIC DINOSAUR *SCOLIDOSAURUS HARRISONI*, OWEN

by B. H. NEWMAN

ABSTRACT. *Scelidosaurus harrisoni* Owen, the type species of the genus, is reconsidered using all available material. Evidence is given that the lectotype chosen by Lydekker is unsuitable, as it is a megalosaur, not an ornithischian, and it is proposed to make an application to the International Nomenclature Commission to designate an alternative specimen.

UNTIL the recent discovery in the Upper Trias of South Africa of *Heterodontosaurus* (Crompton and Charig 1962), *Scelidosaurus* was the earliest recorded ornithischian dinosaur of which we had adequate knowledge. *Scelidosaurus* comes from the Lower Lias of Charmouth, Dorset and is not only the earliest member of the group recorded from the northern hemisphere but its skeleton is the first to be known with any degree of completeness. The genus includes but a single species and is generally accepted as a member of the Sub-order Stegosauria. Specimens referred with the prefixes BM or GSM are respectively in the British Museum (N.H.) or the Geological Survey Museum London.

SYSTEMATIC DESCRIPTION

Genus *SCOLIDOSAURUS* Owen, 1861

Scelidosaurus harrisoni Owen

Plates 7, 8

- 1859 *Scelidosaurus* Owen, p. 150 *nomen nudum*.
- 1860 *Scelidosaurus* Owen, p. 258 *nomen nudum*.
- 1861 *Scelidosaurus harrisoni* Owen, p. 1, pls. I–VI.
- 1863 *Scelidosaurus harrisoni* Owen; Owen, p. 1, pls. I–XI.
- 1888 *Scelidosaurus harrisoni* Owen; Lydekker, p. 181.
- 1890 *Scelidosaurus harrisoni* Owen; Woodward and Sherborn, p. 283.

Lectotype. (BM 39496), a right knee-joint, designated by Lydekker (1888, p. 181).

Paratypes. A skull and skeleton (BM R1111): a femur, tibia, fibula and phalanges with a vertebral centrum of a juvenile individual (Lyme Regis Museum): an imperfect left femur, GSM 109660 and a terminal phalange GSM 109561. All are from the lower Lias of Charmouth, Dorset.

The name *Scelidosaurus* was introduced in 1859 by Owen for 'a saurian with large hollow limb-bones, with the femur, having the third inner trochanter, and with metacarpal and phalangeal bones adapted for movement on land' but it was not until 1861 that Owen gave the first valid description of *Scelidosaurus*, using the trivial name *harrisoni*. He described the left femur of one individual, the knee-joint of another, together with a phalange of a third and a femur, tibia, fibula, and phalanges with a centrum of a dorsal vertebra of a fourth, younger animal. Owen also described the skull of a further individual, of which the rest of the skeleton was discovered on further

excavation, and described in 1863. All reconstructions of *Scelidosaurus harrisoni* and ideas as to its appearance and mode of locomotion have been founded entirely on this last specimen (Pl. 7, fig. 1).

Lydekker (1889) was under the impression that the knee-joint was the type and designated it as such. This subsequent designation gave the knee-joint the status of lectotype whilst the other specimens described in the same paper became paratypes. The additional material of the same individual whose skull had been described may also be considered as a paratype. Later Woodward and Sherborn (1890, p. 283) listed the knee-joint as the type of *Scelidosaurus harrisoni* (Pl. 7, fig. 2).

Description of the type material. An initial examination of the type material indicated that the lectotype (BM 39496), possessed characteristics similar to those of the knee-joint of a bipedal, carnivorous dinosaur. Development of this specimen with acetic acid has confirmed this and it appears to be the knee-joint of a megalosaurid.

Of the remainder of Owen's type material, detailed examination has shown that the right femur, tibia, fibula, phalanges, and vertebral centrum of the juvenile individual, all in the Lyme Regis Museum, probably belong to the genus *Hypsilophodon* or some allied form and in any case are not of the same species as the knee-joint, or the pyrite-coated femur, described by Owen in the same paper, the latter specimen also being part of a megalosaurid. The phalange mentioned and figured by Owen in the same paper is possibly also of a megalosaurid.

The skull (R1111) which Owen described with the above material is definitely that of an ornithischian dinosaur, and this with the remainder of the associated skeleton, is the material usually brought to mind when referring to *Scelidosaurus* (see Pl. 7, fig. 1).

Knee-joint. The specimen (BM 39496) comprises the distal end of the femur with the proximal end of the tibia and fibula (Pl. 7, fig. 2). When the femur was compared with that of an undoubted *Megalosaurus bucklandi* (BM 31806) it appeared to be closely similar, (Pl. 8, figs. 1, 5, 6, 8, 9). On the other hand when compared with the femur of the complete skeleton (BM R1111) it showed little if any similarity (Pl. 8, figs. 1, 5, 2, 7) and is, moreover, very much bigger. The popliteal cavity in both the femur of the knee-joint and the femur of *M. bucklandi* has steep straight sides, parallel throughout their length. On the other hand the popliteal cavity in the femur of the skeleton has sides which slope gently to its floor and are wide apart at the distal end, but gradually converge upwards to meet at the proximal end of the cavity forming an arcuate shape. The outer condyle of the femur in the skeleton is quite different in shape from that of either the knee-joint or *M. bucklandi*, its angle to the main shaft of the femur being about 45°, whereas in the two latter the angle is about 90° (Pl. 8, figs. 1, 2, 5-9).

The tibia of the knee-joint compares closely with that of *M. bucklandi* (BM 31809), particularly in the longitudinal expansion of the proximal end of the bone when viewed externally. The proximal aspect of these two specimens also shows a marked similarity in the shape of the condyles and the forward extension of that part of the bone supporting the procnemial and ectocnemial crests. Comparison of these specimens with the tibia of the skeleton in posterior view shows that the condyles of the latter are relatively smaller, with a larger space between them, whilst the articular surfaces are somewhat flattened, contrasting strongly with the deep, rounded condyles of the other two (Pl. 8, figs. 3, 4, 10-13).

Left femur. This isolated left femur (GSM 109560), one of the paratypes described by Owen, also appears to be that of a megalosaurid, though probably of an immature animal, and when compared with *M. bucklandi* (BM 31806) shows several similar features (Pl. 7, fig. 3a–b). The distal and proximal ends of the femur have been restored by the writer and the bone is figured for comparison with a right femur of *M. bucklandi*. The restored areas are indicated by white lines on the Geological Survey specimen, and similar white lines have been painted in corresponding positions on BM 31806.

Terminal phalange. The phalange (GSM 109561) mentioned and figured by Owen (1861, p. 5, pl. 2) is possibly the terminal phalange of the first digit of a megalosaurian. Comparison of this specimen with the terminal phalanges of the ornithischian skeleton, R1111, showed that whilst the latter are spatulate and hoof-like, the former is claw-like as in *Megalosaurus* and cannot belong to the same species.

Juvenile specimen. The bones of the young individual in the Lyme Regis Museum described by Owen (1861) do not belong to a megalosaurid but are certainly ornithischian possibly related to the Wealden genus *Hypsilophodon*. Comparison with the skeleton (R1111) suggests they are not of the same species but definite opinion must await the development of the skeleton with acid so that the relevant bones may be examined more fully.

DISCUSSION

Since it is now clear that, in his original description of *Scelidosaurus harrisoni*, Owen was dealing with more than one genus, the name should be reserved for that part of the material which is an undoubted ornithischian skeleton. On this basis the skull (BM R1111), together with its associated skeleton, should be the lectotype. Unfortunately, as already pointed out, Lydekker (1889) chose the knee-joint, (BM 39496), as lectotype and was supported in this by Woodward and Sherborn (1890). Consequently an application is to be made to the International Commission on Zoological Nomenclature to set aside Lydekker's selection, and designate BM R1111 as the type of *Scelidosaurus harrisoni*.

EXPLANATION OF PLATE 7

Fig. 1. A complete skeleton of an ornithischian dinosaur, '*Scelidosaurus harrisoni*' left side view. BM R1111.

Fig. 2. A knee joint, lectotype of *Scelidosaurus harrisoni*. BM 39496.

Fig. 3. (a) Posterior view of right femur of *Megalosaurus bucklandi* BM 31806, compared with (b) that of the left femur of an unnamed megalosaurid, GSM 109560.

EXPLANATION OF PLATE 8

Figs. 1, 5, 8. External, posterior and terminal views of distal end of right femur of the lectotype of '*Scelidosaurus harrisoni*', BM 39496.

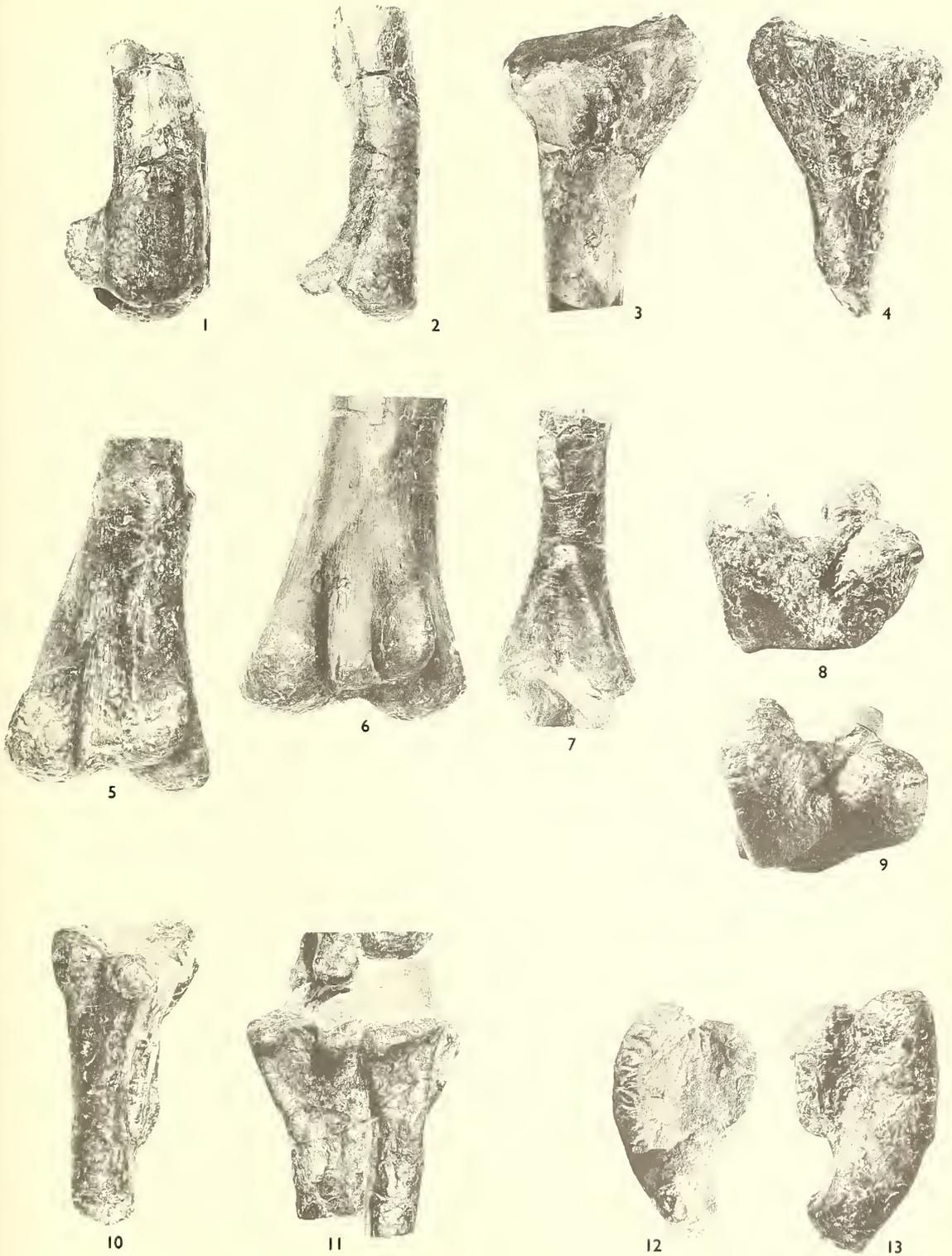
Figs. 2, 7, 11. External and posterior views of distal half of right femur and posterior view of right knee joint of skeleton of an ornithischian dinosaur, BM R1111.

Figs. 3, 12. Terminal and internal views of proximal end of left tibia of *Megalosaurus bucklandi*, BM 31809.

Figs. 4, 10, 13. Internal, posterior and terminal views of right tibia of lectotype of '*Scelidosaurus harrisoni*', BM 39496.

Figs. 6, 9. Posterior and terminal views of distal end of right femur of *Megalosaurus bucklandi*, BM 31806.





Acknowledgements. I wish to thank Dr. E. I. White for his advice and encouragement; Dr. B. G. Gardiner and Dr. W. T. Dean for their help and advice in preparing this manuscript; Dr. A. J. Charig for suggesting that I write this paper; Mr. A. E. Rixon for preparing the material; Mr. J. Brown and Mr. R. Tanner for their patience in preparing the plates; and the authorities of the Geological Survey and Museum (London) and the Lyme Regis Museum for the use of their material.

REFERENCES

CROMPTON, A. W., and CHARIG, A. J. 1962. A New Ornithischian from the Upper Trias of South Africa. *Nature, Lond.* **196** (4859), 1074-7.

LYDEKKER, R. 1889. *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History)*, part 1. London.

OWEN, R. 1859. 'Palaeontology'. In *Encyclopaedia Britannica*, 8th ed. **17**, 91-176. Adam and Black, Edinburgh.

— 1860. *Palaeontology*, 2nd ed. London.

— 1861. The Fossil Reptilia of the Liassic Formations. *Palaeontogr. Soc. [Monogr.]*, **1**, 1-14. London.

— 1863. The Fossil Reptilia of the Liassic Formations. *Ibid.* **2**, 1-26. London.

WOODWARD, A. S. and SHERBORN, C. D. 1890. *A Catalogue of British Fossil Vertebrata*, 209-96. London.

B. H. NEWMAN
 Department of Palaeontology,
 British Museum (N.H.),
 Cromwell Road,
 London S.W. 7.

Typescript received 6 May 1966

TABULATE CORALS FROM THE ILFRACOMBE BEDS (MIDDLE-UPPER DEVONIAN) OF NORTH DEVON

by the late F. J. W. HOLWILL

ABSTRACT. Twenty species of tabulate corals from the Ilfracombe Beds of North Devon are figured and described; of these, *Chaetetes multitalatus* is a new species and most of the others are recorded for the first time from North Devon.

LITTLE or no systematic palaeontological work has been done on the Ilfracombe Beds for the last hundred years; Phillips (1841) and Edwards and Haime (1853) are the only authors who have figured corals from these beds though many others have published fossil lists; of these, Valpy (1867) and Etheridge (1867) are the most important, though Etheridge drew much of his information from Valpy's earlier work. Webby (1964) has described a number of rugose corals from the Ilfracombe Beds of Somerset but has only figured one tabulate coral.

The accompanying table shows all the tabulate corals previously recorded from North Devon (Table 1). Unfortunately, none of these corals is accurately localized and many of the original specimens have been lost; I have therefore re-collected throughout the whole coastal area and this work has largely substantiated previous records, but in addition sixteen other species have been recognized, one of which is new.

STRATIGRAPHY

The Ilfracombe Beds consist of a series of slates, often calcareous, with some arenaceous bands and occasional limestones. Four distinctive limestones have been named and described in earlier papers (Holwill 1962, 1964*b*) and it is from these limestones that the corals have been obtained. The evidence for the age of the limestones has also been discussed in the above two papers and the conclusions are summarized in the following table:

David's Stone Limestone	Frasnian
Combe Martin Beach Limestone	?
Jenny Start Limestone	Givetian
Rillage Limestone	

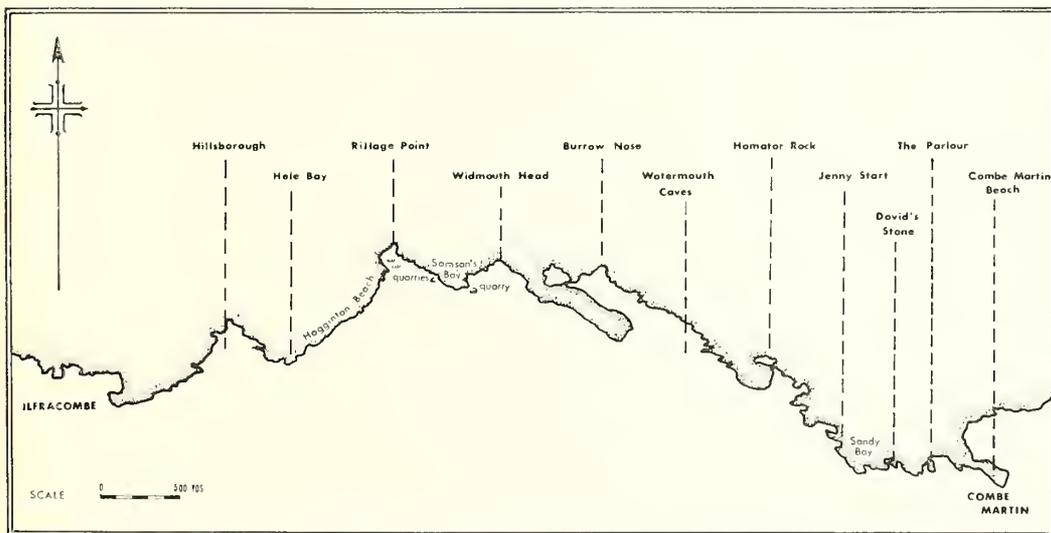
The limestones are separated by thick successions of unfossiliferous slate and the precise boundary between Middle and Upper Devonian cannot be defined.

In the Jenny Start Limestone there is an abundant fauna of rugose corals associated with occasional tabulates; in the David's Stone Limestone however, tabulate corals are locally numerous (for example at Broadstrand near Ilfracombe), while *Rugosa* are almost completely absent. The whole of North Devon is strongly folded and faulted so

that the majority of the corals are distorted and frequently recrystallized. Corals form the dominant element in the fauna though crinoid fragments are widespread and there are occasional brachiopods (especially in the Combe Martin Beach Limestone), gastro-

TABLE 1. *Tabulate corals previously recorded from North Devon*

<i>Species</i>	<i>First recorded</i>	<i>Substantiated</i>	<i>Remarks</i>
<i>Favosites cervicornis</i> (de Blainville)	Etheridge 1867	✓	= <i>Thamnopora cervicornis</i>
<i>F. fibrosa</i> Edwards and Haime	Phillips 1841		
<i>F. polymorpha</i> (Goldfuss)	Phillips 1841	✓	= <i>Thamnopora polymorpha</i>
<i>Heliolites porosus</i> Goldfuss	Etheridge 1867		
<i>Alveolites suborbicularis</i> Lamarck	Etheridge 1867	✓	
<i>Favosites dubia</i> Edwards and Haime	Etheridge 1867	✓	= <i>Thamnopora polyforata</i>
<i>Michelinia antiqua</i> (M'Coy)	Valpy 1867	?	= ? <i>Pleurodictyum</i> sp. recorded in Evans 1929. A single specimen of <i>Pleurodictyum</i> from the British Museum is figured below; it cannot be identified specifically.
<i>Syringopora</i> sp.	Valpy 1867		
<i>Cladochonus</i> sp.	Valpy 1867	?	probably a synonym of <i>Anopora</i> figured below



TEXT-FIG. 1. Map of the North Devon Coast between Combe Martin and Ilfracombe showing the localities mentioned in the text.

pods and orthoceratids (in the Rillage Limestone). The main localities mentioned in the text are shown on the accompanying map (text-fig. 1).

Acknowledgements. The field work connected with this study was carried out with financial assistance from the Central Research Fund of the University of London; this help is gratefully acknowledged.

Note. Dr. C. T. Scrutton (British Museum (Nat. Hist.)) has seen the manuscript through the press.

SYSTEMATIC DESCRIPTIONS

All the specimens discussed below are in the Murchison Museum, Imperial College, London, and their catalogue numbers are prefixed MM in the text. The only exception is *Pleurodictyum* sp. which is in the British Museum (Nat. Hist.).

ORDER TABULATA

Family CHAETETIDAE Edwards and Haime 1850

Sub-family CHAETETINAE Edwards and Haime 1850

Genus CHAETETES Fischer (*in* Eichwald 1829)

1829 *Chaetetes* Fischer (*in* Eichwald), p. 197.

1899 *Litophyllum* Etheridge, p. 178.

1939 *Chaetetes*; Lecompte, p. 154 (*cum syn.*).

1958 *Chaetetes*; Stasińska, p. 224.

Diagnosis. Massive tabulate corals with narrow, straight, or slightly curved, prismatic corallites making an angle of 90° with the outer surface. Septa are absent or represented by rudimentary spines. No mural pores. Tabulae horizontal and tending to occur at the same level in adjacent corallites. Increase by fission.

Remarks. Etheridge (1899, p. 178) erected the genus *Litophyllum* for chaetetid-like forms with thickened walls; in transverse section, the polygonal form of the calice appears rounded as a result of thickening. Lecompte (1939, p. 154) included these thickened forms within the genus *Chaetetes*; this seems justified for within the same colony, thickened and unthickened forms can occasionally be found.

Lecompte (1939) has given a very full review of the literature on *Chaetetes* and he recognizes the following five features as diagnostic of the genus:

1. Exclusively fissipartite (usually bipartite) increase.
2. Tabulae tend to occur at the same level in neighbouring corallites.
3. Mural pores are absent.
4. Corallites are narrow.
5. Walls between corallites are completely amalgamated.

On this last point he admits to some uncertainty. Okulitch (1936, p. 374) has observed a line marking the suture between corallites in *C. radians*, and Oakley (1936a, p. 442) has found an inclusion of dark granular material in the walls of *C. akpatokensis* which he attributed to recrystallization along an original suture. In the species described below, there is some evidence of a suture and although the question remains open, it seems probable that the walls may sometimes be composite.

Smith and Lang (1930, p. 188) pointed out that the walls in *Chaetetes* may be incompletely formed and, in transverse section, the resulting projection gives the appearance of a single septum, or, in extreme cases, where the walls are locally absent, to a meandroid colony.

Sokolov (1955, p. 95) was not prepared to accept the Chaetetidae as a family of the Tabulata since the absence of true septa, the mode of increase and the trabecular structure of the walls, sometimes arranged in isolated columns, was not found in any

other members of the order. He therefore referred them to the Hydrozoa; in this he was followed by Stasińska (1958, pp. 178 et seq., 224).

I have here placed the Chaetetidae in the Tabulata following Hill and Stumm (1956, p. 450) although there is no additional evidence from the North Devon specimens to confirm or contradict either point of view.

Chaetetes lonsdalei Etheridge and Foord 1884

Plate 14, figs. 6, 7

1884 *Chaetetes lonsdalei* Etheridge and Foord, p. 474, pl. 17, figs. 2, 2c.

1889 *Calanopora piliformis* Schlüter, p. 93, pl. 11, fig. 6.

1892 *Chaetetes piliformis* (Schlüter); Rominger, p. 62, pl. 3, figs. 15–16.

1939 *Chaetetes lonsdalei* Etheridge and Foord; Lecompte, p. 161, pl. 21, figs. 1–2.

1958 *Chaetetes* (?) *lonsdalei* Etheridge and Foord; Stasińska, p. 230, pl. 37, figs. 1–3.

Diagnosis. (Modified after Lecompte 1939, p. 162.) Large tabulate corals with straight prismatic corallites from 0.2–0.6 mm. in diameter. The calices may be polygonal or alveolitoid in shape with small granular or pointed spines projecting from the surrounding walls. The tabulae are well developed—three or four in 1 mm. The walls are stout and increase is fissipartite.

Remarks. The North Devon form agrees in all important respects with the species described by Etheridge and Foord from the Middle Devonian of Queensland and by Lecompte from the Couvinian of the Ardennes, though the diameter may be greater than was suggested by Lecompte; the diameter is however very variable. I have also included in the diagnosis the alveolitoid form which seems more typical of the species (the polygonal form is common, but it is almost always associated with granular spines and these, as Lecompte pointed out, are indications of incipient fission).

The tabulae are not regularly spaced but tend to occur at the same height in adjacent corallites; although they are usually horizontal, they occasionally show a slight downward projection at their centre. The walls have no dark median line but they are slightly thickened.

C. lonsdalei differs from *C. multitabulatus* in having much larger corallites and fewer tabulae and from *C. cf. rotundus* in having larger and straighter corallites.

In North Devon, all the specimens of *C. lonsdalei* were obtained from the David's Stone Limestone (Frasnian); in the Ardennes, Lecompte found the species was typical of the upper Couvinian beds, while Stasińska (1958) records it from the Givetian of Skały, Poland. The species therefore seems to have a longer range than was at first thought by Lecompte.

Chaetetes multitabulatus sp. nov.

Plate 9, figs. 4–7

Holotype. MM 11195 from the David's Stone Limestone of David's Stone.

Diagnosis. *Chaetetes* with very numerous tabulae (about 10 in 1 mm.) and thickened walls from which occasional short spines project. Corallites have a diameter of about 0.25 mm.

Description. The holotype consists of a small fragment about 1 cm. square which is embedded in limestone; longitudinal (Pl. 9, fig. 5) and oblique (almost transverse)

sections (Pl. 9, fig. 6) have been cut. The corallites are slightly curved in longitudinal sections and the calices are perpendicular to the outer surface. The tabulae are very thin and approximately correspond in height in neighbouring corallites; they may be horizontal, slightly concave or slightly convex. The wall structure is partially recrystallized but a dark median line is frequently visible suggesting a composite rather than fully amalgamated wall.

Remarks. *C. multitabulatus* differs from *C. cf. rotundus* in having more numerous and thinner tabulae and in the greater thickening of the walls.

Horizon. The David's Stone Limestone is considered to be of Frasnian age.

Chaetetes cf. rotundus Lecompte 1939

Plate 9, figs. 2, 3

cf. 1939 *Chaetetes rotundus* Lecompte, p. 163, pl. 22, fig. 2.

Description. The specimen is part of a massive branching or irregularly lamellar colony measuring approximately 20 × 15 mm. The specimen has been abraded prior to interment.

The corallites are in close contact and polygonal in transverse section though the calices are somewhat rounded due to thickening of the walls. The corallites are mostly curved in longitudinal section but the calices always reach the exterior at right angles to the surface of the corallum.

The diagonal measurements of fully developed corallites vary from 0.2–0.25 mm.; smaller ones can be seen in transverse sections, but that these are immature corallites is confirmed by their appearance in longitudinal section. The thickness of the walls shows a marked variation—the thickest is 0.04 mm., and the thinnest 0.01 mm.; a dark median line is sometimes visible showing that the walls are not fully amalgamated.

No spines or septa are visible, and mural pores are absent. The tabulae are not regularly spaced (about five in 1 mm.) and they tend to become more numerous towards the distal ends of the corallites. Many of the tabulae are slightly convex distally and they do not occur regularly at the same height in neighbouring corallites.

Remarks. The specimen is similar in many respects to *C. regularis* Lecompte [1939, p. 160, pl. 20, fig. 13]; however, the tabulae are more widely spaced and less regular.

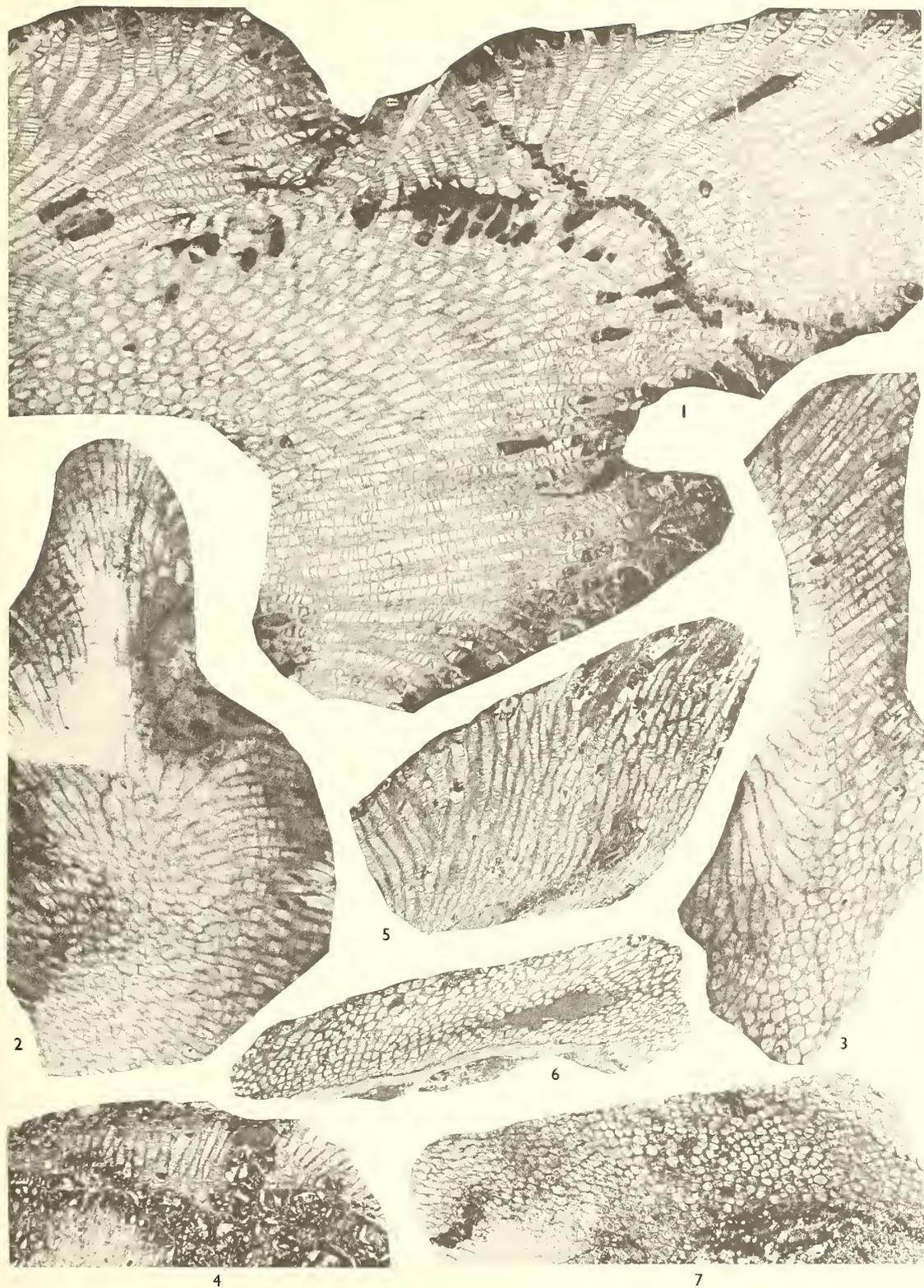
EXPLANATION OF PLATE 9

All figures are thin sections of specimens from the David's Stone Limestone (Frasnian) of North Devon.

Fig. 1. *Thamnopora polymorpha* (Goldfuss). Longitudinal and partly transverse sections cut from a large corallum. MM 11199 from Hillsborough. × 3.5.

Figs. 2–3. *Chaetetes cf. rotundus* Lecompte. Both figures show transverse and longitudinal sections cut from the same specimen. MM 11198 (Hillsborough). × 8.

Figs. 4–7. *Chaetetes multitabulatus* sp. nov. 4. Colony growing on the outer surface of a larger ? bryozoan; the latter shows penecontemporaneous borings which are infilled with calcite and pyrite crystals; MM 11196 from Hillsborough. 5, Longitudinal and 6, transverse sections of the holotype MM 11195 from Sandy Cove. 7, Paratype showing transverse and longitudinal sections; MM 11197 from Hillsborough. All × 6.



HOLWILL, Devonian tabulate corals from North Devon



The specimen is closest to *C. rotundus* Lecompte, differing only in the form of the corallum and in the slight arching of the tabulae.

Material. One specimen (MM 11198) from the David's Stone Limestone (Frasnian) of Hillsborough near Ilfracombe.

Family FAVOSITIDAE Dana 1846
Sub-family ALVEOLITINAE Duncan 1872
Genus ALVEOLITES Lamarck 1801

1933 *Alveolites* Lamarck; Lecompte, pp. 7–15 (*cum syn.*).

1939 *Alveolites* Lamarck; Lecompte, pp. 17–19 (*cum syn.*).

1965 *Alveolites* Lamarck; Schouppé, p. 45 (*cum syn.*).

Diagnosis. See Smith 1933, p. 135.

Remarks. Lecompte (1933, pp. 7–15, 1936, pp. 6–8 and 1939, pp. 17–19) has fully reviewed the literature pertaining to this genus and has pointed out the features which separate it from *Favosites*, *Thamnopora*, and *Coenites*. Although the obliquity of the calice is apparent in most species, occasional individuals within a single colony may open perpendicularly to the outer surface. Lecompte has questioned the reality of a single large septum, suggesting that it is the first stage in fissipartite increase. The material from North Devon is relatively poorly preserved and it is impossible to investigate this matter further.

Range. Silurian and Devonian.

Alveolites suborbicularis Lamarck 1801

Plate 14, fig. 4; Plate 15, figs. 1–5

1933 *Alveolites suborbicularis* Lamarck; Lecompte, pp. 15–18 (*cum syn.*).

1939 *Alveolites suborbicularis* Lamarck; Lecompte, p. 19 (*cum syn.*).

Diagnosis. See Smith 1933, p. 137.

Remarks. Lecompte believed that granular spines were also developed at various positions in the corallite in addition to the prominent septum on the lower side. Smith, however, regarded the granular spines as a recrystallization phenomenon (see comments in Lecompte 1936, p. 7). The recrystallized appearance of the North Devon specimens (see for example, Pl. 15, fig. 1, in which the appearance of additional septa is an illusion resulting from recrystallization) suggest that Smith's interpretation is correct.

In North Devon, this species occurs in the Jenny Start, Combe Martin Beach, and David's Stone Limestones; one specimen collected measured 25 × 35 cm. All the specimens are at least partially recrystallized and distorted; specimens from the Jenny Start Limestone tend to have more widely spaced tabulae (about three in 1 mm.) and larger calices than those from the David's Stone Limestone (about four in 1 mm.). Specimens from the Combe Martin Beach Limestone are relatively small and are frequently found encrusting *Thamnopora*; they are common only at the east end of the Parlour, near Combe Martin; recrystallization has obliterated most of the original wall structure but occasionally the median dark line is discernible; the tabulae are thin and spaced irregularly—about four in 2 mm.

Range. Middle and Upper Devonian. In North Somerset Webby (1964) has identified this species from the Upper Givetian (Roadwater Limestone). In Belgium, Lecompte has not recorded the species below the base of the Frasnian; it is unknown from the Carboniferous.

Alveolites suborbicularis Lamarck forma *gemmans* Lecompte

Plate 16, figs. 1–2

1939 *Alveolites suborbicularis* forma *gemmans* Lecompte, pp. 22–23, pl. 1, figs. 1–12.

Remarks. Most commonly, *A. suborbicularis* is an encrusting coral which tends to develop in relatively thin layers around some convenient object—often another coral colony. Lecompte (1939) has noticed, however, a continuous series away from this simple form through those in which there are slight or moderate swellings on the outer surface (due presumably to the more rapid and successful growth of some corallites), into forms which have developed definite branches and have abandoned the lamellar form completely; the former he classed as forma *gemmans* and the latter as formae *subramosa* and *contortus*. The specimen figured from North Devon still has an essentially lamellar form but it has a marked swelling across its surface; it therefore falls within the morphological group, forma *gemmans*. It occurs in the Jenny Start Limestone (Givetian).

Alveolites multiperforatus Lecompte 1933

Plate 13, figs. 1, 2

1933 *Alveolites multiperforatus* Salée; Lecompte, pp. 39–42, pl. 3, figs. 1, 1a, 1b.

1945 *Alveolites multiperforatus* Salée; Smith, pp. 13–14, pl. 36, figs. 3–5 (*cum syn.*).

Diagnosis. Massive or encrusting tabulate corals. Calices with polygonal or sub-alveoloid form; septal spines rarely seen. The walls are irregularly thickened and mural pores are numerous throughout the corallum. The tabulae are thin, horizontal or slightly convex.

Remarks. The species was fully described by Lecompte (1933) but without a diagnosis. He attributed the authorship of the species to Salée (who named the species in an unpublished manuscript), as did Smith (1945, p. 13) who also discussed the species. However, as Lecompte's is the first published description, the species must be attributed to him.

The abundance of the mural pores, together with the irregular thickening of the walls,

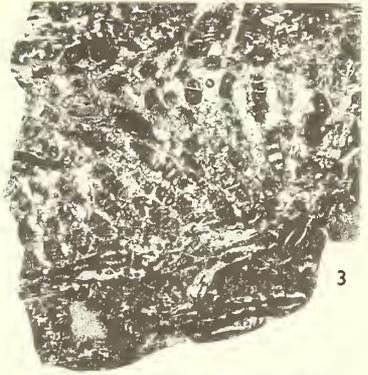
EXPLANATION OF PLATE 10

Figs. 1–5. *Thamnopora polymorpha* (Goldfuss). 1, Longitudinal and 2, transverse thin sections of MM 11200 from the David's Stone Limestone (Frasnian) to the West of the Coastguard Station above Hagginton Beach. 3, Longitudinal thin section of specimen MM 11175 from the David's Stone Limestone (Frasnian) of Sandy Cove. The coral tissue is almost entirely recrystallized. 4, Longitudinal thin section of MM 11201 from the David's Stone Limestone of Hillsborough. 5, A broken corallum weathering out from the David's Stone Limestone at Sandy Cove. MM 11202. All $\times 3$ except fig. 2 $\times 4$.

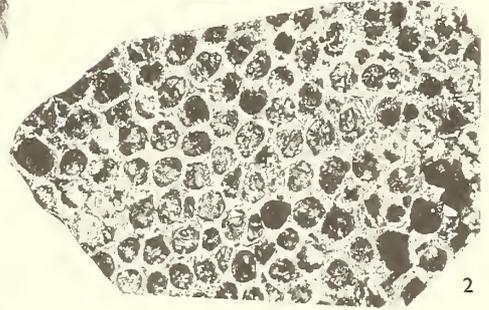
Fig. 6. *Coenites escharoides* (Steininger) Exterior surface of several coralla showing their lamellar form and the slit-like nature of the calices. Specimen MM 11181 from the Jenny Start Limestone (Givetian) of Widmouth Quarry. $\times 2$.



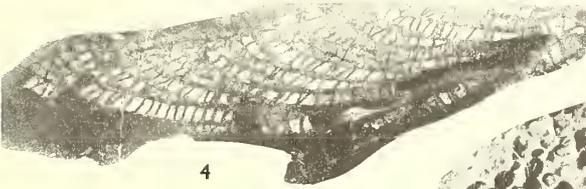
1



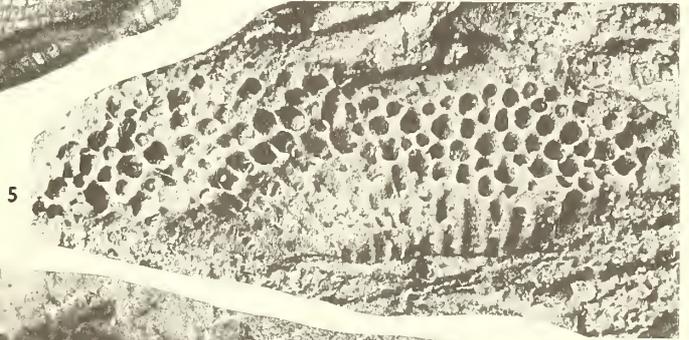
3



2



4



5



6

gives the appearance of 'boudins' in longitudinal section. In North Devon, the species has been obtained from the Jenny Start Limestone of Widmouth; the skeletal structure is partially recrystallized, but the thickening of the walls and the numerous mural pores are readily seen. The tabulae are irregularly spaced—about three in 1 mm.; this agrees well with the specimen figured by Lecompte (1933, pl. 3, fig. 1*b*). The growth of the coral is also irregular and the corallites are rarely straight or parallel for more than short distances. The exterior surface shows the dominantly polygonal form of the calices but with some assuming a more alveolitoïd shape. Their diameter is commonly 0.4–0.6 mm., i.e. similar to the dimensions recorded by Lecompte but slightly larger than in the specimens from the Mackenzie River area. Smith (1945) has described 'numerous minute spines' from some (but not all) of the Canadian specimens and Lecompte mentions them in his description. They have not been observed in the North Devon species but their apparent absence may be the result of the indifferent preservation.

In Canada and in the Ardennes, the species occurs in the Frasnian; in the latter area, it is associated with *Thamnophyllum*, *Stromatopora*, and ?*Hexagonaria*; there is a somewhat similar association in the Jenny Start Limestone (Givetian) of North Devon.

Alveolites obtortus Lecompte 1939

Plate 17, figs. 4, 5

1939 *Alveolites obtortus* Lecompte, pp. 42–43, pl. 6, figs. 4–7.

Diagnosis. See Lecompte 1939, p. 43.

Remarks. One of the distinguishing features of this species is the arrangement of the corallites into fascicles which are irregularly disposed and often interlaced with each other; this feature is well seen in the North Devon specimens. Because of the poor preservation, however, it is not possible to see the concentration of mural pores in the outer parts of the fascicle; there is evidence that the tabulae are more numerous in these peripheral parts and there is some thickening of the corallite walls. The calices agree with the description given by Lecompte, being polygonal or sub-triangular, yet with diameters almost equal.

Lecompte records his species from the Frasnian of the Ardennes; in North Devon, the two specimens assigned to this species occur in the Jenny Start Limestone (Givetian).

Genus *Coenites* d'Eichwald 1829

1829 *Coenites* d'Eichwald, p. 179.

1939 *Coenites*; Lecompte, p. 62.

1955 *Placocoenites* Sokolov, p. 189.

Diagnosis. See Lecompte 1939, pp. 62–63.

Remarks. Some workers (e.g. Lindström 1876, p. 16, Hennig 1906, p. 26) regarded *Coenites* as a bryozoan; Oakley (1936*b*, pp. 25–26) showed conclusively that *Coenites* was, in fact, a tabulate coral. Lecompte (1939) stated that there are three main criteria for recognizing the genus and distinguishing it from *Alveolites* and *Thamnopora*:

- (a) It has considerable distal thickening of the walls.
- (b) It has a slit-like calicular opening.

- (c) It frequently shows three septal processes (though these are not always visible and sometimes, as Oakley observed, there may be six).

The genus is closer to *Alveolites* than to *Thamnopora*, and I agree with Hill and Stumm (1956, p. 466) in placing both *Alveolites* and *Coenites* in the same sub-family.

Sokolov (1955, p. 189) erected a new genus *Placocoenites* for coenitid-like corals having a lamellar form and a 'certain peculiarity in the arrangement of their calicular rim'. I do not regard these differences as significant enough to erect a new genus, especially as many species of *Coenites* have a tendency to grow in a lamellar form. I therefore regard *Placocoenites* as a synonym of *Coenites*.

In North Devon, tectonics and recrystallization (the latter being particularly marked in the preservation of this genus and *Alveolites*) have affected all the specimens to a greater or lesser degree making it difficult to assign specific names in every case; the two specimens described below are however, well represented.

The genus ranges from the Silurian to the Devonian (Hill and Stumm 1956, p. 466) but in the Ardennes, Lecompte found that it characterized the Middle Devonian. In North Devon also, it occurs in the Middle Devonian (Givetian—Jenny Start Limestone), but *C. gradatus* Lecompte is found in the Frasnian (David's Stone Limestone).

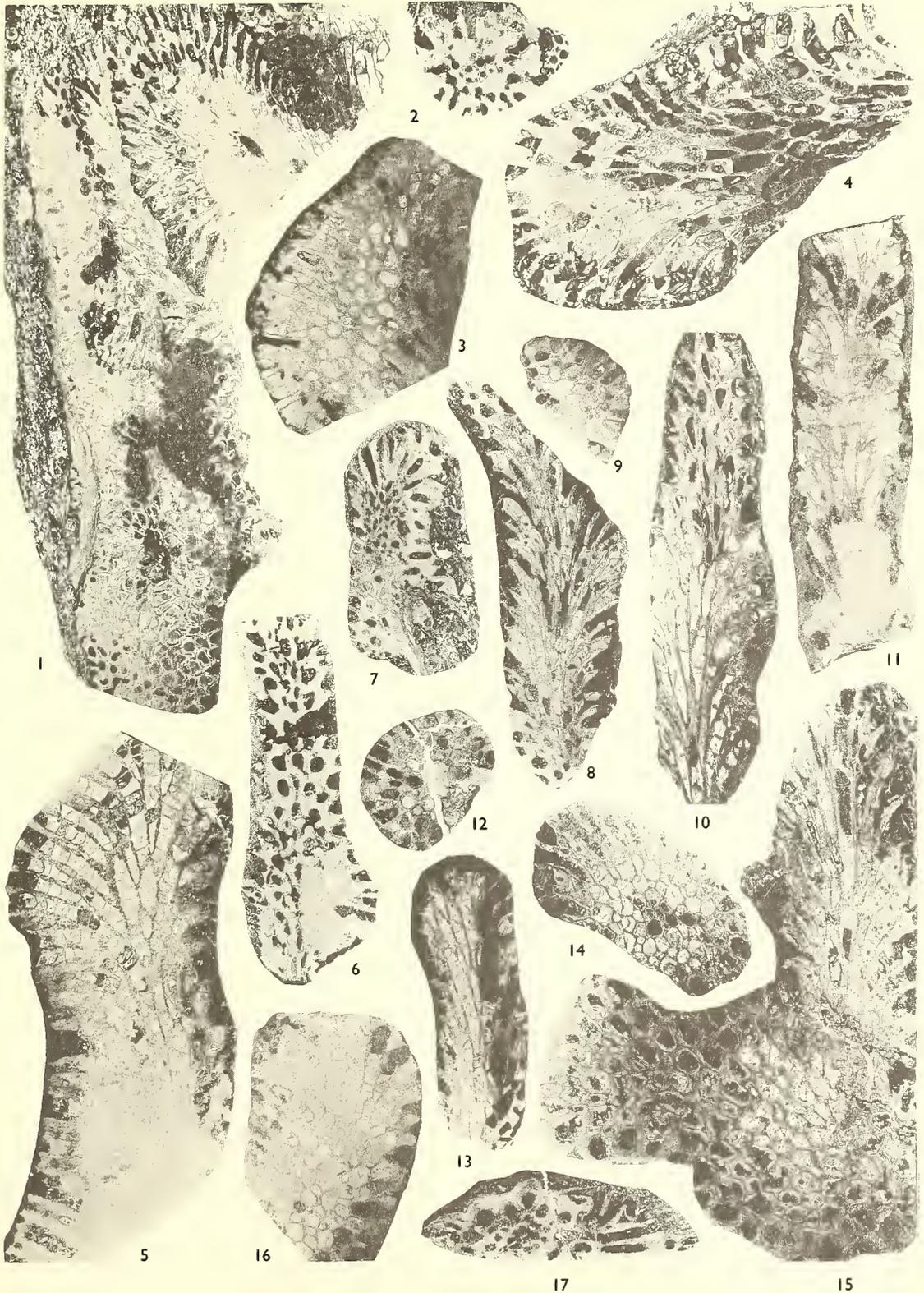
Coenites escharoides (Steininger) 1849

Plate 10, fig. 6; Plate 13, figs. 3-5

- 1849 *Limaria escharoides* Steininger, p. 11.
 1853 *Limaria escharoides* Steininger; Steininger, p. 27.
 1876 *Coenites expansus* Koninck, p. 74, pl. 2, fig. 3.
 1886 *Coenites expansus* Frech, p. 137.
 1889 *Coenites escharoides* (Steininger); Schlüter, p. 126, pl. V, figs. 12-13.
 1896 *Coenites expansa* Frech var. *polonica* Gürich, p. 145, pl. V, figs. 8a-b.
 1898 *Coenites expansus* Koninck, p. 57, pl. 2, fig. 3.
 1901 *Coenites escharoides* (Steininger); Petts (*pars*), p. 193, pl. II, figs. 8a-b.

EXPLANATION OF PLATE 11

- Figs. 1, 4. *Thamnopora cervicornis* (de Blainville). 1, Longitudinal and transverse section of MM 11204 from the Combe Martin Beach Limestone of The Parlour (near Combe Martin). 4, Longitudinal section of MM 11158 from the Rillage Limestone (Givetian) of Smallmouth Beach. Both $\times 3$.
- Figs. 3, 5, 16. *Thamnopora irregularis* Lecompte. All the specimens are from the Jenny Start Limestone (Givetian). 3, Oblique section of MM 11171 (Rillage Quarries). 5, longitudinal, and 16, transverse (partly longitudinal) sections of MM 11170 (Hagginton Beach). All $\times 3$.
- Figs. 2, 6, 7, 17. *Thamnopora tunefacta* Lecompte. All the specimens are from the David's Stone Limestone (Frasnian) of Sandy Cove. 2, Transverse, and 6, longitudinal sections of MM 11169. 7, Longitudinal (partly transverse) sections of MM 11168. 17, Transverse section of MM 11168. All $\times 3$.
- Figs. 8-10, 12-15. *Thamnopora polyforata* (Schlotheim). The following specimens are from the Jenny Start Limestone (Givetian). 8, Longitudinal thin section of MM 11165 (Rillage Quarry); 10, Longitudinal thin section of MM 11166 (Widmouth Quarry). 13, Longitudinal thin section of MM 11164 (Rillage Quarry). 14, Transverse, and 15, longitudinal (partly transverse) sections of 11167 (Hagginton Beach); the latter shows the strong development of spines in the region of bifurcation. All $\times 3$. The remaining specimens are from the David's Stone Limestone (Frasnian). 9, 12, Transverse thin sections of MM 11163 (Sandy Cove). Both $\times 3$.
- Fig. 11. *Thamnopora?* *polyforata* (Schlotheim). Polished longitudinal section of MM 11203 from the Rillage Limestone (Givetian) of Smallmouth. The coral structure is entirely recrystallized. $\times 2.5$.



HOLWILL, Devonian tabulate corals from North Devon

- 1903 *Coenites expansa* Frech var. *polonica* Gürich; Sobolev, p. 27.
 1908 *Coenites escharoides* (Steininger); Reed, p. 25, pl. IV, figs. 4-5.
 1909 *Coenites expansa* Frech var. *polonica* Gürich; Sobolev, p. 519.
 1939 *Coenites escharoides* (Steininger); Lecompte, p. 65, pl. XI, figs. 4-5.
 1947 *Coenites escharoides* (Steininger); Le Maitre, p. 81, pl. 21, fig. 3.
 1951 *Coenites escharoides* (Steininger); Chernyshev, p. 67, pl. XVII, fig. 8.
 1956 *Placocoenites escharoides* (Steininger); Dubatolov, p. 104, pl. 1V, figs. 8a-b.
 1958 *Coenites escharoides* (Steininger); Stasińska, p. 217, pl. 28, figs. 1-3.

Diagnosis. See Lecompte 1939, p. 67.

Remarks. Steininger's brief original diagnosis was amplified by Schlüter (1889), but both described only the external characters. Neither Lecompte nor I have re-examined the type and Lecompte's diagnosis which included the internal characters, is based upon material collected in the Ardennes.

The North Devon specimens are partly affected by recrystallization which obscures the finer details of the structure; I have no hesitation however in identifying them with the specimens described and figured by Lecompte from the Ardennes. Plate 10, fig. 6 shows the foliated form of the colony and the scaly appearance of the exterior surface. Longitudinal sections show a relatively unthickened central area in which the corallites run parallel to the outer surfaces, and abruptly thickened marginal areas where the corallites are sharply bent to become perpendicular to the outer surfaces.

The individual lamellae of the coralla have a thickness of 2-5 mm. and the calicular openings, which are very restricted because of the stereoplasm, have a maximum diameter of 0.3-0.5 mm. The thickening of the surrounding walls may also be as much as 0.5 mm.

Because of recrystallization, the tabulae are not readily seen and in many cases have been completely destroyed; where they are visible, they are numerous, very thin and often slightly concave.

The species is widespread in the European Devonian. Steininger's original specimens were from the Middle Devonian beds of Gerolstein. Lecompte obtained the species from the Couvinian and Givetian beds of the Belgian Ardennes while from Russia, Petts (1901) and Chernyshev (1951) record the species from the Kuznetsk Basin; from Poland, Stasińska records the species from the Couvinian of the Holy Cross Mountains and the Givetian of Skaly. Outside Europe, Reed (1908) found the species in the Middle Devonian of the Shan States (India) and Le Maitre (1947) in the Middle Devonian of Morocco. In North Devon it has been obtained from the Jenny Start Limestone (Givetian) of Widmouth Quarry and Hagginton Beach.

Coenites gradatus Lecompte

Plate 17, figs. 1-3

1939 *Coenites gradatus* Lecompte, pp. 69-70, pl. 11, figs. 11-17.

Diagnosis. See Lecompte 1939, p. 70.

Remarks. This is a very common species in the David's Stone Limestone of Broadstrand (Hillsborough). Some of the specimens are moderately well preserved and the zonation which is typical of the species can be well seen (Pl. 17, fig. 3). This zonation is frequently emphasized by the preservation—the exterior fringe of each zone being better preserved

than the interior parts which are entirely recrystallized. This suggests that recrystallization took place at an early stage, possibly even before the colony finally died. Tabulae are rarely seen, but in one corallum where they are preserved, they are closely spaced—(three in 0.5 mm.). The calices are crescent-shaped and may show a median spine. Sometimes the wall between adjacent corallites is absent (? fissipartite increase) giving the colony a meandroid appearance in transverse sections.

In the Ardennes, the species occurs in both the Couvinian and Givetian. Its occurrence in the David's Stone Limestone indicates that its range extends at least up into the Frasnian.

Coenites sp.

Plate 14, figs. 1–3

Description. Branching corallum with corallites straight at the axis and bending round sharply outside this in order to meet the exterior surface at right angles. The calices are much restricted by the thickening of the walls but they are commonly crescent-shaped and sometimes contain a prominent spine projecting in from the lower side. The diameter of the branches varies from 2–14 mm., but the average is about 8 mm. Thickening is strong in the peripheral areas but is also present to a lesser extent in the axial zone where the tabulae are few and widely spaced (Pl. 14, fig. 3).

Remarks. Only one example of this species has been found. It was obtained from the Jenny Start Limestone of Samson's Cove. In the form of its corallum, it resembles *C. escharoides*, but the branches of the latter are much thinner and the number of corallites in the axial zone is fewer. Generically, it is similar to *Plagiopora* Gürich (= *Scoliopora*—see Lang, Smith, and Thomas 1940, pp. 100, 118), especially *P. kaisini* Lecompte (Lecompte 1939, pp. 144–5, pl. 20, fig. 11), but it lacks polygonal calices with three spines and it has greater thickening of the corallite walls. It is probably a new species, but with such limited material, I have hesitated to erect one.

Sub-family PACHYPORINAE Gerth 1921

Genus THAMNOPORA Steininger 1831

1873 *Pachypora* Lindström, p. 14.

1939 *Thamnopora* Steininger; Lecompte, p. 102, (*cum syn.*).

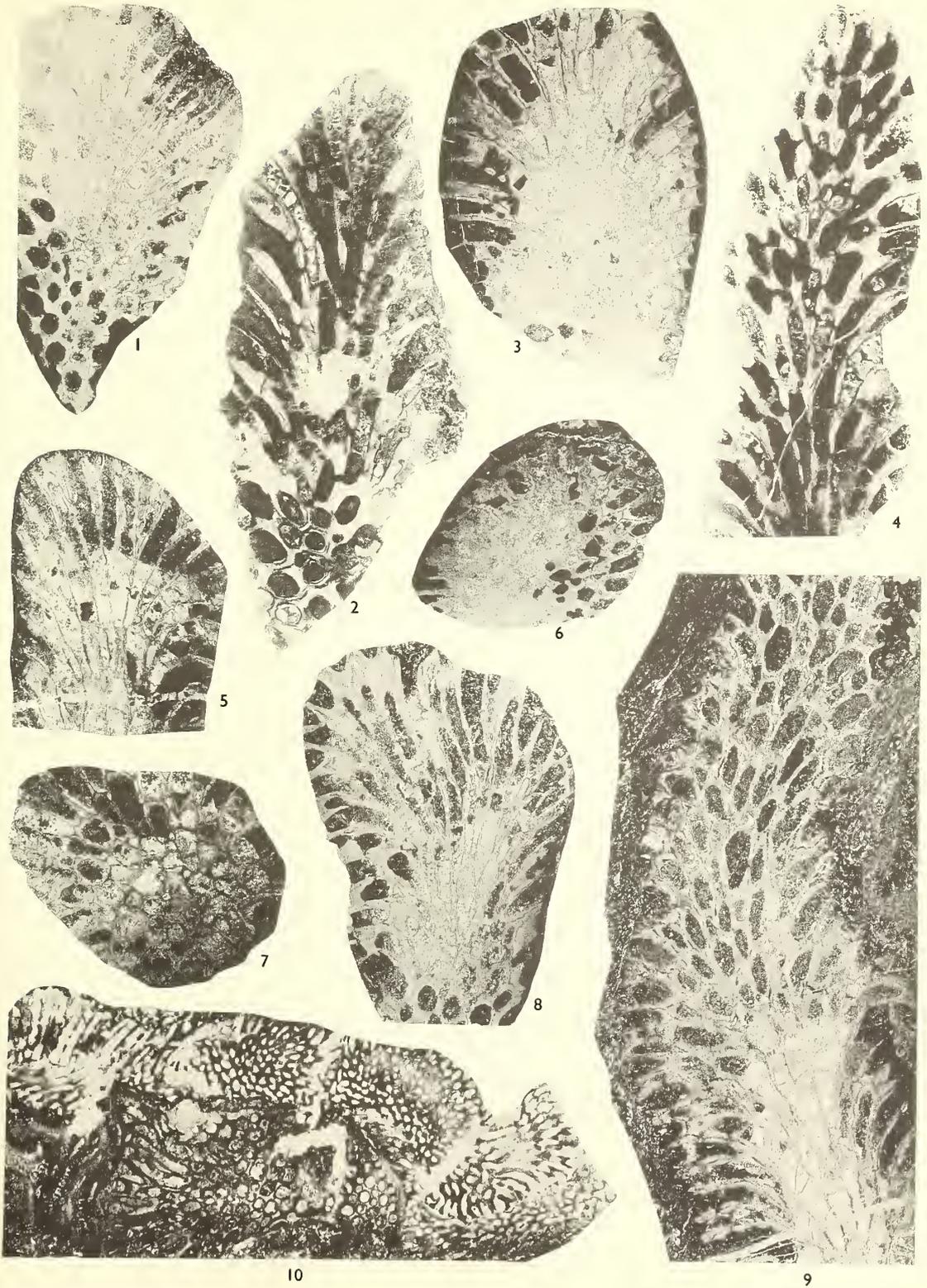
1958 *Thamnopora* Steininger; Lafuste, pp. 3658–60.

EXPLANATION OF PLATE 12

Figs. 1, 3, 5–8. *Thamnopora cronigera* (d'Orbigny). All the specimens come from the Jenny Start Limestone (Givetian) of Widmouth and Rillage Quarries. 1, Longitudinal and partial transverse sections of MM 11159 (Widmouth). 3, Longitudinal, and 7, transverse sections of MM 11160 (Rillage). 5, Longitudinal, and 6, transverse sections of MM 11161 (Rillage). 8, Longitudinal section of MM 11162 (Rillage). All $\times 3$.

Figs. 2, 4, 9. *Thamnopora boloniense* (de Blainville). 2, Longitudinal and partly transverse section of MM 11156, and 4, longitudinal section of MM 11155 from the David's Stone Limestone (Frasnian) of Sandy Cove. 9, Longitudinal and partially transverse sections of MM 11157 from the Jenny Start Limestone (Givetian) of Rillage Quarry. All $\times 3$.

Fig. 10. *Thamnopora cervicornis* (de Blainville). Transverse polished section of MM 11153 from the Combe Martin Beach limestone of the Parlour. *Alveolites suborbicularis* is seen overgrowing the *Thamnopora* colony.



HOLWILL, Devonian tabulate corals from North Devon



1959 *Thamnopora* Steininger; Chudinova, pp. 66–67 (*cum syn.*).

1965 *Thamnopora* Steininger; Schouppé, pp. 38–40 (*cum syn.*).

Diagnosis. See Lecompte 1939, p. 102.

Discussion. Contrary to most other workers (see especially Lang, Smith, and Thomas 1940, p. 92), Lecompte does not regard *Pachypora* Lindström as a synonym of *Thamnopora*. He argues that the lamellar structure seen in *Pachypora lamellicornis* is fundamentally distinct from the fibrous structure of *Thamnopora*. Lindström (1896, p. 25) himself argued most emphatically against the synonymy, and Chernyshev (1951) claimed that certain species of *Pachypora* (*Thamnopora*) possess two types of stereoplasmic microstructure—one concentric (i.e. lamellar) and the other fibrous. Chudinova (1959) has re-examined this material in addition to investigating over three thousand specimens of *Thamnopora* from the U.S.S.R. and she is emphatic that the stereoplasm always has a radial fibrous microstructure. The confused interpretation of the nature of the microstructure arises because incremental layers of *fibrous* CaCO₃ are laid down during growth and if the preservation is not good, the fibrous texture becomes lost and only the layers are readily apparent—hence the impression of a lamellar structure. This confirms the opinion of Hill (see Lecompte 1939, p. 103) that the lamellar structure is a recrystallization phenomenon. This being so, *Pachypora* must be regarded as a synonym of *Thamnopora*.

Range. Silurian to Trias, but it is most common in the Devonian and Permian.

Thamnopora boloniensis (Gosselet) 1877

Plate 12, figs. 2, 4, 9, Plate 14, fig. 5

1958 *Thamnopora boloniensis* (Gosselet); Stasińska, pp. 198–200, pl. 9–11 (*cum syn.*).

1965 *Thamnopora boloniensis* (Gosselet); Schouppé, pp. 42–45, pl. 3, fig. 5–9 (*cum syn.*).

Diagnosis. See Lecompte 1939, pp. 127–8.

Material. Three specimens from the Jenny Start Limestone and two from the David's Stone Limestone.

Description. (a) Jenny Start Limestone: specimens from the Jenny Start Limestone agree with the diagnosis of *T. boloniensis* except that the size of the calices is smaller (maximum diameter about 1.5 mm.). The corallites are, however, markedly larger than all other forms from North Devon. Only fragments of coralla have been collected and from MM 11157 a longitudinal section has been cut. The maximum diameter of the branch is 14 mm. and its length (incomplete) is 50 mm. (Pl. 12, fig. 9). The diameter of the corallites at the periphery varies from 1.1–1.5 mm., and the walls are thickened throughout, though most strongly at the periphery. The obliquity of the corallites varies from 60° to 90°. Mural pores are numerous and are approximately 1.2 mm. apart. Tabulae are moderately numerous in the axial region (4–5 in 2 mm.) but they tend to be irregularly grouped.

(b) David's Stone Limestone: two specimens have been sectioned longitudinally and these agree in all respects with Lecompte's diagnosis. The branches have a diameter of at least 15 mm. and the largest calices are over 2 mm. across. Mural pores are common

and have a diameter of about 0.15 mm. Tabulae are few and are slightly concave. The walls are thickened throughout but most strongly at the distal ends.

Remarks. In the Ardennes, Lecompte found that this species was characteristic of the Frasnian as did Stasińska (1958) in Poland; in Devon it occurs in both the Upper Givetian (Jenny Start Limestone) and the Frasnian (David's Stone Limestone) but the earlier forms appear to show slight variations. Lecompte's studies, however, showed that *T. boloniensis* is a very variable species even within the Frasnian, and its most persistent feature is the large size of the calices. I have, therefore, placed the two forms described above in the same species.

Thamnopora cervicornis (de Blainville) 1830

Plate 11, figs. 1, 4; Plate 12, fig. 10

1939 *Thamnopora cervicornis* (de Blainville); Lecompte, pp. 109–11 (*cum syn.*).

1945 *Thamnopora cervicornis* (de Blainville); Smith, p. 62, pl. 27, figs. 1a–e.

1958 *Thamnopora cervicornis* (de Blainville); Stasińska, pp. 200–2, pl. 12, figs. 1–3.

Diagnosis. See Lecompte 1939, pp. 110–11.

Remarks. The species has been identified from the Rillage and the Combe Martin Beach Limestones. The single specimen from the Rillage Limestone (Pl. 11, fig. 4) is remarkable because of its prominent spines seen in longitudinal section. The calices have a diameter of 1–1.2 mm. and the thickness of the walls is irregular, though most prominent at the distal ends of the corallites. The branch is irregular in diameter but reaches a maximum of 15 mm. Along the sides of the branch the corallites bend round to reach the exterior at right angles, but at its extremity, they make an angle of about 60°. Tabulae are irregularly spaced and may be slightly convex or concave.

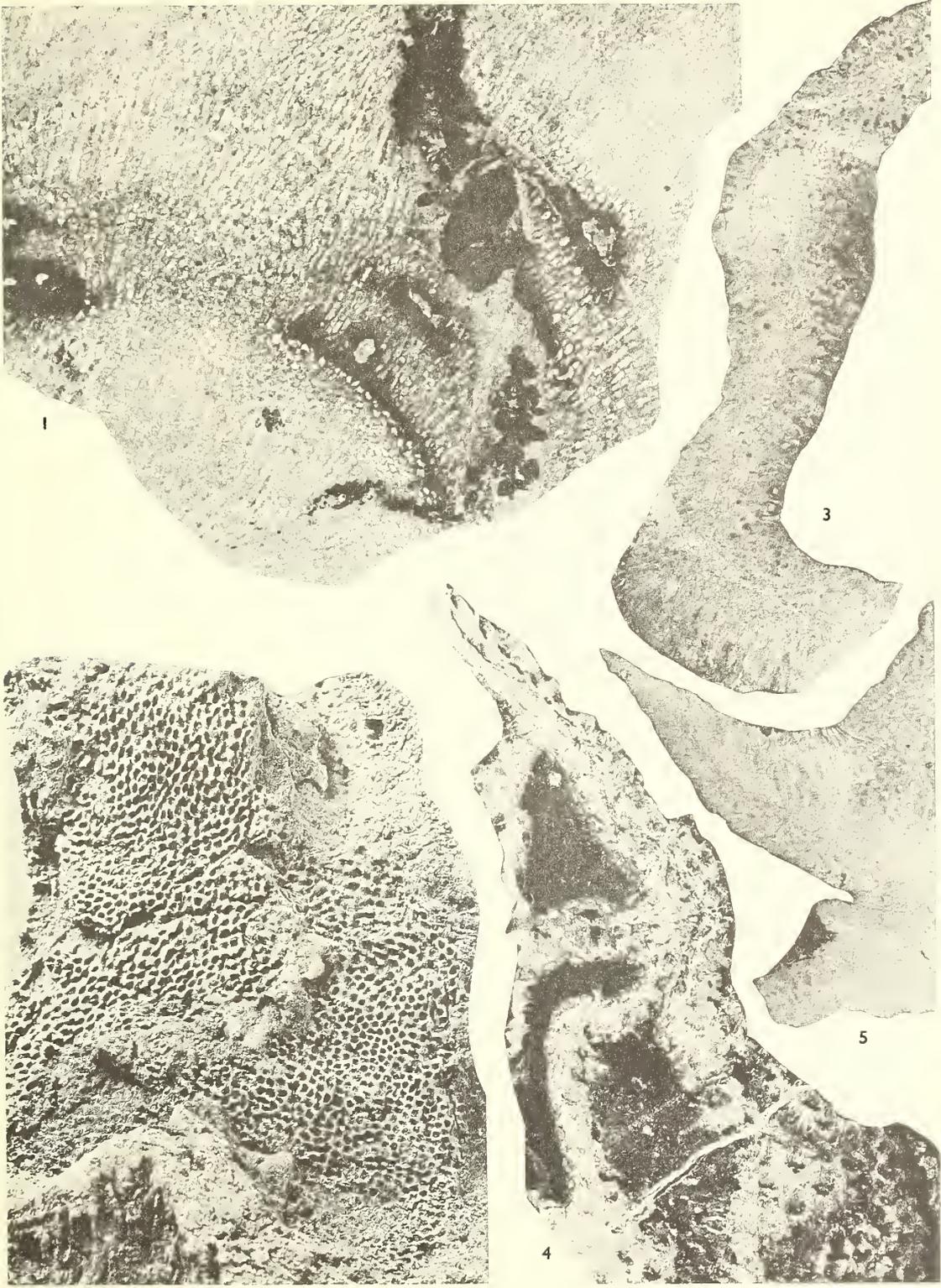
In the Combe Martin Beach Limestone the species is locally common (especially at the entrance to the Parlour). Specimens are frequently overgrown by *Alveolites* and appear to be preserved in their growth positions (Pl. 12, fig. 10). The corallites are

EXPLANATION OF PLATE 13

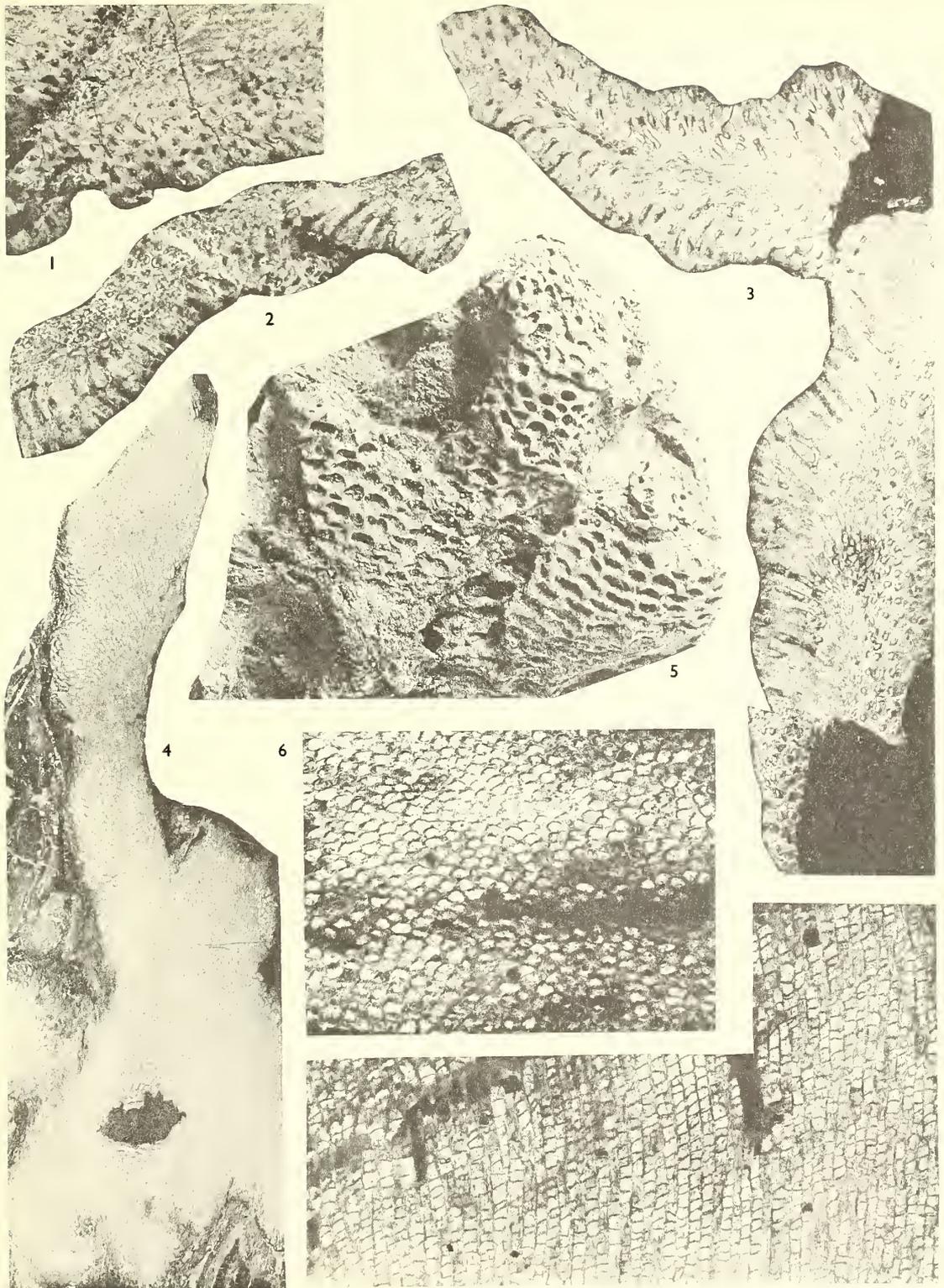
Figs. 1, 2. *Alveolites multiperforatus* Lecompte. 1, Longitudinal thin section ($\times 3$) and 2, external surface ($\times 2.4$) of MM 11177 from the Jenny Start Limestone of Widmouth Quarry. The latter figure shows the form of the calices and the occasional breakdown of the walls between adjacent corallites. Figs. 3–5. *Coenites escharoides* (Steininger). All are longitudinal sections of specimens from the Jenny Start Limestone. 3, and 5, MM 11192 from Hagginton Beach. Both $\times 3$. 4, MM 11181 from Widmouth Quarry. $\times 6$.

EXPLANATION OF PLATE 14

Figs. 1–3. *Coenites* sp. MM 11190 from the Jenny Start Limestone (Givetian) of Samson's Bay. 1, Transverse section showing the thickening around the calices. 2, Longitudinal and partly transverse section. 3, Longitudinal and transverse sections showing the form of the colony and the thickening in the axial and peripheral zones. All $\times 6$.
 Fig. 4. *Alveolites suborbicularis* Lamarck. MM 11150 showing the typical lamellar and encrusting form of the colony. $\times 1.8$.
 Fig. 5. *Thamnopora? boloniensis* (de Blainville). Exterior surface of MM 11193 which has been distorted by tectonic pressure; from the Jenny Start Limestone of Widmouth Quarry. $\times 2.4$.
 Figs. 6, 7. *Chaetetes lonsdalei* Etheridge and Foord. 6, Transverse and 7, longitudinal sections of MM 11176 from the David's Stone Limestone of Hele Bay, near Ilfracombe. Both $\times 6$.



HOLWILL, Devonian tabulate corals from North Devon



HOLWILL, Devonian tabulate corals from North Devon

smaller and more numerous in these coralla than in the specimen from the Rillage Limestone. The corallites have a diameter of about 0.9 mm. and make an angle of 50–60° with the outer surface at the extremity of the branches; along the sides, however, they are perpendicular or even directed posteriorly (see Pl. 13, fig. 1). Thickening of the walls is again irregular but most strong at the distal ends.

In North Somerset, Webby (1964, pp. 4–5) has identified the species from the Upper Givetian (Roadwater Limestone) and in the Ardennes too, Lecompte has found the species confined to the Givetian. Lecompte found that specimens from horizon *Gib* were smaller than those from *Gid* (Upper Givetian). This is most probably an ecological rather than evolutionary variation and although the North Devon specimens approximate more closely to Lecompte's *Gib* specimens, the evidence is too uncertain to draw definite conclusions.

Stasińska (1958) also found the species confined to the Givetian but elsewhere it extends into the Upper Devonian. Smith (1945) records it from the Frasnian of North America and Chudinova (1959, p. 69) mentions its occurrence in Givetian and Frasnian beds of U.S.S.R., Mongolia, and the Sahara; it is however rarer in the higher stages.

Thamnopora cronigera (d'Orbigny) 1850

Plate 12, figs. 1, 3, 5–8

1939 *Thamnopora cronigera* (d'Orbigny); Lecompte, p. 107.

Diagnosis. See Lecompte 1939, p. 109.

Remarks. Lecompte (1939) regarded *T. cronigera* as intermediate between *T. polymorpha* and *T. cervicornis* and he found difficulty in defining the precise limits of each species. Typically, the corallum of *T. cronigera* is smaller and has less tendency to branch than *T. polymorpha*; it also has fewer tabulae. However, it is less thickened by stereoplasm than *T. cervicornis* and the calices are in consequence not so rounded.

The specimens from North Devon referred to this species are all broken fragments but are closely similar to those which were described and figured by Lecompte from the Dinant Basin; these differed from the type (Goldfuss 1831, pl. 27, fig. 3) selected by d'Orbigny (1850, p. 107) in being more 'robuste' and having calices more rounded in the axial zone.

In the Dinant Basin, the species occurs in beds *Gib* and *Gic* of the Middle Givetian. In North Devon, the species is common in the Jenny Start Limestone but has not been identified from any of the other limestones.

Thamnopora polyforata (Schlotheim)

Plate 11, figs. 8–10, 12–15

1820 *Milleporites polyforatus* Schlotheim, p. 365, *partim*.

1826 *Calanopora polymorpha* var. *gracilis, raiuis gracilibus, elougatis* Goldfuss, p. 79, pl. 27, fig. 5.

1936 *Favosites dubius* (de Blainville); Lecompte, p. 54, pl. 10, fig. 1 (*cum syn.*).

1939 *Thamnopora dubia* (de Blainville); Lecompte, p. 120, pl. 18, figs. 7–12.

1945 *Thamnopora polyforata* (Schlotheim); Smith, p. 63, pl. 28, figs. 1, 2 (*cum syn.*).

?1952 *Thamnopora polyforata* (Schlotheim); Smith, p. 301.

1953 *Thamnopora dubia* (de Blainville); Kropfitch and Schouppé, p. 95, pl. 1, figs. 2, 3 (*cum syn.*).

- ?1954 *Thamnopora* cf. *polyforata* (Schlotheim); Hill, p. 31, pl. 1, figs. 7-9.
 1964 *Thamnopora polyforata* (Schlotheim); Webby, pp. 15-17, text-fig. 6.

Diagnosis. See Lecompte 1939, p. 121.

Remarks. The species is common in the Jenny Start Limestone of North Devon. Several specimens have been sectioned and these agree well with those figured and described by Lecompte (1939, pp. 120-2, pl. 18, figs. 7-12). The diameter of the branches is 6-8 mm., except for specimen MM 11167 which is slightly larger (10 mm.). The latter specimen (figured in Pl. 11, fig. 15) shows well the septal spines, though it is possible that recrystallization in the centre of the corallite has accentuated them. The thickening of the walls is well-marked in all the specimens. The average diameter of the calices is 1.7 mm.; none reaches the maximum diameter of 2 mm. mentioned by Lecompte in his diagnosis.

Lecompte (1936) made a detailed study of the species and refigured and described the original of Goldfuss (1826, p. 79), which shows no trace of septal spines. He accepted Quenstedt's (1881, p. 37) view that the species should be interpreted more liberally and framed his diagnosis accordingly. Webby (1964) has reviewed the recent literature and has pointed out that the reference of *T. polyforata* to the genus *Pachypora*, as advocated by Kropfitch and Schouppé (1953), is unsatisfactory, as the corallite walls show both fibrous and lamellar structure. In the light of the recent work by Chudinova (1959)—see discussion on genus above—*Pachypora* must be regarded as a synonym of *Thamnopora*.

In the Ardennes, the species ranges from Givetian to Frasnian. In North Devon it characterizes the Givetian Jenny Start Limestone though a single specimen from the David's Stone Limestone (Frasnian) is doubtfully referred to this species.

Thamnopora irregularis Lecompte 1939

Plate 11, figs. 3, 5, 16

1939 *Thamnopora irregularis* Lecompte, p. 113, pl. 15, figs. 6-9.

Diagnosis. See Lecompte 1939, pp. 114-15.

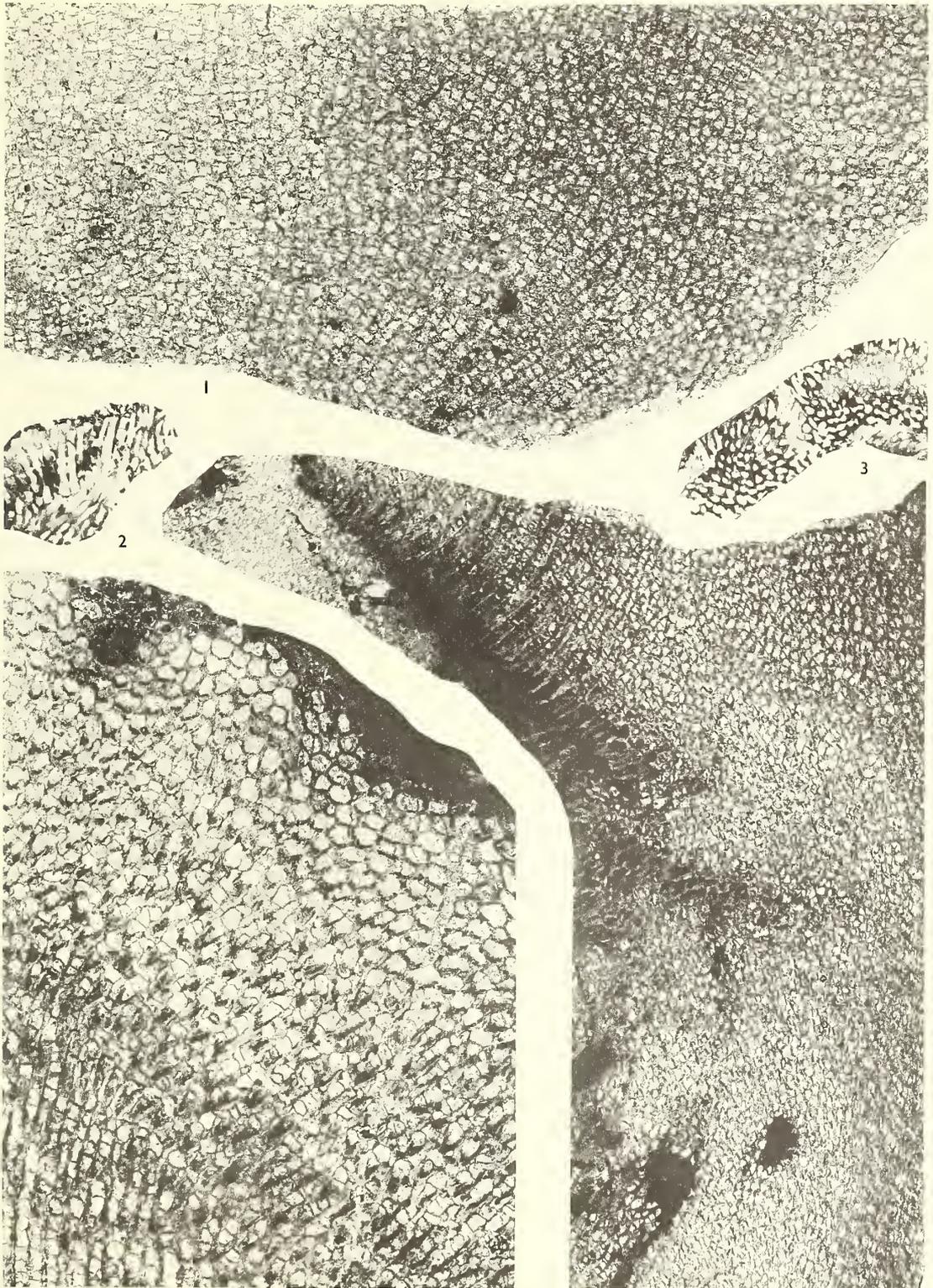
Remarks. The specimens from North Devon agree very closely with the diagnosis and description given by Lecompte though the tabulae tend to be more closely spaced and the distal thickening is somewhat greater than in the holotype. The species has been found only in the Jenny Start Limestone where it frequently forms large ramifying masses. In the Dinant Basin the species occurs in the *Gia* and *Gib* beds of the Givetian.

EXPLANATION OF PLATE 15

Figs. 1-5. *Alveolites suborbicularis* Lamarck. 1, Transverse (partly longitudinal) thin section of MM 11186 from the David's Stone Limestone of Broadstrand Beach, near Ilfracombe ($\times 4$). 2, Longitudinal, and 3, transverse sections of MM 11153 from the Parlour, near Combe Martin ($\times 2.5$). 4, Transverse and longitudinal sections of MM 11154 from the Jenny Start Limestone of Widmouth Quarry ($\times 4$). 5, Transverse and longitudinal sections of MM 11187 from the David's Stone Limestone of Broadstrand Beach, near Ilfracombe ($\times 4$).

EXPLANATION OF PLATE 16

Figs. 1, 2. *Alveolites suborbicularis* Lamarck forma *gemmans* Lecompte. 1, Transverse, and 2, longitudinal sections of MM 11178 from the Jenny Start Limestone of Rillage Quarries. Both $\times 3.5$.



4

5

HOLWILL, Devonian tabulate corals from North Devon



HOLWILL, Devonian tabulate corals from North Devon

Thamnopora polymorpha (Goldfuss)

Plate 10, figs. 1-5

1936 *Favosites polymorphus* (Goldfuss); Lecompte, pp. 34-40, pl. 7, figs. 1-2 (*cum syn.*).1939 *Thamnopora polymorpha* (Goldfuss); Lecompte, pp. 104-7.1964 *Favosites sp.*; Holwill 1964b, p. 128.

Diagnosis. See Lecompte 1939, p. 107.

Remarks. This species is very characteristic of the David's Stone Limestone and has not been found in any of the other limestones of the Ilfracombe Beds. The original fibrous structure is still visible in most of the examples collected. The form of the coralla is irregular but it tends to be branching or lamellar with marked bulbous projections.

The average diameter of the corallites is slightly smaller than in the examples from the Ardennes, but otherwise the North Devon specimens agree closely with the type.

In placing the species within the genus *Thamnopora*, I am following Lecompte (1939, pp. 81-83), who argued that the internal thickening, resulting in rounding of the calice, is never found in true favositids, only in species of *Thamnopora*. He admits, however, that *T. polymorpha* forms a transition between indisputable species of *Favosites* with thin walls and angular calices, and typical *Thamnopora* with well-rounded calices and branching corallum. Lecompte makes the point that *Favosites* is typical of Middle Devonian strata, and does not extend into the Upper Devonian except for occasional aberrant forms, while *Thamnopora* (which he considered to be generically distinct from *Pachypora*) showing intermediate characteristics appears in the Couvinian and by the Givetian and Frasnian has developed the typical thamnoporid features. This leads him to suggest that *Thamnopora* may have evolved from *Favosites* during the Lower Couvinian. Other workers have found similar difficulty in deciding the precise boundary between *Favosites* and *Thamnopora*. Swann (1947, p. 259) in studying his *alpenensis* lineage, found a complete morphological series between favositid and thamnoporid forms. In consequence, he felt it logical to place all the forms in *Favosites*, but he recognized that the thickening of the corallite walls was an evolutionary, not environmental, feature, characteristic of Devonian beds. Hamada (1959, pp. 206 et seq.) agreed that it was an evolutionary feature, but unlike Swann, he found it convenient to retain the generic name *Thamnopora* for (p. 208) 'favositids with wall thickening which makes the cross section of the visceral chambers rounded in the axis as well as the peripheral parts of the corallum'.

I agree with Lecompte and Hamada (1959, p. 208) that the genus *Thamnopora* should be retained, as at the least it provides a useful morphological category, and in most cases the thickening (or lack of it) enables *Thamnopora* and *Favosites* to be separated without difficulty. Earlier, I (Holwill 1964) reported the presence of *Favosites* in the David's Stone Limestone, but I was then interpreting *T. polymorpha* as a favositid; no other species of *Favosites* occurs in this limestone.

In Belgium, *T. polymorpha* occurs in Couvinian and Givetian beds (including bed *Gid*—uppermost Givetian). In North Devon the species appears to persist into the Frasnian, though its presence suggests that the David's Stone Limestone is at a low horizon within the Frasnian.

Thamnopora tumefacta Lecompte 1939

Plate 11, figs. 2, 6, 7, 17

1939 *Thamnopora tumefacta* Lecompte, pp. 117–18, pl. 16, figs. 15–16.1952 *Thamnopora tumefacta* Lecompte; Sokolov, pp. 61–62, pl. 13, fig. 1.1959 *Thamnopora tumefacta* Lecompte; Chudinova, pp. 84–85, pl. 26, figs. 2–4.*Diagnosis.* See Lecompte 1939, p. 118.

Remarks. Three specimens have been referred to this species from North Devon. All of them are fragments but they agree closely with Lecompte's diagnosis and description except that they are somewhat smaller—the maximum diameter of the corallum being 6–7 mm. The maximum diameter of the corallites is 0.9 mm., but the walls are strongly thickened, especially distally, so that the aperture may be reduced to 0.2 mm. or less. The corallites bend round so as to meet the outer surface at right angles.

The type specimen comes from the upper Couvinian beds (Co2d) of Couvin but Lecompte also records it from the Givetian. In Russia, Chudinova (1959) reports it from the Middle Devonian of the Eastern Urals, while in North Devon it occurs in the David's Stone Limestone (Frasnian).

Subfamily MICHELININAE Waagen and Wentzel 1886

Genus PLEURODICTYUM Goldfuss 1829

Pleurodictyum sp.

Plate 17, fig. 6

Remarks. Valpy (1867, p. 35) recorded *Pleurodictyuni* as *Michelinia antiqua* from the Ilfracombe Beds probably at Hagginton Beach. I have not been able to trace his specimen with certainty, but it may be BM R6421; this is the specimen figured. It consists of a very poorly developed mould into which dolomite crystals have grown. There is no precise record of its locality, but its preservation and the nature of the limestone matrix make it almost certain to have been obtained from the Combe Martin Beach Limestone which crops out at many places along Hagginton Beach. Specific identification is impossible.

Family AULOPORIDAE Edwards and Haime 1851

Genus AULOPORA Goldfuss 1829

EXPLANATION OF PLATE 17

- Figs. 1–3. *Coenites gradatus* Lecompte. 1, Transverse and partly longitudinal section of MM 11183 from the David's Stone Limestone of Hillsborough near Ilfracombe. 2, and 3, longitudinal sections of MM 11185 and MM 11184 respectively; the latter shows the lamellar form of the colonies emphasized by the preservation. All $\times 3$.
- Figs. 4, 5. *Alveolites obtortus* Lecompte. Transverse and longitudinal sections through specimens from the Jenny Start Limestone of Widmouth Quarry. 1, MM 11179 and 2, MM 11180. Both $\times 3$.
- Fig. 6. *Pleurodictyum* sp. Mould, BM R6421, probably from the Combe Martin Beach Limestone of Hagginton Beach. $\times 6$.
- Figs. 7, 8. *Aulopora ?tubaeformis* Goldfuss. Two fragments of colonies from the David's Stone Limestone of David's Stone. 7, weathered external surface of MM 11189 and 8, partly eroded surface of MM 11188. Both $\times 4$.



HOLWILL, Devonian tabulate corals from North Devon

Aulopora ?tubaeformis Goldfuss 1826

Plate 17, figs. 7-8

?1826 *Aulopora tubaeformis* Goldfuss, p. 83, pl. 29, fig. 2.

Remarks. Only two small and very incomplete colonies have been collected—both of them from the David's Stone Limestone of David's Stone. One of them (MM 11188), shows two partly broken corallites, revealing a thin horizontal tabula. The other specimen is slightly larger, but is embedded in argillaceous limestone and is not seen in relief. The diameter of the calices is about 1.5 mm., and they are about 5 mm. long; they are linked together in a single chain. The preservation prevents any other specific details of the specimens being observed but the size and the shape of the corallites agree with those of *A. tubaeformis*.

REFERENCES

- BLAINVILLE, H. M. D. DE. 1830. Zoophytes. *Dict. Sci. Nat.* 60 pp.
- CHERNYSHEV, B. B. 1951. Silurijskie i devonskie Tabulata i Heliolitida okrain Kuznetskogo ughenosnogo basseina. *Trudy vses. Nanch.-Issled. Geol. Inst.*, Moscow, 160 pp.
- CHUDINOVA, I. I. 1959. Devonskie Tamnoporidy yuzhnoi Sibiri. *Trudy paleont. Inst.* **73**, 1-146, pls. 1-34 (in Russian).
- DANA, J. D. 1846. U.S. exploring expedition during the years 1838 to 1842 under the command of Charles Wilkes. 7, Zoophytes. 1-740 and atlas.
- DUBATOLOV, V. N. 1956. Tabulyaty i Geliolitidy severo-vostochnogo prisalairya. *Ezheg. vses. paleont. obshch.* **15**, 83-124, pl. 1-5.
- DUNCAN, P. M. 1872. A monograph of British fossil corals, 2nd series. *Palaeontogr. Soc. (Monogr.)* **3**.
- EDWARDS, H. M. and HAIME, J. 1850. A monograph of the British fossil corals. Part I, Introduction etc. i-lxxxv, 1-71, pl. 1-11.
- 1853. A monograph of the British fossil corals. Part IV, Corals of the Devonian formation. Ibid. 211-44, pl. 47-56.
- EICHWALD, C. E. D'. 1829. *Zoologia specialis quam expositis animalibus tum vivis, tum fossilibus potissimum Rossiae in universum et Poloniae in specie.* vi+1-314, pl. 1-5. Vilnae.
- ETHERIDGE, R. 1867. The physical structure of North Devon and the palaeontological value of the Devonian fossils. *Quart. J. geol. Soc. Lond.* **23**, 568-698.
- 1899. On the corals of the Tamworth District chiefly from the Moore Creek and Woolmol Limestones. *Rec. geol. Surv. N.S.W.* **6** (3), 151-82, pl. 14-38.
- and FOORD, A. H. 1884. Two species of *Alveolites* and one of *Amplexopora* from the Devonian rocks of Northern Queensland. *Ann. Mag. nat. Hist.* (5) **14**, 175-9.
- EVANS, J. W. 1929. *Sedimentary rocks.* In EVANS, J. W. and STUBBLEFIELD, C. J. (eds.) *Handbook of the geology of Great Britain*, **5**, Devonian. A, 128-53. London.
- FRECH, F. 1886. Die Cyathophylliden und Zaphrentiden des deutschen Mitteldevon. *Palaeont. Abhandl.* **3** (3), 115-234, pl. 13-20.
- GERTH, H. 1921. Die Anthozöen der Dyas von Timor. *Palaeont. von Timor*, **11**, 67-147, pl. 145-50.
- GOLDFUSS, G. A. 1826-33. *Petrefacta Germaniae.* 1-252, 71 pls. Düsseldorf.
- GOSSELET, J. 1877-8. Le calcaire dévonien supérieur dans le Nord-Est de l'arrondissement d'Avesnes. *Ann. Soc. géol. Nord*, **4**, 238-320, pl. 3-4.
- GÜRICH, G. 1896. Das Palaeozoicum im Polnischen Mittelgebirge. *Verh. Russ.-Kais. Min. Ges.* **32**, 1-539, pl. 1-15.
- HAMADA, T. 1959. On the taxonomic position of *Favosites hindensis* and its Devonian age. *Jap. J. Geol. Geogr.* **30**, 201-13, 16 pl.
- HENNIG, A. 1906. Gotlands Silur-Bryozoer. *Arkiv för Zoologi*, **3**, (2), no. 10, 1-62, pl. 1-7.
- HILL, D. 1954. Coral faunas from the Silurian of New South Wales and the Devonian of Western Australia. *Bur. Min. Resour. Aust. Bull.* **23**, 51 pp., 4 pl.

- HILL, D. and STUMM, E. C., 1956. *Treatise on Invertebrate Paleontology*, Part F, Coelenterata (Tabulata), ed. R. C. Moore, F444-74.
- HOLWILL, F. J. W. 1962. The succession of limestones within the Ilfracombe Beds (Devonian) of North Devon. *Proc. Geol. Ass.* **73**, 281-93.
- 1964a. The coral genus *Metriophylhun* Edwards and Haime. *Palaeontology*, **7**, 108-23, pl. 16-19.
- 1964b. Corals of the Ilfracombe Beds. *Proc. Ussher Soc.* **1**, 126-8.
- KONINCK, L. G. DE. 1876-7. *Recherches sur les fossiles paléozoïques de la Nouvelle-Galles du Sud (Australie)*. 1-373, Atlas (pl. 1-4, 1876; pl. 5-24, 1877). Bruxelles.
- 1898. Descriptions of Palaeozoic fossils of New South Wales (Australia). *Mem. geol. Surv. N.S.W., Palaeont.* **6**, 1-298, pl. 1-24. (Translated from Koninck 1876-7.)
- KROPFITSCH, M. and SCHOUPPÉ, A. VON. 1953. Revision der Tabulaten aus dem Paläozoikum von Graz. I. Thamnoporen und Striatoporen. *Mitt. naturw. Ver. Steierm.* **83**, 90-117, pl. 1.
- LAFUSTE, J. 1958. Sur la microstructure des parois calicinales chez *Thamnopora* Steininger. *C.R. Acad. Sci. Paris*, **246** (26), 3658-60.
- LAMARCK, J. B. 1801. *Système des animaux sans vertèbres*, 1-432. Paris.
- LANG, W. D., SMITH, S. and THOMAS, H. D. 1940. *Index of Palaeozoic coral genera*, 1-231. London.
- LECOMPTE, M. 1933. Le genre *Alveolites* Lamarck dans le Dévonien moyen et supérieur de l'Ardenne. *Mém. Mus. Hist. nat. Belg.* **55**, 50 pp., 4 pl.
- 1936. Révision des tabulés dévoniens décrits par Goldfuss. *Ibid.* **75**, 112 pp., 14 pl.
- 1939. Les tabulés du Dévonien moyen et supérieur du bord sud du Bassin de Dinant. *Ibid.* **90**, 227 pp., 23 pl.
- LE MAÎTRE, D. 1947 Contribution à l'étude du Dévonien du Tafilalet, II. Le récif coralligène de Ouihalne. *Mém. Serv. Géol. Maroc.* **67**, 1-113, Lille.
- LINDSTRÖM, G. 1873. Några anteckningar an Anthozoa Tabulata. *Kongl. Vetensk. Akad. Förhandlingar*, **4**, 3-20.
- 1876. On the affinities of the Anthozoa Tabulata. *Ann. Mag. nat. Hist.*, ser. 4, **18**, pp. 1-17.
- 1896. Beschreibung einiger Obersilurischer Korallen aus der Insel Gotland. *Bihang Kongl. Svensk. Vetensk.-Akad. Handl.* **21** (7), pp. 4-50.
- OAKLEY, K. P. 1936a. On Ordovician species of *Chaetetes*. *Geol. Mag.* **73**, 440-4, pl. 12.
- 1936b. On the Wenlock coral *Coenites seriatopora* (H. M. Edwards and J. Haime). *Summ. Progr. geol. Surv. G.B. for 1934* (2), 20-27.
- OKLITCH, V. J. 1936. On the genera *Heliolites*, *Tetradium* and *Chaetetes*. *Am. Journ. Sc.*, ser. 5, **32**, 361-79.
- ORBIGNY, M. A. D'. 1850 *Prodrôme de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés*. lx+1-394. Paris.
- PETTS, G. FON. 1901. Materialy k poznaniyu fauny devonskikh otlozhenii okrain Kuznetskago ugle-nosnago basseina. *Trav. Sect. geol. Cab. St.-Petersb.* **4**, 1-393, pl. 1-6 (in Russian).
- PHILLIPS, J. 1841. Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon and West Somerset. *Geol. Surv. Great Britain and Ireland*, xii+231, pl. 1-60.
- QUENSTEDT, F. A. 1881. Die Röhren- und Sternkorallen, *Petrefaktenkunde Deutschlands*, **6**, 913-1094. Leipzig.
- REED, F. R. C. 1908. The Devonian faunas of the Northern Shan States. *Mem. geol. Surv. India. Palaeont. indica*, N.S. **2**, no. 5, 1-183, pl. 1-20.
- ROMINGER, C. 1892. On the occurrence of typical *Chaetetes* in the Devonian strata of the falls of the Ohio and likewise in the analogous beds of the Eifel in Germany. *Am. Geol.* **10**, 16-25, pl. 5.
- SCHLOTHEIM, E. F. VON 1820. *Die Petrifaktenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung . . . erläutert*. pp. lxii+1-437.
- SCHLÜTER, C. 1889. Anthozoen des rheinischen Mittel-Devon. *Abh. geol. Specialk. Preuß. Thüring. Staat.* **8** (4), x+259, pl. 1-16. Gothan.
- SCHOUPPÉ, A. VON. 1965. Die Mittel- bis Oberdevonische Korallenfauna von Kuragh (Chitral). *Scient. Rep. Italien Exped. Karakorum (K²) Hindu Kush*, **4**, Paleont.-Zool.-Bot., 13-53, pl. 2, 3.
- SMITH, S. 1933. Sur des espèces nouvelles d'*Alvéolites* de l'Eifelien du Nord de la France et de la Belgique. *Ann. Soc. Géol. Nord*, **58**, 134-45, pl. 2-3.
- 1945. Upper Devonian Corals of the Mackenzie River Region, Canada. *Spec. Pap. geol. Soc. Amer.* **59**, 126 pp.

- SMITH, S. 1952. Notes on corals from Lower Devonian rocks of S.W. Devonshire. *Trans. R. geol. Soc. Cornwall*, **18**, 299–308.
- and LANG, W. D. 1930. Descriptions of the type specimens of some Carboniferous Corals. *Ann. Mag. nat. Hist.* (10)5, 177–94, pl. 7–8.
- SOBOLEV, D. 1903. Devonskiya otlozheniya profilya Grzhegorzhevitse-Skaly-Vlokhi. *Izv. varshav. politekh. Inst.* 1–107 (in Russian).
- 1909. Srednii Devon kletsko-sandomirskago kryazha. *Mater. Geol. Ross.* **24**, 41–536 (in Russian).
- SOKOLOV, B. S. 1950. Khetetidy karbona severo-vostochnoi Ukrainy i sopredelnykh oblastei (s opisaniem nekotorykh tabulyat). *Trudy vses. nefi. nauchno-issled. geol.-razv. Inst.* 144 pp.
- 1952. Tabulyaty paleozoya Evropeiskoi chasti SSSR, IV. Devon Russkoi platformy i zapadnogo Urala. *Ibid.* **62**, 1–291, pl. 1–40 (in Russian).
- 1955. Tabulyaty paleozoya Evropeiskoi chasti SSSR, Vvedenie. Obshchie voprosy sistematiki i istorii razvitiya Tabulyat. *Ibid.* **85**, 1–527, pl. 1–90 (in Russian).
- STASIŃSKA, A. 1958. Tabulata, Helioditida et Chaetetida du Dévonien Moyen. *Acta Palaeont. Polon.* **3**, 161–282.
- STEININGER, J. 1831. *Bemerkungen über die Versteinerungen welche in dem Uebergangs kalkgebirge der Eifel gefunden werden*, 1–44. Trier.
- 1833. Observations sur les fossils du calcaire intermédiaire de l'Eifel. *Mem. Soc. geol. France* (1), **1**, 331–71.
- 1849. *Die Versteinerungen des Uebergangsgebirges der Eifel*, 1–34. Trier.
- 1853. *Geognostische Beschreibung der Eifel*. 1–143, 10 pl. Trier.
- SWANN, D. H. 1947. The *Favosites alpenensis* lineage in the Middle Devonian Traverse Group of Michigan. *Contrib. Mus. Paleont. Univ. Michigan* **6** (9), 235–317, pl. 1–17.
- VALPY, P. 1867. *Notes on the Geology of Ilfracombe*. 38 pp. Twiss and Sons, Ilfracombe.
- WAAGEN, W. and WENTZEL, J. 1886. Salt-range fossils. I. Productus limestone fossils. Part 6, Coelenterata. *Mem. geol. Surv. India. Palaeont. indica*, Ser. 13, pp. 835–924, pl. 97–116.
- WHITEAVES, J. F. 1897. Palaeozoic Fossils, 4; the fossils of the Galena-Trenton and Black River formations of Lake Winnipeg and its vicinity. *Geol. Surv. Canada*, **3**, pt. 3, 129–242, pl. 16–22.
- WEBBY, B. 1964. Devonian corals and brachiopods from the Brendon Hills, West Somerset. *Palaeontology*, **7**, 1–22.

Typescript received from author 16 October 1966

CARBONIFEROUS SCHIZOPHORIID BRACHIOPODS FROM WESTERN EUROPE

by YVONNE P. POCOCK

ABSTRACT. Six species of the genus *Schizophoria* are described from the Carboniferous of western Europe. *Schizophoria annectans* is new. All species are shown to be externally and internally distinct. Stratigraphical ranges and postulated phylogeny are also given.

THE genus *Schizophoria* has been studied from the Carboniferous of Belgium and the British Isles. The precise stratigraphical range and relative abundance of *Schizophoria* from the Dinant Basin of Belgium is unknown, due to absence of extensive collections, and lack of detailed information on horizons. Available information is listed under specific descriptions.

In the British Isles *Schizophoria* has a long stratigraphical and wide geographical range. The genus appears in the K zone, becomes very abundant in the reef facies (C–D zones), and eventually disappears towards the top of the Viséan, except for *S. connivens* (Phillips). *Schizophoria connivens* continues to occur in limestones (E stage) of the Scottish Namurian succession, and marine Cayton Gill Beds (R₁ stage) of the Yorkshire Namurian succession.

Abbreviations. In the descriptions, relevant museum collections listed are as follows: BC—Bedford College, University of London; BM—British Museum (Natural History); GSI—Geological Survey of Ireland (Dublin); GSL—Geological Survey (Leeds); GSM—Geological Survey Museum (London); HMUG—Hunterian Museum, University of Glasgow; IC—Imperial College, University of London; IRSN—Institut royal des sciences naturelles de Belgique; SM—Sedgwick Museum, University of Cambridge; TCD—Trinity College, Dublin; UR—University of Reading.

In each text-figure of serial sections, the numbers represent distances in millimetres measured anteriorly from the umbones. Almost all muscle field patterns and vascular markings are illustrated on figures of internal moulds, since moulds, rather than discrete valves, are the common form of preservation.

SYSTEMATIC DESCRIPTION

Superfamily ENTELETACEA Waagen 1884

Family SCHIZOPHORIIDAE Schuchert and Le Vene 1929

Subfamily SCHIZOPHORIINAE Schuchert and Le Vene 1929

Genus SCHIZOPHORIA King 1850

Schizophoria connivens (Phillips) 1836

Plate 18, figs. 1, 2; text-figs. 1–4

1836 *Spirifera connivens* Phillips, p. 220, pl. 11, fig. 2.

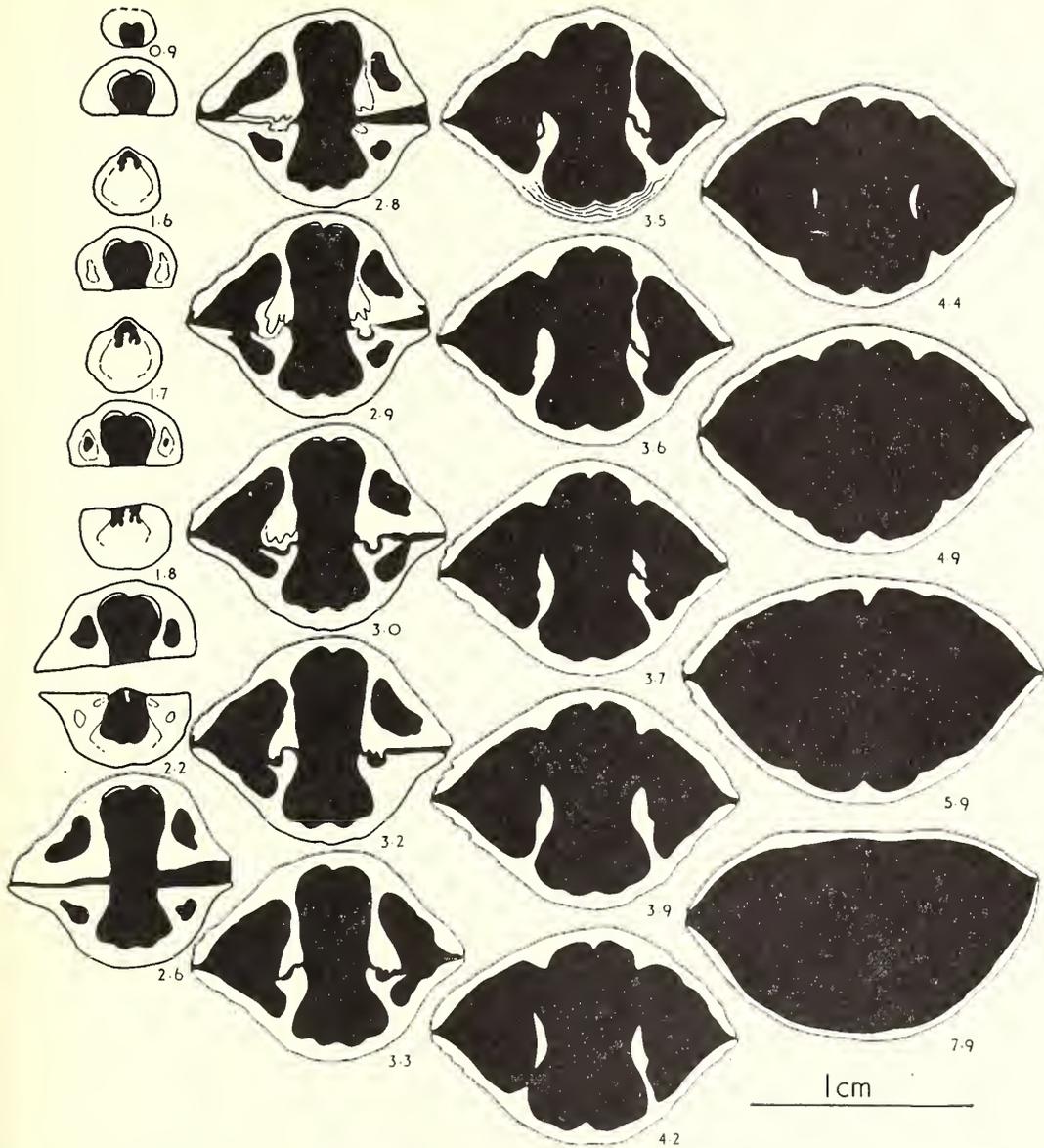
1842–4 *Orthis striatula* De Koninck, p. 224, pl. 13, fig. 11a, b; non pl. 13^{bis}, fig. 6.

1861 *Schizophoria resupinata* var. *connivens* (Phillips); Davidson, p. 131, pl. 29, figs. 6, 7.

1923 *Schizophoria resupinata* var. *connivens* (Phillips); Demanet, p. 121, pl. 5, fig. 3.

1923 *Schizophoria resupinata* var. *gibbera* (Portlock); Demanet, pl. 5, fig. 2.

1932 *Schizophoria hudsoni* George, p. 38, figs. 51–53.



TEXT-FIG. 1. *Schizophoria connivens* (Phillips). Transverse serial sections (IC 11137); D₁ zone, Swinden, Yorkshire; Length 13.7 mm., width 16.7 mm., depth 11.5 mm.

1934 *Schizophoria resupinata* var. *connivens* (Phillips); Demanet, p. 56, pl. 4, figs. 5, 6.

1941 *Schizophoria connivens* (Phillips); Bond, p. 293, text-fig. 35.

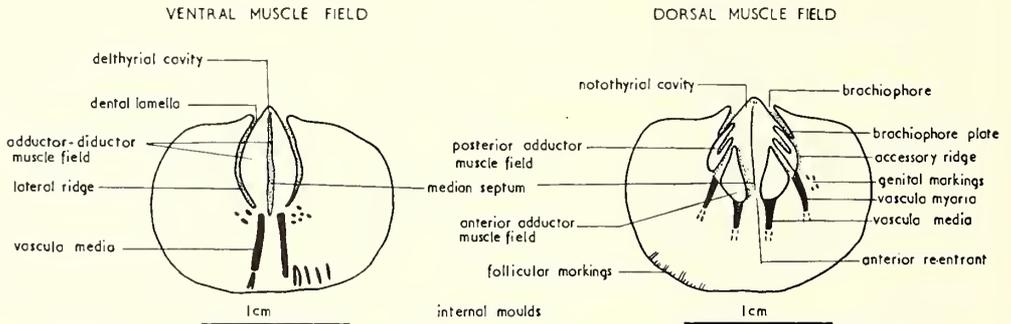
1962 *Schizophoria* aff. *S. resupinata* (Martin); Yanagida, pl. 21, fig. 5.

Type. The holotype is lost. The neotype, chosen and figured by Bond (1941), is deposited in the British Museum (Natural History), B387.

Diagnosis. Small to medium, tumid, rectangular to rounded, with biplicate, sulciphate

or quadrate-uniplicate anterior commissure. Shell coarsely costellate, rugate. Ventral muscle field strongly incised, elliptical to flabellate. Short, strong brachiophore plates.

Description. Shell ventribiconvex to weakly dorsibiconvex, with greatest shell width at or slightly anterior to mid-length. Ventral sulcus ill-defined, originating anterior of umbo, broadening and deepening anteriorly. Dorsal sulcus frequently developed. Anterior commissure varying from biplicate to sulciphate or uniplicate. Costellae coarse, 4 in 1 mm. at 10 mm. from beaks. Scattered costellae thickened, with spine bases developed anteriorly. Prominent growth rugae.



TEXT-FIG. 2. *Schizophoria connivens* (Phillips). Ventral and dorsal muscle fields, based on specimens BC B272, 275; BM B47673, 5709; GSL 2830; UR 13595.

Teeth compound, supported by anteriorly and ventrally divergent dental lamellae (text-fig. 1, sections 2.2–3.3). Articulation supplemented by interlocking ends of brachiophores and dental lamellae. Ventral muscle field (text-fig. 2) one-half valve length, elliptical to flabellate, strongly incised. Median septum varying from narrow to broad, subangular to rounded, broadening and increasing in height anteriorly (text-fig. 1, sections 0.9–5.9). Two slightly divergent vascula media (text-fig. 2).

Myophore compound, average width 1.5 mm., with central ridge bordered by two lateral ridges. Stubby brachiophores fused to strong, short, divergent brachiophore plates (text-fig. 1, sections 2.6–4.2). Dental sockets articulating with ventral teeth (text-fig. 1, sections 2.8–3.3). Dorsal muscle field (text-fig. 2) moderately incised, elliptical to rounded, one-half to two-thirds valve length. Accessory ridges reflexed anteriorly to form shallow, subangular re-entrant. Median septum subrounded, broadening and increasing in height, and becoming sharp crested anteriorly (text-fig. 1, sections

EXPLANATION OF PLATE 18

Figs. 1, 2. *Schizophoria connivens* (Phillips). 1, Ventral view, BC B146 ($\times 2$). 2, Anterior view, SM D.22.B ($\times 2$).

Fig. 3. *Schizophoria gibbera* (Portlock). 3a, b, Dorsal and anterior views, holotype, GSM 70646 ($\times 1\frac{1}{2}$).

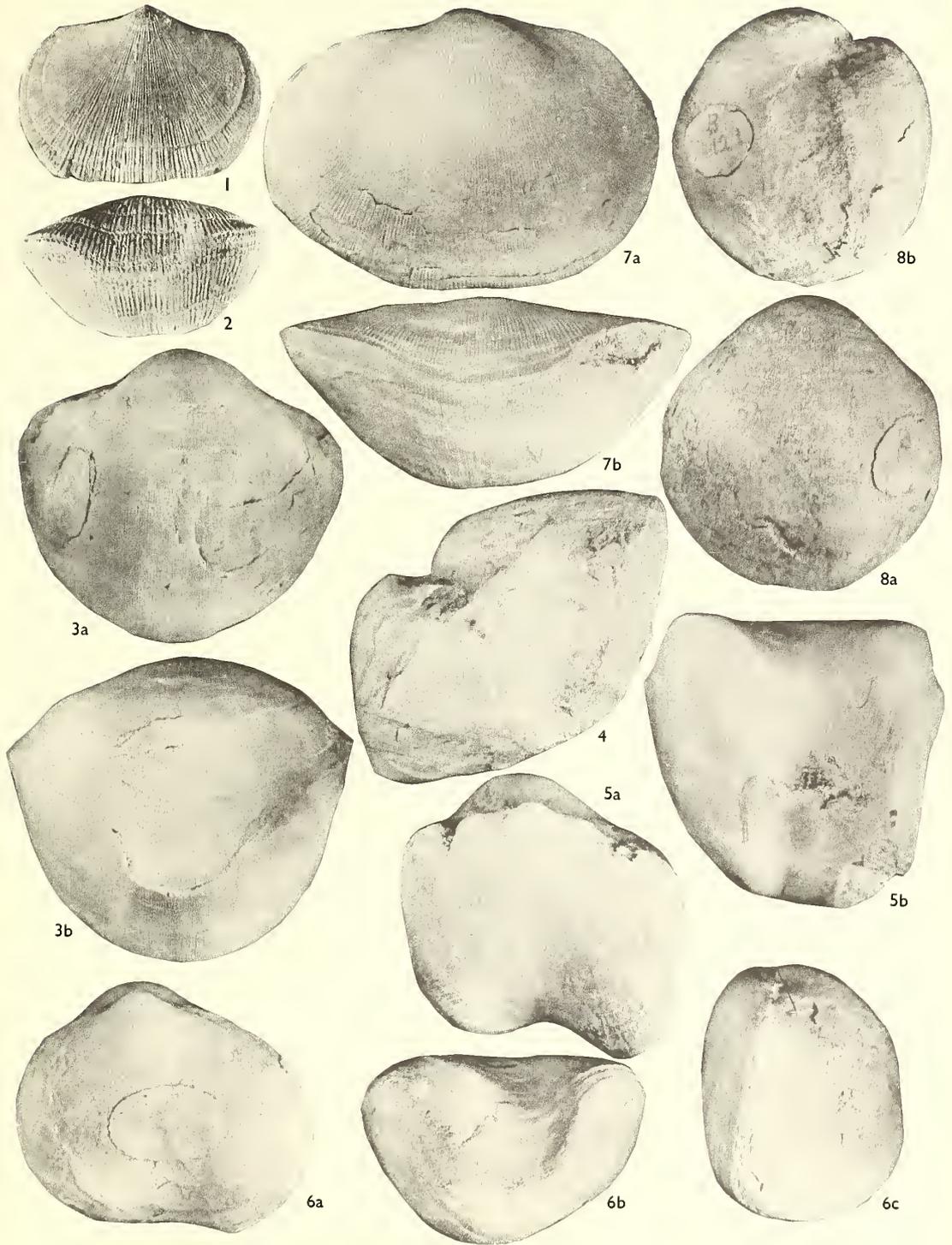
Figs. 4, 5. *Schizophoria linguata* (Quenstedt). 4a, Lateral view, type specimen, Tübingen 55,152 ($\times 2$).

5a, b, Ventral and anterior views, type specimen, Tübingen 55,153 ($\times 2$).

Fig. 6. *Schizophoria annectans* sp. nov. 6a, b, c, Ventral, anterior and lateral views, holotype, BM B40126 ($\times 2$).

Fig. 7. *Schizophoria resupinata* (Martin). 7a, b, Dorsal and anterior views, BC B175 ($\times 1\frac{1}{2}$).

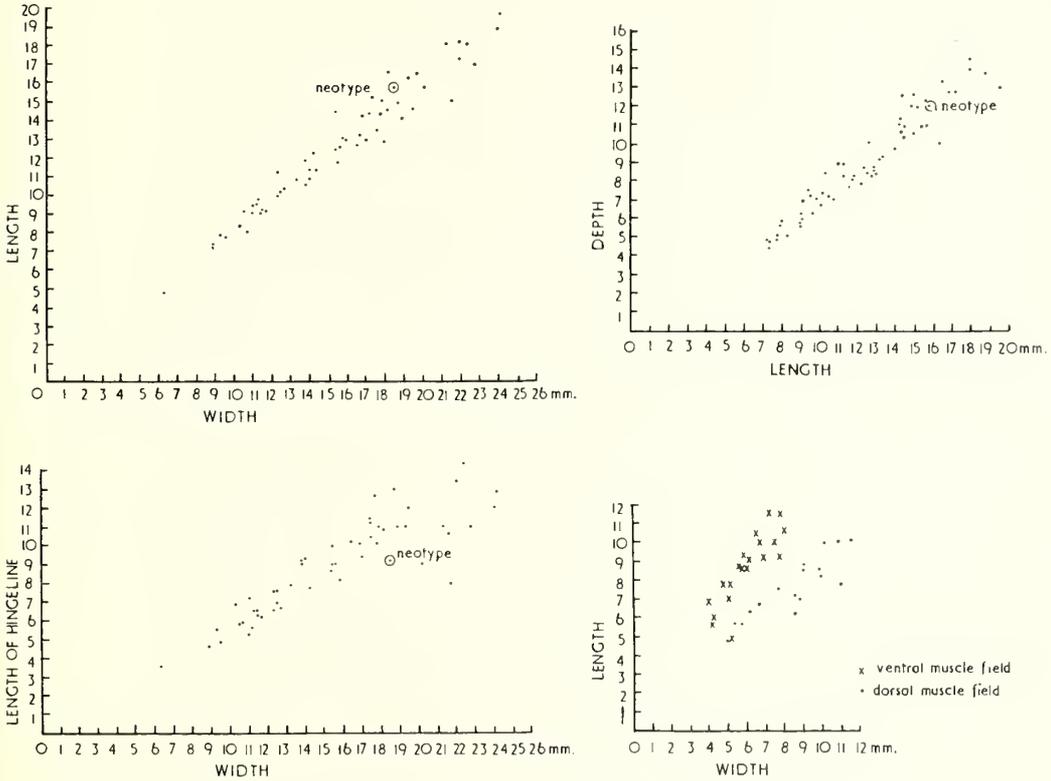
Fig. 8. *Schizophoria woodi* Bond. 8a, b, Dorsal and lateral views, BM B54121 ($\times 1\frac{1}{2}$).



2.6-5.9). Anterior adductor muscle scar pyriform; posterior muscle scar digitate. Two vascula media, two vascula myaria (text-fig. 2). Genital markings developed postero-laterally. Follicular markings occasionally developed peripherally on internal moulds.

Dimensions. External dimensions and muscle field dimensions are plotted on text-fig. 3.

S. CONNIVENS (PHILLIPS)



TEXT-FIG. 3. Dimensions of *Schizophoria connivens* (Phillips).

Remarks. *Schizophoria connivens* superficially resembles small, rugate forms of *S. resupinata* (Martin), but is distinguished externally by its more tumid outline, biplicate or quadrate-uniplicate anterior commissure, and coarser costellae. Internally, the elliptical to flabellate ventral muscle field, short, stout brachiophore plates of *S. connivens* contrast with the more flabellate ventral muscle field, and longer, more slender brachiophore plates of *S. resupinata*.

Schizophoria connivens also superficially resembles older, rugate specimens of *S. woodi* Bond from Treak Cliff, in size, outline, and prominent rugae. But *S. connivens* has coarse costellae, and a biplication or quadrate-uniplication, in contrast to the finer costellae and angular-uniplication of *S. woodi*.

Comparisons with other species are given on text-fig. 4.

	SIZE	OUTLINE	CONVEXITY	ANTERIOR COMMISSURE	ORNAMENT	DENTAL LAMELLAE	VENTRAL MUSCLE FIELD	BRACHIOPHORES BRACHIOPHORE PLATES	DORSAL MUSCLE FIELD
SCHIZOPHORIA RESUPINATA (MARTIN)	medium large	rectangular elliptical	ventribiconvex biconvex moderately dorsibiconvex	rectimarginate uniplicate unisulcate subplicate	costellae fine some thick costellae with spine bases rugae weak absent	ventrally subparallel	broad labellate moderately incised	stubby brachiophores slender divergent brachiophore plates	elliptical moderately incised
SCHIZOPHORIA CONNIVENS (PHILLIPS)	medium small	rectangular rounded	ventribiconvex biconvex moderately dorsibiconvex	quadrate uniplicate biplicate subplicate	costellae coarse with spine bases rugae prominent	ventrally subparallel divergent	moderately narrow oval	stubby brachiophores slender divergent brachiophore plates	elliptical rounded moderately incised
SCHIZOPHORIA GIBBERA (PORTLOCK)	medium large	elliptical rounded	strongly dorsibiconvex	rounded uniplicate	costellae very fine some thick costellae rugae present	ventrally convergent	narrow parallel- sided incised	stubby brachiophores long slender curved brachiophore plates	rectangular elliptical strongly incised
SCHIZOPHORIA LINGUATA (QUENSTEDT)	medium small	rectangular elliptical	great ontogenetic in dorsibiconvexity	rounded uniplicate	costellae very fine some thick costellae rugae present	ventrally subparallel	narrow parallel- sided incised	stubby brachiophores long slender curved brachiophore plates	rectangular elliptical moderately incised
SCHIZOPHORIA ANNECTANS N. SP.	medium small	rectangular elliptical	biconvex moderately dorsibiconvex	rounded uniplicate	costellae very fine some thick costellae rugae prominent	ventrally subparallel	narrow parallel- sided incised	stubby brachiophores long curved brachiophore plates	rectangular elliptical moderately incised
SCHIZOPHORIA WOODI BOND	large small	rounded rectangular elliptical	strongly dorsibiconvex	angular uniplicate	costellae very fine some thick costellae with spine bases rugae prominent	ventrally subparallel	broad labellate strongly incised	stubby brachiophores long slender curved brachiophore plates	labellate moderately incised

TEXT-FIG. 4. Comparisons of Carboniferous species of *Schizophoria*.

Although *S. connivens* is a long ranging species, there is apparently little external and internal variation between early and late forms.

Schizophoria hudsoni George is listed in synonymy with *S. connivens*. *S. hudsoni* from the Cayton Gill Beds of the Millstone Grit are preserved as external and internal moulds. But these moulds resemble *S. connivens* in outline, anterior plication, coarsely costellate and rugate shell, and form of the muscle fields.

Material. Belgium, Visé: Viséan (IRSN 2737). Derbyshire: *Dielasma* Bed, D₁, Treak Cliff, Castleton (BC B137, 138); Carboniferous Limestone, Longnor (BM B34460); Carboniferous Limestone, D₂, Park Hill, Longnor (GSM 34243, 34247, 84682, 84686). Isle of Man (Castletown): Carboniferous Limestone, D₂, Poolvash (HMUG L53461, 2, 5). Ireland: Lower Carboniferous, C₁₋₂, Millicent, Kildare (BM B13184); C₁₋₂ subzones, Ballylin, Limerick (UR 13593, 13595); Viséan, D₁, Meath (TCD 3593-8). Lancashire: Carboniferous Limestone, Clitheroe (SM E6502, 6505, 6506). Scotland: Carboniferous Limestone, D₃, Corrie Burn, Campsie (HMUG L131/2, 3; L4272/2, 3; L5343/1); Carboniferous Calmy Limestone, E₂, Gair, Carluke (HMUG L127; L129/1-5; L130/1, 5); Carboniferous Limestone, Lesmahagow (HMUG L4273/2). Staffordshire: Carboniferous Limestone, D₁, Narrowdale (GSM 84678). Yorkshire: Lower Carboniferous, C₂, Bolland (neotype BM B387); Elbolton Limestone Series, Tufa Beds, middle D₁ subzone, Elbolton Knoll, Cracoe (BC B139-156); Tufa-Cyrtina-Septosa Beds, middle D₁ subzone, same locality (BC B157); Tufa Beds, Stebden Knoll, Cracoe (BC B158-161); Carboniferous Limestone, Swinden, Grassington (IC 11130-11133); S₂ subzone, Stockdale Beck, Scaleber Bridge; Lower Carboniferous, Settle (BM B5709); Millstone Grit, Cayton Gill Beds, R₁, Fewston Bents Quarry, near Harrogate (BC B255-278); Cayton Gill Series, Cayton Gill, Markington (BM B34252); Millstone Grit, Pateley Bridge (BM B47673); Cayton Gill shell bed, near Darley (GSL 2829; 2830; 2914; 2915).

Schizophoria gibbera (Portlock) 1843

Plate 18, fig. 3; text-figs. 5-7

1843 *Atrypa* (*Porambonites*) *gibbera* Portlock, p. 460, pl. 38, fig. 1.

1844 *Orthis gibbera* (Portlock); M' Coy, p. 124, pl. 18, fig. 9.

1861 *Orthis resupinata* var. *gibbera* (Portlock); Davidson, p. 130, pl. 29, fig. 5.

1934 *Schizophoria resupinata* var. *gibbera* (Portlock); Demanet, p. 55, pl. 4, fig. 4, *non* 1-3.

1941 *Schizophoria gibbera* (Portlock); Bond, p. 295, pl. 22, figs. A-D, H.

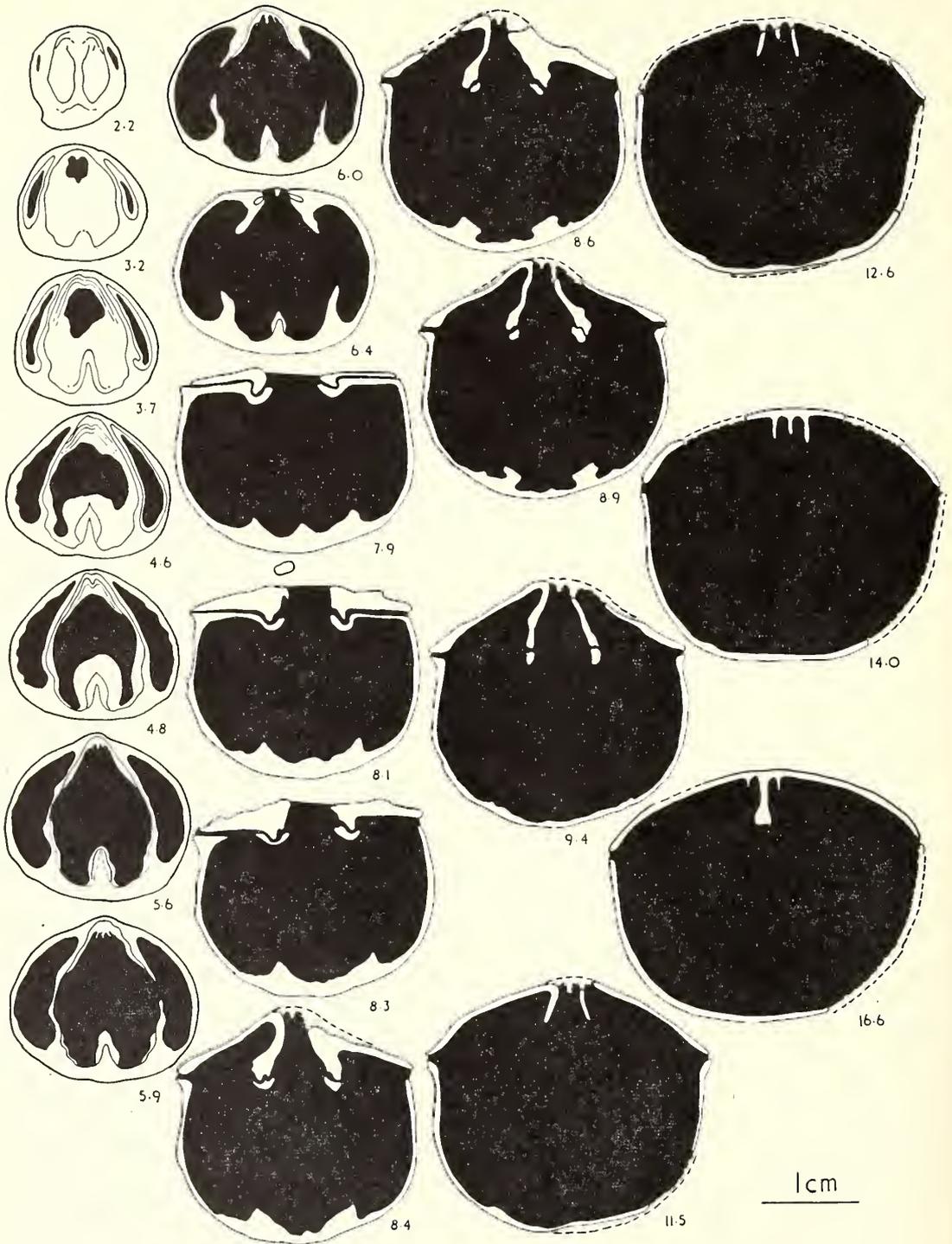
non 1923 *Schizophoria resupinata* var. *gibbera* (Portlock); Demanet, p. 121, pl. 5, fig. 2.

Type. The holotype is deposited in the Geological Survey Museum, GSM 70646.

Diagnosis. Medium to large, elliptical to rounded, deeper than long, strongly dorsibiconvex. Ventral sulcus absent. Dorsal concentric fold. Shell finely costellate, with scattered thickened costellae. Ventral muscle field very narrow, parallel-sided, strongly incised. Dorsal muscle field rectangular to elliptical, strongly incised, bounded posteriorly by curved brachiophore plates.

Description. Shell wider and deeper than long, with greatest width near mid-length. Low, ventral, concentric fold developed anteriorly, decreasing postero-laterally. Concentric dorsal fold developed posteriorly, disappearing laterally. Low, flat-topped, transverse dorsal fold occasionally developed. High, rounded anterior uniplication. Costellae fine, 6 to 7 in 1 mm. at 10 mm. from beaks. Scattered costellae thickened, irregularly spaced, 6 to 15 normal costellae apart. Growth rugae more prominent anteriorly.

Teeth compound, anteriorly parallel ventrally convergent dental lamellae (text-fig. 5, sections 8.3-9.4). Ventral muscle field (text-fig. 6) approximately one-half valve length, narrow, parallel-sided, strongly incised. Median septum narrow, rounded, increasing in



TEXT-FIG. 5. *Schizophoria gibbera* (Portlock). Transverse serial sections (GSI 21/4); C_{1-2} zones, Limerick; Length 26.7 mm., width 31.8 mm., depth 26.2 mm.

height and broadening anteriorly; becoming club-shaped anteriorly, and continuing for a short distance anterior of muscle field (text-fig. 5, sections 8.6–16.6). Two divergent *vascula media*. Genital markings developed postero-laterally (text-fig. 6).

Myophore small, compound, with central ridge bordered by two lateral ridges. Stubby brachiophores fused to slender, long, curved brachiophore plates (text-fig. 5, sections 3.2–6.4). Dental sockets oval, articulating with ventral teeth (text-fig. 5, sections 7.9–8.3). Dorsal muscle field (text-fig. 6) strongly incised, rectangular to elliptical, longer than wide, one-half to two-thirds valve length; anterior boundary ill-defined. Median septum broad, angular, first broadening, then narrowing and decreasing in height, and becoming subrounded anteriorly (text-fig. 5, sections 4.8–8.1). Genital markings developed postero-laterally.

Dimensions. External dimensions and dimensions of muscle fields of *S. gibbera* are as follows (in mm.):

	<i>Length</i>	<i>Width</i>	<i>Depth</i>	<i>Hinge-line (length)</i>
GSM 70646	31.1	34.6	31.2	—
BC B164	26.6	29.3	26.8	—
BM BB7350	29.0	35.6	33.9	25.2
BM BB7351	25.0	27.9	25.0	—
GSM 5758	24.0	26.3	25.6	18.2
GSI 21/4	24.4	30.5	26.0	23.9
21/4	26.7	31.8	26.2	22.3
21/4	29.4	37.7	29.3	—
SME 6577	27.5	31.8	31.0	—
TCD 1265	23.2	31.8	27.5	20.3

Ventral Muscle Field

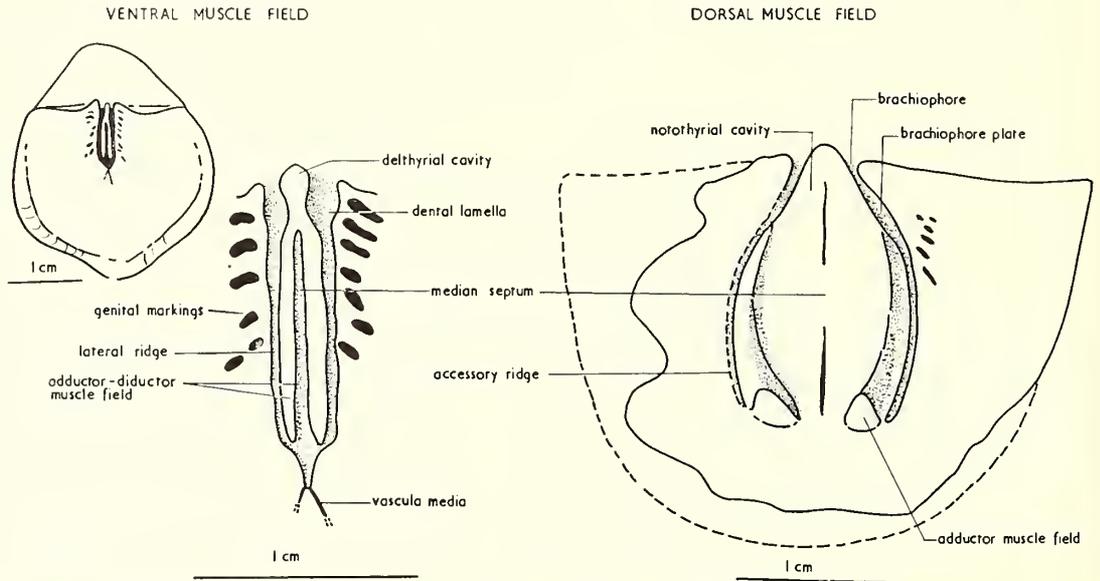
	<i>Length</i>	<i>Width</i>
GSM 5758	13.0	2.8

Dorsal Muscle Field

	<i>Length</i>	<i>Width</i>
BC B165	16.4	11.6
TCD 1270	13.8	11.3

Remarks. *S. gibbera* superficially resembles adult specimens of *S. linguata* (Quenstedt), in outline and costellation. Both species are strongly convex, have concentric folds, a rounded uniplication, and are finely costellate with scattered coarser costellae. But specific differences in size and outline are shown on text-fig. 7A. Internally, there are superficial similarities. Both have a narrow, parallel-sided ventral muscle field with a median septum extending beyond the anterior boundary, and a pair of divergent *vascula media*. *S. gibbera* has a wider muscle field in proportion to valve width, but it is shorter (one-half valve length) and the median septum and diductor muscle field are similar in width. The ventral muscle field of *S. linguata* is one-half to two-thirds valve length, with the median septum broadening anteriorly, and becoming wider than the diductor muscle field (text-fig. 7B). In the dorsal valve, both species have a rectangular to elliptical muscle field, bounded posteriorly by long, slender, curved brachiophore plates. *S. gibbera* has a more strongly incised muscle field, with strong accessory ridges continuous with the brachiophore plates, and a strong median septum (text-fig. 7B).

Schizophoria gibbera also superficially resembles adult forms of *S. woodi* Bond. Demanet (1934, pl. 5, figs. 1–3) figured *S. woodi* under *S. gibbera*. Both species are dorsibiconvex and finely costellate, but *S. gibbera* is more convex, and has a more inflated dorsal umbo. *S. gibbera* is more rounded in outline, and wider than long, while *S. woodi* may be as long as, or longer than, wide. There are other differences. *S. gibbera*



TEXT-FIG. 6. *Schizophoria gibbera* (Portlock). Ventral and dorsal muscle fields, based on specimens GSM 5758; TCD 1270. Ventral muscle field also enlarged.

has a fold on both valves, no ventral sulcus, and a deep, broad, rounded, anterior plication, in contrast to the generally smoother valve profiles or dorsal fold, angular ventral sulcus, and subangular plication of *S. woodi*.

Material. Ireland: Waulsortian, C₁₋₂ zones, Buttevant, Cork (TCD 1265, 1270); Carboniferous Limestone, C₂S₁, Little Island, Cork (GSM 5758); Carboniferous Limestone, C₂S₁-D₂, Tyrone (holotype GSM 70646). Lancashire: Lower Carboniferous, C₂, Bolland (BM BB7350, 7351); Worston Shale Group, C₂S₁ zone, Bellman Quarry, Clitheroe (BC B164, 165).

Schizophoria linguata (Quenstedt) 1871

Plate 18, figs. 4, 5; text-figs. 8–11

1871 *Orthis linguata* Quenstedt, p. 565, pl. 55, figs. 152–4.

1934 *Schizophoria resupinata* var. *palliata* Demanet, p. 58, pl. 4, figs. 7, 8.

1941 *Schizophoria palliata* Demanet; Bond, p. 297, pl. 22, fig. E, fig. 36.

non 1930 *Orthis* (*Schizophoria*) *linguata* Quenstedt; Paeckelmann, p. 175, pl. 9, fig. 15.

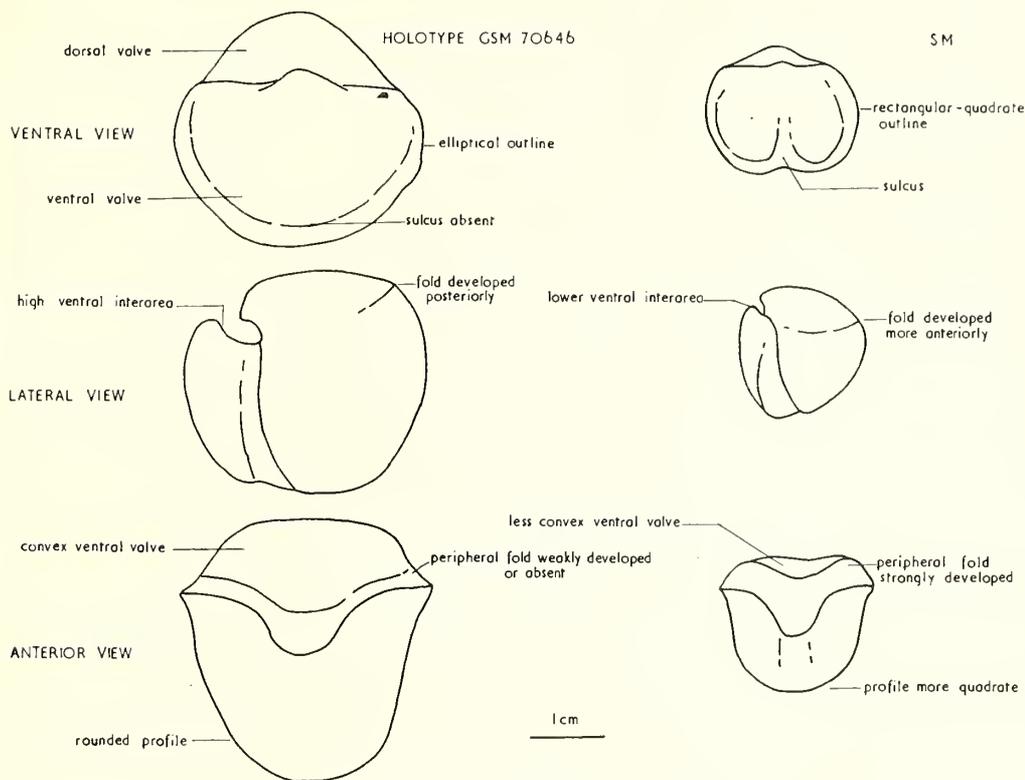
Types. Quenstedt's specimens are deposited in the Museum für Geologie und Paläontologie, Tübingen.

Diagnosis. Medium to small, rectangular to quadrate, with concentric ventral and dorsal folds. Great ontogenetic variation in dorsibiconvexity. Shell very finely costellate, with

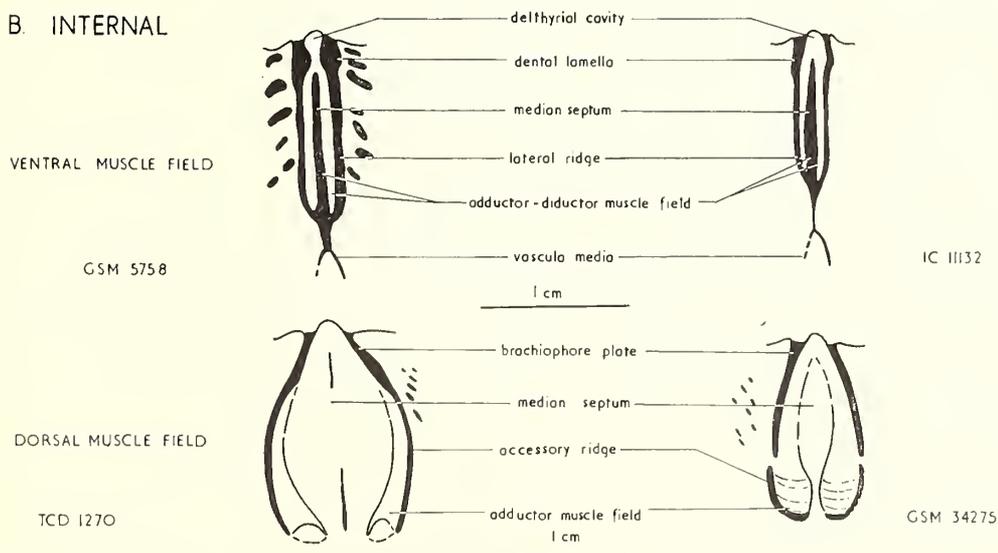
A. EXTERNAL

S. GIBBERA (PORTLOCK)

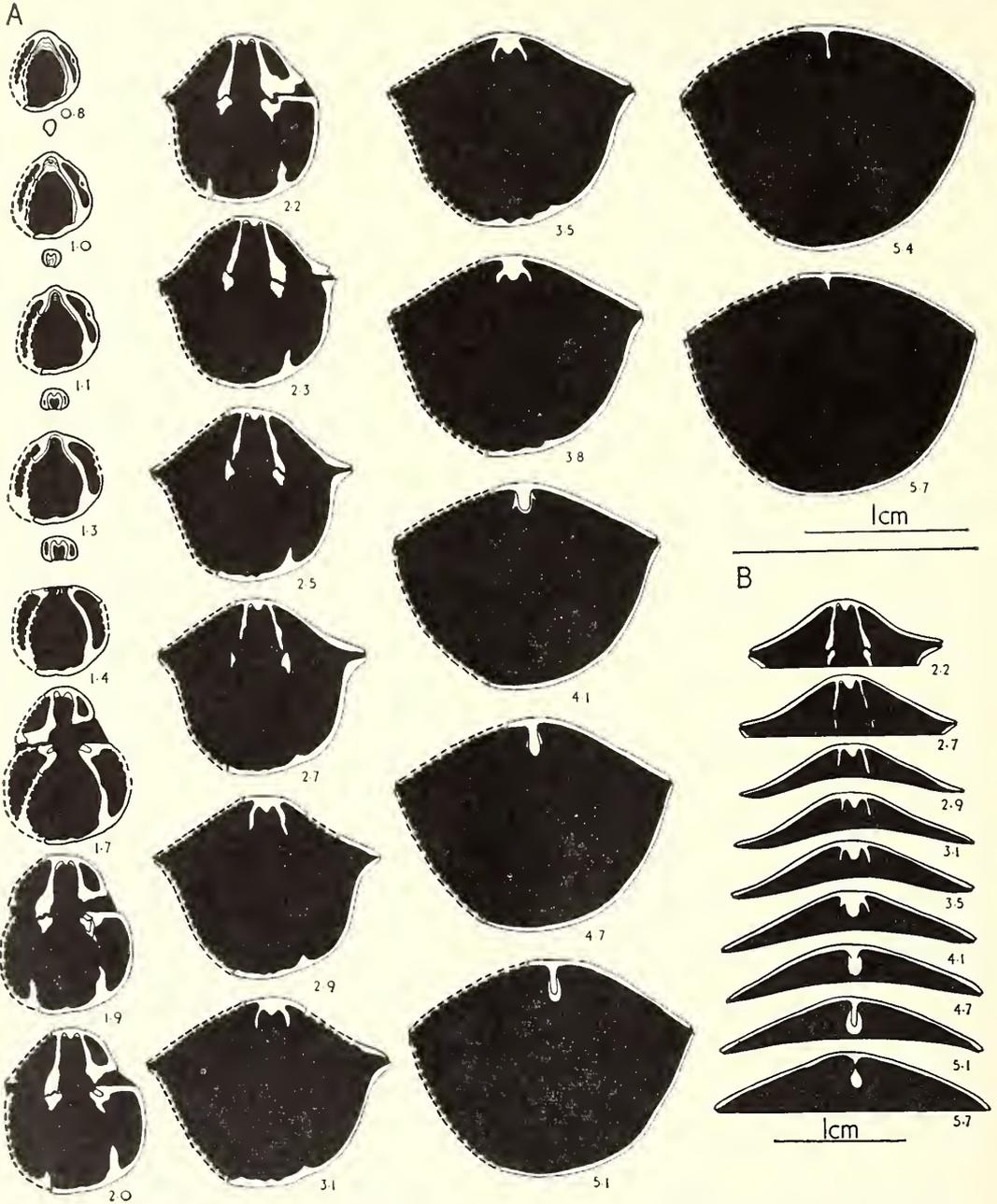
S. LINGUATA (QUENSTEDT)



B. INTERNAL



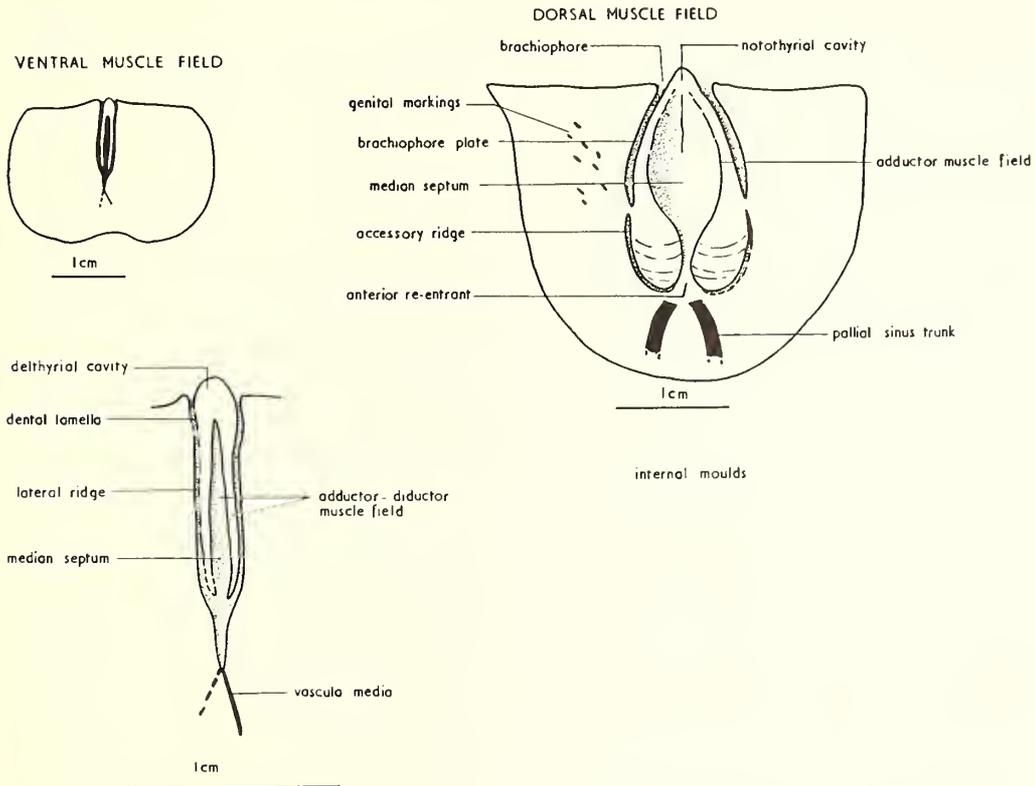
TEXT-FIG. 7. Specific differences between *Schizophoria gibbera* (Portlock) and *Schizophoria linguata* (Quenstedt).



TEXT-FIG. 8. *Schizophoria linguata* (Quenstedt). Transverse serial sections (A—SM D.22.B; B—SM D.22.B); D₁ zone, Craven, Yorkshire; A—length 14.1 mm., width 16.4 mm., depth 9.7 mm.; B—length 14.9 mm., width 18.8 mm., depth 14.4 mm.

scattered thicker costellae. Ventral muscle field strongly incised, very narrow, parallel-sided. Dorsal muscle field rectangular to elliptical, bounded posteriorly by curved brachiophore plates.

Description. Shell, biconvex to dorsibiconvex in young stages, dorsibiconvexity increasing with age, wider than long, with greatest width at mid-length. Ventral concentric fold,



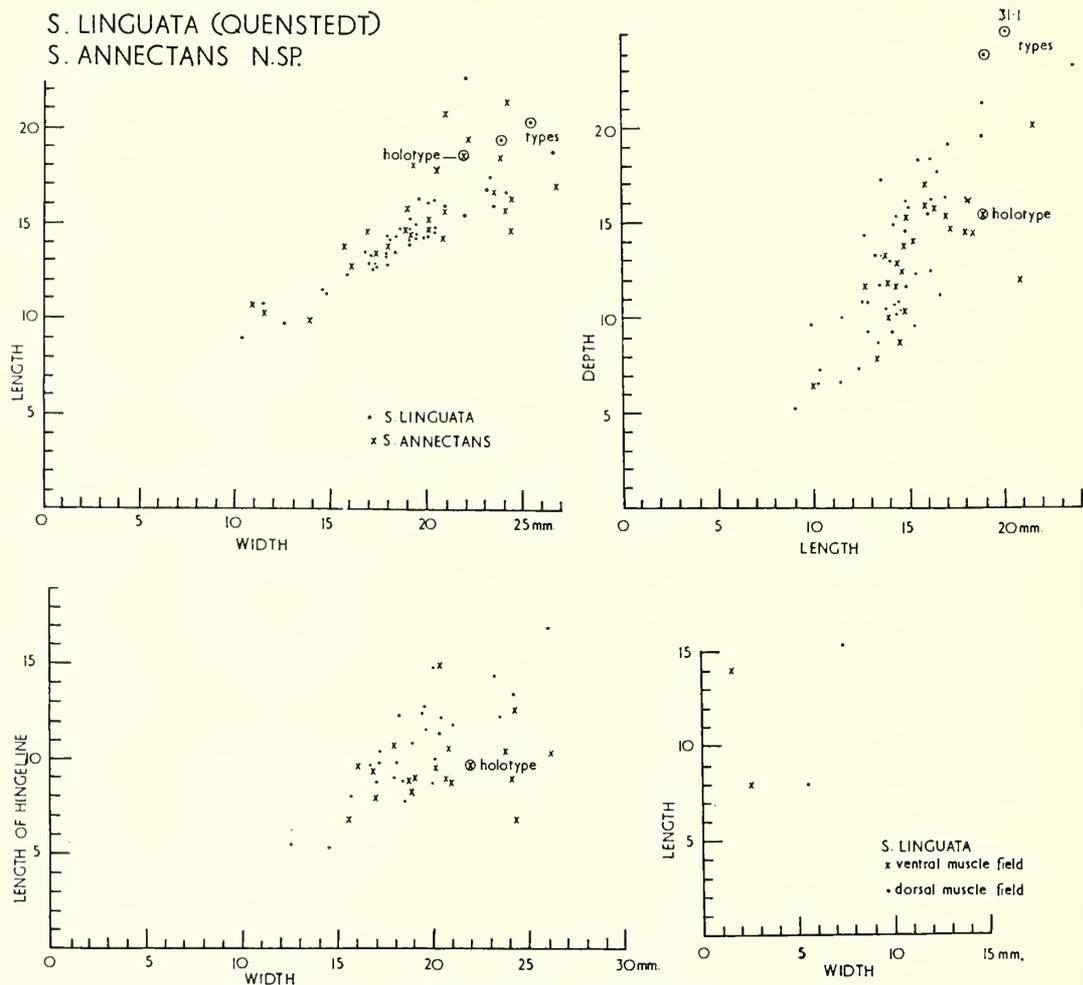
TEXT-FIG. 9. *Schizophoria linguata* (Quenstedt). Ventral and dorsal muscle fields, based upon specimens GSM 34295; IC 11134; SM D.22.B. Ventral muscle field also enlarged.

broken medially by sulcus. Dorsal concentric fold developed; low transverse fold occasionally developed anteriorly. High, broad, rounded anterior uniplication. Costellae very fine, 6 to 7 in 1 mm. at 10 mm. from beaks. Scattered coarser costellae. Rugae developed anteriorly and laterally.

Teeth compound, supported by anteriorly parallel and ventrally parallel to convergent dental lamellae (text-fig. 8A, sections 1.4–2.7). Ventral muscle field (text-fig. 9) one-half to two-thirds valve length, very narrow, parallel-sided, strongly incised. Median septum rounded, increasing in height and becoming subrounded anteriorly, then narrowing and decreasing in height, and extending for short distance beyond anterior of muscle field (text-fig. 8A, sections 1.1–5.7). Two divergent vascula media (text-fig. 9).

Myophore simple, or rudimentarily compound, with central ridge bordered by two

lateral ridges. Stubby brachiophores fused to slender, long, curved brachiophore plates (text-fig. 8A, sections 0.8–1.9). Dental sockets oval, articulating with ventral teeth (text-fig. 8A, sections 1.9–2.2). Dorsal muscle field (text-fig. 9) moderately incised, longitudinally rectangular to elliptical, one-half to two-thirds valve length. Accessory ridges



TEXT-FIG. 10. Dimensions of *Schizophoria linguata* (Quenstedt) and *Schizophoria annectans* sp. nov.

smoothly reflexed anteriorly to form shallow, subrounded re-entrant. Median septum broad, low, narrowing anteriorly (text-fig. 8A, sections 1.3–3.8). Two poorly preserved pallial sinus trunks originating from anterior re-entrant. Genital markings developed postero-laterally (text-fig. 9).

Dimensions. External dimensions are plotted on text-fig. 10. Dimensions of *S. annectans* sp. nov. have been added, to indicate its affinities with *S. linguata*.

Remarks. Quenstedt (1868–71) described and illustrated adult specimens under *Orthis linguata*.

Demagnet (1934) described two specimens under *S. resupinata* var. *palliat*a, but these were youthful forms, unlike the adult, strongly dorsibiconvex specimens of Quenstedt. *Schizophoria linguata* displays a great ontogenetic increase in dorsibiconvexity.

Bond (1941) illustrated this range in dorsibiconvexity. He did not list *S. linguata* in synonymy with *S. palliat*a, but stated that *S. linguata* cannot be considered conspecific with *S. palliat*a, since Demagnet (1934, p. 59) stated that *S. linguata* has only 5 costellae per mm. Although Bond gives 9 to 10 costellae per m., only 6 to 7 costellae have been measured in this study.

Orthis linguata and *Schizophoria palliat*a are thus considered to be synonymous, and *S. linguata* is used in priority over *S. palliat*a.

S. linguata shows close affinities with *S. annectans*. Youthful specimens have a comparable outline, convexity, anterior plication, and costellation (text-fig. 11). Both are rectangular to elliptical, biconvex, and finely costellate with scattered thickened costellae. But *S. annectans* has a narrower anterior plication. Adult specimens of the two species are similarly alike, but *S. annectans* has a more elliptical outline, is less strongly dorsibiconvex, and lacks the characteristic concentric folds (text-fig. 11).

Internally there are also close similarities in muscle fields, dental lamellae, brachio-phores and brachio-phore plates, but *S. annectans* has a more prominent, rounded to anteriorly flat-topped ventral median septum. Although there is variation in the strength of the median septum of *S. linguata* (text-fig. 8B), it is less prominent than that of *S. annectans*.

Adult, strongly dorsibiconvex forms of *S. linguata* resemble *S. gibbera* (Portlock). Similarities and differences are dealt with under the latter species.

Youthful biconvex, rectangular to elliptical forms of *S. linguata* superficially resemble *S. resupinata* (Martin), but *S. linguata* has finer costellae. Internally, the narrower, parallel-sided ventral muscle field, longitudinally rectangular to elliptical dorsal muscle field, and curved brachio-phore plates of *S. linguata* contrast with the broader, flabellate ventral muscle field, transversely elliptical dorsal muscle field, and divergent brachio-phore plates of *S. resupinata*.

Material. Belgium, Dinant: Tournaisian, Tn3bR, Dréhance (IRSN 3200). Caldbeck, Cumberland: Lower Carboniferous, S₂-D₁ (BM B75348). Derbyshire: Viséan, D₁ zone, Treak Cliff, Castleton (BM B40846); Lower Carboniferous, Dovedale (GSM 34274, 5, 34277, 34279); Lower Carboniferous, C₁₋₂, Thorpe Cloud (BM B4108). Staffordshire: Lower Carboniferous, D₁, Narrowdale (GSM 39/29, 84675-7), Wetton (BM B13190, 34459); Lower Carboniferous, D₂ subzone, Narrowdale (BM B49065-8). Yorkshire: Carboniferous Limestone, C₂, Bolland (BM B26199); Lower Carboniferous, Settle (SM E6773); Wharfedale (BM B34453).

Schizophoria annectans sp. nov.

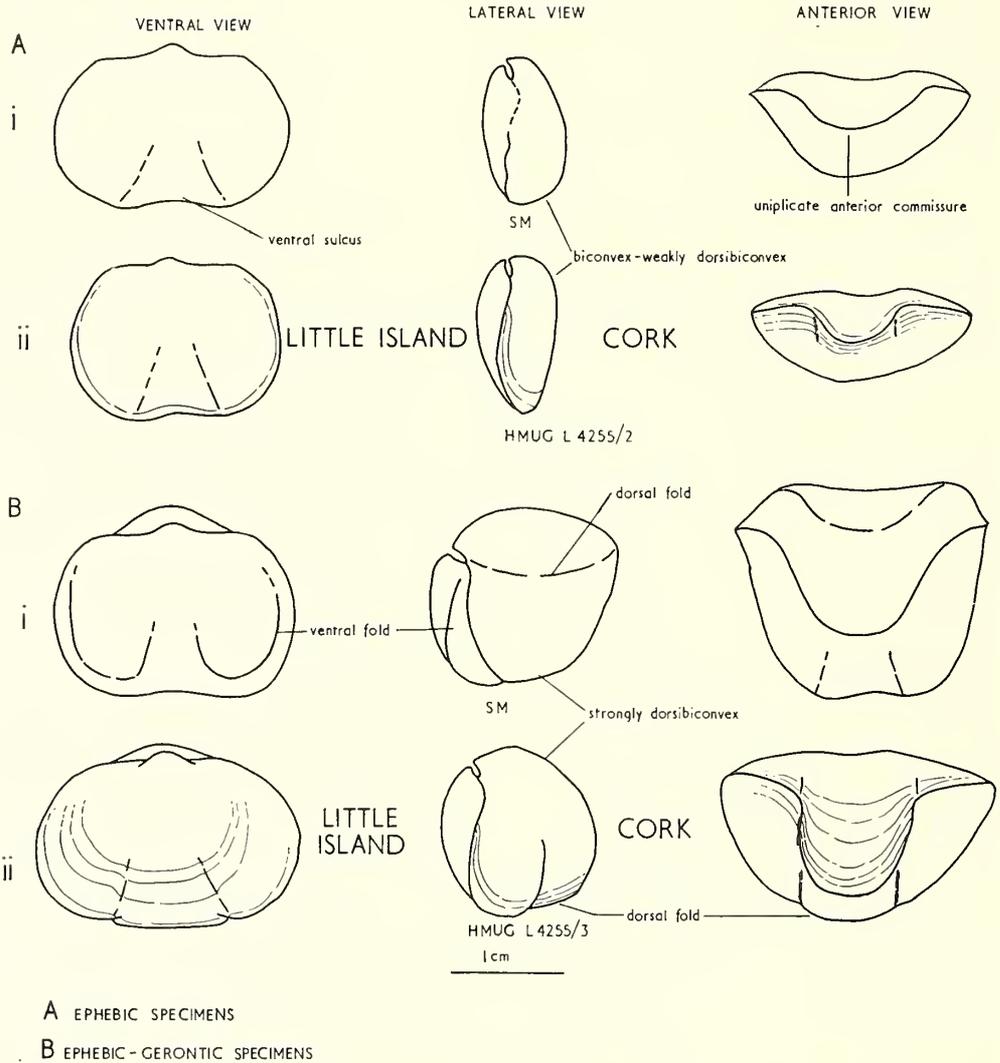
Plate 18, fig. 6; text-figs. 10, 12

1930 *Orthis* (*Schizophoria*) *linguata* Quenstedt; Paeckelmann, p. 175, pl. 9, fig. 15.

Type. The holotype is deposited in the British Museum (Natural History), B40126.

Diagnosis. Medium to small, rectangular to elliptical. Shell very finely costellate, with scattered coarser costellae, and rugate. Ventral muscle field strongly incised, narrow, parallel-sided, with broad, rounded median septum. Curved brachio-phore plates.

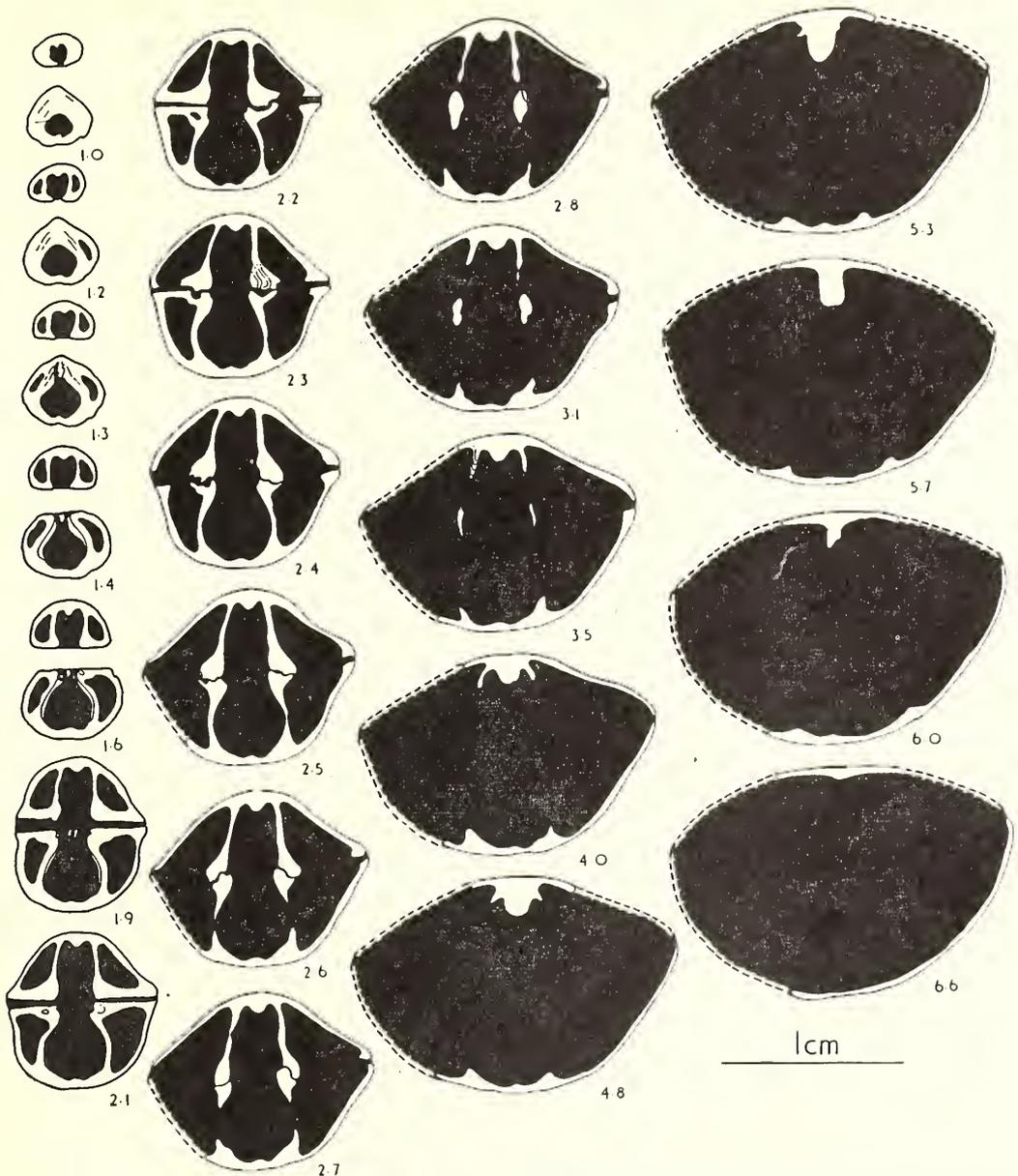
Description. Shell biconvex to moderately dorsibiconvex, wider than long, with greatest width at mid-length. Ventral sulcus originating anterior of umbo, broadening and deepening anteriorly; well-defined laterally in older specimens. Dorsal fold occasionally



TEXT-FIG. 11. Comparison of *Schizophoria linguata* (Quenstedt) (A (i) ephebic shell; B (i) ephebic-gerontic shell) and *S. annectans* sp. nov. (A (ii) ephebic shell; B (ii) ephebic-gerontic shell).

developed anteriorly. High, broad, rounded anterior plication. Costellae very fine, 6 costellae in 1 mm. at 10 mm. from beaks. Scattered coarser costellae. Prominent rugae, concentrated anteriorly and laterally.

Teeth compound, supported by anteriorly parallel and ventrally parallel to convergent dental lamellae (text-fig. 12, sections 1.2-2.8). Articulation supplemented by interlocking ends of dental lamellae and brachiophores (text-fig. 12, sections 2.7-2.8). Ventral



TEXT-FIG. 12. *Schizophoria annectans* sp. nov. Transverse serial sections (HMUG L4255/1); C₂S₁ zone, Little Island, Cork; length 12.8 mm., width 19.8 mm., depth 14.3 mm.

muscle field approximately one-half valve length, narrow, parallel-sided, strongly incised. Median septum rounded, broadening and increasing in height anteriorly, and extending for short distance anterior of muscle field (text-fig. 12, sections 1.0-6.6).

Myophore simple, or rudimentarily compound, with central ridge, bordered by two lateral ridges. Stubby brachiophores fused to strong, long, curved brachiophore plates

(text-fig. 12, sections 1.4–2.7). Dental sockets oval, articulating with ventral teeth. Dorsal muscle field moderately to strongly incised, longer than wide, approximately one-half valve length. Median septum broad, low, rounded, increasing, then decreasing in height anteriorly (text-fig. 12, sections 1.2–6.0).

Dimensions. External dimensions are plotted on text-fig. 10.

Remarks. Internal moulds of *S. annectans* are not available, but in transverse serial sections, the muscle fields have a similar general outline to those of *S. linguata*.

In the British Isles, *S. annectans* is apparently limited to Little Island, Cork and the Valley of the Maine, Ireland, apart from three specimens from the Craven area of Yorkshire.

Although possessing close affinities with *S. linguata*, hence the derivation of *annectans*—linking or connecting form, *S. annectans* does show external and internal differences. These have been described under *S. linguata*.

Paeckelmann (1930, p. 175, pl. 9, fig. 15) described and illustrated a specimen from the Lower Carboniferous of Germany under *Orthis (Schizophoria) linguata* (Quenstedt). This resembles *S. annectans* in outline, fine costellae and prominent rugae, anterior uniplication, and short anterior dorsal fold.

Material. Ireland: Carboniferous Limestone, C₂S₁, Little Island, Cork (BM B40126, 68454; GSI 75/3; GSM 5730, 5732; HMUG L1841/2, 5, 4255/1–5; SME 6875); Valley of the Maine (GSM 3758, 3759); Yorkshire: Lower Carboniferous, D₁, Craven (SM).

Schizophoria resupinata (Martin) 1809

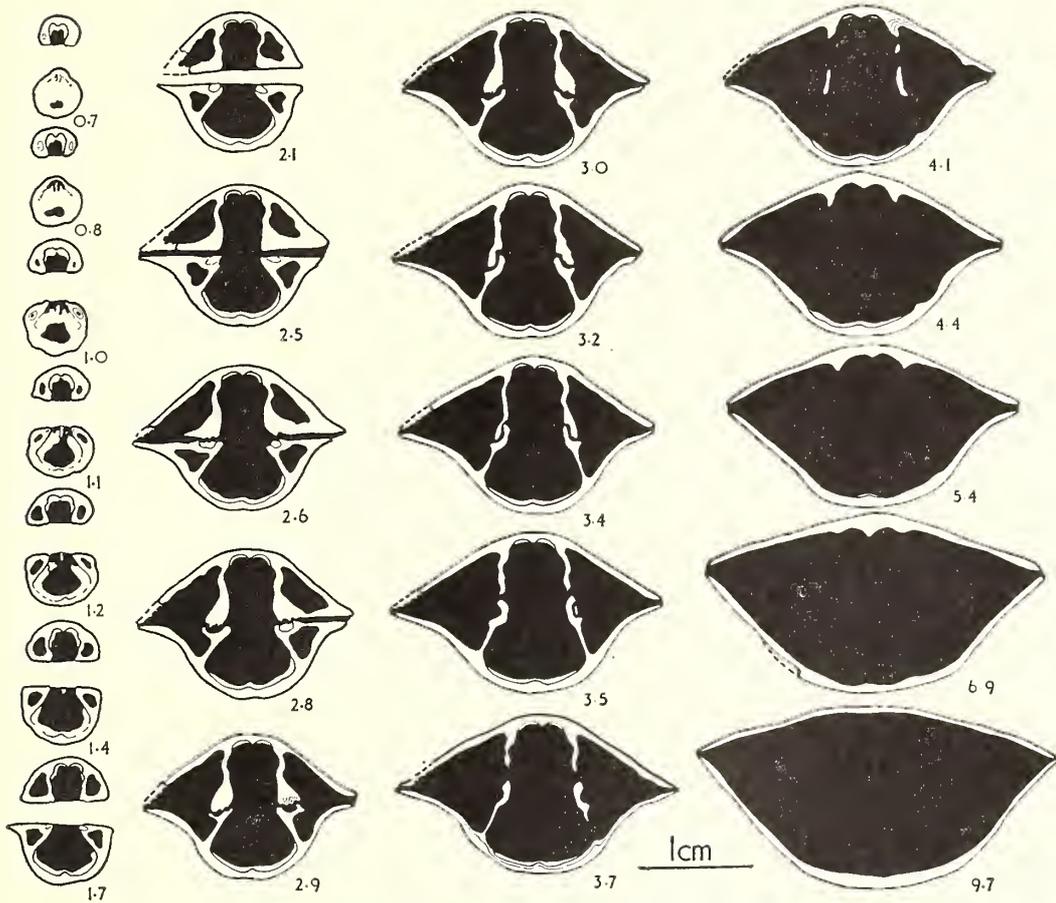
Plate 18, fig. 7; text-figs. 13–15

- 1777 *Anomites* Schröter, p. 352, pl. 5, fig. 2.
 1809 *Conchyolithus anomites (resupinatus)* Martin, pl. 49, figs. 13, 14.
 1823 *Terebratula resupinata* (Martin); Sowerby, pl. 325.
 1836 *Spirifer resupinata* (Martin); Phillips, p. 220, pl. 11, fig. 1.
 1842–4 *Orthis resupinata* (Martin); de Koninck, p. 226, pl. 13, figs. 9, 10.
 1853 *Orthis resupinata* (Martin); Davidson, pl. 7, fig. 135.
 1861 *Orthis resupinata* (Martin); Davidson, p. 130, pl. 29, figs. 1–3; pl. 30, figs. 1–5.
 1871 *Orthis resupinata* (Martin); Quenstedt, p. 563, pl. 55, figs. 146–9 (148—var. *lata?*).
 1873 *Orthis resupinata* (Martin); de Koninck, p. 47, pl. 2, fig. 5b.
 1877 *Orthis resupinata* (Martin); de Koninck, p. 214, pl. 10, fig. 9.
 1923 *Schizophoria resupinata* (Martin); Demanet, p. 119, pl. 5, fig. 1.
 1934 *Schizophoria resupinata* (Martin); Demanet, p. 47, text-fig. 9, pl. 3, figs. 1–5.
 1938 *Schizophoria elboltonensis* George and Ponsford, text-figs. 6, 7.
 1938 *Schizophoria nuda* George and Ponsford, p. 224, pl. 5, figs. 1–5, text-figs. 1–5.
 1941 *Schizophoria resupinata* (Martin); Bond, p. 289, pl. 21, figs. A–C.
 1942 *Schizophoria resupinata* (Martin); Délépine, p. 59, pl. 6, figs. 16, 17; 1946, p. 27, pl. 6, figs. 16, 17.
 1950 *Schizophoria resupinata* (Martin); Termier and Termier, pl. 71, figs. 27–30; pl. 73, figs. 1–7, 10, 11; pl. 77, figs. 8, 9.
 1954 *Schizophoria resupinata* (Martin); Parkinson, p. 368, figs. 1, 2a–e.
 1957 *Schizophoria* cf. *S. resupinata* (Martin); Campbell, p. 48, pl. 12, figs. 1–5; text-figs. 3–5.
 1958 *Schizophoria verulamensis* Cvancara, p. 856, pl. 109, figs. 14–16; pl. 110, figs. 1–5.
 1934 *Schizophoria resupinata* var. *dorsosinuata* Demanet, pl. 3, figs. 14, 15.
 1938 *Schizophoria* cf. *dorsosinuata* Demanet; George and Ponsford, text-figs. 10–14.
 1941 *S. resupinata* var. *dorsosinuata* Demanet; Bond, p. 289, figs. 33, 34.

1923 *Schizophoria resupinata* var. *lata* Demanet, p. 122, pl. 5, fig. 4: 1934, pl. 3, figs. 6-8.

1941 *S. resupinata* var. *lata* Demanet; Bond, p. 290, figs. 33, 34.

1934 *Schizophoria resupinata* var. *gigantea* Demanet, p. 60, pl. 4, figs. 12, 13.



TEXT-FIG. 13. *Schizophoria resupinata* (Martin). Transverse serial sections (IC 11138); D₁ zone, Swinden, Yorkshire; Length 23.0 mm., width 30.0 mm., depth 16.0 mm.

1861 *Orthis resupinata* (Martin); Davidson, pl. 29, fig. 3.

1934 *Schizophoria resupinata* var. *punguis* Demanet, p. 59, pl. 4, figs. 9-11.

1938 *Schizophoria punguis* Demanet; George and Ponsford, text-figs. 8, 9.

1941 *S. resupinata* var. *punguis* Demanet; Bond, p. 290.

1934 *Schizophoria resupinata* var. *rotundata* Demanet, p. 17, pl. 3, figs. 9-13.

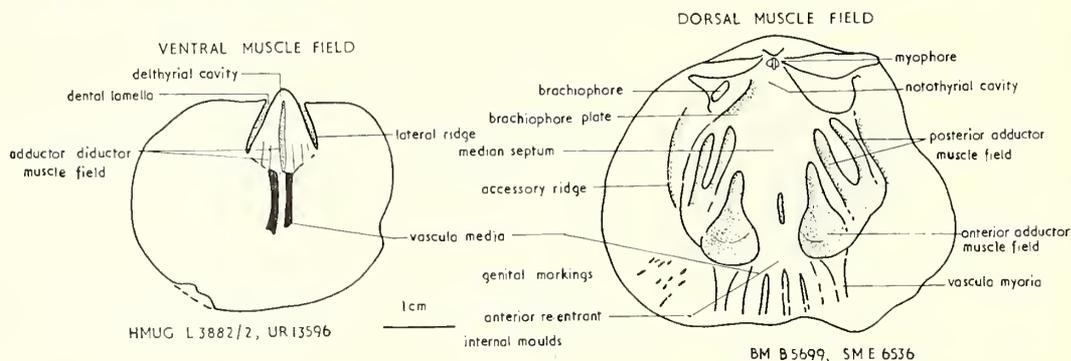
Types. Martin's holotype (1809) is lost. The neotype, chosen by George and Ponsford (1938) and figured by Bond (1941) is deposited in the British Museum (Natural History), BB2420.

Diagnosis. Medium to large, rectangular to elliptical. Ventral muscle field moderately incised, flabellate. Slender divergent brachiophore plates.

Description. Shell ventribiconvex to moderately dorsibiconvex, wider than long, with

greatest width at mid-length. Ventral sulcus generally ill-defined, except for broad, shallow depression developed anteriorly. Dorsal sulcus frequently developed. Anterior commissure varying from rectimarginate to broadly uniplicate, unisulcate or weakly sulcinate. Costellae fine, 4 to 5 in 1 mm. at 10 mm. from beaks. Scattered coarser costellae, with spine bases developed anteriorly.

Teeth compound, supported by anteriorly divergent, ventrally subparallel, dental lamellae (text-fig. 13, sections 1.1–3.5). Articulation supplemented by interlocking ends of dental lamellae and brachiophores (text-fig. 13, sections 3.2–3.5). Ventral muscle field (text-fig. 14) less than one-half valve length, flabellate, moderately incised; anterior boundary often ill-defined. Median septum narrow, subrounded, generally broadening and increasing in height slightly anteriorly (text-fig. 13, sections 0.7–6.9). Two parallel vascula media (text-fig. 14).



TEXT-FIG. 14. *Schizophoria resupinata* (Martin). Ventral and dorsal muscle fields, based on specimens BM B5699; HMUG L3882/2; SM E6536; UR13596.

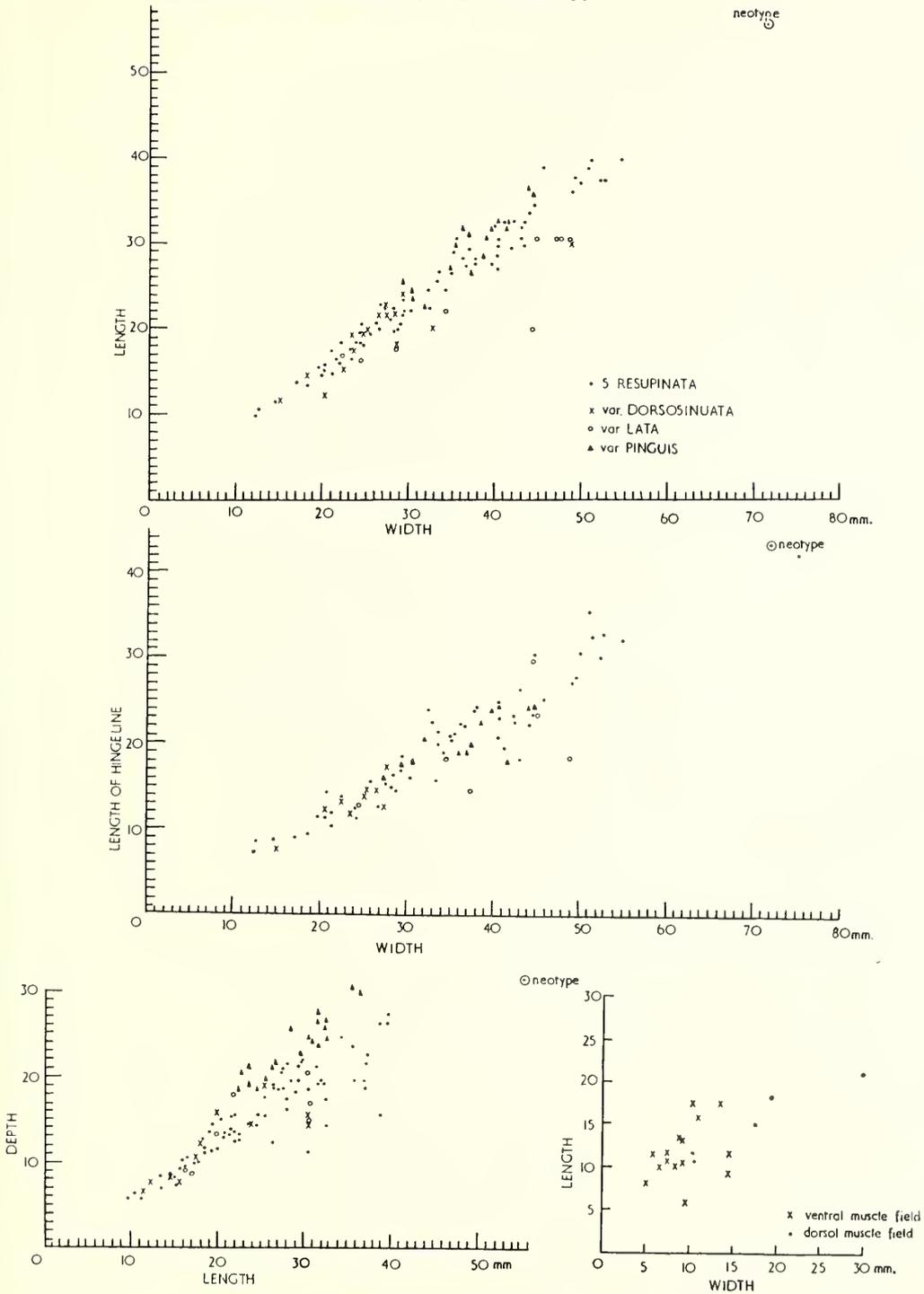
Myophore large, average width 2.5 mm., with central ridge bordered by two or four lateral ridges. Stubby brachiophores fused to slender, divergent brachiophore plates (text-fig. 13, sections 1.4–3.7). Deep dental sockets articulating with ventral teeth (text-fig. 13, sections 2.6–3.0). Dorsal muscle field (text-fig. 14) moderately incised, transversely elliptical, one-third to one-half valve length. Accessory ridges smoothly reflexed to form rounded anterior re-entrant. Median septum subangular, broadening anteriorly (text-fig. 13, sections 1.2–6.9). Four vascula media originating from anterior re-entrant, two vascula myaria originating from ends of anterior adductor muscle scars. Genital markings developed postero-laterally (text-fig. 14).

Dimensions. External dimensions and muscle field dimensions are plotted on text-fig. 15.

Remarks. The neotype chosen by George and Ponsford closely resembles Martin's lost holotype in outline, convexity and dorsal sulcus, but is larger. *S. resupinata* varies in size, but only one other specimen of similar proportions has been plotted on text-fig. 15. Although resembling the holotype, it was an unfortunate choice of neotype, since it is so much larger than an average specimen.

Variation. Although *S. resupinata* is a long ranging species (K–D zones), there is little change in morphology from early to late forms. Slight variations in convexity, outline, anterior plication, and development of a dorsal sulcus and thickened costellae and spine

S. RESUPINATA (MARTIN) & VARIETIES



TEXT-FIG. 15. Dimensions of *Schizophoria resupinata* (Martin).

bases occur within specimens from one horizon and between specimens from different horizons.

Some specimens from Treak Cliff, Derbyshire, differ from the characteristic form of *S. resupinata* in outline, convexity, and costellation. They are more elliptical in outline, biconvex to dorsibiconvex, and have coarser costellae, 3 to 4 in 1 mm. Differences in relative convexity of the valves is correlated with internal variations in the relative lengths of dental lamellae and brachiophore plates. Apart from a broader ventral median septum, the two forms are similar internally.

Varieties. Demanet (1923, 1934) established five varieties of *S. resupinata*, *dorsosinuata*, *gigantea*, *lata*, *pinguis*, and *rotundata*.

Schizophoria resupinata var. *dorsosinuata* is characterized by medium size, quadrate to rectangular outline, a dorsal sulcus, fine costellae, and prominent rugae. The variant resembles *S. resupinata*, except that the dorsal sulcus is more consistently developed, and the rugae more prominent. Internally there is close similarity, except that the ventral muscle field of *dorsosinuata* is more incised, and the median septum broader.

There is a tendency for some specimens to become much wider than long. They resemble the variant *lata* in width, but have the characteristic dorsal sulcus and rugae of *dorsosinuata*.

The variant *gigantea* is recognized by its large size, semi-elliptical outline, and strongly convex dorsal valve. Internally, the ventral muscle field resembles that of *S. resupinata*.

Demanet established var. *lata* on its length : width ratio, elliptical outline and broad anterior ventral sulcus. The ventral muscle field of *lata* is comparable with that of *S. resupinata*.

The variant *pinguis* was diagnosed on its inflated outline. It is characterized by large size, a rounded, strongly dorsibiconvex outline, and prominent rugae. Internally, it closely resembles *S. resupinata*, except that the muscle fields are more incised.

Two specimens from the British Museum, BB40159 and B54136 are more transversely elongate forms of *pinguis*, resembling *lata* in length : width ratio.

Specimens of *S. resupinata* range from weakly dorsibiconvex to more strongly dorsibiconvex forms. These represent Parkinson's (1954) thin and thick forms. Parkinson attempted to show an evolutionary trend from thin to thick forms collected from C and D zones of the Lower Carboniferous. He believed that thick forms are characteristic of the D zone, but although thin forms are characteristic of the C zone, they also occur in the D zone. The variant *pinguis* appears to represent the acme of inflation, and is restricted to the D zone (Parkinson 1954). However, specimen BM B386 was collected from the C₁ subzone of Bolland, and BM B54136 from the C₁₋₂ subzones of Thorpe Cloud, Derbyshire.

Schizophoria resupinata var. *rotundata* was established on small size, rounded outline, even convexity and lack of ventral sulcus. No specimens other than Demanet's type have been recognized.

All variants of *S. resupinata* are rare, and generally recur at different horizons, although most have been examined from the D zone. Out of approximately several hundred specimens of *S. resupinata*, the following numbers of variant specimens have been examined: *dorsosinuata*—22; *gigantea*—4; *lata*—10; *pinguis*—17; *rotundata*—1. Externally they are recognized by their varietal features, but internally they closely

resemble *S. resupinata*, except for slight details of muscle fields. A sporadic appearance of a few variant specimens possibly suggests that they merely represent a few mutant forms showing extreme variation. Many intermediate stages are seen trending towards extreme forms. Combinations of variation are seen in inflated and transversely elongate forms of var. *pinguis*, and elongate forms of *dorsosinuata*.

Extreme variation may have been induced by environmental conditions. Bond (1941, p. 209) stated that *dorsosinuata* may be the result of unfavourable conditions causing stunting and development of rugae, after a period of normal growth. But rugate and non-rugate specimens of *S. resupinata* occur together. *Gigantea* could represent a few large individuals which flourished under favourable conditions. The inflated *pinguis* occurs alongside less convex forms of *S. resupinata*.

The varietal names are descriptive of the several variation trends, but synonymies and descriptions of variants have been included under *S. resupinata* to emphasize their close relationship to the species, and as merely representing extreme individual variation.

Comparisons of species. *Schizophoria elboltonensis* George and Ponsford is distinguished externally from *S. resupinata* by its more quadrate outline. Serial sections by George and Ponsford (1938, text-fig. 7) illustrated stubby brachiophores and short, stout brachiophore plates, in contrast to the more tapered brachiophores and longer, more slender brachiophore plates of *S. resupinata*. Since *S. elboltonensis* differs only in respect of its quadrate outline, brachiophores and brachiophore plates, and no additional specimens have been examined, the species has been listed under *S. resupinata*.

In 1938 George and Ponsford also described *S. nuda*. This is a large form, characterized by an elliptical outline with greatest width near the hinge-line, and strongly incised muscle fields. The ventral muscle field of *S. nuda*, its flabellate outline, median septum, and even variation in muscle field outline, clearly conform to that of *S. resupinata*. In the dorsal muscle field, the outline, digitate posterior adductors, variations in median septum and pallial sinus trunks of *S. nuda* also closely resemble those of *S. resupinata*. The only distinction is relative incision, and incision is in part correlated with age. These large specimens could represent old forms. *Schizophoria nuda* accordingly has been listed in synonymy with *S. resupinata*.

Youthful specimens of *S. resupinata* superficially resemble young forms of *S. woodi* Bond in their rectangular to elliptical outline. But *S. resupinata* has a rectimarginate to rounded uniplicate, unisulcate or sulcate anterior commissure, coarser costellae, and a lack of rugae, in contrast to the rectimarginate to angular uniplication, finer costellae, and more prominent rugae of *S. woodi*. Adult specimens are also distinguished by their outline and convexity. *S. resupinata* is wider than long, and moderately dorsibiconvex, while *S. woodi* may also be as long as wide, or longer than wide, and strongly dorsibiconvex. Internal differences can be seen by comparing text-figs. 13 and 16.

Material. Belgium, Dinant: Viséan, Furfooz (IRSN 1301); Tournaisian, Tn 3, Tournai (var. *dorsosinuata*) (IRSN 3440, 5496, 8261); same stratigraphical level, Furfooz (var. *dorsosinuata*) (IRSN 3200); Tournaisian, Tn3bR, Weve (var. *dorsosinuata*) (IRSN 4447); same level, Dréhance (var. *lata*) (IRSN 3200); Tournaisian, Lez-Fontain (var. *lata*) (IRSN 8760); Tournaisian, Furfooz (var. *pinguis*) (IRSN 1301); Tournaisian, Tn3bR, Vère Chateau (var. *pinguis*) (IRSN 4447). Avon Gorge: Tournaisian, Z₁₋₂ subzones (BC B166). Derbyshire: *Dielasma* Bed, D₁ subzone, Treak Cliff, Castleton (BC B167-9); B₂ subzone, Treak Cliff (BM B14879); Lower Carboniferous, D₂, Park Hill, Longnor (GSM 84670, 84681, 84683); Lower Carboniferous, C₁₋₂, Thorpe Cloud (var. *pinguis*) (BM B54136); Viséan,

D₁ zone, Eldon Hill (var. *pinguis*) (BM BB40159, 40161, 40167, 40169, 40171, 40172; HMUG L5333/1). Isle of Man (Castletown): Poyllvaish Limestone, P_{1a} subzone (D₂), near Poyll Vaaish (BC B170–85); Poyllvaish Limestone, near Poyll Vaaish (var. *gigantea*) (BC B186); same level and locality (var. *lata*) (BC B187); Lower Carboniferous, D_{2a}, Poyll Vaaish (var. *pinguis*), (HMUG L4256; SME 6487). Ireland: Viséan, Carrick syncline (HMUG L3882/2); Viséan, D₁ zone, Curkeen Hill, Dublin (TCD 3019, 3042, 3044, 3048); Waulsortian, C_{1–2} zones, Ballylin, Limerick (UR 13590, 13596); Carboniferous Limestone, C_{1–2}, Ballydoole, Limerick (var. *dorsosinuata*) (GSI 3/4). Lancashire: Worston Shale Group, C₂S₁ zone, Clitheroe (BC B189–94; GSM 3691, 3709, 84666; SME 13607); Carboniferous Limestone, C₂, Bolland (var. *pinguis*) (BM B386). Yorkshire: Carboniferous Limestone, C₂, Bolland (neotype BM BB2420, B384, B8328); Elbolton Limestone Series, *Cyrtina septosa* D₁ subzone, Elbolton Knoll, Cracoe (BC B195); Tufa-*Cyrtina septosa* Beds, D₁ subzone, Elbolton Knoll, Cracoe (BC B196–205); Viséan, D₁ subzone, Elbolton, Cracoe (var. *lata*) (BM BB8149, BS 4027); same level and locality (var. *pinguis*), (BM B54146; IC 11135); S₂ reef limestones, Stockdale Beck, Scaleber, Settle (var. *pinguis*) (BC B207).

Schizophoria woodi Bond 1941

Plate 18, fig. 8; text-figs. 16–19

1934 *Schizophoria resupinata* var. *gibbera* Demanet, pl. 4, figs. 1–3, *non* 4.

1941 *Schizophoria woodi* Bond, p. 299, pl. 22, figs. F, G; text-fig. 37.

1950 *Schizophoria resupinata* (Martin); Termier and Termier, pl. 71, fig. 31.

1952 *Schizophoria resupinata* (Martin); Wright, text-fig. 5 (3).

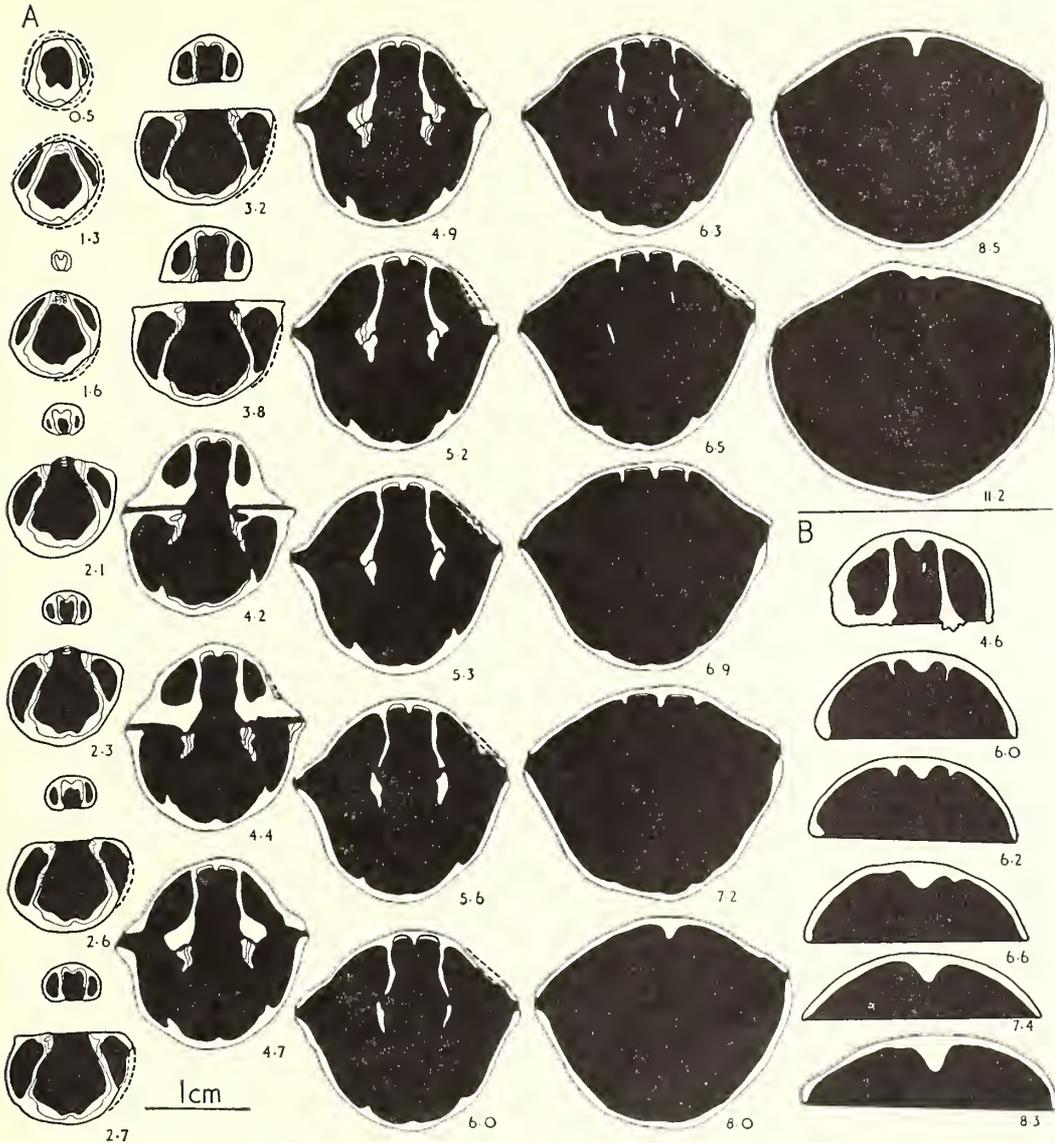
Type. The holotype is deposited in the British Museum (Natural History) BB8152.

Diagnosis. Small to large, rounded to elliptical, generally strongly dorsibiconvex, with narrow, groove-like ventral sulcus, and subangular uniplicate anterior commissure. Shell finely costellate. Ventral muscle field flabellate, strongly incised. Slender, curved brachiophore plates.

Description. Shell biconvex to strongly dorsibiconvex, with greatest width at mid-length. Ventral sulcus angular, originating half way along valve, broadening and deepening anteriorly. Narrow dorsal fold frequently developed anteriorly. Broad, subangular anterior uniplication. Costellae fine, 6 to 7 in 1 mm. at 10 mm. from beaks. Scattered thickened costellae. Prominent growth rugae.

Teeth compound, supported by anteriorly divergent, ventrally subparallel to convergent dental lamellae (text-fig. 16A, sections 2.1–6.3). Ventral muscle field (text-fig. 17) one-third to one-half valve length, flabellate, strongly incised. Deep, subrounded anterior re-entrant. Median septum narrow, rounded, broadening and increasing in height anteriorly (text-fig. 16A, sections 1.6–11.2). Two parallel vascula media (text-fig. 17).

Myophore compound, average width 1.5 mm., with central ridge bordered by two lateral ridges. Stubby brachiophores fused to slender, curved brachiophore plates (text-fig. 16A, sections 2.1–4.7). Deep dental sockets articulating with ventral teeth (text-fig. 16A, sections 4.2–4.4). Dorsal muscle field (text-fig. 17) moderately incised, flabellate, longer than wide, one-half valve length. Accessory ridges smoothly reflexed to form shallow subangular re-entrant. Median septum low, subrounded, slightly increasing in width and height anteriorly (text-fig. 16A, sections 2.1–8.0). Two vascula media originating from anterior re-entrant, two vascula myaria originating antero-laterally (text-fig. 17).

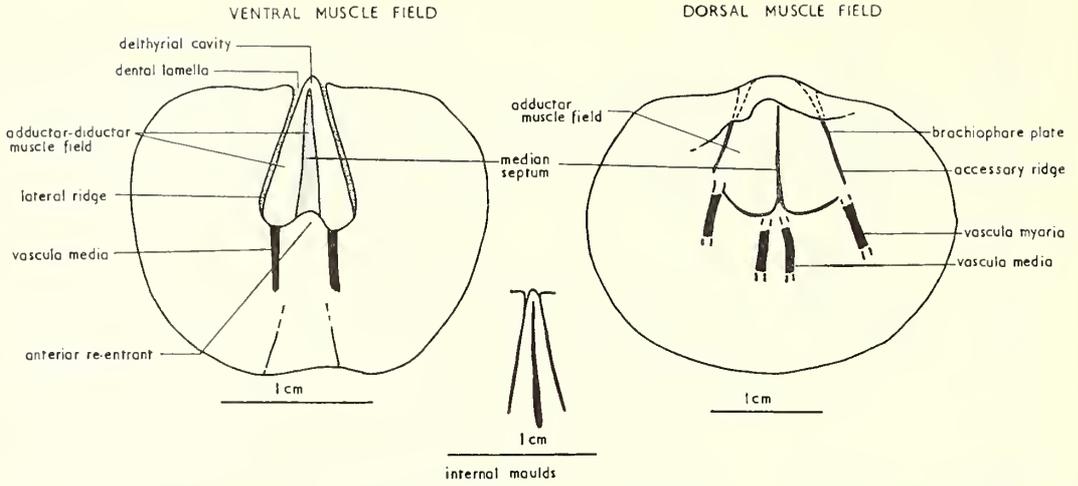


TEXT-FIG. 16. *Schizophoria woodi* Bond. Transverse serial sections (A—BC B248; B—BM B54120); D₂ zone, Isle of Man; A—length 26.1 mm., width 27.1 mm., depth 22.5 mm., B—length 25.7 mm., width 28.0 mm., depth 22.0 mm.

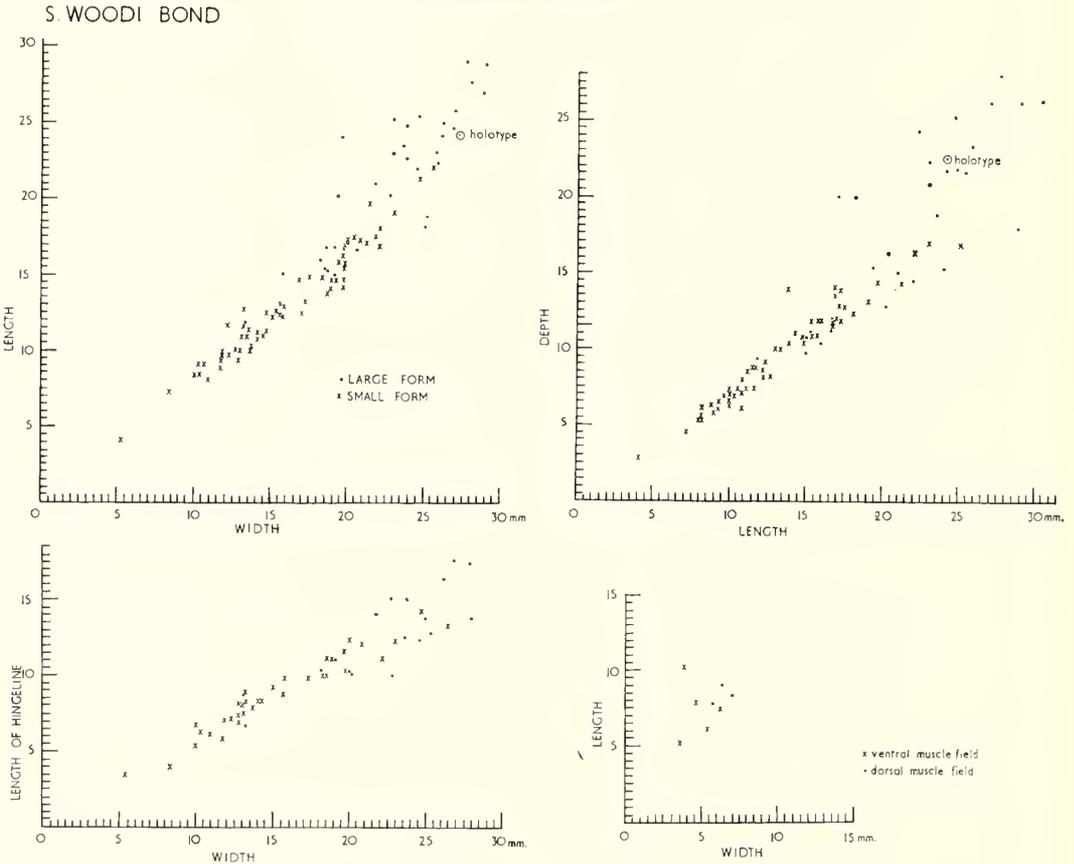
Dimensions. External dimensions and muscle field dimensions are plotted on text-fig. 18. Some smaller forms of *S. woodi* from Cracoe, Ireland and Treak Cliff have been plotted separately.

Remarks. Bond (1941, p. 299, text-fig. 37) illustrated variations in shell outline. Similar trends shown by Belgian specimens are illustrated on text-fig. 19.

Specimens assigned to *S. woodi* from Treak Cliff, Derbyshire and Swinden and Elbolton Knolls, Yorkshire, do not generally attain the same size and dorsibiconvexity



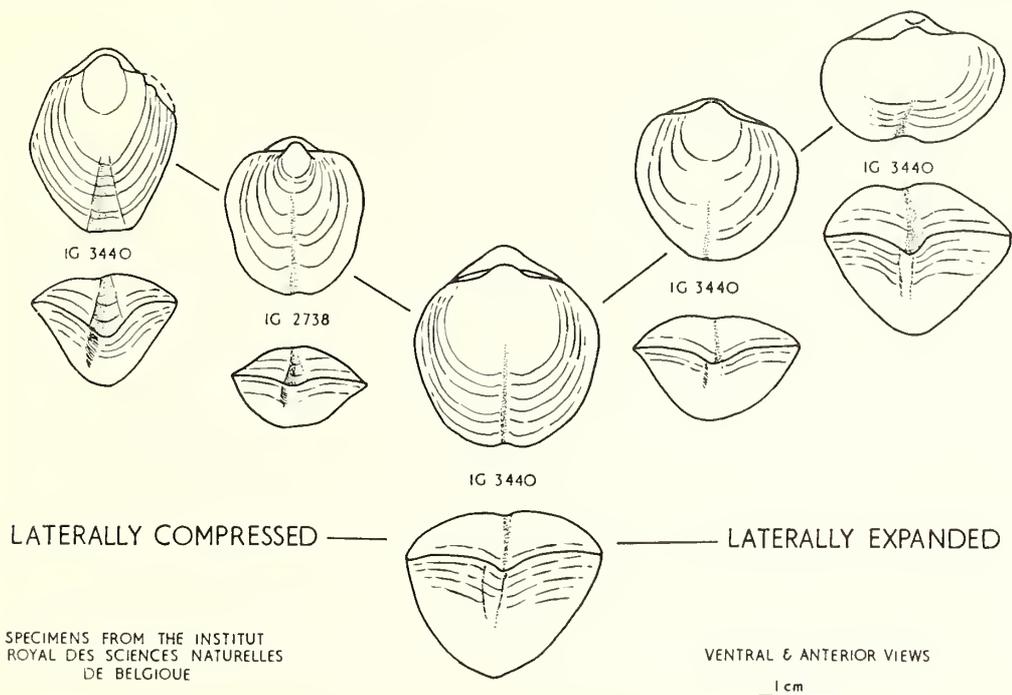
TEXT-FIG. 17. *Schizophoria woodi* Bond. Ventral and dorsal muscle fields, based on specimens BC B239, 250-2; BM BB39953.



TEXT-FIG. 18. Dimensions of *Schizophoria woodi* Bond.

as those from Craven and the Isle of Man. However, external and internal characters of the two forms are very similar.

Small, biconvex forms of *S. woodi*, especially from Elbolton and Swinden Knolls, and Treak Cliff, superficially resemble *S. connivens* (Phillips) in size, tumid outline, and prominent rugae. But *S. woodi* has fine costellae, less prominent rugae, and an angular-uniplicate anterior commissure, in contrast to the coarse costellae, thick rugae, and



TEXT-FIG. 19. External variation in *Schizophoria woodi* Bond.

quadrate-uniplicate or biplicate anterior commissure of *S. connivens*. Internally they are quite distinct (cf. text-figs. 16 and 1).

S. woodi superficially resembles *S. gibbera* (Portlock) in dorsibiconvexity and costellation. Although strongly dorsibiconvex and finely costellate, *S. woodi* has slightly coarser costellae and has rugae, and is less strongly dorsibiconvex. In other characters the two species are readily distinguishable (text-fig. 4).

Strongly dorsibiconvex individuals of *S. woodi* also superficially resemble comparable forms of *S. linguata* (Quenstedt) in outline and costellation. Both are strongly dorsibiconvex and finely costellate, but *S. woodi* is more rounded in outline, and has a narrower, more angular ventral sulcus and anterior plication, in contrast to the quadrate to rectangular outline, and rounded sulcus and plication of *S. linguata*. Internally the two species are distinct (text-figs. 16 and 8). Youthful specimens of the two species are generally distinct. *S. woodi* is more rounded in outline, more convex, and has a sub-angular anterior plication, in contrast to the rectangular to elliptical outline, and rounded plication of *S. linguata*.

Material. Belgium, Visé: Viséan (BM B13197/1, 6, 9; HMUG L1152/1, 2; IRSN 2737, 3440). Derbyshire: *Dielasma* Bed, D₁ subzone, Treak Cliff, Castleton (BC B208-36; BM BB39846, 39852, 39857, 39883, 39885, 39886, 39903, 39906, 39913, 39925, 39926, 39942, 39953); Avonian reef limestones, Treak Cliff (HMUG L5323/5, 9, 14, 44, 45, 63, 68, 70, 84, 87, 95, 123-5, 128). Ireland: Viséan, D₁ subzone, County Meath (TCD M2647b, 27125b). Isle of Man (Castletown): Poyllvaish Limestone, Upper Reef Knoll Limestone, P_{1a} (D₂) subzone, Ghaw Gortagh, near Poyll Vaish (BC B237-52); Lower Carboniferous (BM B54118-21). Yorkshire: Avonian reef limestones, Elbolton Knoll, Cracoe (HMUG L5321/7); Lower Carboniferous, D₁, Craven (BM BB8152—holotype); D₁ zone, Wedber Knoll, Malham (HMUG L3674/2; IC 11136; SM E11,128, 11,129).

PHYLOGENY

The postulated phylogeny of Carboniferous species of *Schizophoria* is shown on text-fig. 20. This chart is based solely on the available material, and could conceivably represent only a part of the true picture of descent.

The phylogeny of Devonian species has previously been described (Pocock, 1966).

The relationship of species has been based externally on outline and costellation, and internally on muscle field patterns and form of the brachiophore plates, correlated with stratigraphical distribution. These features are illustrated on text-figs. 20, 21.

Four main lines of development are recognized in the Carboniferous. The line of development represented by *S. connivens* consists of small to medium-sized, coarsely costellate, rugate forms, with divergent brachiophore plates, and an elliptical to weakly flabellate ventral muscle field.

The line represented by *S. resupinata* and its varieties is characterized by larger forms, with finer costellae, divergent brachiophore plates, and a flabellate ventral muscle field.

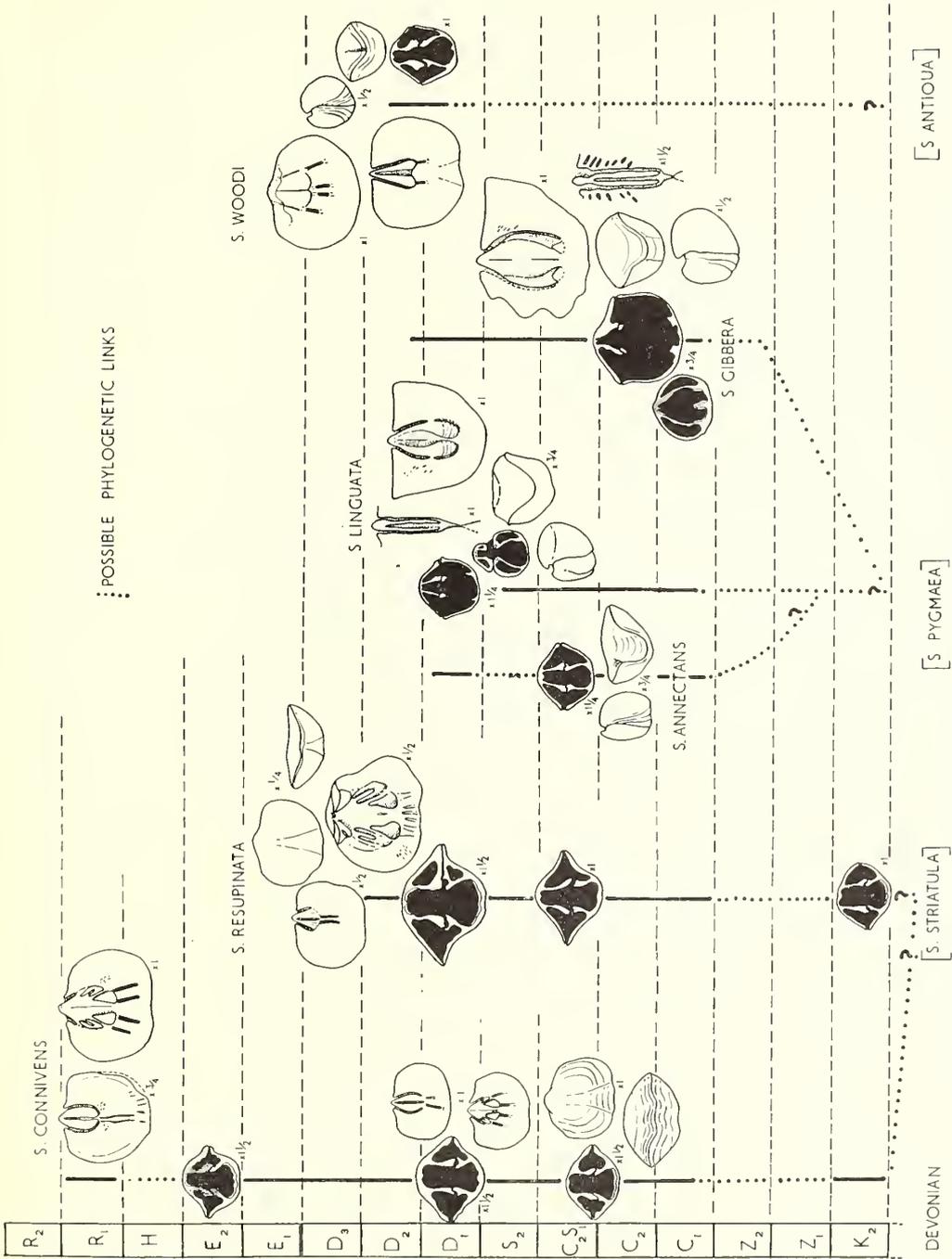
S. gibbera, *S. linguata*, and *S. annectans* represent a line composed of three branches, characterized by greater dorsibiconvexity, very fine ornament, a narrow, parallel-sided ventral muscle field, a rectangular to elliptical dorsal muscle field, and curved brachiophore plates.

S. woodi is the fourth line of development, and is similarly a strongly dorsibiconvex form with fine costellae, and curved brachiophore plates. But *S. woodi* has a flabellate ventral muscle field.

S. resupinata (K-D zones) was probably derived from the *S. striatula* line of development in the Devonian, based on general outline and muscle fields. The varieties of *S. resupinata* are shown as sporadic offshoots, representing extreme variation at different levels.

S. connivens (K zone—R₁ stage) has hereby been derived as an offshoot from *S. resupinata*, possibly in late Devonian or early Carboniferous. Although distinct from *S. resupinata*, there are some resemblances in the dorsal muscle field and brachiophore plates.

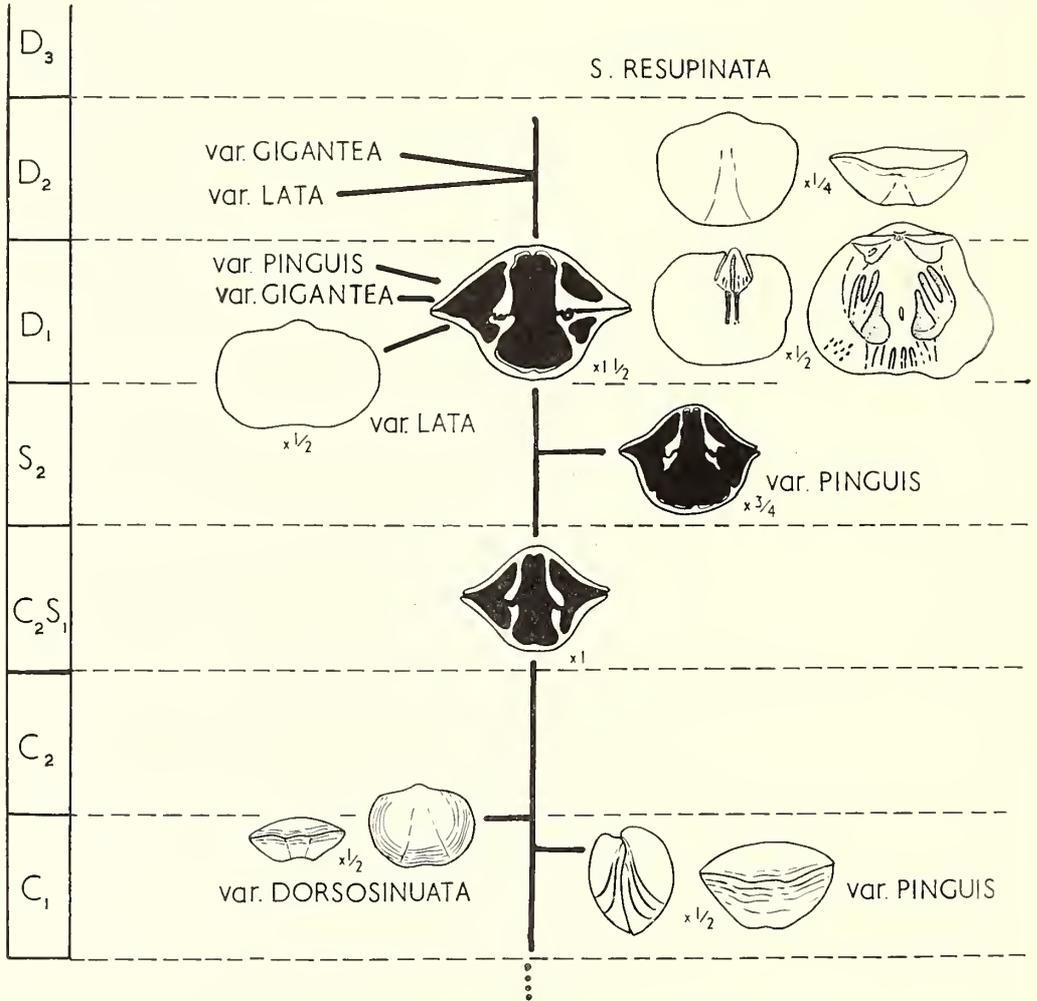
Derivation of the *gibbera-linguata-annectans* line (C-D zones) is difficult to postulate. Although *S. provulvaria* and *S. antiqua* of the Devonian have curved brachiophore plates, they have different external outline and muscle fields. The strongly dorsibiconvex forms, with narrow, parallel-sided ventral muscle fields of the Carboniferous are not represented by any closely comparable forms studied in the Devonian. Although *S. gibbera*, *S. linguata*, and *S. annectans* have been derived from the *S. provulvaria*-*S. pygmaea* line on text-fig.



TEXT-FIG. 20. Postulated phylogeny of *Schizophoria* from the Carboniferous of western Europe.

20, they could have alternatively developed outside the area studied, appearing during the British Lower Carboniferous marine transgression.

S. woodi (D zone) could possibly have developed from *S. antiqua* of the Devonian. Both are dorsibiconvex, rugate forms, with a flabellate ventral muscle field, elliptical to



TEXT-FIG. 21. Varieties of *Schizophoria resupinata*.

flabellate dorsal muscle field, and curved brachiophore plates. But *S. antiqua* is more coarsely costellate, and although smaller in size than the larger form of *S. woodi*, it closely resembles the smaller form of *S. woodi*.

Acknowledgements. The author wishes to thank all museums for allowing access to relevant collections. Thanks are extended to Mr. J. W. Keith, Bedford College, for photographic assistance. This research work formed part of a thesis, written under the supervision of Dr. C. H. Holland of Bedford College, and submitted for a Ph.D. degree, University of London.

REFERENCES

- BOND, G. 1941. Species and Variation in British and Belgian Carboniferous Schizophoriidae. *Proc. Geol. Ass. Lond.* **52**, 285–303, pl. 21, 22.
- CAMPBELL, K. S. W. 1957. A lower Carboniferous Brachiopod-Coral fauna from New South Wales. *J. Paleont.* **31**, 34–98, pl. 11–17.
- CVANCARA, A. M. 1958. Invertebrate fossils from the lower Carboniferous of New South Wales. *Ibid.* **32**, 846–88, pl. 109–113.
- DAVIDSON, T. 1851–5. British Fossil Brachiopoda. 1. Tertiary, Cretaceous, Oolitic, and Liasic species, with a General Introduction. *Palaeontogr. Soc.* [Monogr.].
- 1858–63. A monograph of the British fossil Brachiopoda, 2. Permian and Carboniferous species. *Ibid.*
- DÉLÉPINE, G. 1942. Les faunes marines du Carbonifère des Asturies (Espagne). *Mém. Acad. Inst. France* **66**, 2nd ser., 1–122.
- DEMANET, F. 1923. Le Waulsortien de Sosoye. *Mém. Inst. géol. Univ. Louvain*, **2**, 39–284, pl. 3–14.
- 1934. Les Brachiopodes du Dinantien de la Belgique. *Mém. Mus. roy. d'Hist. nat. de Belg.* (1) **61**, 1–116.
- GEORGE, T. N. 1932. Brachiopoda from the Cayton Gill Beds. *Trans. Leeds geol. Ass.* **5**, 37–48.
- GEORGE, T. N. and PONSFORD, D. R. A. 1938. Notes on the Morphology of *Schizophoria*. *Trans. Leeds geol. Ass.* **5**, 227–45.
- KONINCK, L. G. DE. 1842–4. *Description des animaux fossiles qui se trouvent dans le terrain carbonifère de Belgique*, iv+650 pp., Liège.
- 1873. *Recherches sur les animaux fossiles: pt. 2, Monographie des fossiles carbonifère de Bleiberg en Carinthie*, 116, pp., Bruxelles.
- 1877. *Recherches sur les fossiles paléozoïques de la Nouvelle-Galles du Sud (Australie)*, 368 pp., Bruxelles. Atlas, 24 pl.
- MARTIN, W. 1809. *Figures and descriptions of petrifications collected in Derbyshire*, 28 pp., Wigan.
- M'COY, F. 1844. *A synopsis of the characters of the Carboniferous Limestone fossils of Ireland*, vi+207 pp., Dublin.
- PAECKELMANN, W. 1930. Die Brachiopoden des deutschen Unterkarbons. 1. *Abh. Preuß. geol. Landesanst.* **122**, 143–326.
- PARKINSON, D. 1954. Quantitative studies of brachiopods from the Lower Carboniferous reef limestones of England. *J. Paleont.* **28**, 367–81.
- PHILLIPS, J. 1836. *Illustrations of the geology of Yorkshire; pt. 2. The Mountain Limestone district*, xx+253 pp., London.
- POCOCK, Y. P. 1966. Devonian schizophoriid brachiopods from western Europe. *Palaeontology*, **9**, 381–412, pl. 66.
- PORTLOCK, J. E. 1843. *Report on the geology of the county of Londonderry and parts of Tyrone and Fermanagh*, xi+784 pp., Dublin.
- QUENSTEDT, F. A. 1868–71. *Petrefaktenkunde Deutschlands: Abt. 1, Band 2. Die Brachiopoden*, iv+748 pp., pls. 37–61. Leipzig.
- SCHRÖTER, J. S. 1777. *Abhandlungen der über verschiedene Gegenstände der Naturgeschichte*, **2**, 335–504.
- SOWERBY, J. 1823. *The mineral conchology of Great Britain; or Coloured figures and descriptions of remains of testaceous animals*, **4**, 160 pp., London.
- TERMIER, H. and TERMIER, G. 1950. Invertébrés de l'Ère primaire, fasc. 2, Bryozoaires et Brachiopodes. *Paléont. Maroc*, **2**, 1–253.
- WRIGHT, J. A. 1952. *Brachiopod communities in Avonian reef limestones of the Pennines*. Ph.D. thesis, Univ. of Glasgow, no. 1134, 79 pp.
- YANAGIDA, J. 1962. Carboniferous brachiopods from Akiyoshi, S.W. Japan. *Mem. Fac. Sci. Kynslu Univ.*, ser. D, **12**, 87–127.

Y. P. POCOCC,
Department of Biology and Geology,
Northern Polytechnic,
London, N. 7

PRESERVED LIGAMENTS IN AUSTRALIAN PERMIAN BIVALVES

by BRUCE RUNNEGAR

ABSTRACT. The Australian Permian 'burrowing' bivalves have large external ligaments which may be either replaced by calcite or have their outer surfaces preserved as external and internal moulds. Sections of two such replaced ligaments of *Pyramus laevis* and *Megadesmus nobilissimus* show three layers which probably correspond to the inner, outer, and fusion layers of living bivalves. The presence of fusion layer is to be expected from the lack of pallial attachment above the adductor muscles, and its presence in *Megadesmus* and *Pyramus* may prove to be useful in differentiating these shells from more or less homeomorphic living (and fossil) shells which have no fusion layer.

EXTERNAL ligaments of fossil bivalves may be preserved either as external moulds (Newell 1956, figs. 3*b*, 3*f*, 4*a*; Skwarko 1963, pl. 4, fig. 4; Runnegar 1965, pl. 15, fig. 15) or as silicified replicas (McAlester 1963, p. 6, fig. 65; Ciriacks 1963, pl. 4, fig. 9), and in either case are usually only visible on the outside of well preserved articulated shells. Exceptional specimens, such as the specimen of *Liebea squamosa* figured by Newell (1942, fig. 5, p. 29, pl. 15, fig. 3*b*), show details of the internal structure of the ligament which could only have been produced by selective solution or decomposition of different layers of the ligament; and Jefferies and Minton (1965, fig. 9) and Runnegar (1965, p. 234) have noted the preservation of ligamental structure in shells of Jurassic and Permian age.

Many of the desmodont bivalves of the eastern Australian Permian have large external ligaments which have been more or less completely converted to coarse granular calcite, and it has been possible to prepare transverse thin sections of the shell and ligament. The internal structure of the ligament has frequently been obliterated by recrystallization or replacement, but one specimen of *Pyramus laevis* (Sowerby) and one of *Megadesmus nobilissimus* (de Koninck) show layers which probably correspond to the original layers of the ligament.

The purpose of this paper is to describe the various layers of the ligament of the Permian bivalves and their method of attachment to the shell, and to suggest that the layers are similar in function and origin to those of many living shells such as *Tellina tenuis* and *Glauconome rugosa*.

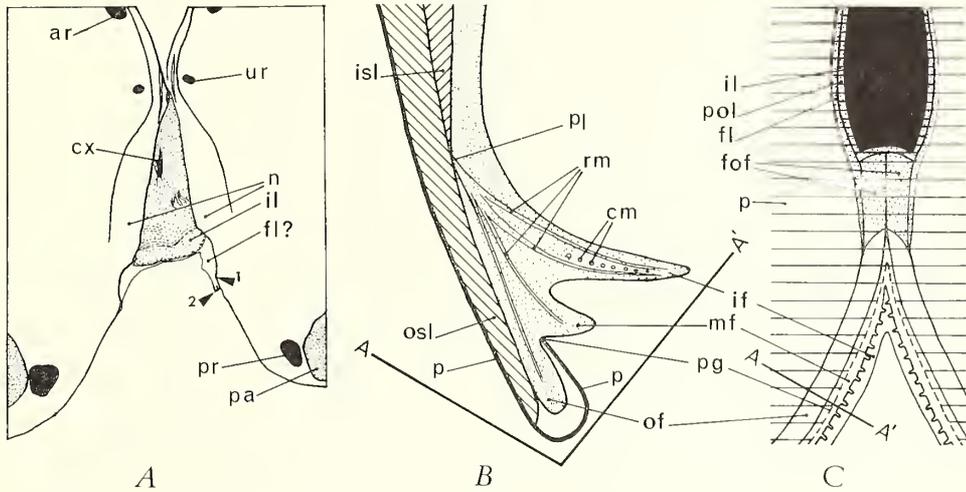
SECRETION OF VALVE AND LIGAMENT

The following is a summary based on the work of Yonge (1948, 1953, 1957), Trueman (1949), Owen (1958, 1959*a*, *b*), and Owen, Trueman, and Yonge (1953).

The bivalved shell of lamellibranchs appears to have resulted from the lateral compression of a primitive uncoiled univalved shell about a median uncalcified strip, termed the ligament (Yonge 1953). Such an explanation is supported by the ontogeny of living bivalves whereby a single larval shell-gland secretes 'a saddle-shaped cuticular pellicle, which becomes calcified at two symmetrical points, right and left of the middle

line' (Pelseener 1906, p. 245). Thus the valves and ligament are parts of a single structure (the shell) and differ only in the degree of calcification of the protein matrix.

The shell is secreted by an envelope of tissue of comparable shape termed the mantle, and the neck of tissue which joins the right and left lobes of the mantle has been called the *mantle isthmus* (Owen, Trueman, and Yonge 1953). The mantle isthmus lies beneath and secretes the ligament, whereas the flanks of the mantle—the mantle lobes—secrete the valves.



TEXT-FIG. 1. A. Line drawing of the specimen of *Myonia valida* shown in Plate 19, figs. 1, 9 and Plate 20, fig. 10; $\times 1$. Note the small piece of fusion (?) layer (2) which appears to extend beyond the posterior edge of the fossette (1).

B. Diagrammatic section of the margin of a bivalve shell and mantle corresponding approximately to the line A-A' in text-fig. 1C.

C. Diagrammatic external view of the posterior part of the ligament to show the relationship of the fusion layer to the secreting surfaces of the mantle.

ar, anterior retractor muscle scar; *cm*, circular muscles; *cx*, cracks in the inner layer of the ligament; *fl*, fusion layer; *fof*, fused outer surfaces of the outer mantle folds; *if*, inner fold of the mantle; *il*, inner layer of the ligament; *isl*, inner shell layer; *mf*, middle fold of the mantle; *n*, nymph; *of*, outer fold of the mantle; *osl*, outer shell layer; *p*, periostracum; *pa*, posterior adductor; *pg*, periostracal groove; *pl*, pallial line; *pol*, posterior outer layer of the ligament; *pr*, posterior pedal retractor muscle scar; *rm*, radial muscles; *ur*, umbonal retractor scar.

The valves and ligament are composed of two layers, the *inner* and *outer layers*, covered by a superficial but continuous *periostracum*. The inner layers of valves and ligament are secreted by cells comprising the external surface of the mantle and isthmus, whereas the outer layers and periostracum are formed only at the growing (peripheral) edge of the valve and ligament. (It is important to note that there is only one growing edge to the shell and that it is continuous from one valve to the other at the anterior and posterior ends of the ligament). Secretion of the periostracum takes place just inside the edge of the mantle in a structure termed the *periostracal groove* (*pg*, text-fig. 1 B-C) which lies between the outer edge of the mantle and the outer of two flaps of tissue that extend around the perimeter of the mantle. These two flaps together with the outer edge

of the mantle, form the *mantle folds*, and are termed *outer*, *middle*, or *inner* according to their position relative to the outside of the shell (text-fig. 1 B-C).

The inner fold of the mantle contains radial (or orbicular) muscles which are attached to the shell along the pallial line as well as circumpallial muscles lying parallel to the mantle margin, and its function is partly protective and partly to control water flow into the mantle cavity. Cross-fusion of the left and right edges of this fold (with the development of appropriate pedal and siphonal orifices) may result in a firm muscular union of the ventral and posterior edges of the mantle lobes to produce siphons and a muscular 'floor' to the mantle cavity. The middle fold of the mantle edge usually bears tentacles and in some cases eye-spots, and its function is essentially sensory. The outer fold (the outermost edge of the mantle) is concerned solely with shell secretion; its outer surface gives rise to the outer shell layer, and, in the region of the mantle isthmus, the outer layer of the ligament, while the periostracum is secreted in the groove between its inner surface and the outer surface of the middle fold.

Most isomyarian bivalves have a more or less external ligament, most of which is situated behind the umbones. Consequently the mantle isthmus and ligament are asymmetric about a plane through the beaks at right angles to the hinge, and the major portion of accretionary growth of the ligament occurs at its larger (posterior) end. It follows that in unspecialized shells, posterior growth of the ligament is essentially like that of the valves, whereas decreased growth causes the anterior end to be somewhat modified. Furthermore, increasing specialization results in the partial or complete fusion of the left and right parts of the outer mantle fold at either or both ends of the ligament, so that the primitive or *primary* ligament (Owen *et al.* 1953) may be secondarily extended either by periostracum or by a new layer called fusion layer (Owen *et al.* 1953). The former is secreted if only the inner surfaces of the outer mantle fold are fused, whereas the latter is produced by the fused *outer* surface of this fold where it bends round from one valve to the other (text-fig. 1c).

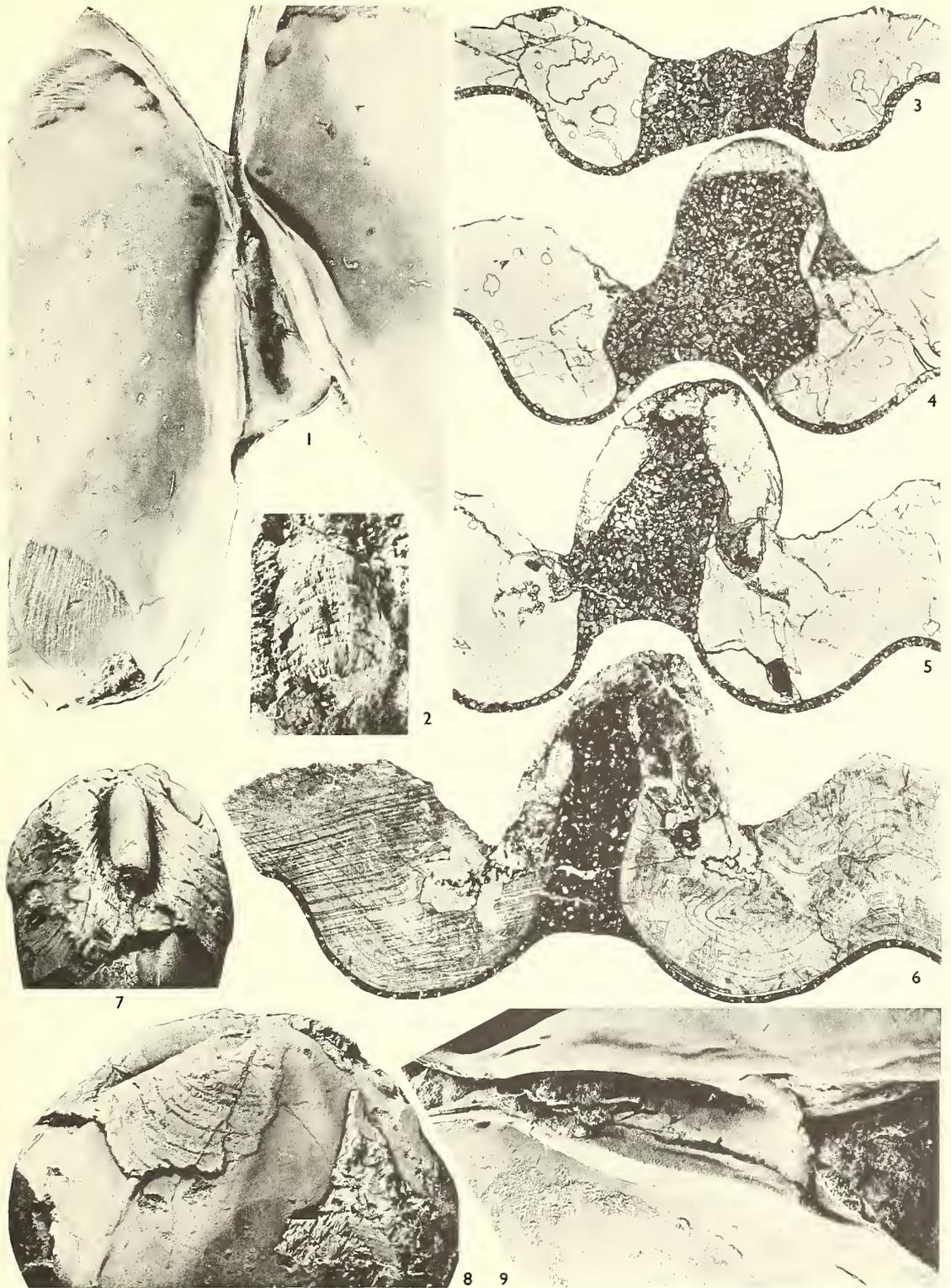
Megadesmus, *Pyramus*, and related members of the Pholadomyidae (Runnegar 1966) have an external C-spring-shaped ligament attached behind the umbos to a deep arcuate groove in each valve; the same type of ligament occurs in many unrelated living shells and has been described in detail from *Tellina tenuis* (Trueman 1942; 1949) and *Glaucanome rugosa* (Owen 1959a). The following summary of the relationships of the various layers of the ligament of *G. rugosa* is taken from Owen (1959a, p. 63).

The interpretation of the structure of the ligament of *G. rugosa* will be more readily understood by comparing the sections shown in figures 4 and 5a to i, [b to f reproduced herein as O to S in text-fig. 3] with the diagrammatic representation of the ligament shown in figure 3 [herein text-fig. 2]. The posterior end of the primary ligament is secondarily extended by fusion layer (FL) and as a consequence,

EXPLANATION OF PLATE 19

Figs. 1, 9. *Myonia valida* Dana. 1, latex cast of internal mould of both valves and the ligament, viewed from the inside, $\times \frac{3}{4}$. 9, the same specimen tilted to show the nymph of the right valve, $\times 1$. See also text-fig. 1A. (AM F8206, Gerringong Volcanics, Wollongong, New South Wales.)

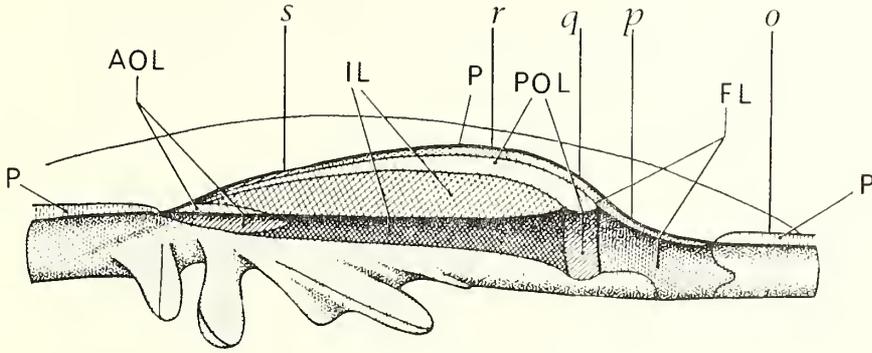
Figs. 2-8. *Pyramus laevis* (Sowerby), 1838. 2, partly decorticated ligament to show the fibrous structure of the inner layer, $\times 4$. (AM F28113, Allandale Formation, Allandale, New South Wales.) 3-6, sections of the ligament of the specimen shown in figs. 7-8, $\times 5$ approx.; compare with text-fig. 3C-F. 7-8, posterior and lateral views of partly decorticated shell with well preserved ligament, $\times 1$. (AM F50457, same location as fig. 2.)



RUNNEGAR, Ligaments in Permian bivalves

the functional ligament is composed of a superficial periostracum (P), fusion layer (FL) and outer (POL) and inner (IL) layers of the ligament. It extends posteriorly from the umbones approximately one-third the distance to the posterior end of the shell. Posterior to the primary ligament, the two valves are joined by an inverted U-shaped structure which is the fusion layer (FL) secreted by the fused outer surfaces of the outer folds of the mantle margins posterior to the mantle isthmus. In the mid-line between the two valves this fusion layer is secreted beneath the periostracum while laterally it extends beneath the calcareous layers of the valves. As growth proceeds the lateral regions of the fusion layer are progressively embedded in the calcareous layers of the shell and it undoubtedly serves to attach the ligament firmly to the valves. Outer layer of the ligament (POL) is secreted beneath the fusion layer by the outer marginal fold at the posterior end of the mantle isthmus where this bends round from one pallial lobe to the other, while the inner layer of the ligament (IL) is secreted by the epithelium of the mantle isthmus.

Underlying the inner layer at the anterior end of the ligament and extending a short distance anterior to the umbones is the anterior outer layer (AOL) secreted by the outer marginal fold at the anterior end of the mantle isthmus. Thus, all the possible constituents of the lamellibranch ligament (Yonge, 1957), with the exception of anterior fusion layer, are present and their relationship to one another particularly at the anterior end, are almost diagrammatically obvious.

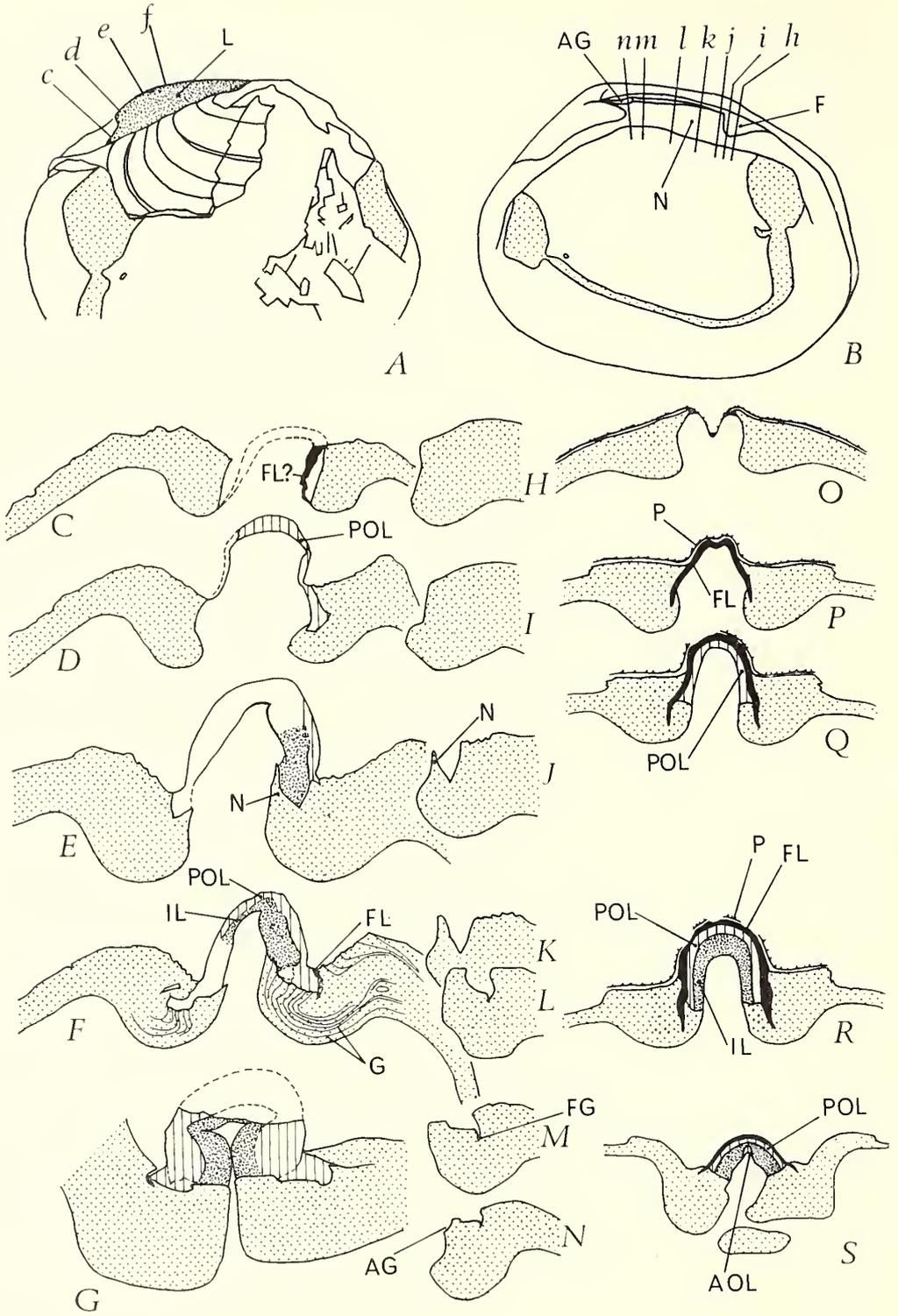


TEXT-FIG. 2. Semi-diagrammatic figure of the ligament of *Glauconome rugosa* cut longitudinally and viewed from the side (after Owen 1959a, fig. 3). AOL, anterior outer layer; FL, fusion layer, IL, inner layer; P, periostracum; POL, posterior outer layer. Sections cut at points s-o are shown in text-fig. 3O-S.

LIGAMENT STRUCTURE OF PERMIAN SHELLS

A detailed study of the ligament of the Permian bivalves has been possible because of two exceptionally well-preserved specimens of *Pyramus laevis* (Australian Museum F50457 and University of Queensland F47938), one of *Megadesmus nobilissimus* (UQ F45401), and one of *Myonia valida* (AM F8206). It seems likely that the ligament is fundamentally similar in related species and that the following description would apply in a general way to all of the Australian Permian members of the family Pholadomyidae (Runnegar 1966).

The ligament of *Pyramus laevis* is a short and robust structure situated externally behind the beaks (Pl. 19, figs. 7-8). Twenty-six acetate peels and one thin section were taken at significant intervals along the ligament of AM F50457, and several of these sections are reproduced in text-fig. 3C-F and Plate 19, figs. 3-6. However, since both



the shell and ligament are composed of crystalline calcite it was often difficult to interpret the somewhat crushed sections. Fortunately a completely undistorted and excellently preserved external mould of *Pyramus laevis* (UQ F47938, Pl. 20, figs. 7-9, text-fig. 3B) showing the ligament groove without the ligament was available. A rubber cast of this specimen was made and serial sections of the ligament groove were cut with a razor blade at intervals of about one millimetre. Camera lucida drawings of several of these sections are shown in text-fig. 3H-N. By comparing these sections with those of the shell plus the ligament it has been possible to suggest that at least three layers may have been present in the posterior part of the ligament of *Pyramus laevis*, and that these were probably inner layer (IL), posterior outer layer (POL), and fusion layer (FL). It is likely that an anterior outer layer and periostracum were present as well.

Attachment of the ligament to the shell. When the shell is viewed from above, the ligament groove is slightly arcuate and extends backwards from the beak (Runnegar 1965, Pl. 14, fig. 4). It is bordered on the inside by a strong vertical plate termed a *nymph* and the gap between the end of the nymph and the posterior (i.e. outside) edge of the ligament groove is the point where the secretory folds of the mantle edge bend round from one valve to the other. (Bernard 1895, p. 109) has called this gap the *fossette ligamentaire secondaire* or secondary ligamentary depression). Consequently, the inner layer of the ligament, which is secreted by the dorsal surface of the mantle isthmus, does not extend beyond the ends of the nymphs and is attached on either side to the upper edges of the nymphs (text-fig. 3F, R). By analogy with *Glaucanome rugosa* (text-fig. 3R), the posterior outer layer appears to have been attached to the inner side of the V-shaped ligament groove (text-fig. 3F), and at the base of the groove is another narrower groove (FG) into which fusion layer was probably inserted (text-fig. 3F, G, L-M, compare with text-fig. 3R, after Owen).

Bernard (1895) has pointed out that the *fossette secondaire* is merely the youngest section of the ligament groove, so that only the outermost layer of the ligament (in this case probably fusion layer) can extend backwards from the bottom of the fossette, since the posterior side of the fossette will eventually become the outer edge of the ligament groove. The posterior limit of the outer layer is therefore at or near the bottom of the fossette if fusion layer is present, and at the posterior end of the fossette if it is absent. However, fusion layer may extend for some distance beyond the ends of the primary ligament (Owen 1958), and, unlike the inner and outer layers, is not necessarily confined to the ligament groove.

Inner layer of the ligament. The boundary between inner and outer layers could be traced through 10 of the 27 sections of the ligament of *Pyramus laevis* and its position corresponds to that found by Owen in *Glaucanome rugosa* and Trueman in *Tellina tenuis* (text-fig. 3). In living shells this layer is fibrous with the fibres perpendicular to the growing surfaces within the layer (Newell 1942, p. 28; Trueman, 1949). The fibrous structure of the layer in *Pyramus laevis* is well shown by the specimen figured in Plate 19, fig. 2,

TEXT-FIG. 3. Sections of the shell and ligament of *Pyramus laevis* (C-F, H-N), *Megadesmus nobilissimus* (G, UQ F45401) and *Glaucanome rugosa* (O-S after Owen 1959a, figs. 4b-e, 5f). The positions of the sections are shown in A (AM F50457, see also Pl. 19, figs. 1, 9), B (UQ F47938, Pl. 20, figs. 7-9), and text-fig. 2.

AG, anterior groove which probably contained AOL; AOL, anterior outer layer; F, *fossette ligamentaire secondaire*; FG, groove into which fusion layer was probably inserted; FL, fusion layer; G, growth-lines; IL, inner layer; L, ligament; N, nymph; P, periostracum; POL, posterior outer layer.

and the upper edge of the nymph of UQ F47938 shows the impression of fibres at right angles to the axis of the ligament (Pl. 20, fig. 8), thus providing additional evidence that the inner layer was attached to the upper edge of the nymph.

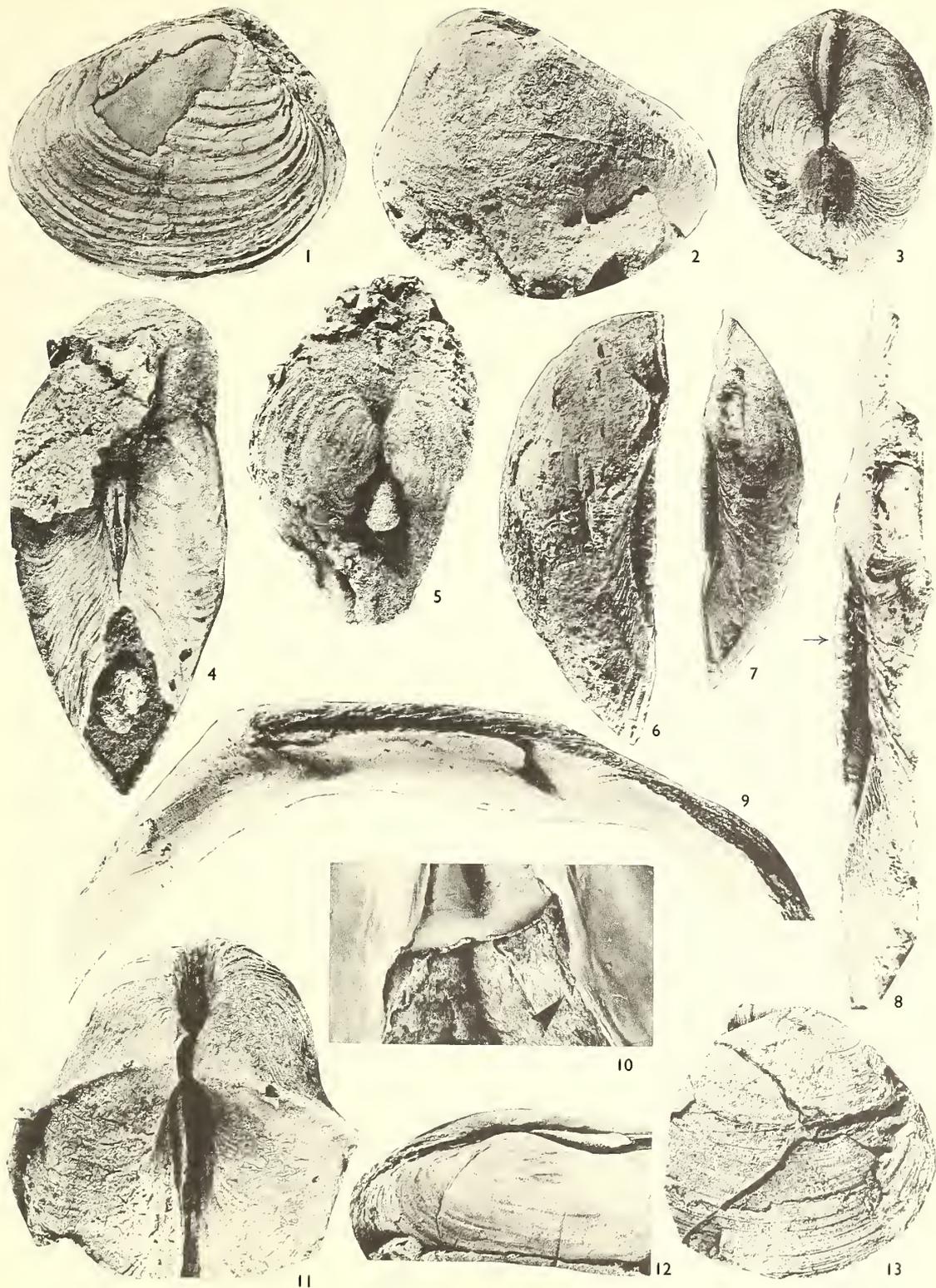
The inside surface of the inner layer is beautifully shown by a specimen of *Myonia valida* (Pl. 19, figs. 1, 9; text-fig. 1A) in which it extends backwards as far as the fossette and becomes very much thinner at its posterior end. The layer has several quite deep cracks in it (CX, text-fig. 1A) and the surfaces of these fractures also show the fibrous nature of the layer. Cracks of this type are common in the desiccated ligaments of shells removed from sea-water and they occur because of the low resistance this layer has to tensional stress.

Growth-lines within the layer are parallel to the inner surface of the ligament, so that the calcareous fibres are at all times perpendicular to the inner and outer surfaces of each growth lamella. Each growth lamella thickens posteriorly, and the younger lamellae overlap the earlier formed ones, so that the outer surface of the inner layer of the ligament is formed from the overlapped ends of the growth lamellae. This is well shown in the partly decorticated ligament of *P. laevis* (Pl. 19, fig. 2) in which the fibres at the posterior end of each lamella almost parallel the outer surface of the layer.

Outer layer of the ligament. The outer layer appears to be somewhat thinner than the inner and is probably composed of two parts—anterior and posterior outer layer. The latter covers the inner layer and probably extends beyond it as far as the base of the fossette. The gross structure of the posterior outer layer could be seen in transverse

EXPLANATION OF PLATE 20

- Figs. 1, 7–9, 13. *Pyramus laevis* (Sowerby). 1, plaster cast of lectotype of *Megadesmus cuneatus* (= *P. laevis*), $\times \frac{3}{4}$. (Brit. Mus. (Nat. Hist.) PL 682, Allandale Formation at Harper's Hill, near Lochinvar, New South Wales.) 7–9, dorsal and lateral views of latex cast of hinge to show the ligament groove nymph, and *fossette*. 7, $\times 1$; 8–9, $\times 2$. Note the fibrous nature of the upper surface of the nymph in fig. 8. (UQ F47938, 200 feet stratigraphically above the unconformity with pre-Permian strata at Durras South, south coast, New South Wales.) In fig. 7 the photograph of the hinge of F47938 has been superimposed on a photograph of another specimen (N.S.W. Geol. and Mining Mus. F7983, same location as fig. 1) to show the shell outline. 13, lateral view of latex cast showing part of the right valve and ligament, $\times \frac{3}{4}$. (UQ F47933, same location as figs. 8–9.)
- Figs. 2, 6. *Megadesmus nobilissimus* (de Koninck). Lateral and dorsal views of left valve showing position of ligament groove. 2, $\times \frac{3}{4}$; 6, $\times 1$. (UQ F46635, Middle Gympie Formation, Chatsworth, north of Gympie, Queensland.)
- Fig. 3. *Astartila cytherea* Dana. Anterio-dorsal view of latex cast showing large external ligament. (AM F4735.)
- Figs. 4, 5. *Vacmella curvata* (Morris). 4, dorsal view of both valves showing well-developed nymphs and long shallow fossette, $\times 1$. (AM F19201, Conjola Formation?, Bawley Point, Termeil, south coast, N.S.W.) 5, latex cast of external mould showing the ligament for comparison with fig. 4, $\times 1$. (Bur. Miner. Resour. Aust. CPC 7357, upper part of Middle Bowen Beds, Clermont area, Queensland.)
- Fig. 10. *Myonia valida* Dana. Enlargement of posterior part of ligament of specimen shown in plate 19, figs. 1, 9, to show the maximum posterior extension of the fusion (?) layer (arrowed) beyond the end of the fossette, $\times 1$.
- Fig. 11. *Myonia morrissi* (Etheridge). Latex cast of external mould showing ligament groove, $\times 1$. (UQ F21224, Homevale Beds, Homevale Homestead, northwest of Nebo, Queensland.)
- Fig. 12. *Vacmella?* sp. nov. Latex cast of external mould showing ligament, $\times 1$. Bur. Miner. Resour. Aust. CPC 7358, Barfield Formation, Jerry Creek, 5 miles east of Baralaba, Queensland.)



RUNNEGAR, Ligaments in Permian bivalves

sections but no special characters could be observed. In living shells it is relatively thin and uncalcified, and is able to withstand a great deal of tensional stress.

Several specimens of *P. laevis* and particularly UQ F47938 (Pl. 20, fig. 9) have a shallow groove on the inside surface of the anterior end of the nymph (AG, text-fig. 3B, N). This groove is in the position one would expect to find the anterior part of the outer layer (AOL, text-fig. 2) and may represent the position of insertion of this layer.

Fusion layer. The fusion layer of living shells is similar in appearance to both the periostracum and the posterior outer layer, and consequently is often difficult to identify. It can be recognized by the following features:

1. The staining reactions of each of the three layers differ so that stains such as Mallory's triple stain can be used to distinguish fusion layer (Trueman 1949, p. 738; Beedham 1958).

2. Both periostracum and fusion layer but not the outer layer may extend beyond the anterior and posterior limits of the ligament groove, with the fusion layer forming what Trueman (1949) has termed the 'anterior and posterior covers'.

3. The pallial line is normally extended above the adductors as far as the anterior and posterior ends of the ligament. Where the ligament has been secondarily extended by fusion layer (but not where it has been extended by periostracum) there is an accompanying loss of pallial attachment, so that the pallial line extends only to the anterior and posterior ends of the fusion layer (Owen 1958).

4. Fusion layer is secreted if the outer surfaces of the outer folds of the mantle are fused at either or both ends of the ligament, so that its presence can be determined indirectly from an examination of sections of the mantle at either end of the ligament.

In the study of fossil bivalves methods (1) and (4) are obviously not available and the identification of fusion layer must depend on an examination of the ligament and shell.

The presence of fusion layer in the ligament of *Pyramus*, *Myonia*, *Vacunella*, and related genera would be expected from the lack of pallial attachment between the posterior adductor and the posterior end of the ligament, best seen in the specimen of *Myonia valida* shown in Plate 19, fig. 1. Sections of the ligament of *Pyramus laevis* and *Megadesmus nobilissimus* showed that a thin layer (FL, text-fig. 3) is present on the outermost part of the ligament, and is inserted in a narrow groove (FG) which occurs at the base of the ligament groove (text-fig. 3L-N). It seems likely that this layer is fusion layer rather than periostracum, firstly because it is relatively thick (50–100 μ) and secondly because it is inserted in a deep groove in the manner of the fusion layer of living shells (text-figs. 3Q-R, after Owen 1959a; see also Trueman 1949, fig. 7). Periostracum is relatively thin, and more importantly, since it covers the valves, should not be inserted in the shell.

It is also unlikely that this presumed fusion layer formed all or part of the posterior outer layer, since it is relatively thin in both small and large specimens (text-fig. 3F-G), and because it is inserted in a separate narrow groove. This possibility could be excluded if the layer could be shown to extend beyond the limits of the ligament groove, or in a posterior direction, beyond the posterior edge of the fossette. Unfortunately it has not been possible to demonstrate such an extension conclusively. In serial sections of *Pyramus laevis* a very thin outer layer could be followed beyond the exposed ligament at least as far as the posterior side of the fossette, but it could not be definitely traced

beyond the end of the fossette. An external layer that may have been fusion layer can be seen in a specimen of *Myonia valida* (Pl. 19, figs. 1, 9; Pl. 20, fig. 10; text-fig. 1A). In this specimen the valves are gaping widely and the outermost layer of the ligament has split into two parts. On each valve the layer is attached to the shell at least as far as the posterior end of the fossette and on the left valve appears to have extended a little way beyond the fossette (Pl. 20, fig. 10; text-fig. 1A).

To summarize, a very narrow external layer which has been interpreted as fusion layer can be seen in thin sections of the ligaments of *Pyranuus laevis* and *Megadesmus nobilissimus*. Although the presence of fusion layer in *Pyranuus*, *Myonia*, *Megadesmus*, and *Vacuella* is to be expected from the lack of pallial attachment between the adductor muscles and the ends of the ligament, it has not been possible to prove that the layer extends beyond the limits of the primary ligament, so that the identification of this layer as fusion layer is, at present, somewhat tentative.

Preservation of the ligaments. The outer layer of the ligament of living bivalves is a tanned fibrous protein and the inner layer a relatively little tanned protein impregnated with a large amount of fibrous calcium carbonate (Trueman *in* Imbrie and Newell 1964, p. 62). The preserved ligaments appear to be composed of granular calcite and it seems likely that the protein has been replaced by calcite soon after the death of the animal. Pieces of woody tissue associated with the shells in the Allandale Formation at Allandale, New South Wales, are similarly replaced so that their cellular structure is retained, suggesting that selective calcification of relatively tough organic tissues may have been common at this (and perhaps other) localities.

DISCUSSION

Yonge (1957, p. 168) considers that each natural group of lamellibranchs has a characteristic pattern of mantle fusion involving the ventral margins of the mantle, the siphons, and the ligament, so that the type and degree of fusion of the peripheral folds of the mantle at either end of the ligament is probably of considerable taxonomic significance. Since the number and arrangement of the layers comprising the ligament depend on the type of dorsal fusion of the mantle folds, the extent of fusion can be inferred from a study of the layers of the ligament. (It is, for example, sufficient to demonstrate the presence of fusion layer to be able to assume that the outer surfaces of the outer mantle folds have been fused.) Secondly, Owen (1958) has been able to suggest that the type of fusion can to some extent be inferred from the degree of extension of the pallial line above the adductor muscle scars, since the pallial line normally extends to the end of the ligament unless the ligament has been secondarily extended by fusion layer.

Fusion layer is thought to occur in the ligament of *Pyranuus*, *Megadesmus*, and other Permian members of the Pholadomyidae, and there is a corresponding lack of pallial attachment above the adductors. Unfortunately the structure of the ligament of related living genera such as *Pholadomya* or *Laternula* is not known to me, but the absence of dorsal extensions of the pallial line in both genera would suggest that the ligament has been secondarily extended by fusion layer. By contrast the more or less homeomorphic burrowing bivalves *Mya*, *Panope*, and *Hiatella* have the pallial line extended dorsally as far as the ends of the ligament, and in *Mya* and *Hiatella* at least, there is a corresponding absence of fusion layer (Hunter 1949, p. 276; Owen 1958, p. 647).

Acknowledgements. This study was financed by a Commonwealth Postgraduate Award. Mr. H. O. Fletcher of the Australian Museum, Sydney, allowed the sectioning of a specimen of *Pyramus laevis* and made other specimens available for the study. The manuscript has been read at various stages by Professor Dorothy Hill and Mr. J. S. Jell of the University of Queensland, Brisbane, and Dr. J. M. Dickins, Bureau of Mineral Resources, Canberra, and their assistance in both this and other ways is gratefully acknowledged.

REFERENCES

- BEEHDHAM, G. E. 1958. Observations on the non-calcareous component of the shell of the Lamellibranchia. *Q. Jl microsc. Sci.* **99**, 341–57.
- BERNARD, F. 1895. Première note sur le développement et la morphologie de la coquille chez les lamellibranches. *Bull. Soc. géol. Fr.* (3) **23**, 104–54.
- CIRIACKS, K. W. 1963. Permian and Eotriassic bivalves of the Middle Rockies. *Bull. Am. Mus. nat. Hist.* **125**, 100 pp., 16 pl.
- HUNTER, W. R. 1949. The structure and behaviour of *Hiatella gallicana* (Lamarck) and *H. arctica* (L), with special reference to the boring habit. *Proc. R. Soc. Edinb.* B **63**, 271–89.
- IMBRIE, J. and NEWELL, N. D. (eds.). 1964. *Approaches to paleoecology*. Wiley and Sons, New York, London, and Sydney, 432 pp.
- JEFFERIES, R. P. S. and MINTON, P. 1965. The mode of life of two Jurassic species of 'Posidonia' (Bivalvia). *Palaeontology*, **8**, 156–85, pl. 19.
- MCALISTER, A. L. 1963. Revision of the type species of the Ordovician nuculoid pelecypod genus *Tancrediopsis*. *Postilla*, **74**, 1–19.
- NEWELL, N. D. 1942. Late Palaeozoic pelecypods: Mytilacea. *Publ. State geol. Surv. Kans., Univ. Kans.* **10**, 1–115, 15 pl.
- 1956. Primitive desmodont pelecypods of the Australian Permian. *Am. Mus. Novit.* **1799**, 13.
- OWEN, G. 1958. Shell form, pallial attachment and the ligament in the Bivalvia. *Proc. zool. Soc. Lond.* **131**, 637–48.
- 1959a. Observations on the Solenacea with reasons for excluding the family Glaucomyidae. *Phil. Trans. R. Soc.* **B242**, 59–97.
- 1959b. The ligament and digestive system in the taxodont bivalves. *Proc. malac. Soc. Lond.* **33**, 215–23.
- TRUEMAN, E. R., and YONGE, C. M. 1953. The ligament in the lamellibranchia. *Nature, Lond.* **171**, p. 73.
- PELSENEER, P. 1906. In Lankester, E. R. *A treatise on Zoology, Part 5, Mollusca* London, 355. (Facsimile reprint by A. Asher and Co., Amsterdam, 1964.)
- RUNNEGAR, B. 1965. The bivalves *Megadesmus* Sowerby and *Astartila* Dana from the Permian of eastern Australia. *J. geol. Soc. Aust.* **12**, 227–52, pls. 12–15.
- 1966. Systematics and biology of some desmodont bivalves from the Australian Permian. *J. geol. Soc. Aust.* **13**, 373–86.
- SKWARKO, S. K. 1963. Australian Mesozoic Trigoniids. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* **67**, 55, 6 pl.
- TRUEMAN, E. R. 1942. The structure and deposition of the shell of *Tellina tenuis*. *Jl R. Microsc. Soc.* **62**, 69–92.
- 1949. The ligament of *Tellina tenuis*. *Proc. zool. Soc. Lond.* **119**, 717–42.
- YONGE, C. M. 1948. Formation of siphons in Lamellibranchia. *Nature, Lond.* **161**, 198–9.
- 1953. The monomyarian condition in the Lamellibranchia. *Trans. R. Soc. Edinb.* **62**, 443–78.
- 1957. Mantle fusion in the Lamellibranchia. *Pubbl. Staz. zool. Napoli*, **29**, 151–71.

B. RUNNEGAR
Department of Geology and Mineralogy,
University of Queensland,
Brisbane, Australia

BISCALITHECA (COENOPTERIDALES) FROM THE UPPER PENNSYLVANIAN OF ILLINOIS

by TOM L. PHILLIPS and HENRY N. ANDREWS

ABSTRACT. The frond anatomy and sporangial attachments of *Biscalitheca musata* Mamay are described from the Upper Pennsylvanian locality near Berryville, Illinois.

BISCALITHECA MUSATA has been allied with the Zygopteridaceae because of sporangial similarities with *Etapteris lacattei* and species of *Zygopteris*; however, the attachment of these to anatomically identifiable coenopterid genera has not been previously demonstrated. The vegetative parts of *Biscalitheca* and sporangial attachments in stalked soral groups were not known when the genus was established by Mamay (1957).

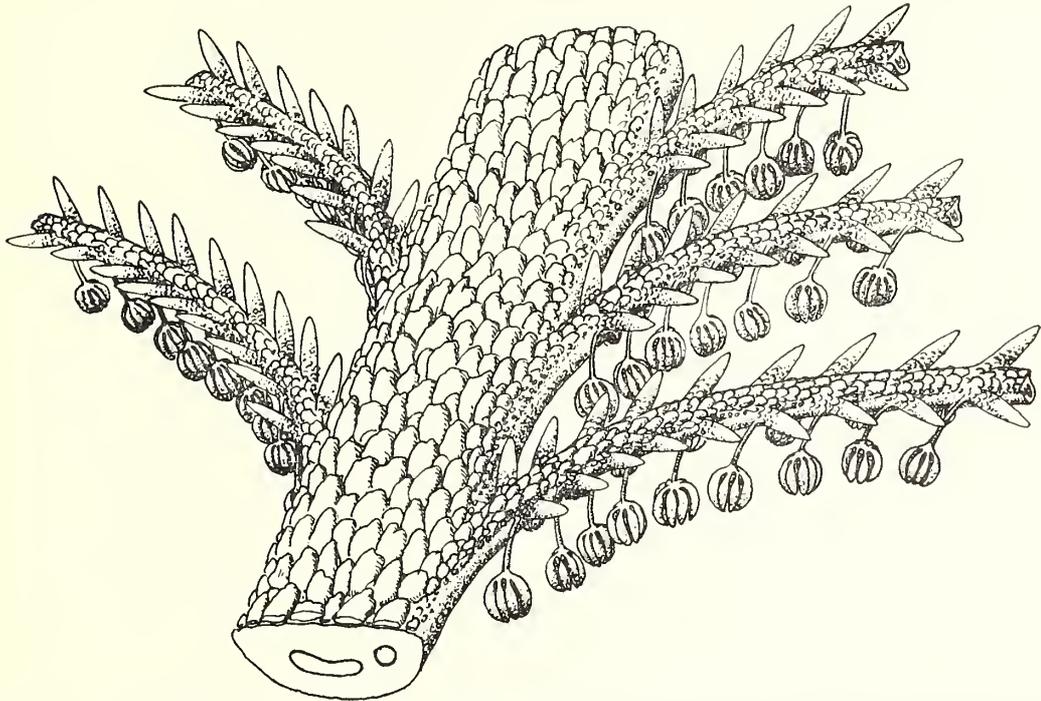
Materials. Two coal balls (Nos. 1271 and 7051) were collected from the Calhoun Coal near Berryville, Illinois, where the type material was obtained by Mamay (1957). The Calhoun Coal occurs in the Mattoon Formation, McLeansboro group, and is Upper Pennsylvanian in age. Coal ball 7051 contained compact sporangial masses scattered over a length of 8 cm. and a width of about 3 cm. along one edge of the coal ball. Specimen 1271 lacked the massive compaction of sporangial aggregations and included, in section, pinnately arranged soral groups along with three orders of connected frond divisions which extended across about 12 cm. in the widest section of the coal ball and was traced through a length of about 10 cm. Our description is based on specimen 1271 for the most part.

GENERAL MORPHOLOGY

The recovered portion of the frond of *Biscalitheca musata* included three orders of foliar members in a bipinnate arrangement. A stalked soral group, usually of seven sporangia, extended from the trailing edge of the base of each of the ultimate non-laminate divisions. The suggested reconstruction of a frond portion in text-fig. 1 includes a rather broad rachis with two rows of alternating primary pinnae. Soral stalks are attached on the rachis side at the junction of primary and ultimate pinnae; the relative lengths of the soral stalks are slightly exaggerated for clarity. An enlarged restoration of a sorus with a segment of the soral stalk is shown in text-fig. 2. The rachis and primary pinnae are covered by scale-like emergences exclusively and uniformly along upper or adaxial surfaces (Pl. 23, fig. 1), and similar multicellular outgrowths were preserved around the basal one-half of the ultimate divisions (Pl. 24, fig. 5).

The rachis is flattened in the plane of the primary pinnae, but the ultimate or secondary pinnae are directed slightly upward away from the rachis and out of the plane described by previous divisions (Pl. 21, fig. 1). By far the largest frond segment, which we descriptively refer to as the rachis, extended diagonally between adjacent broken edges of the coal ball for a length of only 3.5 cm. (Pl. 21, fig. 2; Pl. 22, fig. 1). Coal-ball sections including the rachis revealed a maximum of 2 primary pinnae on one side and 5 on the

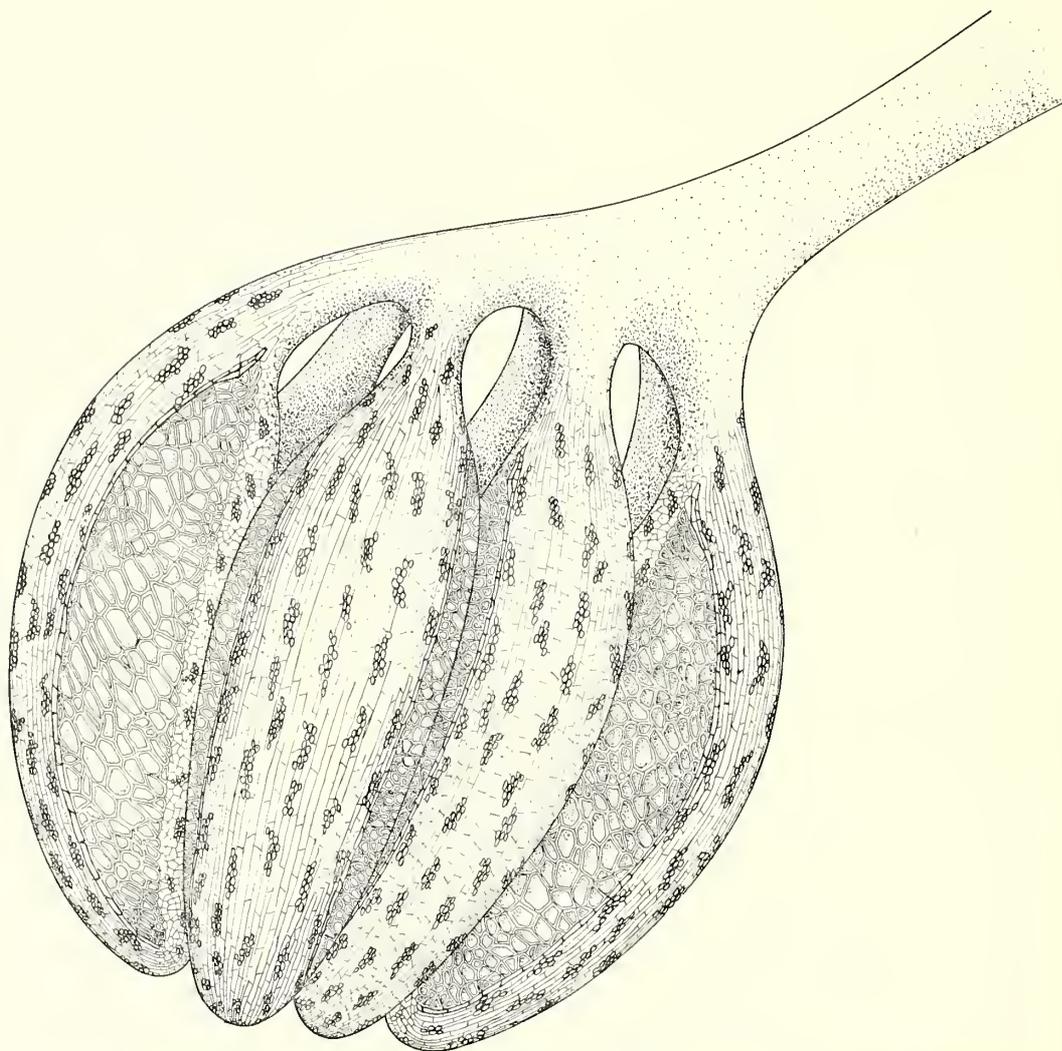
other. In the broadest sectioned part of the frond, excluding the rachis, 10 primary pinnae, apparently from the same side of the rachis, were observed about 8.5 mm. from each other. It is estimated that about 12 cm. of the length of the frond was represented in the coal ball. In transverse section the rachis is broadly ellipsoidal with the lower surface more rounded than the upper. The upper surface appears to have been almost



TEXT-FIG. 1. Suggested reconstruction of a portion of the fertile frond of *Biscalitheca musata*. Three orders of foliar divisions are represented with ultimate pinnae extending upward distally out of the plane of previous divisions. The stalked, circular sori occur in two rows.

flat, but this may be somewhat exaggerated, as is the width, because of crushing in the plane of the primary pinnae. The width of the crushed rachis was about 15 mm. with a maximum thickness of 3 mm.; despite inaccuracies in the dimensions attendant on crushing and the proximity of successive pinnae bases, the rachis seems to have been at least 2-3 times wider than thick. Primary pinnae were traced up to lengths of 7.5 cm., and the distance between successive primary pinnae on the same side of the rachis ranged from 7 to 11.5 mm. Measurements from the centres of primary pinnae, however indicated that the distance between pinnae was usually 8.5 mm. Primary pinnae have a maximum diameter of 3 mm. with 1.5-2.0 mm. the most common diameters encountered. Each primary pinna exhibits a striking branching pattern in which opposite to sub-opposite pairs of short cylindrical divisions arise distichously (Pl. 21, fig. 1). The bases of successive pairs of secondary pinnae are 7-8 mm. apart and the distal portions, without emergences, are oriented slightly upward and distinctly toward the end of the primary pinna. The secondary, or ultimate pinnae, are approximately 1.8-2.1 mm. in

basal diameter and tapered distally through a length which preservationally did not exceed 8 mm. The smoothly cylindrical to slightly angular soral branches are 4–5 mm. long and 0.5–0.7 mm. in diameter (Pl. 22, fig. 3; Pl. 23, fig. 2). Representative sections



TEXT-FIG. 2. Suggested reconstruction of stalked, circular sorus of *Biscalitheca musata* with apparently the region of dehiscence of each sporangium facing outward.

through a sorus showing the general arrangement of the soral stalk and attached sporangia are shown in Pl. 23, figs. 2, 3 and Pl. 24, fig. 3. The banana-shaped sporangia are 3–4 mm. in length, and spatially, in the coal ball, the two sori from an opposite pair of ultimate divisions extended toward the rachis to very near the base of the pair of ultimate divisions next behind. The sori were frequently appressed alongside the primary

pinna, directed toward the rachis; in Plate 22, fig. 6, the soral stalk is shown above, one of the sporangia below, and the junction of primary and ultimate pinnae at the bottom.

FROND ANATOMY

Rachis. The width of the xylem strand of the rachis is about 0.85 mm. with a minimum thickness at the ends of 0.4 mm. prior to prominent trace formation. The somewhat bar-shaped xylem appears to have a slight median, adaxial groove, and the adaxial to slightly lateral trace formation and emission imparts some adaxial curvature to the strand (Pl. 21, fig. 2; Pl. 22, fig. 1). The abaxial side of the strand is relatively flat. In accurate transverse sections, the xylem strand appears to be flattened laterally. Trace formation and emission are marginal, and in cross section, the crescent to semicircular-shaped pinna traces are about twice as wide as thick. Trace formation consists of an increase of tracheids along the adaxial portions with lateral extension beyond the sides of the abaxial portion of the band (Pl. 21, fig. 2); with departure of the pinna trace, the associated portion of the adaxial face is flattened and the other adaxial edge exhibits trace formation (Pl. 22, fig. 1). Distinct adaxial arms are not distinguishable. Tracheid diameters in the rachis xylem range from 20–80 μ . Protoxylem groups are not usually distinct, and tracheids of smallest diameter appear to be limited to the median portion along the adaxial face or immediately beneath the median portion of the adaxial face. One protoxylem group may be observed associated with incipient traces, but during trace emission the protoxylem could not be clearly followed. The vascular strand of the rachis is outlined by a narrow dark band of amorphous material which is separated from the tracheids by an unpreserved zone of about 100 μ in width.

Primary pinnae. Xylary strands of primary pinnae differ somewhat in transverse configuration from that of the rachis and also from those of the ultimate pinnae. The abaxial face, both sides and, at certain stages, even the adaxial face of the xylem is flattened in primary pinnae (Pl. 21, fig. 3; Pl. 22, fig. 2). The xylem strand is about 0.4 mm. thick, and the maximum width, which is attained across the abaxial portion, is slightly less than the thickness. The strand becomes narrower adaxially, and during trace formation and emission two adaxial extensions develop. The xylem strand usually exhibits a slight median adaxial groove which becomes more prominent immediately prior to trace emission (Pl. 24, fig. 4). Extending abaxially from the slight groove, a narrow zone of smaller tracheids frequently gives the appearance that the strand is essentially U-shaped with the arms of the U appressed (Pl. 21, fig. 1; Pl. 22, fig. 2). In well-preserved specimens the continuity of the tracheids along this zone can be seen. Along the adaxial face of the strand, the proximity of the two extended trace portions may temporarily enclose a small non-tracheidal zone between them. The zone between the trace-contributing edges of the xylem strand frequently appears as an unpreserved peripheral loop (Pl. 21, fig. 3). The dimensions of the loop are approximately $50 \times 75 \mu$.

Sori and their attachment. The minute traces from the primary pinnae branch at the base of the ultimate pinnae and a small vascular segment passes into the soral stalk (Pl. 24, fig. 4). The soral stalk consists of a central xylem core, cylindrical to slightly elliptical in cross-section, and there is a zone of ground tissue with scattered secretory

cells along the innermost edge (Pl. 22, fig. 3; Pl. 24, fig. 4). Secretory cells extended throughout the length of the soral stalk into the slightly expanded and branched portion where sporangia are attached (Pl. 23, figs. 2, 3; Pl. 24, fig. 3).

The sporangia are borne in compact clusters of 6–9 with 7 being a quite regular number. Three representative sections through a sorus of 7 sporangia are shown in Plate 23, fig. 4 and Plate 24, figs. 1, 2 with portions of all 7 appearing in Plate 24, fig. 1. The sporangia exhibit a distinct orientation in many sori, and it is suggested that this was probably the initial arrangement with all the sori (text-fig. 2). The distal end of each sporangium arches toward the centre of the sorus. The dorsiventral faces of sporangia are oriented toward and away from the centre of the soral aggregation with annuli directed more or less toward those of laterally adjacent sporangia. The lower surface of the sporangium (according to Mamay's description) with smaller, irregularly shaped and oriented cells, faces toward the inside of the soral group. The orientation of sporangia in the sori, with the outer wall composed of slender cells with the elongate dimension parallel to the sporangial axis, suggests that the outer face constituted a region of dehiscence.

Sporangia and spores. The sporangia and spores have been described in detail by Mamay (1957), and our specimens agree with the type material in the gross morphology of the sporangium and spores. We have calculated that a sporangium 3.6 mm. long and 0.9 mm. diameter contains about 8,000 spores of $65\ \mu$ diameter. All the sporangia of a given sorus either exhibited (Pl. 22, fig. 5) or lacked (Pl. 23, fig. 2) dark coloured, endosporal contents.

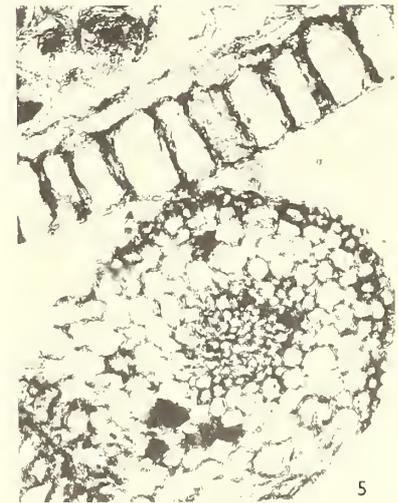
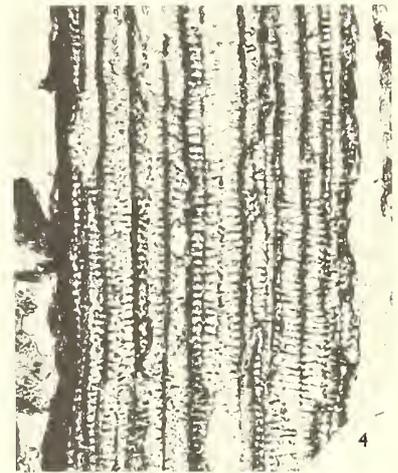
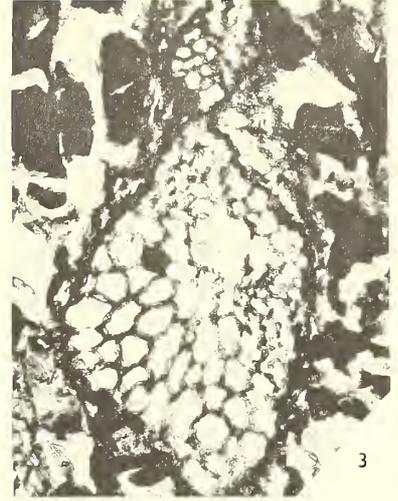
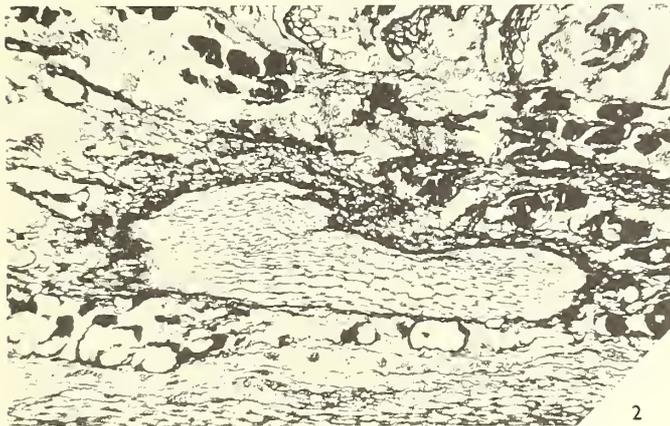
Non-vascular tissue with moderately thick cell walls occupies the central region of each sporangial pedicel (Pl. 21, fig. 5) and joins the divisions of vascular tissue from the soral stalk. In some sporangia an inner wall layer 1–2 cells in thickness of non-indurated cells is frequently observed (Pl. 22, fig. 5); in particularly well-preserved sporangia the inner wall layer is 4–5 cells in thickness. In longitudinal section these cells measure approximately $30 \times 160\ \mu$.

Ultimate pinnae. The xylary strand of the ultimate pinna in cross-section is band-shaped with a slight adaxial curvature. The xylem band is 4–5 cells thick and up to 15 tracheids wide (Pl. 21, fig. 1, upper left), and tissues immediately surrounding it are thin-walled, parenchymatous cells of extremely small diameter (Pl. 24, fig. 5).

Vascular tissue. Tracheids are generally scalariform in all the foliar members and in the soral stalks (Pl. 21, fig. 4; Pl. 22, fig. 4). Along the adaxial and lateral faces of the xylem of the primary pinnae is a rather well-preserved narrow band of up to 4 cells which apparently constituted a phloem zone (Pl. 22, fig. 2); no sieve areas were observed.

EXPLANATION OF PLATE 21

Figs. 1–5. *Biscalitheca musata*. 1, Primary pinna, T.S., with secondary pinnae laterally, oblique. Note soral stalk left of primary pinna, T.S. Slide 1950, $\times 34$. 2, Rachis with vascular strand at incipient stage of trace formation. Multicellular outgrowths on adaxial (upward) surface. Slide 1919, $\times 34$, T.S. 3, Primary pinna with peripheral adaxial loop and departing trace. Slide 1929, $\times 135$, T.S. 4, Scalariform thickenings of xylem of primary pinna. Slide 1943, $\times 96$, L.S. 5, Multistratose annulus wall and pedicel of sporangium. Slide 1948, $\times 135$, T.S.



During pinna trace emission, tissue from this zone accompanied the xylem portion of the trace. The phloem zone was separated from the xylem and, in turn, from cortical tissues by distinct dark lines or narrow bands of apparently crushed parenchyma.

Cortex. The cortical anatomy of the rachis and primary pinnae is essentially the same. The inner cortex is about one-half the width of the outer cortex. The most conspicuous components of the inner cortex are large, moderately thick-walled cells measuring about $150\ \mu$ in diameter and $230\ \mu$ in length. The large cells are arranged in vertical series end to end, and the lumens of many are filled with a black substance; 2–4 of these secretory chains of cells may be seen along a given radius of the inner cortex. Intermixed among the vertical series of large cells are numerous small, isodiametric parenchyma cells. The inner portion of the outer cortex is composed of larger parenchyma cells, minimally of $85\ \mu$ diameter and isodiametric; these centrifugally give way to successively longer parenchyma cells attaining lengths from 150 – $250\ \mu$ with a maximum diameter of $95\ \mu$ within a band of some 5–6 cells in thickness. The end walls are transverse. The outer and larger portion of the outer cortex exhibits progressively longer cells with smaller diameters, slightly thicker walls, and tapered end walls. The ground tissue of ultimate pinnae is composed of uniformly parenchymatous cells, usually longer than wide (Pl. 21, fig. 1, right), attaining maximum diameters of $160\ \mu$. Secretory cells observed in the ultimate pinnae were limited to the lower portion and frequently were entirely absent.

Epidermis and emergences. Epidermal cells of the primary pinna are quite small and somewhat rectangular in cross-sections of a pinna; the epidermis is not well preserved in the rachis. Hairs are not present. The adaxial surface of the rachis and primary pinnae and the lower half of the roughly cylindrical ultimate pinnae are covered with emergences which vary from 450 – $625\ \mu$ in width and up to $240\ \mu$ in thickness. The emergences are irregular to ellipsoidal in section; they appear to be slightly indented or notched at the tip (Pl. 21, fig. 2). These multicellular outgrowths are composed of uniformly thin-walled cells with a maximum diameter of $85\ \mu$; the outermost cells are slightly smaller and frequently contain dark coloured material. Stomata were not observed.

SYSTEMATIC TREATMENT

Genus *BISCALITHECA* Mamay 1957

Type species. *B. musata* Mamay 1957.

Emended diagnosis. Fertile frond bipinnate, non-laminate, rachis up to 15 mm. wide, 12 cm. long; alternate penultimate pinnae, 8.5 mm. (7–11.5 mm.) apart, 3–1.5 mm. wide, up to 7.5 cm. long; opposite to subopposite ultimate pinnae 7–8 mm. apart, 2.1–1.8 mm. in diameter, up to 8 mm. long; ultimate pinnae extend distally out of plane of other frond divisions.

Emergences, scale-like, slightly bifid, uniformly along adaxial surface of rachis and primary pinnae and around proximal one-half of ultimate pinnae.

Xylary strands in transverse section, shallow C-shaped in rachis and ultimate pinnae, and quadrilateral in primary pinnae with broad abaxial face tapering laterally to narrow adaxial face; protoxylem groups adaxial where distinct; tracheidal thickenings scalariform.

Cortex, two-zoned; inner cortex one-half width of outer, composed of large, moderately thick-walled cells ($150 \times 230 \mu$) with long axes end to end in vertical chains, intermixed small, isodiametric parenchyma cells; outer cortex centrifugally exhibits gradation from isodiametric to elongate parenchyma cells with transverse end walls to narrow, fusiform.

Soral stalk, attachment at trailing edge of junction of primary and ultimate pinnae, 7–8 mm. apart, probably pendant to trailing, terete to slightly angular, 0.5–0.7 mm. diameter, 4–5 mm. long, with terete xylary strand branching into 7 (6–9) divisions near base of as many terminal, sporangial pedicels; scattered secretory cells in inner cortical zone. Sorus, circular, with 7 (6–9) sporangia distally curved toward centre with annuli lateral and region of dehiscence away from centre. Sporangial pedicels terete, to 0.35 mm. in diameter, non-vascularized, attached to divisions of soral stalk.

Sporangia banana-shaped, 3–4 mm. long, 0.9–1.1 mm. in diameter, bilateral, dorso-ventral; sporangial wall unistratose to multistratose with a pair of lateral multiseriate, longitudinal annuli, 10–12 cells wide; outer sporangial wall between annuli containing elongate, double-rowed sclerotic nests ($250 \times 80 \mu$) and elongate-fusiform ($100 \times 20 \mu$) cells in the region of dehiscence, paralleling sporangial axis on outer face; cells of inner face between annuli, smaller and less regular in shape, intermixed with sclerotic nests less uniformly oriented.

Spores spherical, trilete, usually 58–70 μ in diameter (range 38–100 μ) endosporal contents frequent.

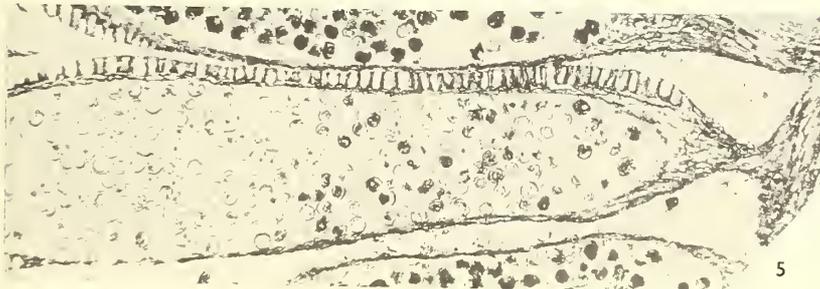
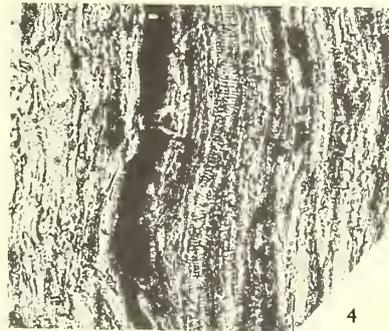
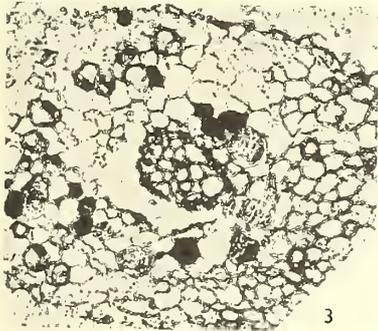
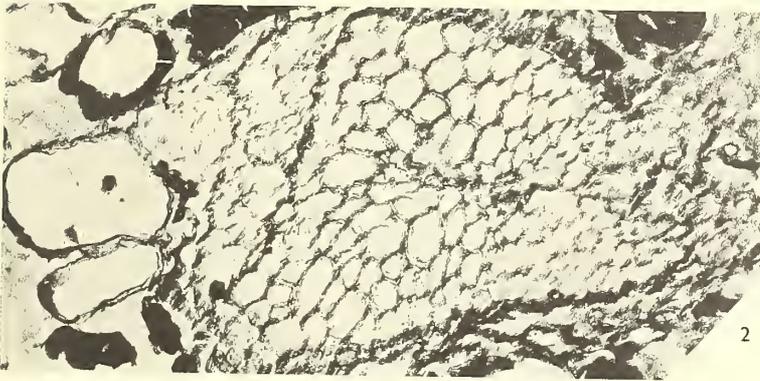
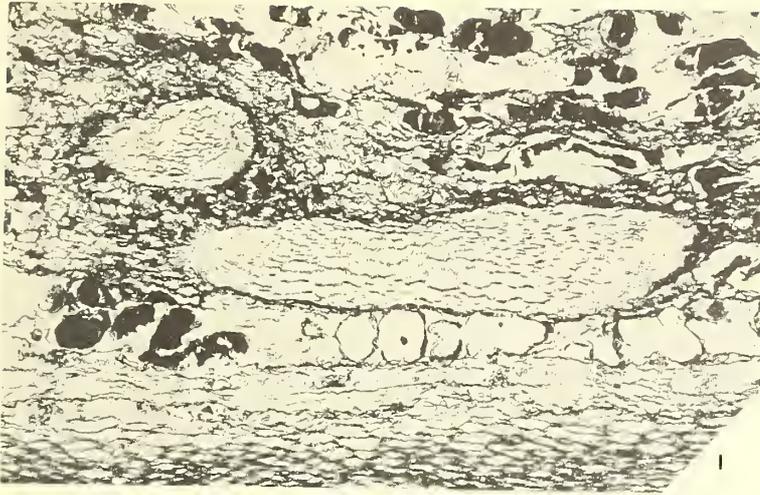
Remarks. Additional details on sporangia and spores are to be found in the original diagnosis by Mamay (1957) and need not be repeated here. This amended diagnosis is based on specimen 1271, slides 1917 through 1950, and peel preparations in the paleobotanical collection (Morrill Hall), Botany Department, University of Illinois, Urbana, Illinois.

Discussion. *Biscalitheca* presents certain points of close similarity to those of *Etapteris lacattei* (Renault) Bertrand although Mamay (1957) did not regard them as congeneric. We agree with Mamay's treatment, but the sporangia described under these two generic names are so striking in their size, shape, and massive lateral annuli that their close relationship is strongly suggested. Our description of *Biscalitheca musata* affords information on the vegetative parts, and certain features of the vascular anatomy are quite different from the frond parts of *Etapteris lacattei*. In view of the sporangial similarities and anatomical dissimilarities of the fronds of *Biscalitheca* and *E. lacattei*, it seems desirable to summarize the rather confusing nomenclatural history of the sporangia presently referred to *E. lacattei*.

The distinctive features of vascular tissues in the frond axes of *Zygopteris elliptica* and *Z. lacattei* were first described and figured by Renault (1869, pl. 7, figs. 10, 12); Bertrand

EXPLANATION OF PLATE 22

Figs. 1–6. *Biscalitheca musata*. 1, Trace departure from vascular strand of rachis. Slide 1921, $\times 34$, T.S. 2, Vascular strand of primary pinna; adaxial side on right. Slide 1923, $\times 135$, T.S. 3, Soral stalk. Slide 1936, $\times 135$, T.S. 4, Tracheids of soral stalk with scalariform thickenings. Slide 1918, $\times 135$, L.S. 5, Pedicellate sporangium with multistratose wall sectioned through annulus. Slide 1917, $\times 34$, L.S. 6, Primary pinna, right, oblique L.S., ultimate pinna, lower left, soral stalk, upper left, sporangium from soral stalk, middle left. Slide 1945, $\times 34$.



(1909, 1911) later concluded that *Z. elliptica* was a foliar division of *Z. lacattei*, and he substituted the new combination, *Etapteris lacattei*. The identity of *Zygopteris* and *Etapteris* has been demonstrated by Sahni (1932), and reference may be made to the informative study of stem and frond anatomy of *Zygopteris* by Baxter (1952); it is not necessary to review that point here.

In 1876 Renault described as 'fructifications of *Zygopteris*' terminal clusters of sporangia which are about 2.5 mm. long, banana-shaped, and with a massive, multi-seriate annulus running along opposite sides of each sporangium (1876, pl. 1, figs. 1, 2, 2 *bis*, 3). Renault also included a figure of the petiole of *Zygopteris lacattei* (1876, pl. 1, fig. 4), but he did not demonstrate that the sporangia were attached to *Z. lacattei*; Bertrand (1909, 1911) also held the opinion that the sporangia, as originally figured by Renault, were borne by *Etapteris lacattei*, but no evidence of this was presented. The attachment and affinity of this anatomically known, stalked, soral group, therefore, has been inferred.

An additional series of binomials were simultaneously introduced with accompanying illustrations of zygopterid frond compressions by Renault (1876, pl. 1, figs. 12–17), by Grand'Eury (1877) and by Renault and Zeiller (1888, pl. 32, figs. 5–7). Renault (1876, p. 23, text) employs the name *Androstachys* for the fertile frond parts (= *Audrophyllum* on his pl. 1, figs. 14, 15) and *Schizopteris pinnata* Grand'Eury for sterile ones. Grand'Eury (1877, p. 201, text) in turn, employed the binomial, *Schizostachys frondosus* (= *Androstachys frondosus* in his pl. 17, fig. 3). Finally, both the sterile and fertile frond parts were figured under the binomial, *Zygopteris pinnata*, by Renault and Zeiller (1888, pl. 32, figs. 5–7).

Certain points seem to be especially critical in clarifying the nature of this group of fossils in which the taxonomy is hardly less complex than the structure of the sporangium wall. The sporangia of the two suites of fossils (petrifications and compressions) originally figured by Renault (1876) and referred to *Etapteris lacattei* and *Zygopteris pinnata* respectively display the characteristic, massive, lateral annuli suggesting rather strongly that they represent the same genus if not the same species. While the massive annuli are highly distinctive, the lack of details and inconsistencies in subsequent French illustrations render exact comparisons impossible. The sporangia described by Renault on the basis of petrified specimens and compressions are probably closely related to the American *Biscalitheca*; detailed comparisons of sporangial morphology with *Biscalitheca niusata* have been previously made by Mamay (1957).

Further comparisons of *Biscalitheca* may be made with the soral aggregation and soral stalk of *Etapteris lacattei* in addition to the fertile frond compressions of *Zygopteris pinnata* and *Monoscalitheca fasciculata* which are not known anatomically. Terminal, stalked clusters of sporangia were borne by all four taxa, ranging in number from 3–8 in *Etapteris lacattei* to 10–16 in *Monoscalitheca fasciculata*; the range of sporangial number per sorus is more restricted in *Biscalitheca*, and seven is the usual number. The sporangia in all four taxa are pedicellate; however, the soral stalks of *Zygopteris pinnata* are quite short compared to those of *Monoscalitheca* and *Biscalitheca*. Soral stalks in the last two genera attained lengths of 4–5 mm. which are approximately comparable to the maximum lengths attained by their sporangia. The soral stalks of *Biscalitheca* are 0.5–0.7 mm. in diameter compared to 1 mm. in *Monoscalitheca*. In *Etapteris lacattei* the sorus was borne on a small cylindrical axis (Renault 1876, pl. 1, fig. 4 *bis*) with a minute

stele of 12–14 small cells, presumably tracheids, and scattered secretory cells are present in the surrounding ground tissue. These anatomical features seem important because they compare closely with the corresponding soral stalk of *Biscalitheca*. The soral stalk of *Etapteris lacattei* was approximately 1.3×1.8 mm. in a slightly oblique transverse section based on measurements of Renault's illustration. There is, however, no conclusive evidence that the soral stalk figured by Renault and in other publications cited above was borne on a *Zygopteris* frond. Despite regular soral arrangements in *Biscalitheca* and *Etapteris lacattei*, compact sporangial aggregations of both taxa have been encountered (Mamay 1957; specimen 7051, this study; Renault 1896, fig. 8, pl. 31), and in these specimens attachment of soral stalks to the frond was not established. Although the anatomy of the highest orders of frond divisions of *Zygopteris* is not presently known, the differences in the anatomy of foliar members of *Biscalitheca* and *Zygopteris* or *Etapteris* seem to emphasize the difficulty in relating *Biscalitheca* to any previously described zygopterid or in clarifying the possibility of soral attachment of sporangia referred to *Etapteris lacattei*.

The vascular strands of the frond of *Biscalitheca*, except in the soral stalks, exhibit bilateral symmetry, and the rachis and primary pinnae occur in the same plane. The primary pinnae of *Etapteris lacattei* and *E. scotti*, which are on the order of 4–5 mm. in diameter, also possess bilateral symmetry, and both species give rise to two rows of arch-shaped pinna traces. Subsequent changes of the xylary strands of the secondary pinnae are not known. A pair of antennae are present on one face of the xylary strand of the primary pinna of *E. lacattei*, and traces to secondary pinnae arise from a pair of ridges associated with protoxylem on the opposing face. This is distinct from *Biscalitheca* which exhibits no antennae; the abaxial face of the two trace-bearing orders (i.e. rachis and primary pinnae) is more or less flattened.

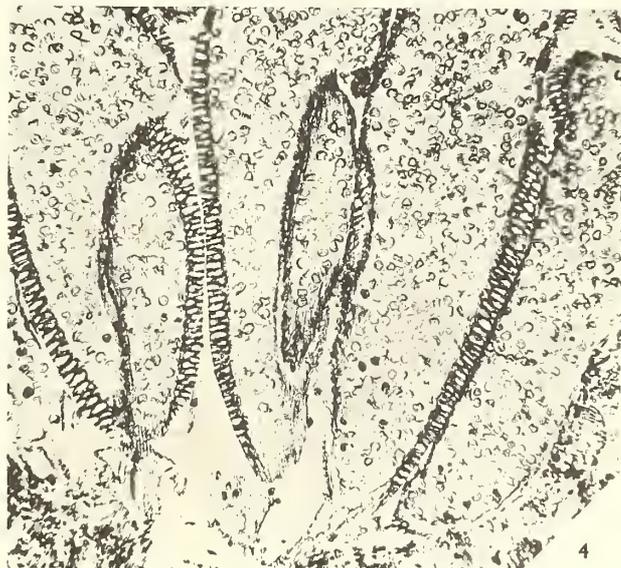
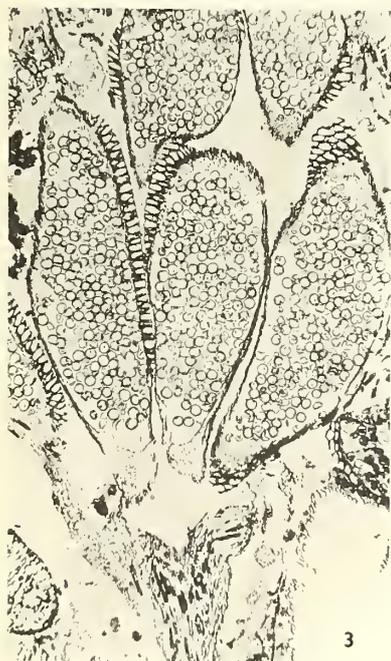
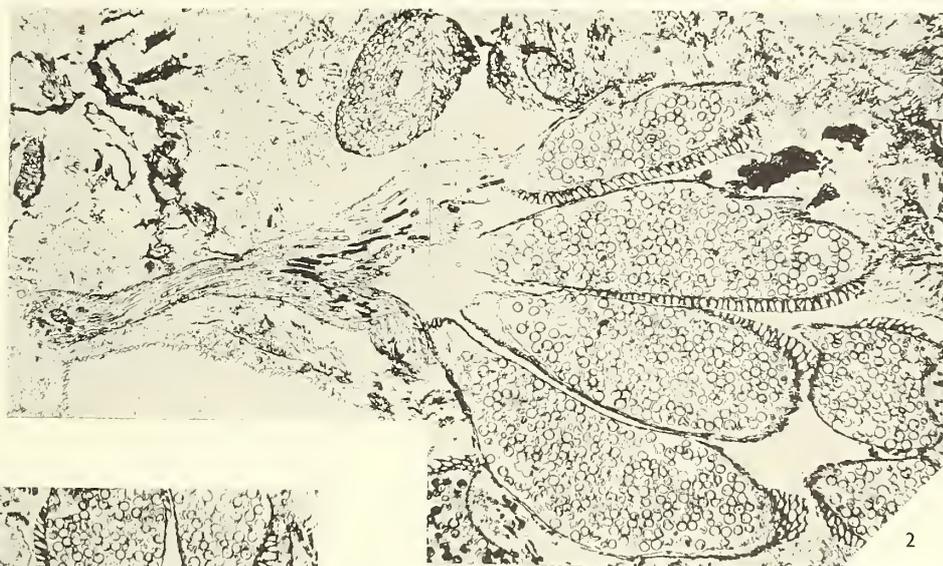
The transverse xylary configuration of the primary pinnae of *E. scotti*, as figured diagrammatically by Bertrand (1909, text-fig. 21), bears some resemblance to that of the primary pinnae of *Biscalitheca* (Pl. 21, fig. 3; Pl. 22, fig. 2). Both types of vascular strands are widest along the abaxial face, and a small peripheral loop-like zone is sometimes formed during trace formation in *Biscalitheca*. The median groove of the abaxial portion of the xylem in *E. scotti* is not evident in *Biscalitheca*. Although there appear to be several similarities in primary pinna strands of *E. scotti* and *Biscalitheca* (the range of zygopterid tracheids includes scalariform thickenings), no close relationship can be suggested. There is no evidence at present that the frond portion of *Biscalitheca*, which we have described, originated from a quadriseriate phyllophore as in *Etapteris*.

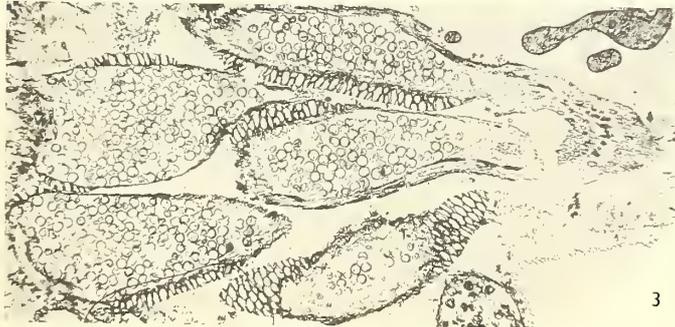
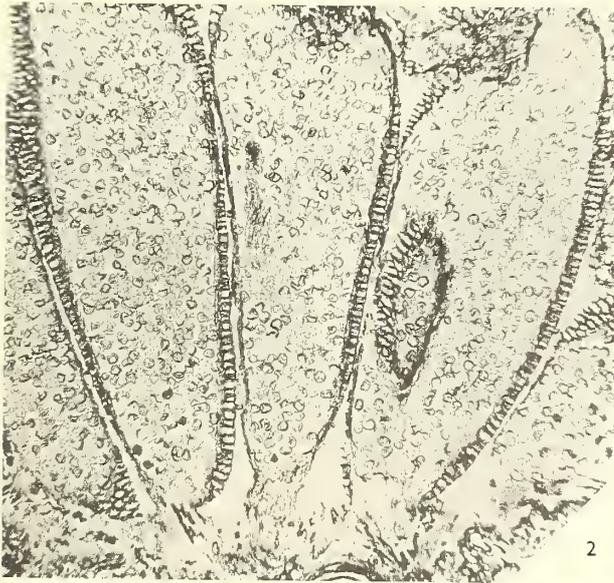
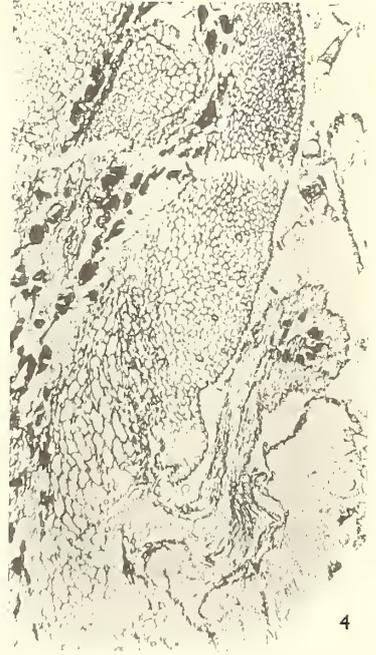
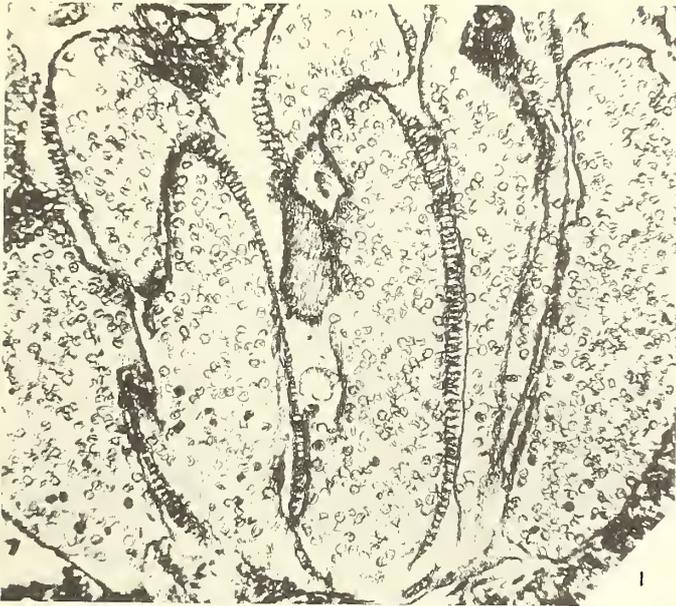
EXPLANATION OF PLATE 23

Figs. 1–4. *Biscalitheca musata*. 1, Primary pinna with stalk of sorus at left. Common trace to soral stalk and ultimate pinna at right. Multicellular outgrowths on adaxial (upward) surface. Slide 1944, $\times 34$, T.S. 2, Sorus and stalk. Slide 1937, $\times 22.5$, L.S. 3, Sorus; see also fig. 2 and plate 24, fig. 3. Slide 1939, $\times 22.5$, L.S. 4, Sorus; see also Plate 24, figs. 1, 2. Slide 1927, $\times 22.5$, L.S.

EXPLANATION OF PLATE 24

Figs. 1–5. *Biscalitheca musata*. 1, Sorus with 7 sporangia, Slide 1925, $\times 22.5$, L.S. 2, Sorus; see also fig. 1, and Plate 23, fig. 4. Slide 1926, $\times 22.5$, L.S. 3, Sorus; see Plate 23, figs. 2, 3. Slide 1941, $\times 22.5$, L.S. 4, Primary pinna with attached soral stalk, at right. Slide 1928, $\times 34$ T.S. 5, Ultimate pinna in proximal region. Slide 1945, $\times 34$, T.S.





The foliar anatomy of *Biscalitheca* appears to be distinct from that of previously described coenopterids. It has been previously pointed out (Phillips and Andrews 1966) that the filicoid foliar member illustrated by Mamay (1957, fig. 12) is similar to *Catenopteris simplex*; however, there is presently no further evidence that *Catenopteris* and *Biscalitheca* may be complementary plant parts. A shallow C-shaped vascular strand occurs in the petiole of *Catenopteris*, tracheidal thickenings are scalariform as in *Biscalitheca* and the two genera are presently known only from the Berryville locality. The distinctive anatomy of the inner cortex of the rachis and primary pinnae of *Biscalitheca* has not been observed in the petiolar bases of *Catenopteris*. The ultimate divisions of the frond of *Biscalitheca* also exhibit a narrow band of tracheids forming a shallow C-shape in cross-section (Pl. 21, fig. 1, upper left) and do not exhibit the distinctive inner cortical anatomy of previous divisions. Multicellular scale-like emergences partially cover the ultimate divisions and occur along the adaxial surface of the rachis and primary pinnae. These have not been observed in *Catenopteris*.

The exact order of division represented by the unattached specimens of *Biscalitheca*, *Monoscalitheca*, and *Zygopteris pinnata* are uncertain. It seems quite probable, however, that the largest frond members, which in each genus are markedly broad, are primary pinnae if not rachises and, on the basis of size and location of sori, that we are comparing similar parts of the three taxa. Grand'Eury (1877) described a rachis fragment of *Zygopteris pinnata* (= *Androstachys frondosus*) about 15 cm. long with primary pinnae having a maximum length of 8 cm. The sori are borne for the most part along one side of the primary divisions, but his figures reveal little in the way of significant details. The orientation of the short-stalked sori of *Z. pinnata* appears to be more or less toward the distal end of the primary pinnae which bear them, and the orientation in *Monoscalitheca* is similar. The sori are about 3 mm. apart in *Monoscalitheca*, and one slightly overlaps the base of the next. According to Abbott (1961): 'The sori are borne almost immediately on the acrostichous or lower side of the branch as the branch leaves its larger axis.' The portion of the recovered frond of *Monoscalitheca* was 6–8 cm. in length with primary divisions attaining lengths up to 6 cm. and about 5 mm. apart. At least 12 cm. of the *Biscalitheca* frond was recovered with primary divisions usually 8.5 mm. apart and lengths of 7.5 cm. attained. *Biscalitheca* exhibits one additional order of division, one which projects out of the plane of the remainder of the frond segment. If the ultimate members of the frond of *Biscalitheca* were removed, an arrangement of sori (i.e. linear on the lower to lateral margins of the primary pinnae) somewhat similar to *Monoscalitheca* and *Zygopteris pinnata* would result. The question may be raised concerning the presence of an additional division in these last two taxa which, if not in the same plane as previous divisions, may not be readily apparent in the splitting of compression specimens.

The similarities of frond size, soral arrangement, and, to a certain extent, the number and arrangement of frond divisions further add to the close comparisons of sporangial morphology among *Biscalitheca*, *Monoscalitheca*, and *Zygopteris pinnata*.

The high degree of specialization evident in well-preserved sporangia of *Biscalitheca* and *Monoscalitheca* is unparalleled among ferns outside of those attributed to the zygopterid group. The sporangia are much more complex than any living free sporangiate types. Although the evidence is indirect, the bulk of information available suggests that the sporangium of *Biscalitheca* developed in a eusporangiate manner; this includes

the massive size of the sporangium, large spore output (8,000 per sporangium), extensive annulus development and the preservation of a wall more than one cell in thickness. The development of an extensive annulus or annuli is exhibited by *Botryopteris globosa*, *Anachoropteris involuta*, and a number of other coenopterids of the late Paleozoic, but none compare closely with the extent and precise annulus orientation of *Biscalitheca* and the presumed sporangia of zygopterid ferns.

Acknowledgements. This research has been financed in large part by the United States National Science Foundation. Support was also provided by the University of Connecticut Research Foundation. We also thank Stanley Jones, Botany Department, the University of Illinois at Urbana, for the preparation of the restoration drawings.

ADDENDUM

Sometime after this study was completed and submitted for publication a new species of the genus, *Biscalitheca kansana*, was described by Cridland (1966). His fossil is a compression specimen and was collected from the Lawrence shale in the Upper Pennsylvanian of eastern Kansas. This horizon is only slightly above the Calhoun coal from which *B. musata* was obtained (Cridland, Morris, and Baxter 1963, p. 63).

The sporangia of *B. kansana* lack the small nests of minute sclerotic cells in their wall; otherwise they appear to be identical with those of *B. musata*. If we are dealing with two species it is evident that they are very closely related. Cridland, of course, receives full credit for discovering the frond, or frond fragment, on which these unique sporangia were borne. It seems interesting and significant that his restorations of a portion of the frond, and the individual sporangial aggregates, are very close to ours, since his study was based on a compression and ours on a coal ball petrification. It is convincing evidence that modern techniques enable us to reach essentially identical conclusions when dealing with a fossil that is preserved in two very different ways. That the two species are closely related is obvious but beyond this our studies have yielded almost wholly different kinds of information. Our study of *B. musata* has been concerned primarily with anatomical features and these in turn have enabled us to deal with certain previously described fossils. Since this in no way duplicates Cridland's contribution it has not seemed necessary to alter our manuscript.

REFERENCES

- ABBOTT, M. L. 1961. A coenopterid fern fructification from the Upper Freeport, No. 7, coal in southeastern Ohio. *J. Paleont.* **35**, 981-5.
- BAXTER, R. W. 1952. The coal-age of Kansas. II. On the relationships among genera *Etapteris*, *Scleropteris* and *Botrychioxylon*. *Amer. J. Bot.* **39**, 263-74.
- BERTRAND, P. 1909. *Études sur la fronde des Zygoptéridées. Text and Atlas*. Lille.
- 1911. Nouvelles remarques sur la fronde des Zygoptéridées. *Mém. Soc. Hist. nat. d'Autun*, **25**, 1-38.
- CRIDLAND, ARTHUR A. 1966. *Biscalitheca kansana* sp. n. (Coenopteridales, Zygopteridaceae), a compression from the Lawrence shale (Upper Pennsylvanian), Kansas, U.S.A. *Amer. J. Bot.* **53**, 987-94.
- MORRIS, JOHN E., and BAXTER, R. W., 1963. The Pennsylvanian plants of Kansas and their stratigraphic significance. *Palaeontographica*, **112B**, 58-92.
- GRAND'EURY, F. C. 1877. Flore carbonifère du département de la Loire et du centre de la France. *Acad. Sci. Inst. France, Mém.* **24**, Text and Atlas, Paris.
- MAMAY, S. H. 1957. *Biscalitheca*, a new genus of Pennsylvanian coenopterids based on its fructification. *Amer. J. Bot.* **44**, 229-39.

- PHILLIPS, T. L. and ANDREWS, H. N. 1966. *Catenopteris simplex* gen. et sp. nov., a primitive pteridophyte from the Upper Pennsylvanian of Illinois. *Bull. Torrey Bot. Club.* **93**, 117–28.
- RENAULT, B. 1869. Étude sur quelques végétaux silicifiés d'Autun. *Ann. Sci. nat., Bot.* **XII**, **5**.
- 1876. Recherches sur la fructification de quelques végétaux provenant des gisements silicifiés d'Autun et de Saint-Étienne. *Ibid.* **VI**, **3**, 5–29.
- 1896. Études des Gîtes Minéraux de la France. Bassin Houiller et Permien d'Autun et d'Épinac. **4**, Text and Atlas. Paris.
- and ZEILLER, R. 1888. Études sur le terrain houiller de Commentry, flore fossile, pt. 1. *Bull. Soc. Industrie minière*, **2**, Text and Atlas, Saint-Étienne.
- SAHNI, B. 1932. On the structure of *Zygopteris primaria* (Cotta) and on the relations between the genera *Zygopteris*, *Etapteris* and *Botrychioxylon*. *Phil. Trans. Roy. Soc., London*, **222B**, 29–46.

TOM L. PHILLIPS,
 Department of Botany,
 University of Illinois,
 Urbana, Illinois 61801,
 U.S.A.

HENRY N. ANDREWS,
 Department of Botany
 University of Connecticut,
 Storrs, Connecticut 06268,
 U.S.A.

Manuscript received 20 September 1966

A TOURNAISIAN SPORE FLORA FROM THE CEMENTSTONE GROUP OF AYRSHIRE, SCOTLAND

by H. J. SULLIVAN

ABSTRACT. A well-preserved spore flora containing elements diagnostic of a Tournaisian age has been obtained from a horizon approximately 100 ft. above the base of the Cementstone Group in Ayrshire. A total of twenty-two species of spores have been recognized in the assemblage; of these, eight are new. Comparison with assemblages from other parts of the world has indicated regional variations in the composition of the Tournaisian spore floras.

THE oldest Carboniferous sediments in the Midland Valley of Scotland are assigned to the Cementstone Group of the Calciferous Sandstone Measures (MacGregor 1960). The sequence consists of thin argillaceous dolomites ('cementstones') interbedded with grey to green shales and mudstones. Films of gypsum, halite pseudomorphs, and mud cracks which are present on many of the bedding surfaces are evidence of the arid environment under which these sediments were laid down. The nodular development and unfossiliferous nature of the cementstones favour the view that much of the material was chemically precipitated from hypersaline waters. The Cementstone Group displays considerable lateral variation in thickness and lithology; for details, see MacGregor (1930, pp. 491-4), George (1958, pp. 304-9), Francis in Craig (1965, pp. 311-17). At many localities, the Cementstone Group succeeds the Upper Old Red Sandstone with apparent conformity. The change from the red sandstones and concretionstones of the Upper Old Red Sandstone into the shales and cementstones of the Cementstone Group is continuous and transitional, and frequently the lithologies are interbedded in a passage zone between the two formations. The base of the Cementstone Group is drawn at the lowest occurrences of the cementstones.

PREVIOUS RECORDS OF FOSSILS FROM THE CEMENTSTONE GROUP

The lack of diagnostic fossils which are used for the conventional zonal subdivision of Dinantian sequences in Britain and Europe has precluded a reliable palaeontological age determination for the Cementstone Group. The fauna consists of ostracods, entomostracans, inarticulate brachiopods, fish teeth and scales, and lamellibranchs. Plant compressions and petrefactions are also common at many horizons and their distribution is adequately documented (Crookall 1932). Spores have been illustrated and described from fructifications (e.g. Smith 1962*a*, 1962*b*; Alvin 1965). Knox (1959, p. 92) has also recorded the presence of fourteen genera of dispersed spores in the Calciferous Sandstone Measures which was penetrated in an unspecified borehole in Dumfriesshire. The palynological data so far published have little stratigraphical application.

Marine limestones are intercalated with cementstones in the lower part of the Cementstone Group at Randerstone, Fife (Kirkby 1902). The faunas had been dated as Tour-

naisian in age by comparison with the occurrences in northern England. George (1958) has challenged the validity of this age determination (and also the evidence of conformable contact between the Cementstone Group and the Upper Old Red Sandstone) and has suggested the faunas at Randerstone may be of Viséan age. He concludes (p. 304): 'The precise age of the oldest Carboniferous sediments remains unproved. On the evidence of the earliest goniatite beds, and on general palaeogeographical grounds of comparison with the developments in Ulster and Northumbria, it is not likely to be greater than latest Caninian or perhaps Seminulan.'

LOCATION AND PREPARATION OF THE SAMPLES

The sample of cementstone was collected by Dr. E. C. Freshney from a horizon approximately 100 ft. above the base of the Cementstone Group in Bracken Bay, Heads of Ayr, Ayrshire (Grid ref.: 2830 1860). The location of the sample is shown in text-fig. 1.

The cementstone was first treated with hydrochloric acid and then with hydrofluoric acid. The residue was oxidized with Schulze Solution for 10 minutes and washed with 5% caustic potash and distilled water.

The slides containing the holotypes and all illustrated specimens have been deposited in the collection of the Research Centre, Pan American Petroleum Corporation, Tulsa. The slides are identified with a preparation number and the coordinates are those of a Leitz Ortholux microscope (No. 618559).

SYSTEMATIC DESCRIPTIONS

Anteturma SPORITES H. Potonié 1893

Turma TRILETES (Reinsch) Potonié and Kremp 1954

Subturma AZONOTRILETES Luber 1935

Infraturma APICULATI (Bennie and Kidston) R. Potonié 1956

Genus BACULATISPORITES Thomson and Pflug 1953

Type species. *B. primarius* (Wolff) Thomson and Pflug 1953.

Baculatisporites fusticulus sp. nov.

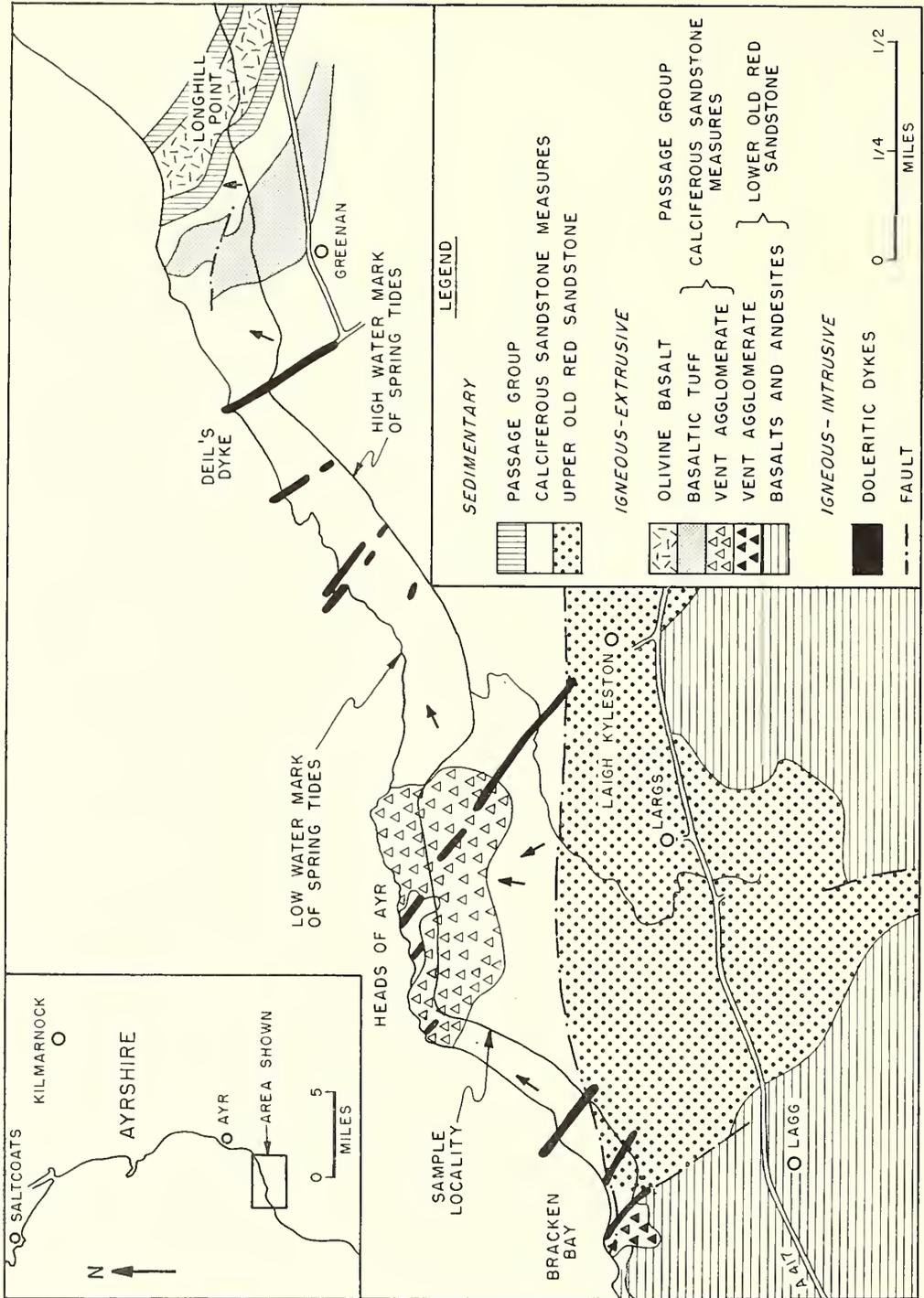
Plate 25, figs. 1, 2

Holotype. Slide P26381-A-04, 115·0 53·0. Size 86 μ .

Diagnosis. Size 73–100 μ , mean 89 μ (34 specimens); amb oval to circular; exine 1·5–2 μ thick, ornamented with bacula and pila up to 1 μ high and 0·7 μ wide.

Description. Amb circular to oval, may be irregular due to presence of secondary folds. Trilete mark visible to indistinct, rays exceed half radius of spore, simple and slightly sinuous. Exine yellow in colour, 1·5–2 μ thick. Ornamentation consists of bacula and pila which are of uniform size and comprehensively distributed. Elements are up to 1 μ high, 0·5–0·7 μ wide and 1–2 μ apart. Occasionally the ornament may be absent from a narrow zone bordering the rays. Secondary folds common.

Remarks. The spores described above cannot conveniently be accommodated in any known Palaeozoic genus. The elements are of a different shape to those in *Cyclogranisporites*



TEXT-FIG. 1. Geological map of the Heads of Ayr region (after Bassett 1958) showing location of sample.

Potonié and Kremp 1954, and are considerably smaller than the bacula in *Raistrickia* Schopf, Wilson and Bentall 1944. The ornament in *Bullatisporites* Allen 1965 is exclusively pilose.

Genus PUSTULATISPORITES Potonié and Kremp 1954

Type species. *P. pustulatus* Potonié and Kremp 1954.

Pustulatisporites gibberosus (Hacquebard) Playford 1964

Plate 25, fig. 3

Remarks. This species occurred rarely in the Cementstone Group assemblage. The specimens agreed closely with the emended description of *P. gibberosus* given by Playford (1964, pp. 18–19).

Previous records. Horton Group (Tournaisian) of eastern Canada (Hacquebard 1957, Playford 1964).

Genus RAISTRICKIA Schopf, Wilson, and Bentall 1944

Type species. *R. grovensis* Schopf in Schopf, Wilson, and Bentall 1944.

Raistrickia clavata Hacquebard emend. Playford 1964

Plate 25, figs. 4, 5

Remarks. A total of 30 specimens of *R. clavata* were identified in the Cementstone Group assemblage. They showed a similar morphological variation to the examples illustrated by Playford (1964, pl. 6, figs. 5–10) from the Horton Group.

Previous records. Horton Group (Tournaisian) of eastern Canada (Hacquebard 1957, Playford 1964).

Raistrickia corynoges sp. nov.

Plate 25, figs. 6–8; text-fig. 2

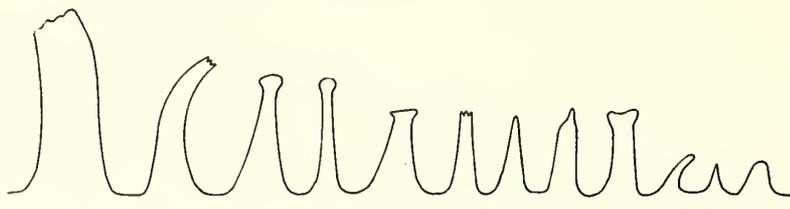
1963 *Acaulotriletes macrurus* (non Lubert and Waltz 1938, p. 30; pl. 7, fig. 94) Kedo, p. 44; pl. III, fig. 58.

Holotype. Slide P26381-A-04, 109·4 45·3. Size, 58 μ .

Diagnosis. Size (excluding ornament) 50–75 μ , mean 64 μ (44 specimens); amb circular to oval; exine ornamented with bacula, coni and verrucae; equatorial elements baculose, up to 15 μ high and 5 μ wide; trilete rays may be obscured by ornamentation.

Description. Amb circular to oval. Trilete mark may be distinct or obscured by ornamentation. Rays extend half to two-thirds radius of spore, straight, vertex high. Exine up to 4 μ thick, yellow to brown in colour. Ornamentation extremely variable in size and shape on any individual specimen. In the spore (Pl. 25, fig. 8), the proximal polar region is ornamented with dispersed broad-based cones and verrucae up to 2 μ high and wide and up to 4 μ apart. Towards the equator, the elements become larger, more densely distributed, and baculose in shape. Equatorial bacula 8–10 μ high and 4–5 μ (rarely 7 μ) wide. The bacula usually have rounded tops; less frequently, the tops are pointed or blunted (text-fig. 2). The distal polar region of the specimen is ornamented with cones

and verrucae which may be discrete or coalescent and up to $4\ \mu$ high and wide. The equatorial elements in the specimen (Pl. 25, fig. 6) are up to $15\ \mu$ high and $3\text{--}5\ \mu$ wide. The distal surface is also covered with bacula but with a few broad based cones among them. The proximal polar region is ornamented with verrucose and spatulate processes up to $4\ \mu$ in height and $8\ \mu$ in width. In the spore (Pl. 25, fig. 7), the elements are dominantly baculose and are connected at the base by low ridges. Secondary folds rare. Spores frequently preserved in off-polar compression.



TEXT-FIG. 2. Profile view of sculptural elements of *Raistrickia corynoges* sp. nov.

Comparison. The species *Acanthotriletes sphaerites* Kedo 1963 (p. 44; pl. 3, fig. 58) is similar to *R. corynoges*, but differs in possessing longer trilete rays, and larger (up to $24\ \mu$ high) and more uniform processes. *Archaeotriletes hamulus* (Naumova 1953, p. 52; pl. 6, fig. 54) from the Middle Frasnian of the Moscow Platform is inadequately described and illustrated, but the ornamentation appears to be of a larger size, more uniform in shape, and less densely distributed than in *R. corynoges*.

Remarks. Kedo's illustration of *Acanthotriletes macrurus* differs considerably from the drawing of Lubert in Lubert and Waltz (1938, 1941) and those of other Russian authors (e.g. Ishchenko 1956, pl. 4, fig. 43; 1958, pl. 2, figs. 28, 29). The photograph given by Playford (1962, pl. 81, fig. 3) is of a specimen similar to the original drawing of Lubert.

Raistrickia sp. described and illustrated by Sullivan (1964, p. 1252, pl. 1, fig. 8) from the Lower Limestone Shales of the Forest of Dean is undoubtedly *R. corynoges*.

Previous records. The Tournaisian (Cherepet horizon) of the Pripyat Basin of eastern Russia (Kedo 1963). Lower Limestone Shales (Tournaisian) of the Forest of Dean, Gloucestershire (Sullivan 1964).

EXPLANATION OF PLATE 25

All figures $\times 650$.

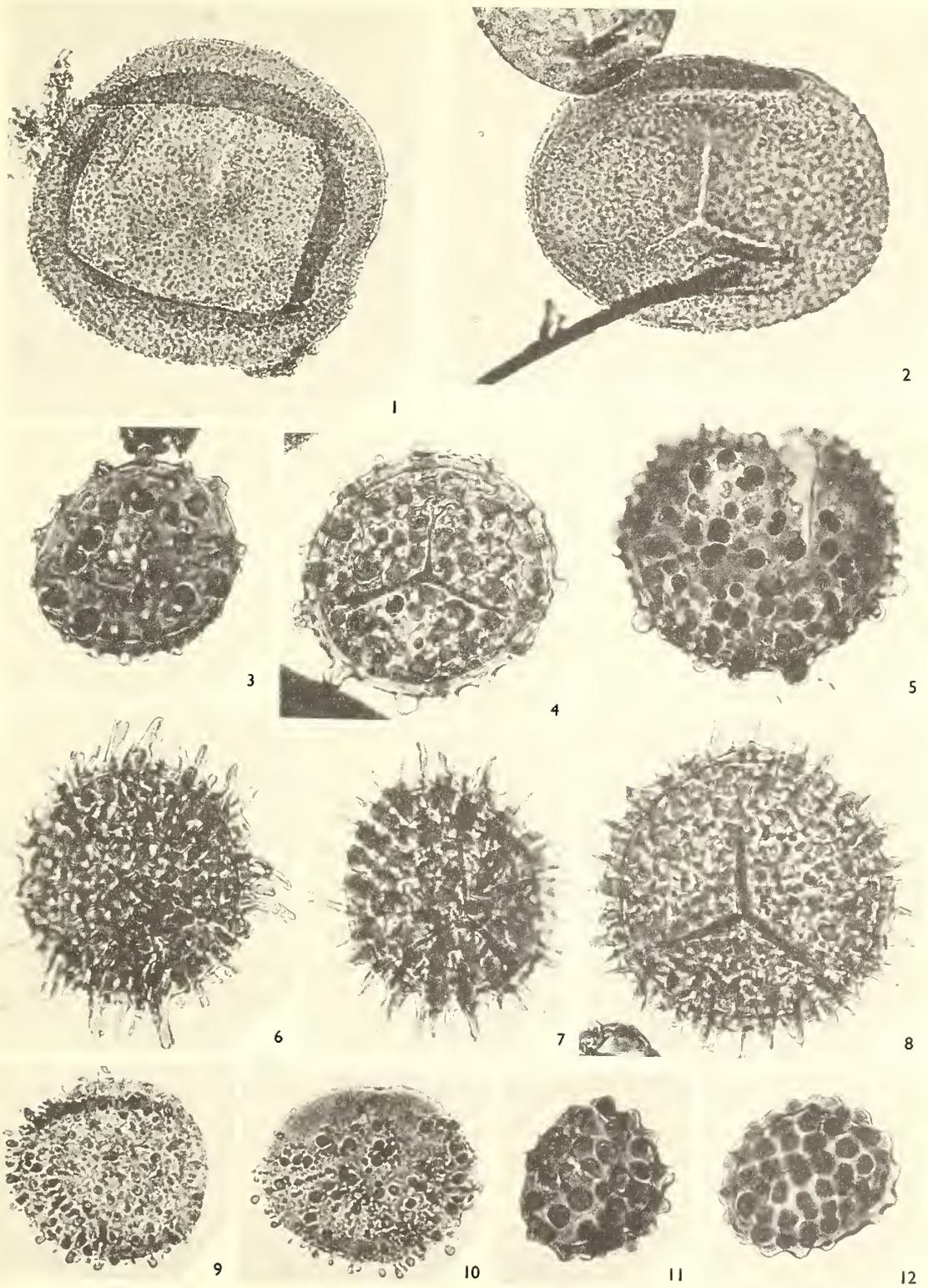
Figs. 1–2. *Baculatisporites fusticulus* sp. nov. 1, Holotype, distal surface, slide P26381-A-04, 115.0 53.0. 2, Proximal surface, slide P26381-A-04, 127.7 30.6.

Fig. 3. *Pustulatisporites gibberosus* (Hacquebard) Playford 1964; distal surface, slide P26381-A-01, 119.6 37.9.

Figs. 4–8. *Raistrickia* spp. 4–5, *Raistrickia clavata* Hacquebard emend. Playford 1964. 4, Proximal surface, slide P26381-A-08, 120.0 40.8. 5, Oblique view, slide P26381-A-08, 109.7 41.5. 6–8, *Raistrickia corynoges* sp. nov. 6, Holotype, distal surface, slide P26381-A-04, 109.4 45.3. 7, Proximal surface, slide P26381-A-03, 123.6 43.2. 8, Proximal surface, slide P26381-A-01, 118.8 40.4.

Figs. 9–10. *Schopfites claviger* sp. nov. 9, Holotype, ? distal surface, slide P26381-A-03, 125.0 26.5. 10, Oblique view, slide P26381-A-02, 125.2 57.3.

Figs. 11–12. *Verrucosisorites scoticus* sp. nov. 11, Holotype, distal surface, slide P26381-A-08, 116.9 43.9. 12, Distal surface, slide P26381-A-03, 123.9 44.5.



SULLIVAN, Scottish Tournaisian miospores

Genus SCHOPFITES Kosanke 1950

Type species. *S. dimorphus* Kosanke 1950.

Schopfites claviger sp. nov.

Plate 25, figs. 9, 10

Holotype. Slide P26381-A-03, 125.0 26.5. Size, 50 μ .

Diagnosis. Size 40–52 μ (excluding ornament), mean 47 μ (28 specimens); trilete rays not observed; exine ornamented with clava and bacula up to 4 μ high and 3 μ wide; portion of exine without ornamentation.

Description. Amb circular to oval. Trilete rays not observed. Exine thin, thickness not determinable, finely and densely infrapunctate. Ornamentation consists of clava and bacula, up to 4 μ high and 3 μ wide, which cover between 60–80% of the total exine surface. Parallel-sided compression folds are sometimes located near the equator.

Comparison. *S. augustus* Playford (1964, p. 26, pl. 7, figs. 2–7) is larger (up to 122 μ), has a more pronounced ornamentation and a distinct trilete mark.

Genus VERRUCOSISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *V. verrucosus* (Ibrahim) Ibrahim 1933.

Verrucosisporites scoticus sp. nov.

Plate 25, figs. 11, 12

Holotype. Slide P26381-A-08, 116.9 43.9. Size, 42 μ .

Diagnosis. Size 38–45 μ , mean 42 μ (18 specimens); exine 2–3 μ thick, ornamented with discrete dome-shaped verrucae or mammilate elements, 2–4 μ high, 2–6 μ wide; ornament mainly confined to distal surface.

Description. Amb circular, rounded triangular or oval. Trilete mark distinct to visible, rays straight or gently curved, exceed two-thirds radius of spore. Exine 2–3 μ thick, laevigate, reddish-brown in colour. Exine ornamented with discrete verrucae which usually have rounded tops, only occasionally truncated. In some specimens, the equatorial elements are mammilate. Verrucae 2–4 μ high (excluding exine thickness), 2–6 μ in basal diameter, and 1–4 μ apart. Ornamentation confined mainly to distal and equatorial surfaces. Some elements may be present on the proximal hemisphere where they are usually located at the termini of the rays. The number of elements visible at the outline varies between 14 and 25. Secondary folds are absent.

Comparison. *Pustulatisporites gibberosus* (Hacquebard) Playford 1964 bears a superficial resemblance to *V. scoticus*. It may be differentiated by its more discrete and larger verrucae and by the infragranulate exine.

Verrucosisporites variotuberculatus sp. nov.

Plate 26, figs. 1–4

Holotype. Slide P26381-A-01, 114.7 38.3. Size, 64 μ .

Diagnosis. Size 57–90 μ , mean 72 μ (45 specimens); amb circular to oval; trilete rays half to two-thirds radius; exine 4–10 μ thick, verrucae 1–3 μ high and 2–10 μ wide, reduced in size towards proximal pole.

Description. Amb circular to oval. Trilete mark distinct, sometimes gaping, rays extend one-half to two-thirds radius of spore. Exine 4–10 μ thick; thickness constant in any single specimen. Exine ornamented with low, dome-shaped verrucae 1–3 μ high (excluding exine thickness), surface smooth to irregularly pitted (corrosion?). Verrucae are polygonal in basal view (usually irregularly pentagonal), rarely circular, and are 4–10 μ wide. Elements are separated by narrow, stripe-like channels which form a discontinuous negative reticulum. Characteristically, there is a reduction in size of the ornament in the region of the proximal pole (Pl. 26, figs. 1, 2, 4). Secondary folds are absent.

Comparison. *V. congestus* Playford 1964 and *Convolutispora stigmoidea* Bharadwaj and Venkatachala 1962 can easily be differentiated from *V. variotuberculatus* by the fact that there is no reduction in the size of the verrucae at the proximal pole. *V. grumosus* (Naumova) Sullivan 1964 resembles *V. variotuberculatus*, but is smaller in size (up to 70 μ), has a thinner exine and a less distinct trilete mark.

Infraturma MURORNATI Potonié and Kremp 1954

Genus CONVOLUTISPORA Hoffmeister, Staplin, and Malloy 1955

Type species. *C. florida* Hoffmeister, Staplin, and Malloy 1955.

Convolutispora cf. *mellita* Hoffmeister, Staplin, and Malloy 1955

Plate 26, figs. 5–7

Description. Size 60–95 μ , mean 81 μ (40 specimens). Amb circular to oval. Trilete mark distinct, but may be obscured by ornamentation, rays exceed half radius of spore, straight to slightly curved. Exine 6–8 μ thick, ornamented with broad, low anastomosing ridges which rarely exceed 2 μ in height (excluding exine thickness) and 8 μ in width. Lumina are of two kinds: one set is circular to oval in shape and up to 4 μ in the longest diameter, and a second set consists of narrow, irregularly sinuous depressions less than 3 μ wide and up to 25 μ long. Margin smooth to slightly undulating.

Comparison. A detailed examination of the holotype is necessary before it can be established whether the specimens described above are truly conspecific with *C. mellita*.

EXPLANATION OF PLATE 26

All figures $\times 650$.

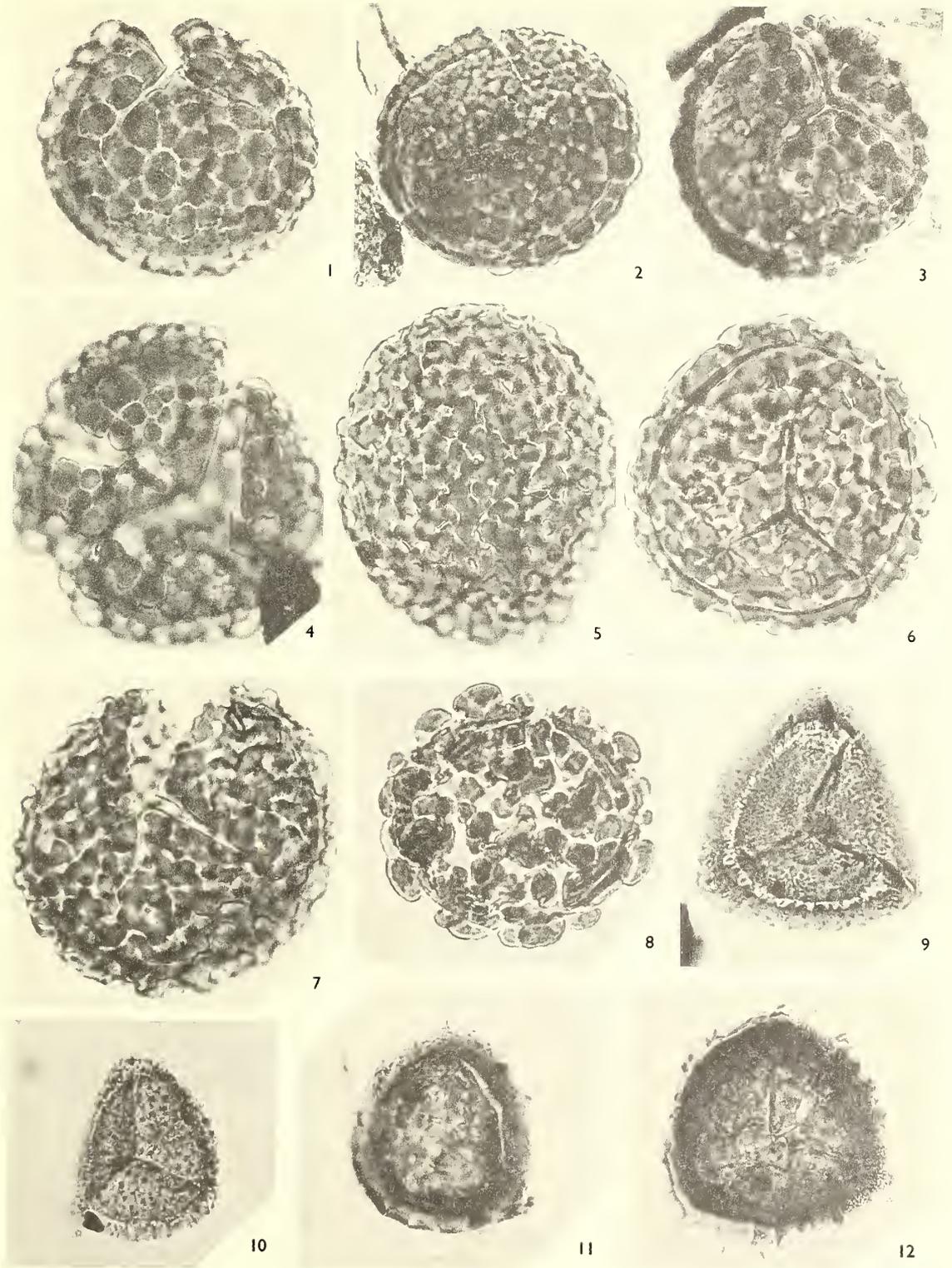
Figs. 1–4. *Verrucosporites variotuberculatus* sp. nov. 1, Semi-oblique view, slide P26381-A-01, 125·0 54·4. 2, Holotype, semi-oblique view, slide P26381-A-01, 114·7 38·3. 3, Proximal surface, slide P26381-A-08, 117·3 43·7. 4, Proximal surface, slide P26381-A-03, 123·8 22·1.

Figs. 5–8. *Convolutispora* spp. 5–7, *Convolutispora* cf. *mellita* Hoffmeister, Staplin, and Malloy 1955. 5, Distal surface, slide P26381-A-08, 120·0 44·2. 6, Proximal surface, slide P26381-A-04, 119·7 28·5. 7, Proximal surface, slide P26381-A-04, 117·9 30·8. 8, *Convolutispora* cf. *tuberosa* Winslow 1962. Proximal surface, slide P26381-A-02, 124·3 43·3.

Fig. 9. *Vallatisporites vallatus* Hacquebard 1957. Proximal surface, slide P26381-A-03, 116·0 39·2.

Fig. 10. *Lycospora torulosa* Hacquebard 1957. Proximal surface, slide P26381-A-02, 122·6 22·4.

Fig. 11–12. *Hymenozonotrites?* *hastulus* sp. nov. 11, Proximal surface, slide P26381-A-04, 122·1 50·2. 12, Holotype, proximal surface, slide P26381-A-04, 125·9 52·7.



SULLIVAN, Scottish Tournaisian miospores

The width of the ridges exceed the dimensions quoted by Hoffmeister, Staplin, and Malloy (1955, p. 385), but otherwise they are similar to the published description.

Convolutispora cf. *tuberosa* Winslow 1962

Plate 26, fig. 8

Description. Size 65–72 μ (5 specimens). Amb subcircular. Trilete mark not observed. Exine 2 μ thick, ornamented with verrucae, frequently with expanded tops, up to 6 μ high and 10 μ wide. The verrucae may be fused laterally into broad irregular ridges up to 12 μ long. Bacula up to 2.5 μ high and 4 μ wide are interspersed among the ridges.

Comparison. Winslow (1962, p. 71) stated that the ‘tuberculate ridges’ in *C. tuberosa* tended to lie parallel to the rays. This feature could not be demonstrated in the five specimens examined.

Turma ZONALES (Bennie and Kidston) R. Potonié 1956

Subturma ZONOTRILETES Waltz 1935

Infraturma CINGULATI Potonié and Klaus 1954

Genus LYCOSPORA Schopf, Wilson, and Bentall 1944

Type species. *L. micropapillata* (Wilson and Coe) Schopf, Wilson, and Bentall 1944.

Lycospora torulosa Hacquebard 1957

Plate 26, fig. 10

Remarks. A total of seven specimens were identified from the Cementstone Group assemblage. They agreed closely with the forms described by Hacquebard (1957, p. 312) and Playford (1964, p. 35), from the Horton Group (Tournaisian) of eastern Canada.

Genus VALLATISPORITES Hacquebard 1957

Type species. *V. vallatus* Hacquebard 1957.

Vallatisporites vallatus Hacquebard 1957

Plate 26, fig. 9

Remarks. Only five specimens were observed. For description see Hacquebard (1957, pp. 312–13) and Staplin and Jansonius (1964, p. 112).

Previous records. Horton Group (Tournaisian) of eastern Canada (Hacquebard 1957, Playford 1964). Banff Formation (Tournaisian) of Alberta (Staplin and Jansonius 1964).

Genus KNOXISPORITES (Potonié and Kremp) Neves 1964

Type species. *K. hageni* Potonié and Kremp 1954.

Knoxisporites pristinus sp. nov.

Plate 27, figs. 1–5

Holotype. Slide P26381-A-08, 123.1 48.9. Size, 66 μ .

Diagnosis. Size 62–103 μ , mean 85 μ (63 specimens); distal thickenings ill-defined and

of variable form; cingulum one-fifth to one-seventh of the total radius; rarely preserved in good proximo-distal orientation.

Description. Amb sub-circular, may be irregular due to folding. Trilete rays extend three-quarters radius of spore cavity, usually bifurcating at their termini. Cingulum varies between one-fifth and one-seventh total radius of spore, uniform in thickness, but may be variable in width. Exine thickened on distal surface: thickenings are variable in shape and usually ill-defined. In some cases (e.g. Pl. 27, fig. 5), they are visible only as a slight colour differentiation of the distal exoexine. The thickened bands may extend from the interradial regions of the spore cavity or cingulum and fuse at the distal pole, (Pl. 27, figs. 1, 3). The muri may also enclose a small unthickened circular area near the distal pole (Pl. 27, fig. 2). In other specimens (Pl. 27, fig. 4), there may be a circular thickened band with short interradial extensions. The spores are rarely preserved in good proximo-distal orientation. Compression frequently results in the splitting of the exine and the presence of at least one parallel-sided secondary fold.

Remarks. This species is distinguished from other previously described species of *Knoxisporites* by the ill-defined thickenings and the lack of good proximo-distal orientation.

Subturma PSEUDOSACCITRILETES Richardson 1965
Infraturma INTRORNATI Butterworth and Williams 1958
Genus AURORASPORA Hoffmeister, Staplin and Malloy 1955

Type species. *A. solisortus* Hoffmeister, Staplin, and Malloy 1955.

Auroraspora macra sp. nov.

Plate 27, figs. 6-10

Holotype. Slide P26381-A-04, 120.2 34.6. Size, 49 μ .

Diagnosis. Size 48-68 μ , mean 58 μ (65 specimens); amb subcircular to irregular; exoexine laevigate, intexine laevigate to scabrate; trilete mark exceeds two-thirds radius of spore body.

Description. Amb subcircular, frequently irregular due to folding. Intexine 1.5 μ thick, laevigate to scabrate. Trilete rays straight, simple, extend two-thirds to three-quarters of the radius of the spore body. Exoexine thin, thickness not determinable, often finely folded in an irregular pattern. Exoexine usually pitted and torn (Pl. 27, figs. 9, 10).

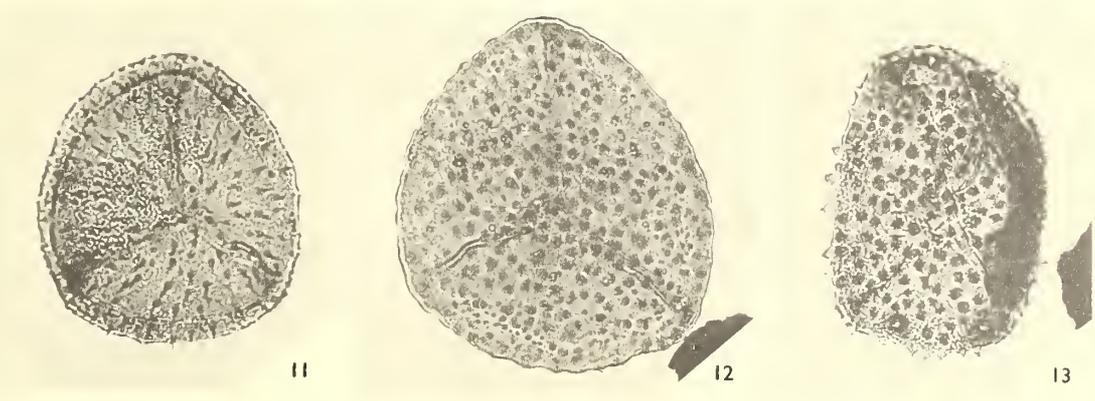
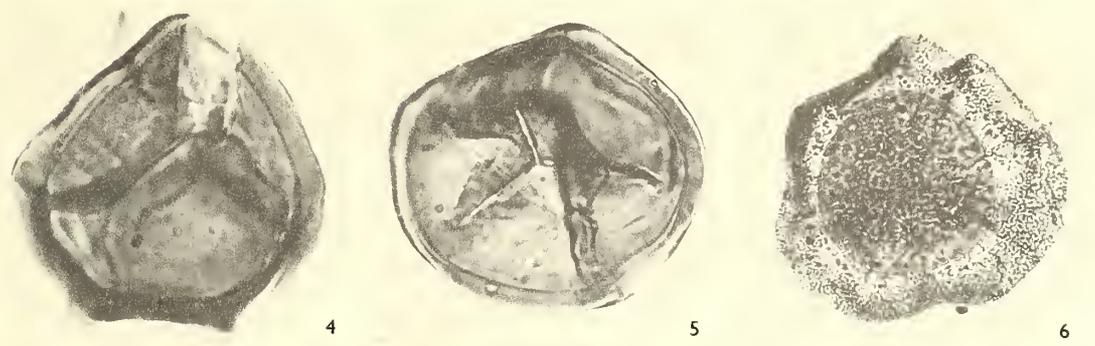
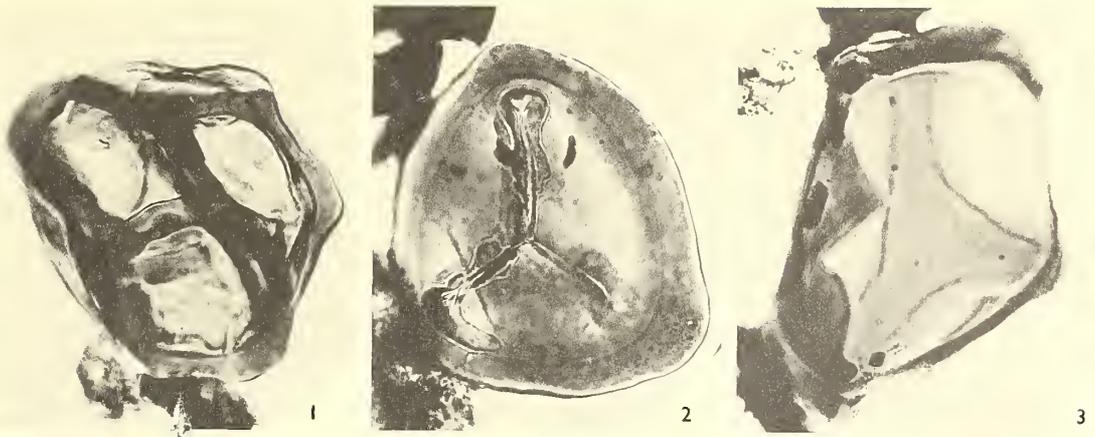
EXPLANATION OF PLATE 27

All figures $\times 650$.

Figs. 1-5. *Knoxisporites pristinus* sp. nov. 1, Distal surface, slide P26381-A-01, 108.8 37.4. 2, Distal surface, slide P26381-A-03, 115.4 56.8. 3, Distal surface, proximal surface missing, slide P26381-A-08, 111.7 38.4. 4, Holotype, distal surface, slide P26381-A-08, 123.1 48.9. 5, Proximal surface, slide P26381-A-03, 114.0 55.3.

Figs. 6-10. *Auroraspora macra* sp. nov. 6, Distal surface, slide P26381-A-03, 114.0 50.0. 7, Holotype, proximal surface, slide P26381-A-04, 120.2 34.6. 8, Proximal surface, slide P26381-A-09, 117.2 42.9. 9, Proximal surface, slide P26381-A-04, 111.2 27.7. 10, Proximal surface, slide P26381-A-01, 112.9 30.9.

Figs. 11-13. *Grandispora echinata* Hacquebard 1957. 11, Distal surface, slide P26381-A-08, 123.3 32.1. 12, Distal surface, slide P26381-A-08, 120.3 36.4. 13, Distal surface, slide P26381-A-01, 118.9 42.0.



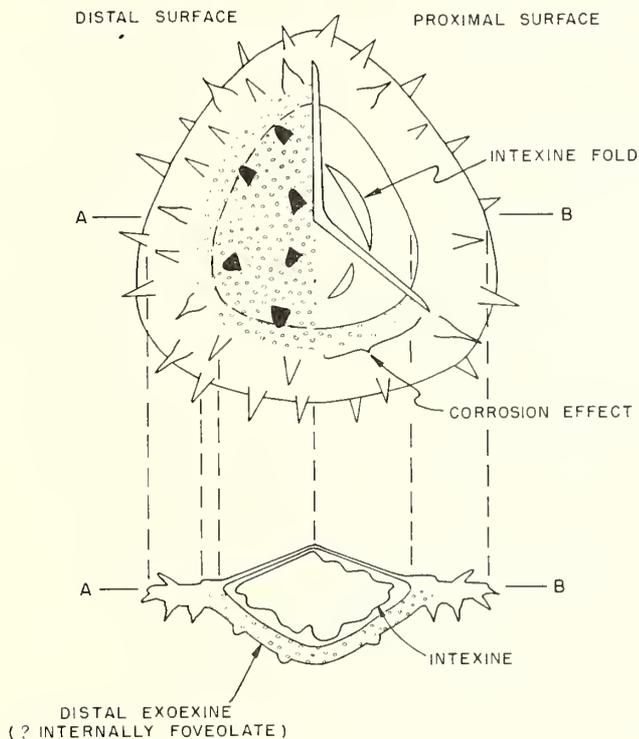
Comparison. *Auroraspora solisortus* is larger (up to 78 μ), has longer trilete rays, and the folds of the exoexine are usually arranged in a radial pattern.

Infraturma EXTRORNATI Butterworth and Williams 1958

Genus HYMENOZONOTRILETES (Naumova 1937?, 1939) Potonié 1958

Type species. *H. polyacanthus* Naumova 1953.

Remarks. The genus *Hymenozonotriletes* as interpreted by Russian palynologists includes species which can be more conveniently assigned to other zonate genera, e.g. *Grandispora* Hoffmeister, Staplin, and Malloy 1955, *Spinozonotriletes* Hacquebard 1957, *Vallatisporites* Hacquebard 1957, *Densosporites* (Berry) Potonié and Kremp 1954, and *Lycospora* Schopf, Wilson, and Bentall 1944. This broad circumscription of *Hymenozonotriletes* is inconsistent with the principles of classification of Potonié and Kremp and, if



TEXT-FIG. 3. Diagrammatic representation of *Hymenozonotriletes?* *hastulus* sp. nov. and its hypothetical cross-section.

it is to be incorporated into this system, a redefinition will be necessary. Such an emendation is not possible at this time because of the doubts concerning the details of structure and exine stratification of the type species, *H. polyacanthus*. The species *H. hastulus* sp. nov. described below is provisionally assigned to *Hymenozonotriletes* since it conforms with the most recent interpretation of the genus (Staplin and Janzonius 1964).

Hymenozonotriletes? hastulus sp. nov.

Plate 26, figs. 11, 12; text-fig. 3

Holotype. Slide P26381-A-04, 125.9 52.7. Size, 58 μ .*Diagnosis.* Size 42–63 μ , mean 54 μ (31 specimens); distal exoexine thickened, infrapunctate (? internally foveolate) sparsely ornamented with cones; cingulum covered with spines up to 9 μ high and 5 μ wide.*Description.* Amb circular to rounded triangular. Trilete rays, when preserved, extend to margin of spore cavity. Rays usually accompanied by folds which may reach on to the cingulum. Intexine thin, laevigate, frequently torn and folded. Distal exoexine thickened beneath spore cavity, finely and densely infrapunctate (? internally foveolate). Proximal exine over spore cavity laevigate. Cingulum one-third to one-half of the total radius; bizonate, dark zone wider than light zone. Cingulum ornamented with prominent solid spines up to 9 μ high and 5 μ wide in basal diameter. Spines may be evenly tapered or may arise from a swollen base. Cones are occasionally present on the distal exoexine beneath the spore cavity. Proximal surface low and pyramidal, distal surface markedly inflated.*Comparison.* In *Hymenozonotriletes? gregarius* Staplin and Jansonius 1964, the proximal as well as the distal exoexine has a prominent structure. The cingulum also has internal vacuoles and the ornament is more variable in shape.*Remarks.* All the specimens examined of *H. ? hastulus* showed evidence of exine damage caused by tearing and corrosion. The infrapunctation of the distal exoexine imparts a spongy appearance to the spores. This may be a surface feature of the exine or may be due to the accentuation, by corrosion, of an internal foveolation.

Genus GRANDISPORA Hoffmeister, Staplin, and Malloy 1955

Type species. *G. spinosa* Hoffmeister, Staplin, and Malloy, 1955.*Grandispora echinata* Hacquebard 1957

Plate 27, figs. 11–13

Description. Size 52–70 μ (1 specimen 80 μ), mean 62 μ (42 specimens). Amb rounded triangular. Trilete rays accompanied by folds which are up to 5 μ high at the apex. Folds extend almost to equator of spore. Intexine thin (less than 1 μ thick), laevigate, frequently folded. Exoexine 1.5 μ thick, often displays an irregular punctation due to corrosion. Ornamentation variable among specimens but generally uniform on individuals. It may consist of spines (Pl. 27, fig. 11), galeae (Pl. 27, fig. 13), or cones (Pl. 27, fig. 12). Ornamentation usually confined to distal exoexine, but may occasionally be present on the equatorial portion of the proximal exoexine. Spines and galeae are up to 5 μ high and 2 μ wide; cones up to 2 μ high and wide with broadly rounded tops.*Remarks.* The shape of the ornament is more variable than in previously described specimens of *G. echinata*.*Previous records.* Horton Group (Tournaisian) of eastern Canada (Hacquebard 1957,

Playford 1964). Laurel Formation of Western Australia (Balme 1960). Upper Sedimentary Group and Lower Limestone Group (Viséan) of the Midland Valley of Scotland (Sullivan and Marshall 1966).

COMPOSITION AND AGE OF THE ASSEMBLAGE

The following twenty-two species were identified in the Cementstone Group spore flora: *Punctatisporites irrasus* Hacquebard 1957, *P. planus* Hacquebard 1957, *P. viriosus* Hacquebard 1957; *Retusotriletes incohatus* Sullivan 1964; *Baculatisporites fusticuhus* sp. nov.; *Pustulatisporites gibberosus* (Hacquebard) Playford 1964; *Raistrickia clavata* Hacquebard emend. Playford 1964, *R. corynoges* sp. nov.; *Schopfites claviger* sp. nov.; *Verrucosisporites scoticus* sp. nov., *V. variotuberculatus* sp. nov.; *Convolutispora* cf. *mellita* Hoffmeister, Staplin and Malloy 1955, *C.* cf. *tuberosa* Winslow 1962; *Reticulatisporites textilis* Balme and Hassell 1962; *Perotriletes magnus* Hughes and Playford 1961; *Lycospora torulosa* Hacquebard 1957; *Vallatisporites vallatus* Hacquebard 1957; *Knoxisporites pristinus* sp. nov.; *Auroraspora macra* sp. nov.; *Endosporites micromanifestus* Hacquebard 1957; *Hymenozonotriletes? hastulus* sp. nov.; *Grandispora echinata* Hacquebard 1957.

The assemblage was dominated by species of *Punctatisporites*. Present in proportions between 5 and 1% were *Retusotriletes incohatus*, *Verrucosisporites variotuberculatus*, *Convolutispora* cf. *mellita*, *Knoxisporites pristinus* and *Auroraspora macra*. The remaining species individually comprised 1% or less of the total.

The assemblage from the Cementstone Group contains eight species whose known occurrences are restricted to rocks of Tournaisian age. *Pustulatisporites gibberosus*, *Raistrickia clavata*, *Vallatisporites vallatus* and *Lycospora torulosa* are present in the Horton Group of eastern Canada (Hacquebard 1957, Playford 1964). *Retusotriletes incohatus* was a dominant element of the assemblages from the Lower Limestone Shales of the Forest of Dean, Gloucestershire (Sullivan 1964), and is also very common in the Tournaisian of the Ardenno-Rhine region of Belgium and Germany. *Raistrickia corynoges* (*Raistrickia* sp. A. of Sullivan 1964) has been recorded from the Tournaisian of the Forest of Dean, the Ardenno-Rhine region and (as *Acanthotriletes macrurus*) from the Pripyat Depression of White Russia (Kedo 1963). Two newly described species, *Baculatisporites fusticuhus* and *Knoxisporites pristinus*, have also been observed in the Lower Limestone Shales in the Cement Works quarry, near Mitcheldean, Forest of Dean (Sullivan, M. S.).

Punctatisporites irrasus, *P. viriosus*, *Endosporites micromanifestus* and *Grandispora echinata* have more extended ranges than the taxa referred to above, but are common constituents of Tournaisian assemblages. Indeed, they were first described by Hacquebard (1957) from the Horton Group of Nova Scotia.

Thus, there is convincing evidence that the assemblage from 100 ft. above the base of the Cementstone Group is of Tournaisian age. It differs markedly in composition from the spore floras described by Sullivan and Marshall (1966) from the Upper Sedimentary Group of the Calciferous Sandstone Measures, which were all of Viséan age. The Tournaisian/Viséan boundary in the western part of the Midland Valley of Scotland would, therefore, lie within the interval between the upper part of the Cementstone Group and the lowermost horizons of the Upper Sedimentary Group. The Clyde

Plateau Lavas, which over much of the region separate the Cementstone Group and the Upper Sedimentary Group, may represent a volcanic episode spanning the Tournaisian/Viséan boundary.

COMPARISON WITH OTHER TOURNAISIAN ASSEMBLAGES

The Cementstone Group spore flora closely resembles the assemblages described by Playford (1964) from the Horton Bluff Formation (the lower of the two divisions of the Horton Group) of eastern Canada. The principal difference would appear to be the greater relative abundance of *Vallatisporites* species and *Lycospora torulosa* in the Canadian assemblages. The Cheverie Formation of the Horton Group has a markedly dissimilar composition from the Horton Bluff Formation. *Vallatisporites* species and *Lycospora torulosa* are absent from the Cheverie Formation, and the most abundant and characteristic species is *Pustulatisporites pretiosus* Playford 1964. No species shown to be restricted to the Cheverie Formation (Playford 1964, Table 1, pp. 38–39) was present in the Cementstone Group.

The Tournaisian spore floras of the Forest of Dean (Sullivan 1964) and the Ardenno-Rhine region (Streel 1966) are very similar. The assemblages are dominated by species of *Punctatisporites* and *Retusotriletes incohatus* and several important accessory spores are common to both areas (Streel 1966, fig. 6).

The Tournaisian spore floras recorded by Winslow (1962) from Ohio display some similarities to those from eastern Canada, Britain, and the Ardenno-Rhine region. The early Kinderhookian assemblages from Ohio contain species of *Vallatisporites* (as *Cirratriradites hystricosus* Winslow, *C. sp. A*, *Lycospora sp. A*), whereas the later ones are characterized by *Punctatisporites? logani* Winslow (a species which resembles *Pustulatisporites pretiosus* in all characters except size). This distribution reflects the differences noted by Playford (1964) between the spore floras from the Horton Bluff and Cheverie Formations. Other taxa reported by Winslow and which may occur in other Tournaisian assemblages are: *Convolutispora tuberosa* Winslow (related to *Verrucosiporites congestus*), *Convolutispora sp.* (similar to *Convolutispora flexuosa* forma *major* Hacquebard), and *Anapiculatisporites tersus* (resembles *Schopfites augustus* Playford).

Two assemblages from the Laurel Formation of north-western Australia have been reported by Balme (1960). Comparison at specific level with spore floras from other areas can only be of a tentative nature since the spores were not formally named and only briefly described. The following characteristic Tournaisian taxa are probably represented in the Laurel Formation: *Vallatisporites* (as *Cingulati* gen. et sp. nov.), *Retusotriletes incohatus* (as *Retusotriletes sp.*) *Punctatisporites irrasus* (as *Punctatisporites B*), *Raistrickia abtrusa* Playford (as *Apiculatisporis sp.*), and *Grandispora echinata* (as *Grandispora cf. G. spinosa*).

The *Rarituberculatus* Assemblage of Tournaisian age from Spitsbergen (Playford 1962, 1963) contrasts markedly with contemporaneous floras from eastern Canada, Britain, and western Europe. The Spitsbergen spore floras contain the following species in abundance: *Punctatisporites glaber* (Naumova) Playford 1962, *Acanthotriletes multisetus* (Luber) Potonié and Kremp 1955, *Tripartites incisotrilobus* (Naumova) Potonié and Kremp 1956, *Anulatisporites anulatus* (Loose) Potonié and Kremp 1954, *A. labiatus* Hughes and Playford 1961, *Densosporites dentatus* Potonié and Kremp 1956, *D. spits-*

bergensis Playford 1963, *D. variomarginatus* Playford 1963, *Lophozonotriletes rarituberculatus* (Luber) Kedo 1957 and *Vallatisporites foveolatus* (Hughes and Playford) Staplin and Jansonius 1964. With the exception of two possible specimens of *Lophozonotriletes rarituberculatus* recorded by Streel (1966) from the Ardenno-Rhine region, none of these species have so far been observed from the Tournaisian of eastern Canada, western Europe, and Britain.

The Tournaisian assemblages described from Russia by Ishchenko (1952, 1956, 1958) and Luber and Waltz (1938, 1941) have a similar composition to the Spitsbergen spore floras.

Species of *Anulatisporites* and *Densosporites* are absent from the Tournaisian spore floras reported by Kedo (1963) from White Russia, but in other respects they are closely comparable to the Russian and Spitsbergen assemblages.

It is proposed to refer to the Tournaisian spore floras of Russia and Spitsbergen as the *Lophozonotriletes* suite because this genus is a particularly characteristic component of the assemblages from these areas.

It is more difficult to select a suitable name for the spore floras of eastern Canada, Britain and the Ardenno-Rhine region. No genus which has both a common and widespread occurrence is at present known to be restricted to the Tournaisian assemblages of these areas. The term *Vallatisporites* suite is provisionally applied because the genus *Vallatisporites* has certainly a greater numerical abundance and a more extended stratigraphical range in the Tournaisian of eastern Canada and western Europe than in Russia or Spitsbergen.

Tournaisian spores have been illustrated from North Africa (Wray 1964, Hemer 1965). However, there are insufficient data currently available to decide whether they belong to either the *Lophozonotriletes* suite or the *Vallatisporites* suite.

Playford (1964, pp. 41–42) has drawn attention to the marked contrast displayed by the Horton Group assemblages from those of Spitsbergen and Russia. He observed: 'The extensive northern floral province, implied by the remarkably similar microfloras of Russia and Spitsbergen . . . , evidently did not encompass eastern Canada. . . .'

Differences in composition of Upper Mississippian (Viséan and Namurian A) spore assemblages have been interpreted by Sullivan (1965) to be the result of a regional differentiation of the parent floras. Three distinctive spore associations were recognized:

1. The *Monilospora* suite—typically present in western Russia, Spitsbergen and western Canada.
2. The *Grandispora* suite—found in Mid-continent United States, eastern Canada and western Europe.
3. The *Kazakhstan* suite—known only from Kazakhstan.

It is apparent that the areas characterized by the *Monilospora* suite in Viséan and Namurian A time are essentially those in which the *Lophozonotriletes* suite is present during the Tournaisian; the *Grandispora* suite, on the other hand, has the same general geographical limits as the *Vallatisporites* suite. One possible exception to this distribution pattern may be the Lower Carboniferous assemblages of Australia. The single Viséan spore flora known from Australia (Venkatachala 1964) appears to belong to the *Monilospora* suite, whereas the Tournaisian assemblages (Balme 1960) have more in common with the *Vallatisporites* suite.

The oldest spore floras described by Luber (1955) from Kazakhstan were from the Ashliarik Series whose age has not been defined more precisely than Tournaisian-Viséan. Until a more accurate age determination is available, there is no means of knowing whether the Kazakhstan suite was recognizable as a separate entity during Tournaisian times.

REFERENCES

- ALLEN, K. C. 1965. Lower and Middle Devonian spores of north and central Vestspitsbergen. *Palaeontology*, **8**, 687-748, 15 pl.
- ALVIN, K. L. 1965. A new fertile lycopod from the Lower Carboniferous of Scotland. *Ibid.* **8**, 281-93, 3 pl.
- BALME, B. E. 1960. Notes on some Carboniferous microfloras from Western Australia. *C.R. 4th Congr. Strat. Geol. Carb., Heerlen* (1958), **1**, 25-31, 2 pl.
- BASSETT, D. A. 1958. Geological excursion guide to the Glasgow district. Geol. Soc. Glasgow, xv+104 pp.
- BUTTERWORTH, M. A. and WILLIAMS, R. W. 1958. The small spore floras of coals in the Limestone Coal Group and Upper Limestone Group of the Lower Carboniferous of Scotland. *Trans. Roy. Soc. Edinb.* **58**, 353-92, 4 pl.
- CRAIG, G. Y. (ed.) 1965. *The Geology of Scotland*. Oliver and Boyd, Edinburgh and London, xv+556 pp.
- CROOKALL, R. 1932. The stratigraphical distribution of British Lower Carboniferous plants. *Summ. Progr. Geol. Surv. Gt. Britain* (1931), **2**, 70-104.
- GEORGE, T. N. 1958. Lower Carboniferous palaeogeography of the British Isles. *Proc. Yorks. geol. Soc.* **31**, 227-318.
- HACQUEBARD, P. A. 1957. Plant spores in coal from the Horton Group (Mississippian) of Nova Scotia. *Micropaleontology*, **3**, 301-24, 3 pl.
- HEMER, D. O. 1965. Application of palynology in Saudi Arabia. *Fifth Arab Petroleum Congress, Cairo* (1965), 1-27, 10 pl.
- HOFFMEISTER, W. S., STAPLIN, F. L., and MALLOY, R. E. 1955. Mississippian plant spores from the Hardinsburg Formation of Illinois and Kentucky. *J. Paleont.* **29**, 372-99, 4 pl.
- ISHCHENKO, A. M. 1956. Spores and pollen of the Lower Carboniferous deposits of the western extension of the Donets Basin. *Akad. nauk Ukrainian S.S.R., Tr. Inst. geol. nauk. Ser. Strat. Paleont.* **11**, 1-185, 20 pl. (in Russian).
- 1958. Sporo-pollen analysis of the Lower Carboniferous sediments of the Dnieper-Donets Basin. *Ibid.* **17**, 1-188, 13 pl. (in Russian).
- KEDO, G. I. 1963. Spores of the Tournaisian stage of the Pripjat Depression and their stratigraphical significance. *Palaeontology and Stratigraphy of the B.S.S.R., Symposium IV, Nauka I tekhnika*, 3-120, 11 pl. (in Russian).
- KIRKBY, J. W. 1902. On Lower Carboniferous strata and fossils from Randerstone, near Crail, Fife. *Trans. Edinb. Geol. Soc.* **8**, 61-75.
- KNOX, E. M. 1959. Some aspects of microspore morphology. *Trans. Bot. Soc. Edinb.* **38**, 89-99, 2 pl.
- LUBER, A. A. and WALTZ, I. E. 1938. Classification and stratigraphical value of the spores of some Carboniferous coal deposits in the U.S.S.R. *Trans. Central Geol. Prosp. Inst.* **105**, 1-45, 10 pl. (in Russian).
- — 1941. Atlas of microspores and pollen grains of the U.S.S.R. *Tr. All-Union Geol. Sci. Res. Inst. (V.S.E.G.E.I.)* **139**, 1-107, 16 pl. (in Russian).
- MACGREGOR, A. G. 1960. Divisions of the Carboniferous on Geological Survey Scottish maps. *Bull. Geol. Surv. Gt. Britain*, **16**, 127-30.
- MACGREGOR, M. 1930. Scottish Carboniferous stratigraphy: an introduction to the study of the Carboniferous rocks of Scotland. *Trans. Geol. Soc. Glasgow*, **18**, 442-558.
- NAUMOVA, S. N. 1953. Spore-pollen complexes of the Upper Devonian of the Russian Platform and their stratigraphic value. *Akad. nauk S.S.S.R. Inst. geol. nauk*, **143**, *Geol. Series*, **60**, 1-203, 19 pl. (in Russian).

- PLAYFORD, G. 1962. Lower Carboniferous microfloras of Spitsbergen—Part One. *Palaeontology*, **5**, 550–618, 10 pl.
- 1963. Idem.—Part Two. *Ibid.* **5**, 619–78, 8 pl.
- 1964. Miospores from the Mississippian Horton Group, eastern Canada. *Bull. Geol. Surv. Canada*, **107**, 1–47, 11 pl.
- POTONÉ, R. and KREMP, G. 1955. Die Sporae dispersae des Ruhrkarbons, ihre Morphographie und Stratigraphie mit Ausblicken auf Arten anderer Gebiete und Zeitabschnitte. Teil I. *Palaeontographica*, **B 98**, 1–136, 16 pl.
- — 1956. Idem.—Teil II, *Ibid.* **B 99**, 85–191, 22 pl.
- SCHOPF, J. M., WILSON, L. R., and BENTALL, R. 1944. An annotated synopsis of Paleozoic fossil spores and the definition of generic groups. *Rept. Inv. Ill. State Geol. Surv.* **91**, 1–72, 3 pl.
- SMITH, D. L. 1962a. The spores of *Alicornopteris lallei* Walton. *Ann. Bot.* n.s. **26**, 267–77, 1 pl.
- 1962b. Three fructifications from the Scottish Lower Carboniferous. *Palaeontology*, **5**, 227–35, 2 pl.
- STAPLIN, F. L. and JANSONIUS, J. 1964. Elucidation of some Paleozoic densospores. *Palaeontographica*, **B 114**, 95–117, 4 pl.
- STREEL, M. 1966. Critères palynologiques pour une stratigraphie détaillée du Tn la dans les Bassins ardenno-rhenans. *Ann. Soc. geol. Belgique*, **89**, 65–96, 2 pl.
- SULLIVAN, H. J. 1964. Miospores from the Lower Limestone Shales (Tournaisian) of the Forest of Dean Basin, Gloucestershire. *C.R. 5th Carb. Congr. Strat. Geol. Carb. Paris* (1963), **3**, 1249–58, 2 pl.
- 1965. Palynological evidence concerning the regional differentiation of Upper Mississippian floras. *Pollen et Spores*, **7**, 539–63, 2 pl.
- and MARSHALL, A. E. 1966. Viséan spores from Scotland. *Micropaleontology*, **12**, 265–85, 4 pl.
- WINSLOW, M. R. 1962. Plant spores and other microfossils from Upper Devonian and Lower Mississippian rocks of Ohio. *U.S. Geol. Surv. Prof. Paper*, **364**, 1–93, 22 pl.
- WRAY, J. L. 1964. Paleozoic palynomorphs from Libya. *Palynology in Oil Exploration, S.E.P.M. Special Publication 11*, 90–96, 1 pl.

HERBERT J. SULLIVAN
Research Center,
Pan American Petroleum Corporation,
P.O. Box 591,
Tulsa, Oklahoma 74102,
U.S.A.

A SINUS-BEARING MONOPLACOPHORAN AND ITS ROLE IN THE CLASSIFICATION OF PRIMITIVE MOLLUSCS

by H. B. ROLLINS and R. L. BATTEN

ABSTRACT. The discovery of symmetrically disposed multiple muscle scars in *Bellerophon acutilira* Hall, a middle Devonian form assigned to the bellerophontoid genus *Sinuitopsis* Perner, indicates that *Sinuitopsis* is a cyclomyan monoplacophoran. Deployment of the muscle scars shows affinity with the cyclomyan genera *Yochelsonellis* (Horný) and *Cyrtolites* Conrad. A ridge-furrow complex is interpreted as a reflection on the inside of the shell of a dorsally situated rectal tract. The presence of a deep anal sinus and notch in *S. acutilira* demands a reconsideration of monoplacophoran-gastropod relationships. Such a sinus or slit can no longer be always considered anterior, and thus, evidence of torsion in fossil archeogastropods. Quite possibly sinus-bearing cyclomyans were the direct ancestors of the primitive archeogastropods (i.e. the Bellerophontina). The use of the sinus as a tool for the recognition of bellerophontids is discouraged in favour of parietal deposits and posterior trains. A posterior anal sinus was probably advantageous in the achievement of maximum separation of respiratory currents and excretory products.

No molluscan group has provided more controversy and speculation than the bellerophontoids (here including the 'true' bellerophontids and the coiled monoplacophorans), with the exception of such enigmatic Cambrian miscellanea as *Matthevia*. Historically, the main problem has been whether or not these bilaterally symmetrical and isostrophically coiled forms were gastropods, i.e. had undergone the process of torsion. Two schools of thought have developed. Wenz (1938), Moore (1952), and others were convinced that the bellerophontoids were untorted forms. Their ideas were based, in part, on recapitulatory concepts of Naef (1913) and others who stated that, since the ontogenetic development of the gastropods clearly show that larval torsion is linked to the assumption of an asymmetrical shell, the same process must have occurred in the phylogeny of the gastropods. Thus, since the bellerophontoids are symmetrical, they did not undergo torsion. This concept was formalized by Simroth (1906), who erected the class Amphigastropoda for the bellerophontoids, and later modified by Thiele (1935). Crofts (1955) has shown in her brilliant studies of *Haliotis* that torsion and asymmetry in fact are separate ontogenetic processes and that torsion itself is a gradational process. In consequence we feel that the original concept of this school is considerably weakened.

The other school, maintained by J. B. Knight (1952), Yonge (1947, 1960), and others, was of the opinion that the bellerophontids had, in fact, undergone torsion. Three lines of evidence were cited. Their most compelling argument was that the bellerophontids possess an anal sinus or slit in the plane of symmetry and such an attribute would have been unnecessary in an untorted form since the mantle cavity with the anus, ctenidia, and associated organs was posterior, posing no threat of fouling. Secondly, bellerophontids possess parietal deposits which could not form if the head were lying beneath the earlier whorls. Finally, the primitive forms have an elongate trail which would impede the manoeuvrability of the protracted head. An additional piece of evidence was described by Knight (1941*b*) when he illustrated, in a restoration of the genus *Knightites*, functional

inhalant siphons on either side of the anal slit, making mandatory the assumption that the mantle cavity lay in an anterior (torted) position.

No fruitful purpose would be served here by undertaking a detailed review of the history of various theories regarding the development of torsion and coiling (but see Knight *et al.* 1960, Ghiselin 1966, Batten, Rollins, and Gould 1967). It is germane to say, however, that we should not eliminate speculation until a living bellerophont is found. Some light can be shed on the problem by examining some new facts that have recently come to light as a by-product of the intense study of the monoplacophorans and bellerophontids, notably by R. Horný of Praha (Horný, 1963-5).

Horný has presented a modified classification of the monoplacophorans based primarily on the shape, distribution, and number of paired muscle scars in relation to the apex. He has suggested that evolution and taxonomic diversity are greater in this group than originally believed. It is interesting to note that those taxa possessing the greatest number of muscle scar pairs are patelliform and morphologically the most primitive, and that the cyclomyans, which are coiled and may have fused lateral muscles, are probably the most advanced and had greater survival value.

In a paper dealing with the bellerophontid classification Horný (1963) described a number of variations in the shapes of sinuses and slits. He alluded to the possibility that these patterns may be useful in classification. In scanning the morphological range through the course of bellerophontid diversification, with Horný's allusion in mind, we have been struck by several rather consistent distributions. Primitive bellerophontids, with some exceptions, have rather shallow sinuses and slits. This has been noted before and at least one evolutionary trend is based on the deepening of the slit through time. However, along with the shallowness of the sinus and slit we have observed that the majority of these primitive forms lack parietal deposits, and in only a few forms, such as *Anconochilus*, is a trail developed which would impede the organism during the protractile stage.

Our contention, evidence for which is cited below, is this: those bellerophontids which possess sinuses or slits, lateral columellar retractor muscles, parietal deposits, posterior trails, platforms, and/or other similar apertural modifications (see Rollins 1966) are true gastropods. Horný (1965a) has constructed the monoplacophoran subclass Cyclomya to include coiled bilaterally symmetrical forms which possess multiple pairs of muscle scars (which may be fused). We would emend his definition to include those forms which, in addition, have a sinus or slit. Primitive bellerophontids similar to *Sinuitopsis*, which have a sinus and no parietal inductura, might well prove to be Monoplacophora. It is possible that a search through the bellerophontid families will reveal more of these sinuate cyclomyans.

On the basis of the discovery of symmetrical, multiple and partially fused muscle scars in sinus-bearing *Sinuitopsis acutilira* (Hall) from middle Devonian rocks, a new interpretation for the origin of the Gastropoda is now possible.

Previously, it had been stated that torsion occurred and then a sinus-slit developed, presumably for sanitary efficiency. Our hypothesis is that the sinus-slit developed *prior* to torsion and only because it did exist when torsion occurred was viability and a positive selective advantage assured.

With the picture just developed, a reasonable conclusion to come to is that the sinuate cyclomyans originated during the Cambrian, gave rise to the true gastropods

and that phylogenetic diversification developed in both groups. However, in reviewing the genera of primitive Gastropoda in the Cambrian through Devonian, we have been forcibly struck by the fact that the Cambrian bellerophontids, for example, are distinct and do not seem to be ancestral or related to later genera. It appears that the Ordovician and Silurian genera are equally unrelated to the Devonian forms.

The phylogenetic picture, as we envisage it, is the development of a sinus in middle Cambrian cyclomyans which in turn were ancestral to the first bellerophontid and pleurotomarian gastropods. Following this Cambrian event, another sinuate cyclomyan group appeared giving rise to the Ordovician and Silurian primitive gastropods. The final iterative phase occurred in the Devonian when yet another sinuate cyclomyan group, or a surviving group, originated gastropod groups which underwent a very rapid period of adaptive radiation. This picture appears more consistent with the fossil record and helps explain the large morphological gaps between families of bellerophontids, but, of course, it does admit a polyphyletic origin of the gastropods. We are advancing this different hypothesis for the origin of some of the primitive gastropods in order to stimulate discussion and further testing. We do not wish, at this time, to discuss the various ideas regarding the origin of the pleurotomarians. We suspect that, rather than being derived from the bellerophontids as Knight (1952) has suggested, they were derived directly from the cyclomyans. Consideration of some of these statements will appear in subsequent papers by the authors.

From the evidence of the reduction of symmetrical multiple paired muscles scars and the development of cyclomyan reduced or fused musculature, we are convinced that there was a concomitant reduction in the associated multiple paired organs. This, coupled with the trend in the cyclomyans for increased coiling, accounts for the confusing convergence upon the bellerophontids.

SYSTEMATIC DESCRIPTION

- Class MONOPLACOPHORA Wenz in Knight 1952
 Subclass CYCLOMYA Horný 1965
 Order CYRTONELLIDA Horný 1963
 Superfamily CYRTOLITACEA S. A. Miller 1889
 Family CYRTOLITIDAE S. A. Miller 1889
 ? Subfamily CYRTOLITINAE S. A. Miller 1889
 Genus SINUITOPSIS Perner 1903

Simuitopsis acutilira (Hall)

Plate 28, figs. 1-8

EXPLANATION OF PLATE 28

Fig. 1-8, *Simuitopsis acutilira* (Hall). 1-2, USNM 156725, dorsal and oblique lateral views showing discrete dorsal pair of muscle scars and partially fused right lateral and right ventral muscle scars $\times 3$. 3, paralectotype AMNH 28470, dorsal view of one of Hall's types showing nature of sinus and notch $\times 4$. 4, AMNH 28469, dorsal view showing muscle scars, 'migration tracks', and ridge-furrow complex $\times 3$. 5, USNM 156723, latex mould of dorsal muscle scar pair and ridge-furrow complex $\times 3.5$. 6, 8, USNM 156722, posterior dorsal and lateral views showing sinus and umbilicus 6, $\times 2$, 8, $\times 3$. 7, USNM 156724, dorsal view showing muscle scar and sinus $\times 4$.



1



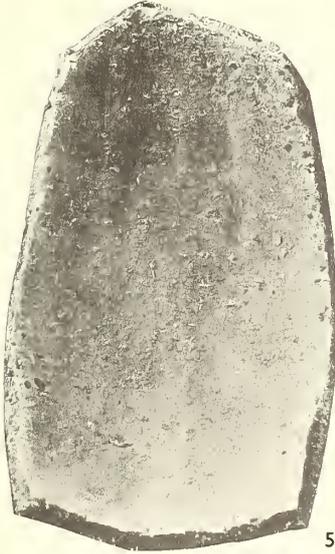
2



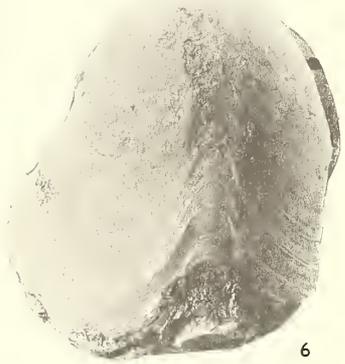
3



4



5



6



7



8

ROLLINS and BATTEN, A sinus-bearing monoplacophoran

1861 *Bellerophon acutilira* Hall, p. 28 (also 1876, Pl. 25, figs. 19–21 and 1879, p. 106, pl. 25, figs. 4–8).

Description. Large symmetrically coiled monoplacophorans with a deep obtusely V-shaped posterior sinus, three pairs of prominent muscle scars arranged in a posterior field, and a possible obscure second anterior field of scars; in main field dorsal pair most distinct, depressed, slightly ovoid in outline, and symmetrically placed anteriorly on either side of medial ridge-furrow complex; lateral scars situated anterior to dorsal scars, elongate in outline, depressed, and often composed of at least two centrally fused parts; lateroventral scars obscure, depressed, slightly anterior to lateral pair, elongate, and may consist of two or more fused parts; possibly secondary anterior field extremely obscure, with variable number of pits or depressions on steinkern, and no distinct positional patterns; growth structures on muscle scars suggested but not clearly defined; 'migration tracks' usually well developed and complex, typically extending posteriorly from margins of main field muscle scars; the medial dorsal ridge-furrow complex extends on steinkerns from a point just posterior to the main field dorsal scars to the apex of the posterior sinus, which is usually reflected on the steinkern as a V-shaped elevated area; rapidly expanding whorls slightly impressed, profile bluntly rounded dorsally, gently convex laterally, but entering the deep open umbilicus with a moderately sharp ventral flexure; aperture rather wide, lateral lips rounded, but not lobe-like; posterior sinus deep and roundly V-shaped terminating in a rounded notch; ornament dominantly collabral, with closely spaced growth-lines often fused into thicker growth increments; faint spiral ornament sometimes visible, primarily on the lateral whorl slopes; parietal and columellar inducturas absent; shell microstructure imperfectly known, apparently a combination of prismatic and lamellar.

Discussion. The type specimens of *S. acutilira* (Hall) bear the locality label, Hamilton Group, Madison County, New York, and are poorly preserved composite moulds, most of them moderately compressed. Nevertheless, there is little doubt that they are conspecific with the individuals from the Pompey member of the Skaneateles formation near Morrisville, New York. The two samples are identical in details of shell morphology, but Hall's specimens are uniformly of smaller size.

In the literature *Simuitopsis* has formerly been reported only from the Ordovician of Bohemia and north-east Asia. Horný (1963) has most recently dealt with the species of *Simuitopsis* and has concluded primarily from the lack of lateral apertural lobes that *Simuitopsis* is indeed quite far removed from the genus *Simuites*, to which it bears a superficial resemblance. At that time, *Simuitopsis* was generally considered a subgenus of *Simuites* (Knight *et al.* 1960).

Although Horný did not find muscle scars on the Bohemian representatives of *Simuitopsis*, the material is reported to be rather poorly preserved and it is probable that future investigations will show the Bohemian species to be monoplacophorans. Perner (1903) reported and figured dorsal nodes in *Simuitopsis nodosa* Perner which, according to Horný, occur sporadically and only in some specimens. Perhaps these nodes are muscle scars. It is significant that the Bohemian species also lack parietal inductura deposits.

S. acutilira (Hall) is very similar in external morphology to the Bohemian species,

S. neglecta Perner, *S. nodosa* Perner, and *S. hornýi* Marek, usually differing only in small details of ornament and degree of circumumbilical angulation.

<i>Measurements.</i>	<i>Total width (mm.)</i>	<i>Total height (mm.)</i>
USNM 156723	17.70	25.00
USNM 156724	17.25*	21.15*
USNM 156725	16.70	20.95*
AMNH 28469	17.40	20.90*
,,	18.75	22.90*
,,	18.80	23.70
,,	20.00*	24.90
,,	16.75*	21.70
,,	20.55	23.45
,,	—	20.10
,,	20.45*	27.55*

* Estimated.

Material. Sixteen specimens from the Pompey member of the Skaneateles formation in central New York State, U.S.A. Fifteen specimens were obtained from exposures along Electric Light Stream, two miles south-west of Morrisville, Madison County, N.Y. One specimen is from Pratts Falls, five miles south of Manlius, Onondaga County, N.Y.

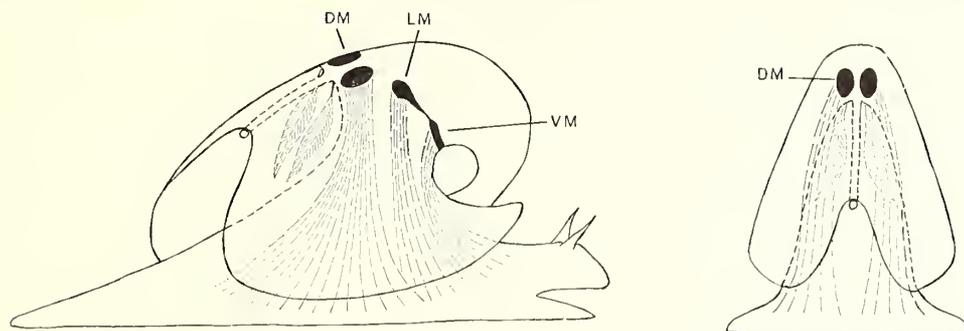
Depositories. American Museum of Natural History, New York, N.Y. (AMNH) and U.S. National Museum, Washington, D.C. (USNM).

ANATOMY AND FUNCTIONAL MORPHOLOGY OF *SINUITOPSIS ACUTILIRA* (HALL)

Muscle-field(s). Symmetrical multiple muscle pairs, of the pattern displayed by *S. acutilira*, have been observed on other planispirally coiled fossil molluscs and have been used as evidence for non-torsion. The occurrence of multiple muscle pairs, coupled with the lack of an anal sinus, has led to the assignment of these closely related lower Palaeozoic molluscs to a specialized subclass of monoplacophorans, the Cyclomya (Horný 1965a). Among the better-known cyclomyans, *Yochelsonellis*, *Cyrtolites*, and *Sinuitopsis*, there is a high degree of similarity in muscle emphasis and position.

In the three cyclomyan genera mentioned above, the dorsal muscle scar pair of the main field is deep and very distinct, suggesting strong retractor muscle emplacements. The other pairs of the main field are always less distinct, often fused, and located laterally or even ventrally on the shell. Functionally, they seem best explained as subsidiary pedal retractors. However, the arrangement of the muscle scars in *S. acutilira* might preclude the possibility that they functioned as pedal retractors. Pedal retractors in gastropods are anchored in the columellar region to provide maximum leverage for rapid retraction or protraction of the foot mass. An alternative functional explanation of these muscle pairs involves their use not as retractors but merely as pedal muscles positioning and drawing the shell down over the head-foot mass. However, the sinuous shape (at least in *Sinuitopsis*), and unexpanded nature of the aperture, coupled with the large planispiral shell and centralized mantle cavity, would make a limpet-like habitat very unlikely in these forms. A third possibility would be the use of the muscle-field solely in

pedal positioning, implying a large protruded foot mass and, possibly, a highly specialized locomotory behaviour. Unfortunately, we are unable at this time to speculate constructively upon the special function of the second less distinct muscle field of the cyclomyans. It is important to note, however, that *S. acutilira* reaffirms a major phylogenetic trend of the cyclomyans, the general reduction and fusion of muscle pairs (Horný 1965b).



TEXT-FIG. 1. Hypothetical reconstruction of *Simuitopsis acutilira* (Hall); lateral (left diagram) and posterior (right diagram) views. Muscle scars in solid black. DM = dorsal retractor muscle scar pair, LM = right lateral retractor muscle scar, VM = right latero-ventral retractor muscle scar.

The relation of multiple muscle pairs to the question of torsion in these forms will be considered in a later section.

Ridge-furrow complex. The dorsal ridge-furrow complex of *Simuitopsis* is not unique to that genus, for a strikingly similar feature occurs in a Bohemian cyclomyan, *Yochelsonellis*. In both genera the complex extends adapically (anteriorly) along a medio-dorsal line, terminating between or immediately posterior to the prominent dorsal muscle scars. The sudden disappearance of the ridge-furrow complex anteriorly probably denotes the extremity of the mantle cavity. Visualization of this feature on the inside of the shell of *Simuitopsis* suggests a medial trough formed by lateral secondary shell deposition, probably resulting from reflection of the mantle over a dorsally situated rectal-hypobranchial gland system.

Steinkerns of *Cyrtolites ornatus* Conrad display an accentuated medio-dorsal angulation on the adult whorl also immediately posterior to the main dorsal muscle scars. Conceivably, this angulation reflects a trough on the inner shell surface with a function analogous to that of *Simuitopsis* and *Yochelsonellis*. Similar furrows or troughs in the presumed position of the anus are known in some gastropod groups (e.g. the euomphalids). Maximum separation within the mantle cavity of the anus and the ctenidia may have been functionally advantageous to the cyclomyans for adequate separation of excretory products and respiratory currents.

Sinus and the question of torsion. One of the most evident and commonly discussed trends in gastropod evolution documents the post-torsional modifications of the mantle cavity for efficient manipulation of respiratory currents and elimination of excretory products. In the Bellerophonacea and Pleurotomariacea, fouling of the inhalant currents was presumably circumvented by the development of an anterior emargination

of the mantle into a sinus or slit, permitting separation of the anus from the immediate region of the head. Presence of a sinus or slit has therefore been interpreted as a primary indication of torsion in fossil archeogastropods.

Prior to the discovery of muscle scars in *Sinuitopsis*, all known cyclomyans were easily distinguished from bellerophonts, for, in addition to symmetrical multiple muscle pairs (considered a pre-torsional character), they lacked a sinus. Quite logically then, they found a taxonomic home within the Class Monoplacophora. The presence of a deep sinus in *Sinuitopsis* emphatically demonstrates the need for reconsideration of the basic anatomical relationships of the Monoplacophora and Gastropoda.

Within the framework of our knowledge of the anatomy of early Monoplacophora and Gastropoda the sinus of *Sinuitopsis* is functionally interpretable as the locus of a recessed anus. We are then immediately tempted to question whether the anus was anterior (post-torsional) or posterior (pre-torsional); i.e. was *Sinuitopsis* a gastropod or a monoplacophoran? If we take the view that *Sinuitopsis* is a bellerophontiform gastropod we can explain the sinus (now anterior) in the conventional manner, a response to the problem of fouling. However, we are then faced with the necessity of explaining the symmetrically placed multiple pairs of muscle scars, a radical departure from the documented bellerophontid muscle arrangement—a single pair of columellar retractors (Knight 1947). All the muscle pairs except perhaps the ventrolateral pair would have to have developed after larval torsion to fulfil some highly specialized function.

On the other hand there exists considerable evidence in support of an untorted anatomical reconstruction of *S. acutilira*. There is a lack of parietal inductural deposits, a feature often (perhaps always) present on bellerophonts and interpreted as an excellent indication of torsion, since they are most logically the result of shell deposition over the posterior portion of the foot. The shell microstructure, although inadequately known, appears to be dominantly prismatic and lamellar, but not crossed lamellar as is the case with known bellerophontid shell structure. Finally, the ridge-furrow complex and especially the muscle scar arrangement are typical of cyclomyans that do not bear a sinus.

Evaluation of the evidence suggests to us a posteriorly situated anal sinus in *S. acutilira*, functionally understandable in terms of the achievement of maximum separation of respiratory currents and excretory products.

TAXONOMIC IMPLICATIONS

The existence of a sinus-bearing monoplacophoran necessitates a reappraisal of the taxobases employed in fossil monoplacophorans and archeogastropods. Evaluation of *S. acutilira* suggests that a sinus (or slit) is not a character developed only in response to torsional problems but may have preceded phylogenetic torsion in those early molluscs. Indeed, if this were the case, the fouling situation concomitant with torsion would not have existed, thus giving the newly tormented form a selective advantage.

Sole reliance upon the presence or absence of a sinus for the differentiation of monoplacophorans and archeogastropods is no longer justified. The definition of the superfamily Bellerophontacea should be modified to reduce emphasis on the sinus in favour of secondary parietal deposits and posterior trains, since the latter seem better indices of torsion. Concurrently, of course, the morphological conception of the Class Mono-

placophora must be expanded to include forms with a posterior sinus. Quite probably certain other sinuitid bellerophontids will be revealed as cyclomyan monoplacophorans by further investigations. Particularly suspect are those bellerophonts possessing neither parietal deposits nor posterior train (e.g. *Owenella*, *Sinuella*, *Gamadiscus*, *Cyrtodiscus*, etc.).

ECOLOGY

Monoplacophoran palaeoecology has been recently studied by Horný (1963), who concluded from an analysis of the associated fauna and the sedimentary environment that both the *Tergomya* and the *Cyclomya* were shallow water benthic groups. *Sinuitopsis acutilira* occurs with a typical near shore molluscan fauna in limestone lenses in a cross-bedded calcareous siltstone. Almost invariably, both umbilici of *S. acutilira* are covered by a bryozoan and it may prove possible to reconstruct the living attitude of this cyclomyan species from a detailed study of the encrusting bryozoan.

SUMMARY

1. *Sinuitopsis acutilira* (Hall) is the first documentation of the genus in North America and the only known occurrence younger than Ordovician.
2. *Sinuitopsis*, because of its monoplacophoran muscle scar pattern, is removed from the Bellerophontina and is assigned to the Cyrtolitidae of the Subclass Cyclomya.
3. The muscle scar pattern in *S. acutilira* is analysed and functional interpretation of it is given.
4. The function and taxonomic significance of a sinus in molluscs is discussed and evaluated.
5. In contradistinction to previous ideas regarding the development of a sinus after torsion, evidence is given to show that a sinus was necessary before viability could be achieved in forms undergoing torsion.
6. A radically different phylogenetic concept of the gastropods is advanced involving the iterative origin of bellerophontids from sinuate cyclomyans.

Acknowledgements. We are indebted to Dr. G. A. Cooper whose extensive Devonian collections at the U.S. National Museum furnished us the bulk of the specimens studied. Thanks are due S. J. Gould, N. Eldredge, and B. Cameron, all of Columbia University, for critically reading the manuscript and aiding in the collection of additional material. Dr. Vera Fretter of the University, Reading, England, made helpful suggestions in interpretation of the reconstructed soft anatomy. We are grateful to R. Morris of Columbia University who kindly prepared the text-figure and R. Adlington of the American Museum of Natural History who photographed the specimens. The authors, however, assume full responsibility for the views and interpretations presented in this paper.

REFERENCES

- BATTEN, R. L., ROLLINS, H. B., and GOULD, S. J. 1967. Comments on 'the adaptive significance of gastropod torsion'. *Evolution*, **21**, 405-6.
- CROFTS, D. R. 1955. Muscle morphogenesis in primitive gastropods and its relation to torsion. *Proc. zool. Soc. London*, **125**, 711-50.
- GHISELIN, M. T. 1966. The adaptive significance of gastropod torsion. *Evolution*, **20**, 337-48.
- HALL, J. 1861. Descriptions of new species of fossils from the Upper Helderberg, Hamilton, and Chemung groups. *Fifteenth Ann. Rpt., Regents of the Univ. of the State of N.Y.* 1862, (D) *Contrib. to Paleont.* 29-80 (advanced pub. 1861).

- HALL, J. 1879. Containing descriptions of the Gastropoda, Pteropoda, and Cephalopoda of the Upper Helderberg, Hamilton, Portage, and Chemung groups. *In Natural History of New York, Paleontology*, Albany, **5**, pt. 2, 1-138, pl. 1-30.
- HORNÝ, R. 1963a. New finds of Silurian Drahomirinae (Monoplacophora) in Bohemia and notes on their ontogeny and bionomy. *Čas. národ. Muz., přírod.* **132**, (2), 79-89.
- 1963b. On the systematic position of Cyrtoneiloids (Mollusca). *Ibid.* **132**, (2), 90-94, 2 pl.
- 1963c. Lower Paleozoic Bellerophonina (Gastropoda) of Bohemia. *Sb. geol. Véd. Paleontologie*, **2**, 57-164, pl. 1-44.
- 1965a. On the systematical position of *Cyrtolites* Conrad, 1838 (Mollusca). *Ibid.* **134**, no. 1, 8-10.
- 1965b. *Cyrtolites* Conrad, 1838 and its position among the Monoplacophora (Mollusca). *Sb. národ. Muz. Praze*, **21**, (2), 57-70, pl. 1-2.
- KNIGHT, J. B. 1941a. Paleozoic gastropod genotypes. *Spec. Pap., geol. Soc. Am.*, **32**, 1-510, figs. 1-32, pl. 1-96.
- 1941b. Physiological significance of paired tubular prominences in bellerophonitids. *In* Moore, R. C., Upper Pennsylvanian gastropods from Kansas. *Bull. St. geol. Surv. Kansas*, **38** (4), 156-61, fig. 7.
- 1947. Bellerophonit muscle scars. *J. Paleont.* **21**, 264-7, pl. 42.
- 1952. Primitive fossil gastropods and their bearing on gastropod classification. *Smithson. Misc. Collus.*, **117** (13), (Pub. 4092), 1-56, pl. 1-2.
- and others. 1960. *Treatise on invertebrate paleontology*. Lawrence, Kansas. **I**, Mollusca 1, 1-351.
- MOORE, R. C., LALICKER, C. G., and FISCHER, A. G. 1952. *Invertebrate fossils*. McGraw-Hill (New York). 1-766.
- MORTON, J. E. and YONGE, C. M. 1964. Classification and structure of the Mollusca. *In* K. M. Wilbur and C. M. Yonge, ed., *Physiology of Mollusca*, **1**, 1-57.
- NAEF, A. 1913. Studien zur generellen Morphologie der Mollusken. I Teil. Über Torsion und Asymmetrie der Gastropoden. *Ergebnisse u. Fortschr. Zool.*, ed. Spengel, **3**, 73-164.
- PERNER, J. 1903. Patellidae et Bellerophonitidae. *In* J. Barrande, *Système Silurien du centre de la Bohême*, **4**, Gasteropodes, tome 1, 1-164, pl. 1-89.
- ROLLINS, H. B. 1966. Morphological observations on the bellerophonit *Ptomatis patulus* (Hall) (Gastropoda, Bellerophonitacea). *Amer. Mus. Novitates*, **2242**, 1-7.
- SIMROTH, H. 1906. Mollusca. *In* H. G. Bronn, *Klassen und Ordnungen des Tier-reichs*, 2nd ed. **3**, 85-89, pl. 59-62.
- THIELE, J. 1935. *Handbuch der systematischen Weichtierkunde*, **2**, Jena, 779-1154.
- WENZ, W. 1938. Gastropoda. Allgemeiner Teil und Prosobranchia. *In* O. H. Schindewolf, ed., *Handbuch der Paläozoologie*, **6**, pt. 1, 1-240.
- YONGE, C. M. 1947. The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Phil. Trans. R. Soc.* **B232**, 443-518.

H. B. ROLLINS
Department of Earth Sciences,
Antioch College,
Yellow Springs, Ohio.

R. L. BATTEN
Department of Fossil Invertebrates
American Museum of Natural History,
New York, U.S.A.

Typescript received 24 November 1966

MARINE-BRACKISH BANDS AND THEIR MICROFAUNA FROM THE LOWER PART OF THE WEALD CLAY OF SUSSEX AND SURREY

by T. I. KILENYI *and* NEIL W. ALLEN

ABSTRACT. A brackish-marine microfauna is described from the lower part of the Weald Clay (*Cypridea tuberculata* Zone) of Sussex. The fauna is dominated by ostracods; eight species are described, one subgenus and three species are new. One species of arenaceous foraminifera, and cirripedes, have also been found. The salinity range of the various species is critically examined and the fauna is compared with other Lower Cretaceous microfaunas outside the Weald.

THE molluscan faunas of the Weald Clay fall into two groups; those dominated by *Viviparus*, normally considered freshwater, and a less common fauna believed to show marine influence. Records of the occurrence of certain brackish/marine molluscs, including *Filosina gregaria* Casey (Worssam 1963, p. 14), *Melanopsis attenuatus* J. de C. Sowerby, *Cassiope* cf. *hujani* (de Verneuil) (Dines and Edmunds 1933, pp. 37–38), *Corbula*, *Nemocardium*, *Ostrea* (Gallois 1965, p. 29) and *Ostrea distorta* (J. de C. Sowerby), indicate that the Weald Clay is not purely freshwater in origin. It has long been suspected that the uppermost Weald Clay represents 'a temporary incursion of the sea before the true Lower Greensand transgression' (Arkell 1947, p. 151) and the occurrence of foraminifera and echinoid spines together with marine molluscs (Casey 1961) indicates that conditions at that time were probably marine.

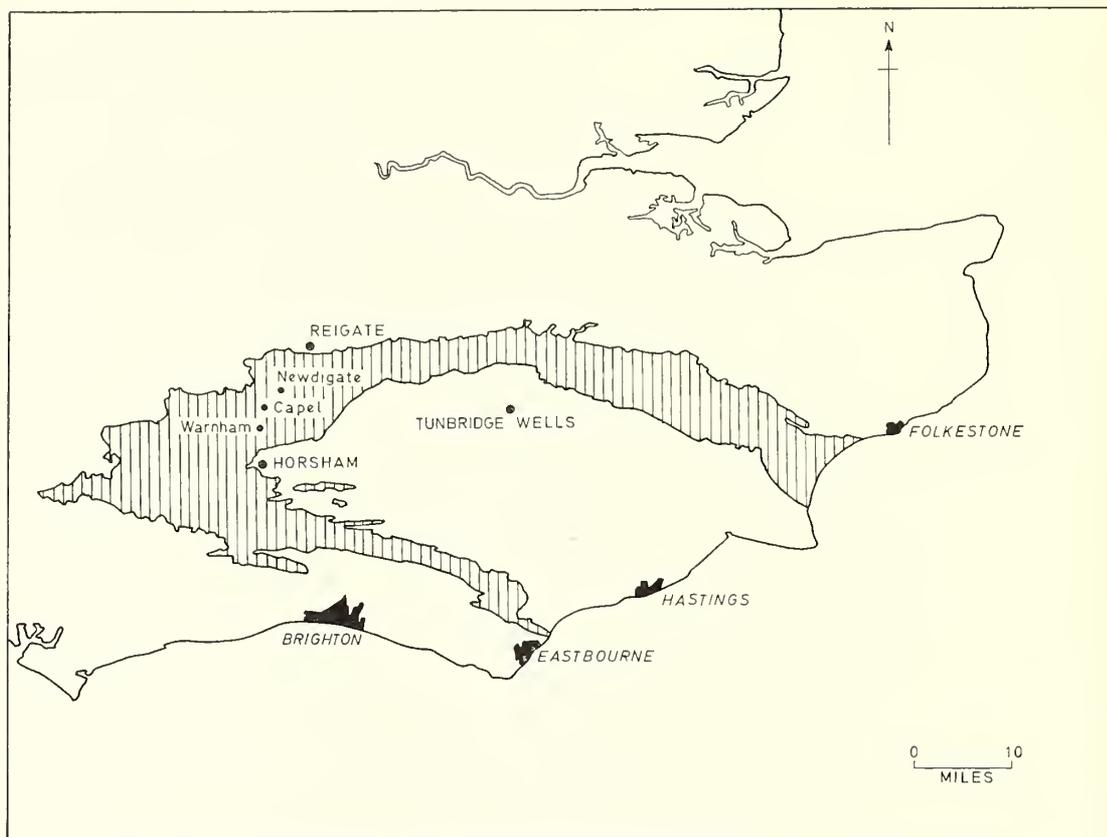
In 1957 Anderson and Casey, besides demonstrating the brackish origin of the highest Weald Clay, indicated that there is a 'marine band, the mid-Weald Clay brackish/marine band, some 400 ft. below the top of the formation' (Anderson and Casey 1957, p. 51) with brackish/marine molluscs, foraminifera, and marine ostracods. In 1963 Anderson (in Worssam 1963, pp. 16–19) gave a list of the ostracods he considered to be 'marine or quasi-marine' and stated that they occur at numerous horizons within the Weald Clay. Allen and Keith (1965) using carbon isotope ratios demonstrated the fluctuations of palaeosalinities in Purbeck and Wealden carbonates.

Worssam (1965, pp. 46–47) indicated that two marine bands had been located in the Weald Clay cores of the Survey's Warlingham borehole, the higher of the two (approx. 1424 ft.) being the mid-Weald Clay marine band and the other (approx. 1446 ft.) 20–25 ft. below it marked by a mudstone with *Cassiope*, *Gervillia*, and *Ostrea*.

In the course of a study of Weald Clay microfaunas, the authors have located certain clay bands crowded with *Cassiope*, *Filosina* and oysters, containing brackish/marine ostracods, foraminifera, and cirripedes. These bands have been found at the Newdigate brick pit (Grid Ref., TQ 205245), the Clock House brick pit near Capel (TQ 176384) and in boreholes from the Warnham brick pit and vicinity (TQ 173345) (text-fig. 1).

The marine horizon at Warnham can be matched quite well with that at Capel both lithologically and palaeontologically. At both places it consists of two beds with *Cassiope* separated by 2 ft. of clay with few ostracods and much lignite (text-fig. 8). We

believe that this Warnham/Capel band is the equivalent of the two marine bands of the Warlingham borehole, with the mid-Weald Clay brackish/marine band (of Anderson and Casey 1957, p. 51) being represented by the upper of the two separate *Cassiopae* bands. The *Cassiopae* band at Newdigate lies above a red clay and therefore cannot be correlated with the Warnham/Capel band. Worssam and Thurrell (1967) suggest that it may represent the upper of the two bands in the Warlingham borehole, i.e. the mid-Weald Clay brackish/marine band. We suggest it is some distance above this band, thus



TEXT-FIG. 1. The outcrop of the Wealden in south-east England with localities worked.

much nearer to the top of the Weald Clay, and that it is not represented in the Warlingham borehole. According to MacDougall (personal communication) the Warnham/Capel band is 280 ft., the Newdigate band 320 ft. above the top of the Horsham Stone.

Acknowledgements. The authors acknowledge the help and advice received from Dr. F. W. Anderson, Mr. J. S. H. Collins, Mr. J. D. S. MacDougall, Dr. J. W. Neale, and Dr. J. E. Prentice. We are grateful to Dr. J. Wolburg for his advice and criticism and many of his ideas were incorporated in text-fig. 3. Mr. H. K. Roberts and Mr. E. C. Burchell assisted in the preparation of the microphotographs. Permission to examine the borehole material from Warnham was received from Mr. M. S. Whitehouse and Mr. R. T. Laird of Redland Bricks. We are grateful for the ready access granted by the London Brick Co. Ltd. to their pit at Clock House, Capel, and to Mr. J. H. Milstead of Woodside Bricks

(Croydon) Ltd. to their pit at Newdigate. N. W. A. acknowledges a research grant from the Natural Environments Research Council.

Abbreviations. In giving dimensions, which are given in millimetres, the following abbreviations are used: L, length; H, height; W, width. The holotypes are deposited in the British Museum (Natural History). Paratypes and the rest of the material are in the collection of the Geology Department, Sir John Cass College, London, and these specimen numbers are prefixed by the index letters SJCC.

SYSTEMATIC DESCRIPTIONS

Subclass OSTRACODA Latreille 1806

Order PODOCOPIDA Müller 1894

Superfamily CYPRIDACEA Baird 1845

Family ILYOCYPRIDIDAE Kaufmann 1900

Rhinoocypris jurassica jurassica (Martin 1940)

Plate 29, figs. 6-7

1940 *Ilyocypris jurassica jurassica* n. ssp. Martin, p. 313, pl. 4, figs. 51-55.

1953 *Ilyocypris jurassica* Martin; Grekoff, p. 376.

1955 *Ilyocypris jurassica jurassica* Martin; Schmidt, p. 52.

1960 *Ilyocypris jurassica jurassica* Martin; Donze, p. 12, pl. 1, figs. 8-11.

1962 *Ilyocypris jurassica jurassica* Martin; Klingler, Malz, and Martin, p. 171, pl. 25, fig. 10.

1963 *Rhinoocypris jurassica jurassica* (Martin); Oertli (1963a), p. 18, pl. 5, figs. 25-27.

1963 *Rhinoocypris jurassica* (Martin); Anderson, p. 16.

Material. Eleven valves and carapaces (SJCC 66/1.1-11).

Dimensions

	L	H	W
Left valve	0.58	0.31	0.14
Right valve	0.54	0.27	0.13

Description. The left valve is larger than the right with slight overlap on all margins. Anterior margin broadly rounded, the posterior margin less so. Dorsal margin straight with a weakly marked anterior cardinal angle, the ventral margin is concave. The ventral and dorsal margins diverge anteriorly, so the carapace is higher anteriorly. The greatest width of the carapace occurs in the inflated posterior region.

The surface of the valve is heavily punctate and finely spinose. From the dorsal margin two narrow sulci extend to the centre of each valve, one of them arises mid-dorsally and produces a deeper, rounded sulcus in the centre of the valve. The other lateral sulcus is in the anterior of the valve and is less extended ventrally. On the anterior margin of each sulcus is a rounded tubercle. Internal view of the valve shows the tubercles to be hollow and the sulci appear as ridges.

Hinge structure could not be seen as the carapaces were partially pyritized, and the muscle scars were obliterated by mineralization. Probably the central sulcus acted as a boss for muscle attachment.

The inner lamella is rather wide anteriorly and postero-ventrally. Selvage is poorly developed and there are several weak lists developed. A narrow vestibulum occurs anteriorly.

Occurrence. From Newdigate in and vicinity of the 'marine band'.

Family CYPRIDIDAE Baird 1845

'*Cypris*' *henfieldensis* Anderson 1939

Plate 29, figs. 11–12

- 1885 ? *Cypris purbeckensis* Jones (part.), pl. 9, fig. 2.
 1939 *Cypris henfieldensis* Anderson, pp. 307–8, pl. 12, figs. 9a–b.
 1953 *Neocytheridea henfieldensis* (Anderson); Grekoff, p. 377.
 1956 '*Cythereis*' *henfieldensis* (Anderson); Anderson, p. 54.
 1963 '*Cypris*' *henfieldensis* (Anderson); Anderson, pp. 16–19.

Material. 2029 valves (SJCC 66/2.1–2029).

Average dimensions

	L	H	W
Left valve	0.86	0.48	0.16
Right valve	0.83	0.46	0.15

Diagnosis. A smooth valved, sub-reniform ostracod of the subfamily *Cypridinae*. Posterior margin is broadly pointed ventrally. Left valve slightly larger than right, overlapping it slightly along the ventral margin and at the anterior cardinal angle. Hinge simple, a fine ridge on the right valve fits into a corresponding groove on the left. Inner lamella wide, with a narrow fused portion and a wide free portion and conspicuous vestibulum at both ends. Muscle scars typical of *Cypridinae*, six scars arranged in two groups.

Remarks. Occurs commonly throughout the Weald Clay but is reduced in numbers in the vicinity of the 'marine bands'.

Superfamily DARWINULACEA Brady and Norman 1889

Family DARWINULIDAE Brady and Norman 1889

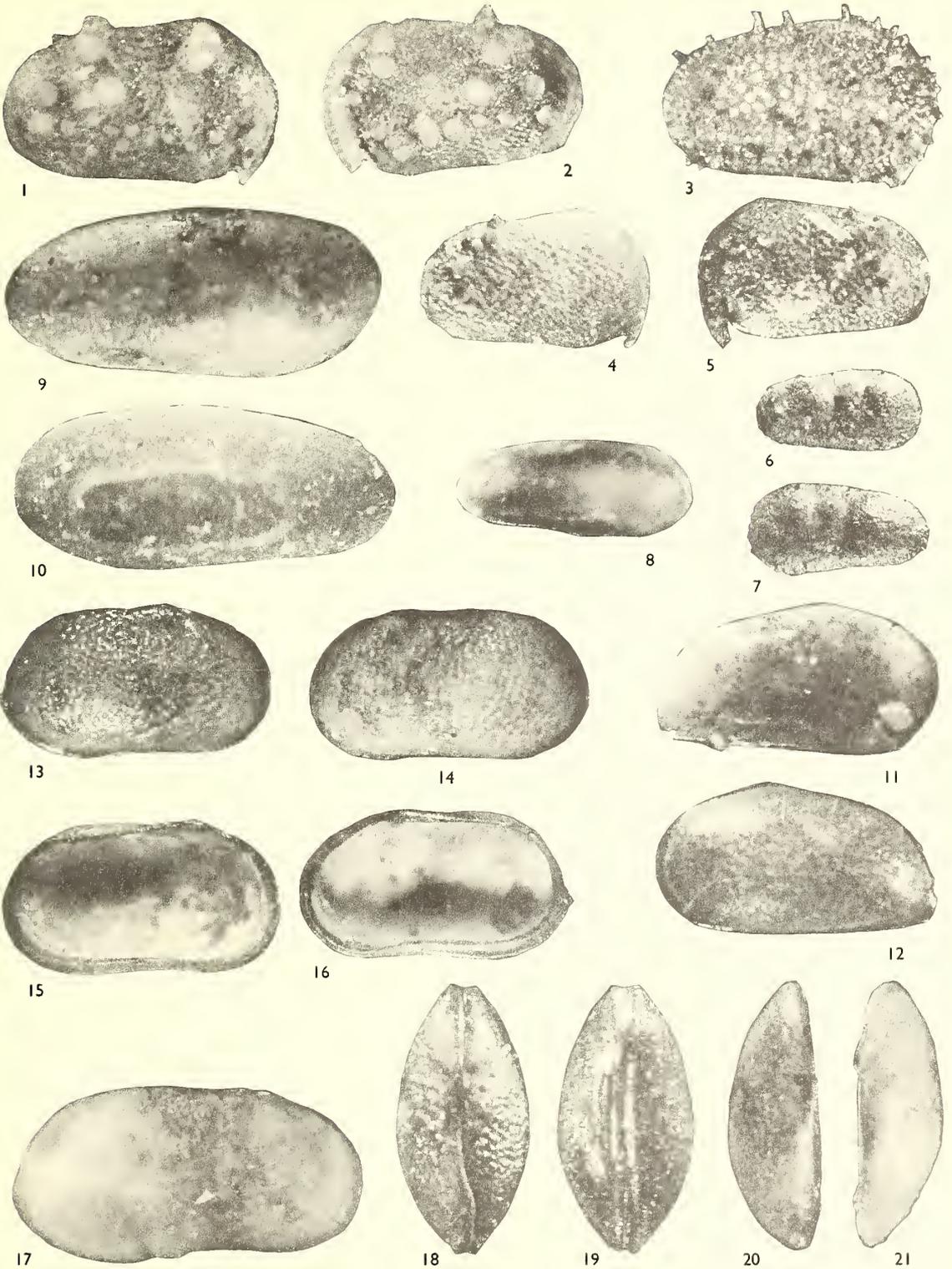
Darwinula leguminella (Forbes 1855)

Plate 29, fig. 8

EXPLANATION OF PLATE 29

All figures $\times 50$.

- Figs. 1–2. *Cypridea marina* Anderson, M. S., Newdigate, Surrey. 1, Right valve, external view, SJCC 66/9.1. 2, Left valve, external view, SJCC 66/9.2.
 Fig. 3. *Cypridea tuberculata* (J. de C. Sowerby), Capel. Right valve, external view, SJCC 66/10.1.
 Figs. 4–5. *Cypridea punila* Anderson, M. S., Clock House pit, Capel. 4, Right valve, external view, SJCC 66/11.1. 5, Left valve, external view, SJCC 66/11.2.
 Figs. 6–7. *Rhinocypris jurassica jurassica* Martin, Newdigate, Surrey. 6, Right valve, external view, SJCC 66/1.1. 7, Left valve, external view, SJCC 66/1.2.
 Fig. 8. *Darwinula leguminella* (Forbes), Warnham, Sussex. Left valve, external view, SJCC 66/3.1.
 Figs. 9–10. *Darwinula oblonga* (Roemer), Newdigate, Surrey. 9, Left valve, external view, SJCC 66/4.1. 10, Right valve, external view, SJCC 66/4.2.
 Figs. 11–12. '*Cypris*' *henfieldensis* Anderson, Newdigate, Surrey. 11, Right valve, external view, SJCC 66/2.1. 12, Left valve, external view, SJCC 66/2.2.
 Figs. 13–21. *Fabanella bononiensis* (Jones), Newdigate, Surrey, and Warnham, Sussex. 13, Female right valve, external view, SJCC 66/5.1. 14, Female left valve, external view, SJCC 66/5.2. 15, Female left valve, internal view, SJCC 66/5.2. 16, Female right valve, internal view, SJCC 66/5.1. 17, Male right valve, external view, SJCC 66/5.3. 18, Female carapace, dorsal view, SJCC 66/5.4. 19, Female carapace, ventral view, SJCC 66/5.6. 20, Female left valve, dorsal view, SJCC 66/5.2. 21, Female right valve, dorsal view, SJCC 66/5.1.



- 1855 *Cypris leguminella* Forbes in Lyell, p. 294, fig. 334c.
 1855 *Darwinula leguminella* (Forbes) Jones, pp. 346–7, pl. 8, figs. 30–31.
 1886 *Darwinula leguminella* (Forbes); Jones, p. 147, pl. 4, figs. 4a–c.
 1888 *Darwinula leguminella* (Forbes); Jones, p. 538.
 1940 *Darwinula leguminella* (Forbes); Martin, p. 317, pl. 4, figs. 58–61.
 1940 *Darwinula* (450) *leguminella* (Forbes); Wicher, p. 268, pl. 2, fig. 8.
 1953 *Darwinula leguminella* (Forbes); Grekoff, p. 376.
 1959 ? *Darwinula leguminella* (Forbes); Zalányi, pp. 425–8, text-figs. 12a–d, 12/a, 13a–c.
 1961 *Darwinula leguminella* (Forbes); Martin (1961b), p. 119, pl. 14, fig. 19.
 1962 *Darwinula leguminella* (Forbes); Klingler, Malz, and Martin, pp. 187–8, pl. 25, fig. 14.
 1963 *Darwinula leguminella* (Forbes); Christensen, pp. 21–23, pl. 2, figs. 2a–c; text-figs. 3, 4b.
 1963 *Darwinula leguminella* (Forbes); Oertli (1963a), p. 20, pl. 6, fig. 40.

Material. 107 valves and carapaces (SJCC 66/3.1–107).

<i>Average dimensions</i>	L	H	W
Carapace	0.77	0.31	0.29

Description. Small, sub-cylindrical carapace. Dorsal margin only very slightly arched, ventral margin slightly concave in anterior half and diverging posteriorly, greatest height in the posterior half of the carapace. Posterior margin smoothly and broadly rounded, anterior more sharply pointed ventrally. In dorsal view the carapace is lanceolate, the posterior region is inflated. The left valve is larger than the right with overlap at all margins, especially ventrally, where there is a knurl in the left valve margin coinciding with the position of greatest concavity. Hinge margin is straight.

Carapace is thin, the surface smooth, often shiny. Muscle scars in the usual rosette arrangement, typical of all species of the genus. Hinge is peculiar in that the smaller (right) valve bears a median groove. It appears that the larger left valve has a median ridge with shallow, elongated sockets anterior and posterior to it. There seem to be no corresponding teeth present on the right valve and it is very likely that the margin of this valve fits into these sockets. The structure of the inner lamella could not be observed.

Occurrence. Common at all three localities, and right through the Weald Clay, much reduced or in cases completely missing in the 'marine bands'.

Remarks. There seems to be some disagreement in the hinge structure as described by Christensen (1963) according to whom the hinge comprises two elements only.

Darwinula oblonga (Roemer 1839)

Plate 29, figs. 9–10

- 1839 *Cypris oblonga* Roemer, p. 52, pl. 20, fig. 21.
 1843 *Cypris oblonga* Roemer; Dunker, p. 39.
 1846 *Cypris oblonga* Roemer; Dunker, p. 60, pl. 13, figs. 26a–b.
 1862 *Cypridea oblonga* (Roemer); Jones, p. 128, pl. 5.
 1940 *Cyprione* (628) *bristovii* Jones; Wicher, p. 268, pl. 2, fig. 7.
 1940 *Cyprione oblonga* (Roemer); Martin, pp. 319–22, pl. 4, figs. 62–63.
 1949 *Cyprione oblonga* (Roemer); Wolburg, p. 353.
 1951 *Cyprione oblonga* (Roemer); Steghaus, p. 209, pl. 14, fig. 8.
 1953 *Darwinula oblonga* (Roemer); Grekoff, p. 376.
 1955 *Cyprione oblonga* (Roemer); Schmidt, p. 53.
 non 1960 *Cyprione oblonga* (Roemer); Neale, p. 214, pl. 1, figs. 6, 8, pl. 3; figs. 9a–b, 11a–b, pl. 4, figs. 1–4.

- 1962 *Darwinula oblonga* (Roemer); Klingler, Malz, and Martin, p. 188, pl. 27, fig. 18.
 1963 *Darwinula oblonga* (Roemer); Christensen, pp. 23–25, pl. 2, figs. 5a–c, text-fig. 4a.
 1963 *Darwinula oblonga* (Roemer); Oertli (1963 a), pp. 20–21.

Material. 149 valves and carapaces (SJCC 66/4.1–149).

Average dimensions

	L	H	W
Carapace	1.11	0.57	0.50

Description. Carapace ovate, oblong to somewhat trapezoidal in shape. Dorsal margin is long and lowly arched; ventral margin slightly concave, the two margins diverge posteriorly. Anterior margin is bluntly pointed ventrally; posterior margin is more broadly rounded with larger angle ventrally than dorsally. Greatest height of carapace is in the posterior region. Carapace is slightly wider in posterior half with posterior end less pointed than the anterior. Left valve is larger than the right with overlap on all margins, but less pronounced at the hinge.

Shell is thin, smooth, and often shiny and transparent with large, prominent, sub-central muscle scars arranged in the pattern of a rosette, with a small antennal scar in front of and ventral to the main group. The faintly visible normal pore canals are widely spaced.

The hinge consists in the left valve of a long narrow groove with an anterior shallow socket. The margin of the right valve fits into the groove and a low tooth is produced anteriorly. The hinge line is very long with the anterior elements occurring about 10% of the valve length from the anterior.

The inner lamella is very narrow, noticeable only at the anterior and posterior margins and completely fused with the outer lamella. About fifteen thin, short, and straight radial pore canals occur anteriorly, and about twenty-five at the posterior.

Occurrence. Occurs throughout the Weald Clay following in its distribution various species of *Cypridea*. Only rarely found with *D. leguminella* and like it its numbers drop markedly in the 'marine bands'.

Superfamily CYTHERACEA Baird 1850

Family CYTHERIDEIDAE Sars 1925

Fabanella bononiensis (Jones 1880)

Plate 29, figs. 13–21; text-figs. 2a–g

- 1880 *Cythere boloniensis* Jones, pp. 615–16.
 1885 *Candona bononiensis* (Jones); Jones, pp. 348–9, pl. 9, figs. 7–8.
 1940 *Cyprideis polita* Martin, pp. 350–3, pl. 7, figs. 110–13, pl. 9, figs. 149–51.
 1951 '*Candona*' *bononiensis* (Jones); Anderson, pp. 209–11.
 1953 *Neocytheridea bononiensis* (Jones) Grekoff, p. 377.
 1961 *Fabanella polita polita* (Martin); Wolburg, p. 199, pl. 1, fig. 3, text-figs. 1–2.
 1961 *Fabanella polita polita* (Martin); Martin (1961a), p. 113, pl. 14, fig. 9.
 1961 *Fabanella polita polita* (Martin); Martin (1961b), p. 186, pl. 1, figs. 1–4, 10–12.
 1962 *Neocytheridea bononiensis bononiensis* (Jones); Wick and Wolburg, pp. 218–19, pl. 32b, figs. 1–2.
 1963 *Neocytheridea bononiensis bononiensis* (Jones); Christensen, pp. 36–38, pl. 3, figs. 2a–e, text-fig. 11.
 1963 *Fabanella boloniensis* (Jones); Anderson, p. 16.

Material. 385 valves and carapaces (SJCC 66/5.1-385).

Average dimensions

	L	H	W
♀ carapace	0.83	0.45	0.45
♂ carapace	1.00	0.48	0.47

Description. Carapace exhibits sexual dimorphism. Males are about 15% longer than females. Anterior and posterior margins are broadly and equally rounded. The ventral margin shows an anterior concavity and is extended below posteriorly. There is a well-marked anterior, but hardly noticeable posterior cardinal angle. A swelling at the anterior cardinal angle marks the ocular region. The greatest height of the valve falls in the posterior half. The carapace is moderately inflated with the greatest width at mid-point. The valves are equal in size and no overlap occurs apart from that at the hinge.

The carapace is heavily calcified. Its surface is covered with punctae, the size of which increases towards the centre of the valve. There is sometimes a suggestion of a concentric pattern of punctae on the valves.

The hinge is lophodont. In the right valve two terminal teeth are found and a median groove, which may not extend from tooth to tooth but only occupy the anterior half of that distance. The anterior tooth occupies roughly 20% of the hinge length and is slightly larger than the posterior one. The median groove appears to slope down from the top of the anterior tooth across the median part of the hinge. In the left valve are corresponding anterior and posterior sockets and a median ridge.

The inner lamella is narrow with a well-developed selvage. The inner margin and line of concrescence do not coincide; there is a narrow anterior vestibulum. Radial pore canals are spindle-shaped, thick in the middle and thinning at each end. There are about twenty anteriorly and ten posteriorly.

The muscle scar pattern consists of a sub-vertical row of four and two separate scars in front of the row, one in line with the first and second (from the dorsal side) and the other below the fourth.

Occurrence. In the 'marine bands' at Warnham, Capel, and Newdigate.

Remarks. There seems to be great confusion as regards the specific status of *F. bononiensis*. Originally described by Jones in 1880 as *Cythere boloniensis*, he amended it (1885) to *Candona bononiensis*. *Cyprideis polita* Martin 1940 is a junior synonym of *C. bononiensis* Jones 1880. In the German literature several subspecies of *F. polita* have been described, all based on the varying degree of punctuation of the valves (Martin 1961), and on the degree of inflation of the posterior half of the carapace (Wolburg 1961). Our specimens are closest to those described by Martin as *F. polita polita* although the surface of the valves is not entirely smooth. It is very likely that we are faced with one species only and the variation in ornamentation is of phenotypic nature.

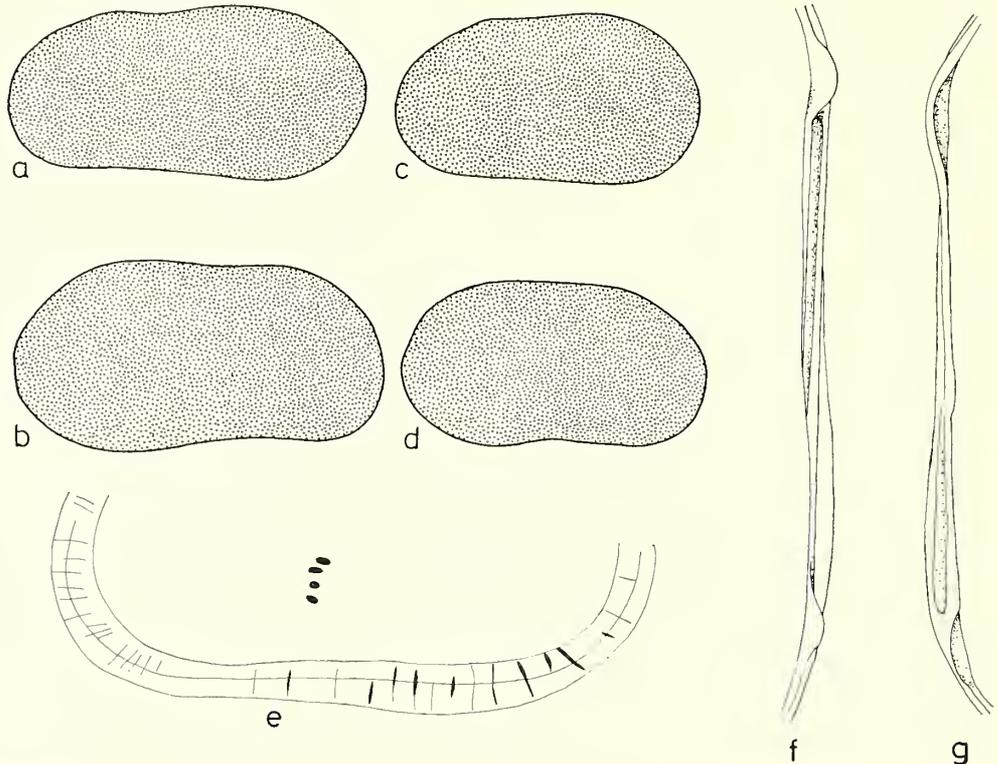
Subgenus *Sternbergella* (*Parasternbergella*) subgen. nov.

Type species. *Sternbergella* (*Parasternbergella*) *wolburgi* sp. nov.

Diagnosis. A subgenus of *Sternbergella* with lophodont hinge.

Remarks. In all respects *S.* (*Parasternbergella*) subgen. nov. agrees with *Sternbergella* but the strikingly different hinge warrants the establishment of a new subgenus.

Wolburg (personal communication) observed a gradual reduction of the hinge of *Sternbergella* from the antimerodont towards lophodont in the higher German Wealden. *Cypris cornigera* Jones 1888 on the basis of its lophodont hinge should also be considered belonging to this new subgenus. *Dolocysteridea* Triebel 1938 seems to be closely allied to *Sternbergella* and Dr. Wolburg (personal communication) drew our attention to the



TEXT-FIG. 2. *Fabanella bononiensis* (Jones 1880). *a*, Left valve, male, outline, $\times 50$. *b*, Right valve, male, outline, $\times 50$. *c*, Left valve, female, outline, $\times 50$. *d*, Right valve, female, outline, $\times 50$. *e*, Free margin, right valve, female, $\times 100$. *f*, Right valve hinge, $\times 150$. *g*, Left valve hinge, $\times 150$.

strikingly similar parallel evolution of the two genera. A suggested tentative evolutionary relationship is shown on text-fig. 3.

Sternbergella (*Parasternbergella*) *wolburgi* sp. nov.

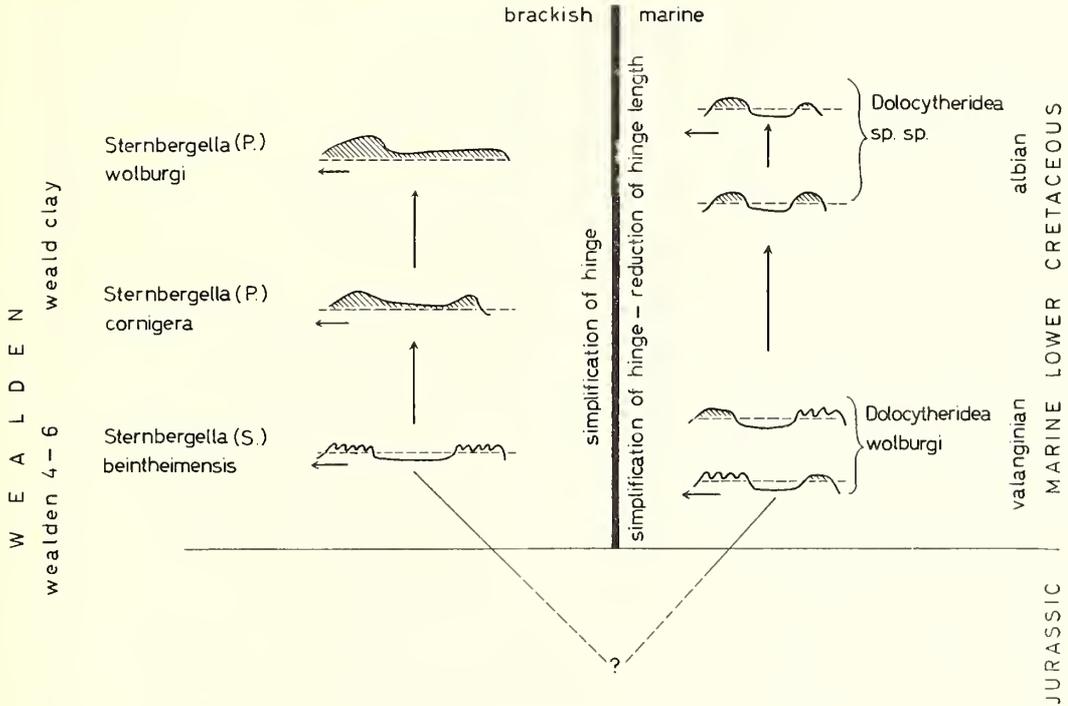
Plate 30, figs. 7-12; text-figs. 4*a-b*, 5*a-f*

Holotype. A female carapace, Io. 3949. *Paratypes*, 286 valves and carapaces (SJCC 66/7.1-286).

Locus typicus Clock House brick pit, Capel, Surrey; 'marine band', lower part of Weald Clay.

Diagnosis. A species of *Sternbergella* (*Parasternbergella*) with a trapezoid (♀♀) or oval (♂♂) carapace. The greatest height of the valves is at the posterior cardinal angle. Fused part of the inner lamella uniformly narrow along the free margin with a broad inner

lamella anteriorly. Hinge unusual; all positive elements are in the right valve consisting of a sharp long anterior tooth and a very poorly developed posterior tooth, the two being connected by a sharp but low median ridge. The left valve carries a corresponding structure, but only the deep anterior socket is conspicuous.



TEXT-FIG. 3. Suggested evolutionary relationship between *Dolocytheridea*, *Sternbergella* s. str. and *S.* (*Parasternbergella*).

Dimensions

	L	H	W
Holotype	1.08	0.65	0.47

Average dimensions of paratypes

♀ Left valve	0.99	0.59	0.24
♀ Right valve	0.96	0.58	0.20
♂ Left valve	1.20	0.65	0.29
♂ Right valve	1.18	0.62	0.25

Description. Carapace shows strong sexual dimorphism; females are shorter, higher, and more trapezoid shaped, males about 15% longer and more oval in outline. Both sexes are characterized by the position of the greatest height in the carapace which is at the posterior cardinal angle. The left valve is larger than the right and the overlap is especially marked ventrally and at the hinge. The carapace is not much inflated, the greatest width occurs in the median to posterior regions.

The anterior margin is broadly rounded, the posterior broadly pointed at mid-height in males and more ventrally in females. The ventral margin is almost straight but in the male right valves there is a short concave portion anteriorly. The hinge margin is straight

in both of the female valves, sloping towards the anterior at a slightly greater angle in the right valve. In males the hinge margin is gently arched. The cardinal angles are rounded and inconspicuous with the exception of the posterior cardinal angle in females which is well developed, situated about two-thirds of the length from the anterior. It also marks the highest point of the valve.

The surface of the valve is smooth and often translucent; there are few, well spaced large normal pore canals. The fused portion of the inner lamella is relatively narrow and of almost uniform length along the length of the free margin. At the anterior the inner margin and the line of concrescence do not coincide and there is a wide free portion of the inner lamella present forming a wide vestibule. Elsewhere the line of concrescence and inner margin coincide. The well-developed selvage is prominent right round. Radial pore canals are trumpet shaped, widening towards the surface, numbering about twenty-four anteriorly and eighteen posteriorly. They are rather irregular mainly in length and width.

The central muscle scar pattern consists of a slightly backwardly arched row of four scars, the second of which (from top) is often attenuated. Two scars occur in front of the main group, one in line with the top or second one in the row, and the other one well below the bottom scar of the row. Often two more groups of scars can be observed, one group consisting of two scars is situated anteroventrally from the main group and represents probably the mandibular muscles; the other group of scars is above the vertical row and consists of a large and a small scar.

The hinge is rather unusual and it is difficult to fit it into any of the established hinge types. It is probably closest to the lophodont hinge, but all the positive hinge elements are carried by the right valve so it cannot be definitely identified with the lophodont type where the median element of the right valve is negative. The right valve hinge consists of a large peg like tooth at the anterior which projects well above the margin of the valve in side view. The posterior element is a weakly developed narrow ridge connected to the anterior element by a very ill-defined smooth ridge. The left valve carries the corresponding negative hinge features, only the anterior deep socket being conspicuous.

Occurrence. In great numbers in the 'marine band' at Capel and less common in the 'marine bands' at Warnham and Newdigate.

EXPLANATION OF PLATE 30

All figures $\times 50$ unless otherwise stated.

Figs. 1-6. *Hutsonia capelensis* sp. nov., Capel, Surrey. 1, Carapace, female, from right, holotype, Io 3948. 2, Carapace, female, from left, holotype, Io 3948. 3, Carapace, male, from right, SJCC 66/6.1. 4, Carapace, male, from left, SJCC 66/6.1. 5, Carapace, female, dorsal view, holotype, Io 3948. 6, Carapace, male, dorsal view, SJCC 66/6.1.

Figs. 7-12. *Sternbergella (Parasternbergella) wolburgi* sp. nov., Capel, Surrey. 7, Carapace, female, from right, holotype, Io 3949. 8, Carapace, female, from left, holotype, Io 3949. 9, Carapace, male, from right, SJCC 66/7.1. 10, Carapace, male, from left, SJCC 66/7.1. 11, Carapace, female, dorsal view, holotype, Io 3949. 12, Right valve, female, dorsal view to show hinge, $\times 150$, SJCC 66/7.2.

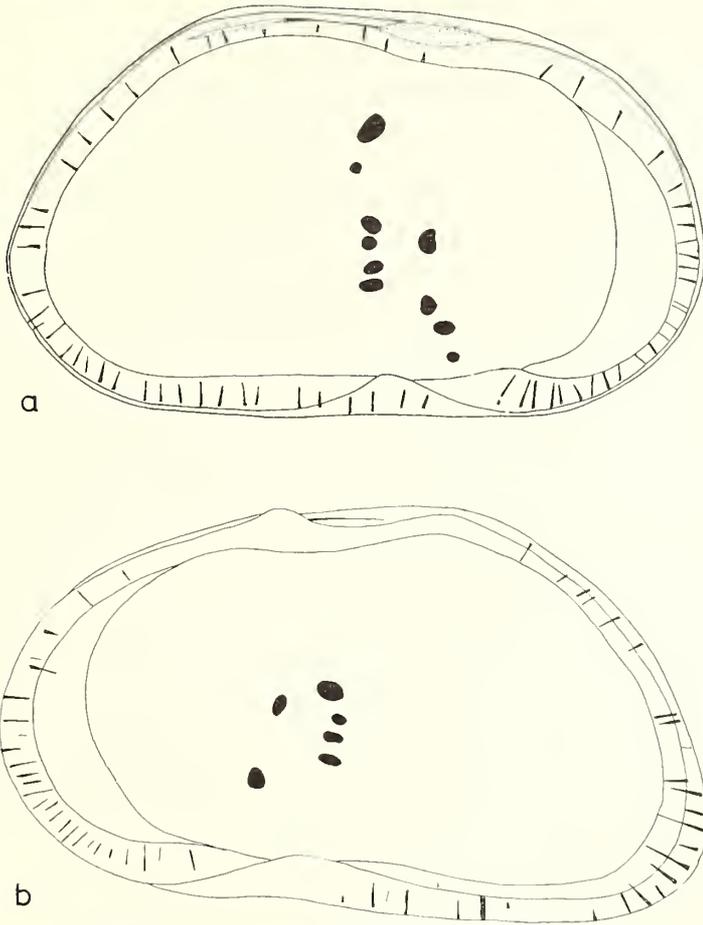
Figs. 13-17. *Schuleridea (Eoschuleridea) wealdensis* sp. nov., Newdigate, Surrey and Warnham, Sussex. 13, Carapace, female, from right, holotype, Io 3950. 14, Carapace, female, from left, holotype, Io 3950. 15, Right valve, male, external view, SJCC 66/8.1. 16, Left valve, male, external view, SJCC 66/8.2. 17, Carapace, male, dorsal view, SJCC 66/8.3.

Figs. 18-21. *Ammobaculites* sp., Capel, Surrey.



KILENYI and ALLEN, Wealden microfossils

Remarks. *S. (P.) wolburgi* sp. nov. differs from *S. (P.) cornigera* (Jones 1888) in its forwardly sloping hinge margin, stronger hinge, and lack of well-developed posterior spines.



TEXT-FIG. 4. *Sternbergella (Parasternbergella) wolburgi* sp. nov. *a*, Female left valve, internal view, $\times 90$. *b*, Female right valve, internal view, $\times 90$.

Family SCHULERIDEIDAE Mandelstam 1959

Schuleridea (Eoschuleridea) wealdensis sp. nov.

Plate 30, figs. 13–17; text-figs. 5a–c

Holotype. A female carapace, Io 3950. *Paratypes*, 524 valves and carapaces (SJCC 66/7.1–524).

Locus typicus 'Marine band', lower part of Weald Clay; Newdigate, Surrey.

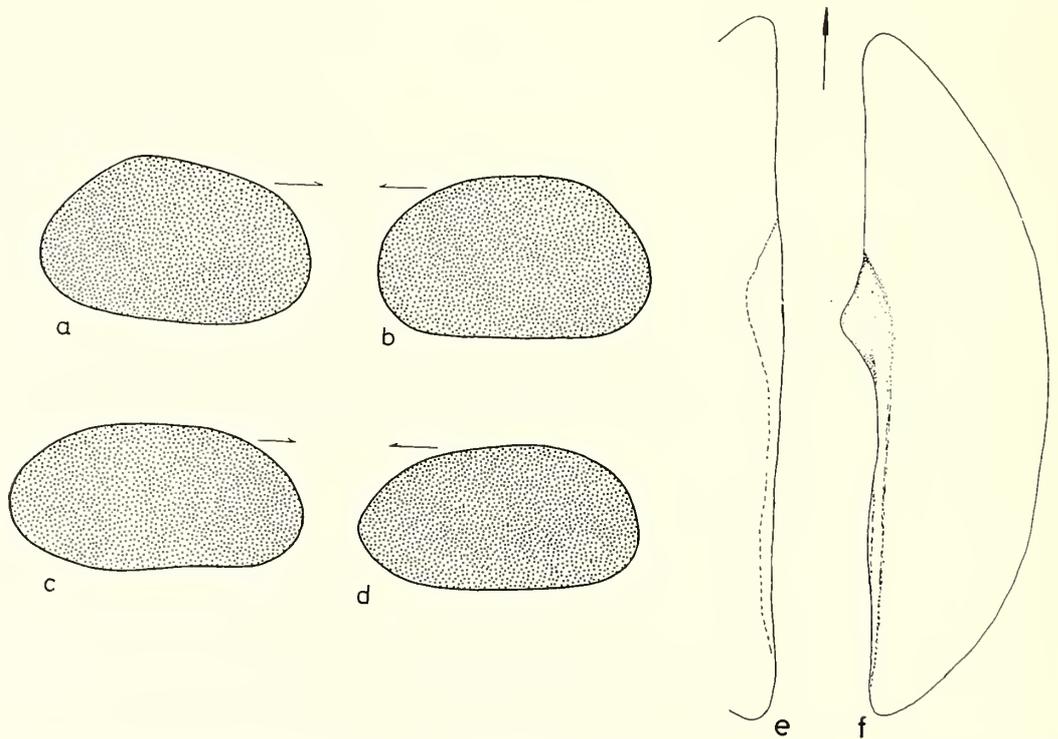
Diagnosis. A species of *Schuleridea (Eoschuleridea)* with a relatively narrow duplicature and only about fifteen radial pore canals on the anterior margin. Carapace is small with very strong sexual dimorphism.

Dimensions of holotype. L, 0.47; H, 0.34; W, 0.27

Average dimensions of paratypes

	L	H	W
♀ Left valve	0.50	0.37	0.17
♀ Right valve	0.45	0.31	0.12
♂ Left valve	0.63	0.37	0.17
♂ Right valve	0.59	0.31	0.12

Description. The carapace is ovoid (♀♀) or more elongated (♂♂). The left valve is larger than the right and overlaps it along the entire margin. The degree of overlap is strongest



TEXT-FIG. 5. *Sternbergella* (*Parasternbergella*) *wolburgi* sp. nov. *a*, Outline of female right valve, $\times 35$. *b*, Outline of female left valve, $\times 35$. *c*, Outline of male right valve, $\times 35$. *d*, Outline of male left valve, $\times 35$. *e*, Left valve hinge, female, $\times 90$. *f*, Right valve hinge, female, $\times 90$.

ventrally and dorsally, least noticeable along the posterior end. The right valve is smaller, on the average by 7–10% (length). The sexual dimorphism is very strong, the males being about 25% longer than the females.

In side view the two valves are very different in shape. The left valve in both sexes has a convex dorsal margin, rounded anterior and slightly pointed posterior end. The ventral part of the valve shows a slight swelling, more pronounced in the females. In the females the posterior cardinal angle is more conspicuous, the anterior being more rounded; in males the opposite is the case. The maximum height of the valve is at the anterior cardinal angle which is about one-third of the length from the anterior in females and one-quarter in males. The right valve is much more angular in both sexes,

both cardinal angles being conspicuous. The dorsal and ventral margins are almost straight. The posterior end is more pointed than in the left valve.

The surface of the valve is smooth with large but few normal pore canals. The shell is thick and heavy, often transparent. A slight ocular depression is present.

The hinge conforms to the usual paleomerodont type found in *Schuleridea* but is less strongly developed than in most Jurassic or Cretaceous species. The hinge in the left valve consists of two crescentic loculate terminal sockets connected by a locellate median groove. The anterior socket is the larger of the two and it contains eight loculi, the posterior having only six or seven. The median groove is situated on top of a bar that is derived from the upper lip of the terminal sockets. The groove is finely locellate with sixteen to eighteen fine locellae. A deep spindle-shaped accommodation groove is found above the median element. The corresponding hinge structure in the right valve comprises three positive elements, two terminal dentate ridges with a finely denticulate bar in between. The average length of the hinge is 0.28 mm. in females and 0.38 mm. in males.

The anterior duplicature is narrow. The inner margin and line of conrescence seem to coincide although in some specimens a very narrow vestibule was observed. The radial pore canals are rather thick, getting rapidly narrow towards both ends. The typical fan-shaped arrangement of the radial pore canals, characteristic of *Schuleridea*, is hardly recognizable; only the last two or three pore canals on each side turn slightly outwards. The number of radial pore canals is between fifteen and seventeen on the anterior margin, same in both males and females.

The muscle scar pattern consists of four scars in a nearly vertical row with two anterior scars in line with the top and bottom scars of the vertical row.

Occurrence. In 'marine bands' from Warnham, Capel, and Newdigate.

Remarks. Species of *Schuleridea* (*Eoschuleridea*) have been described so far only from the Bathonian Estuarine Series of Eastern England (Bate 1967).

Family PROTOCYTHERIDAE Ljubimova 1955

Hutsonia capelensis sp. nov.

Plate 30, figs. 1-6; text-fig. 7a-d

Holotype. A female carapace, Io 3948. *Paratypes*, 32 valves and carapaces (SJCC 66/6.1-32).

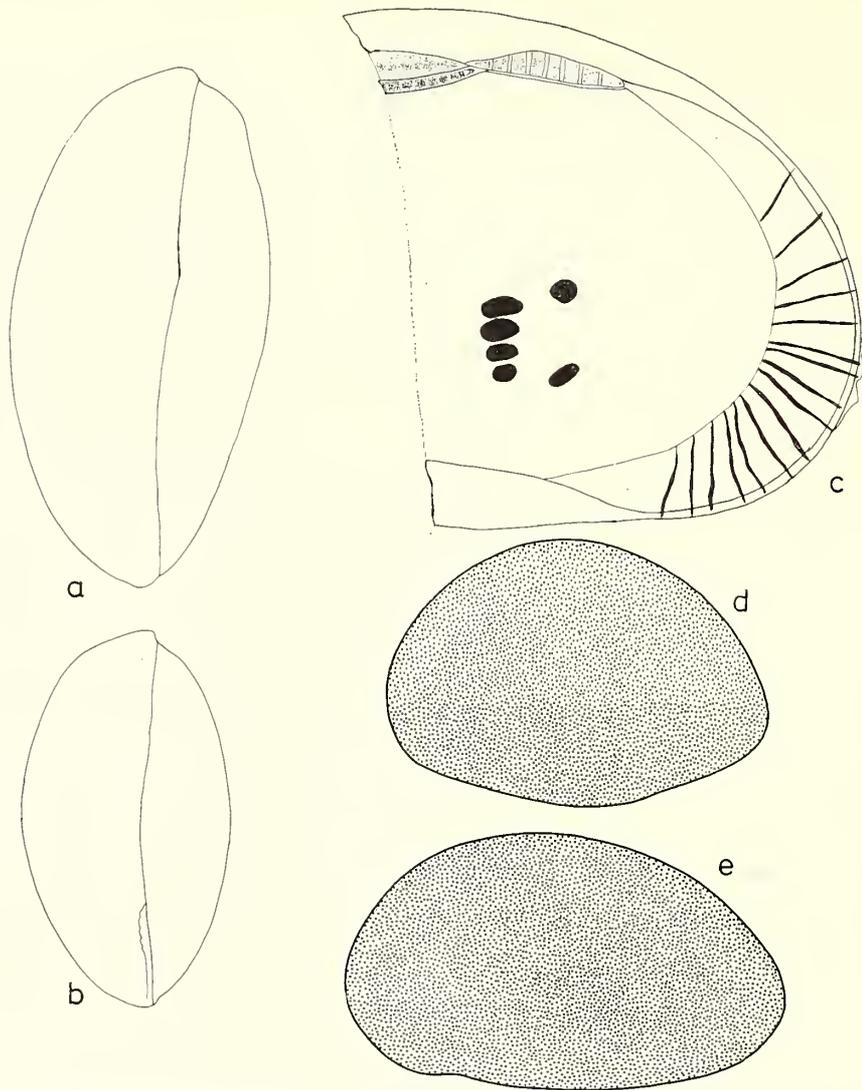
Locus typicus 'Marine band', Lower Weald Clay; Capel, Surrey.

Diagnosis. A species of *Hutsonia* with well-developed bisulcate anterior ornamental complex. Sulci are deep, crescent-shaped, inclined forward, with an elongated median lobe running full length between the sulci. Under this complex, slightly posteriorly, two pits occur in a horizontal row. The central and posterior part of the valve is ornamented by three quasi-horizontal ribs. Sexual dimorphism is very pronounced.

Dimensions of holotype. L, 0.60; H, 0.36; W, 0.31.

Average dimensions of paratypes

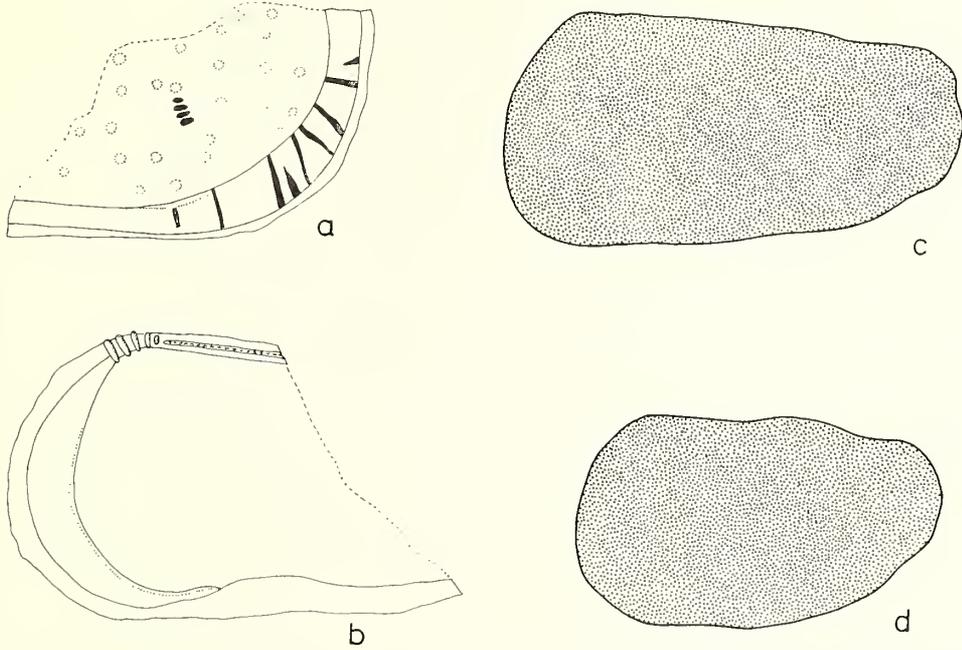
	L	H	W
♀ Left valve	0.60	0.36	0.19
♀ Right valve	0.58	0.34	0.13
♂ Left valve	0.79	0.40	0.19
♂ Right valve	0.76	0.37	0.13



TEXT-FIG. 6. *Schuleridea (Eoschuleridea) wealdensis* sp. nov. *a*, Carapace, male, dorsal view, $\times 100$. *b*, Carapace, female, dorsal view, $\times 100$. *c*, Female left valve, anterior margin and muscle scars, $\times 200$. *d*, Outline of female left valve, $\times 100$. *e*, Outline of male left valve (? juvenile), $\times 100$.

Description. Carapace sub-pyriform in side view. The left valve is larger, overlapping the right slightly along the ventral margin. In males the overlap is more pronounced and extends to the anterior and posterior margins. Sexual dimorphism is extremely strong, males being about 25% longer than females. The two valves are almost identical in shape. The dorsal margin is straight with a slight convexity which is anteriorly in males and at about mid-length in females. The two cardinal angles are well marked. Anterior margin is broadly rounded, the posterior ends in a blunt point well above the mid-height. The ventral margin rises slightly sinuously towards the posterior end. At about

three-eighths length from the anterior there is a short concave portion in the ventral margin; this is much more in evidence in males. The greatest height of the valve is at the anterior cardinal angle, about one-eighth distance from the anterior. In dorsal view carapaces of the two sexes are considerably different in shape, males being almost elliptical with the greatest width only slightly posterior to mid-length; in females, however, the position of the greatest width falls in the posterior third of the carapace. Females are also much more pointed towards the posterior in this view.



TEXT-FIG. 7. *Hutsonia capelensis* sp. nov. *a*, Female left valve, anterior margin and muscle scars, $\times 110$. *b*, Female right valve, anterior margin and anterior portion of hinge, $\times 110$. *c*, Outline of male left valve, $\times 75$. *d*, Outline of female left valve, $\times 75$.

The surface ornamentation consists of an anterior complex of two sulci separated by a lobe and a central and posterior system of ribs. The anterior sulci are crescent-shaped, slightly oblique forwards. The median lobe extends the full length of the sulci and it is thickest at its middle. Two pits occur antero-ventrally arranged parallel to the ventral margin, the first of these two lying just under the ventral end of the posterior sulcus, the second a short distance behind.

A near horizontal system of sharp crested ribs form the rest of the ornamentation. Three of these ribs form a constant feature, running on the lateral side of the valve starting from below the lobe and converging slightly towards the posterior. The upper two of these ribs are deflexed ventrally at their anterior end. On male valves an additional but much shorter rib is situated above. Several very fine ribs run on the ventral side of the valve. The whole surface seems to be finely punctate.

The internal characteristics could be only partially observed as most of the material is in the form of closed carapaces. The hinge is antimerodont with five to seven

crenulations on the anterior element and a locellate median groove in the right valve. Normal pore canals are large and numerous. Radial pore canals appear to be thick and few, about eight on the anterior margin. The duplicature is heavily calcified, and a narrow vestibulum may be present anteriorly.

Remarks. Species of *Hutsonia* have been described from Upper Jurassic–Lower Cretaceous brackish/marine deposits, mainly from North America. *Hutsonia capelensis* sp. nov. appears to be closest to the type species *H. vulgaris* Swain 1946, but differs from it by the presence of well-defined longitudinal ribbing and the lack of reticulation.

Class CIRRIPEDIA

Plates of a lepadomorph cirripede assigned to *Zenigmatolepas hausmanni* Dunker and Koch, by Anderson (1963, p. 63) are abundant in the lower of the two *Cassiope* bands at the Clock House brick pit, Capel. Carinae, scuta and terga are found in association with *Sternbergella* (*Parasterubergella*) *wolburgi* sp. nov. and *Hutsonia capelensis* sp. nov. Scutal plates are the most common at Capel but carinal plates form the bulk of the cirripede fauna at Warnham. There is rather wide variation in the size and shape of the carinae which suggests that there may be more than one species present. The abundant lignite associated with the 'marine bands' may indicate that the cirripedes were probably attached to floating plant debris.

Order FORAMINIFERIDA Eichwald 1830

Family LITUOLIDAE de Blainville 1825

Ammobaculites sp.

Plate 30, figs. 18–21

Material. Several hundred specimens.

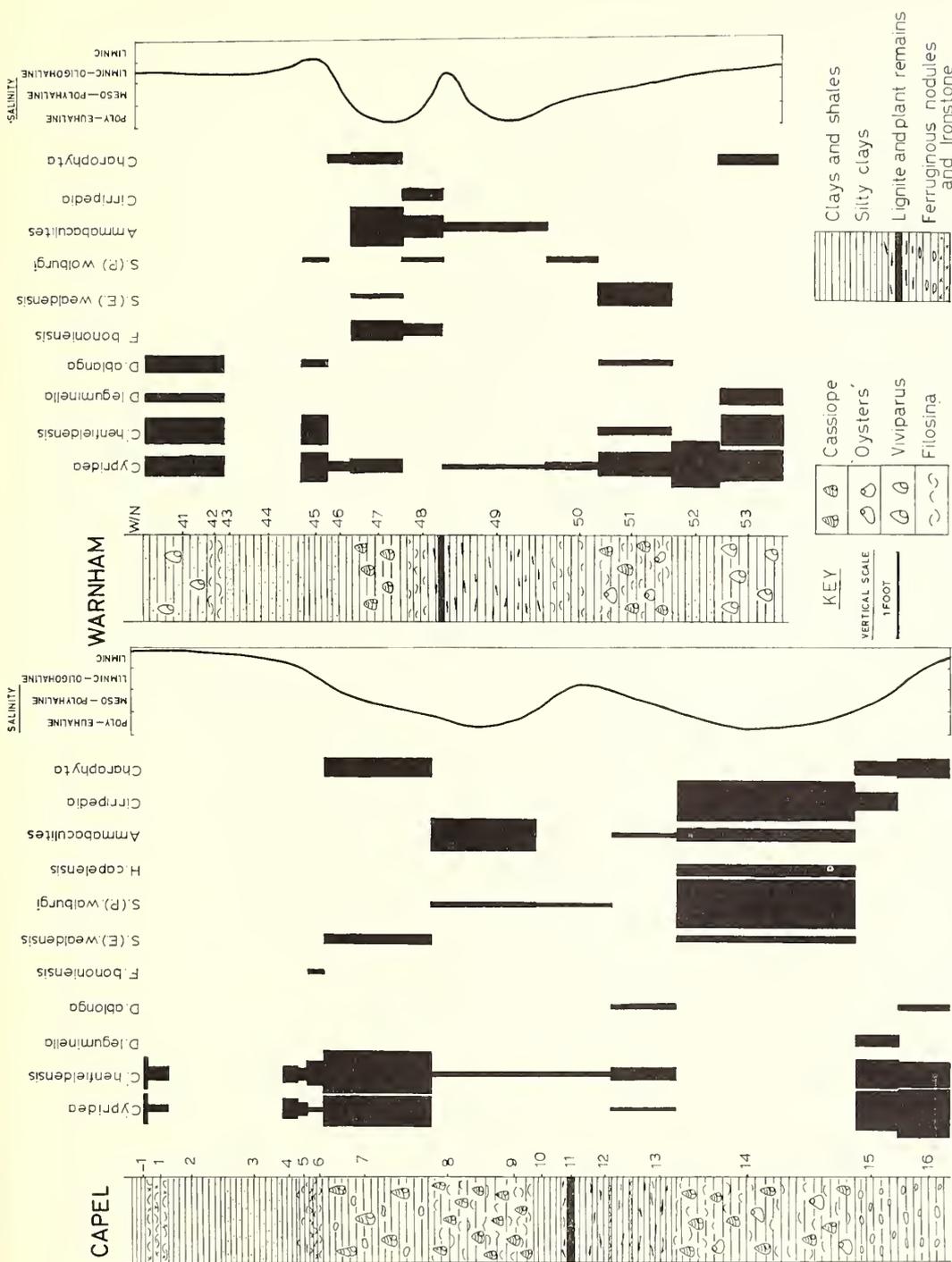
Average dimensions. Length: 0.6–0.8 mm.; Diameter of coil: 0.3–0.5 mm.; Breadth of last chamber: 0.2–0.25 mm.

Remarks. The material is rather poorly preserved, all chambers are usually flattened and therefore specific identification is not attempted. Fairly extensive variation can be observed in the examined population but it appears nevertheless monospecific. The material of the tests consists of fine uniform grade quartz grains.

Occurrence. From the 'marine bands' at Newdigate, Capel, and Warnham.

INTERPRETATION OF ENVIRONMENTS

It is generally accepted that some species of ostracods are accurate indicators of various environmental parameters, including salinity. Two methods of approach can be used in determining the original salinity: (a) Comparison with the living representatives of the genus, if any. This is, at least theoretically, the most reliable approach, but serious errors may be introduced by not differentiating between biocenosis and thanatocenosis in the study of modern ostracod faunas. Wagner (1964) pointed out that this is especially important in the study of estuarine or delta environments where considerable transportation of empty shells takes place. (b) Shell characteristics can be indicative of the degree of salinity. Weakly calcified valves, weak hinge structure and narrow fused



TEXT-FIG. 8. Stratigraphical distribution of microfossils in and in the vicinity of the marine bands at Capel and Warnham. (The relative abundance of various microfossils is expressed by the width of the columns.)

zone are typical of freshwater forms. On the other hand, strongly calcified, heavy shelled forms with strongly developed hinges are more characteristic of marine (mainly benthonic) forms (Hartman 1964). In brackish water species the overall size and degree of calcification decreases with salinity. The inferred salinity range of various microfossils found in or near the 'marine bands' is examined below. On this basis four distinct micro-fossil assemblages are recognized.

A. *Freshwater assemblage*

Genus *Cypridea* Bosquet 1852

Many species of *Cypridea* are abundant throughout the Weald Clay. A sharp fall in their numbers heralds the establishment of brackish conditions and they are absent from some parts of the 'marine bands'. At Warnham and Capel the dominant species in the vicinity of the 'marine band' are a form close to *Cypridea punila* Anderson, M. S. (Pl. 29, figs. 4-5) and the heavily ornamented *C. tuberculata* (J. de C. Sowerby) (Pl. 29, fig. 3) in which the size and shape of the tubercles vary while the pattern remains the same. At Newdigate the dominant species is *Cypridea marina* Anderson, M. S., a large form with a number of stout rounded tubercles (Pl. 29, figs. 1-2). We consider all species of *Cypridea* in the 'marine bands' to be transported specimens and therefore we are not concerned with them in this study.

Genus *Theriosynoecum* Branson 1936

Theriosynoecum fittoni (Mantell 1844) occurs in large numbers in the freshwater deposits of the Weald Clay but is exceedingly rare in the 'marine bands'. *T. fittoni* follows the distribution of the various species of *Cypridea* and is considered to be a completely freshwater genus.

B. *Limnic-oligohaline assemblage*

This assemblage includes forms that are assumed to be generally freshwater dwellers with some tolerance of brackish conditions. The evidence of recent species of *Darwinula* and *Ilyocypris* from slightly brackish environments (Wagner 1957, Neale 1964, and Hartman 1964) is supported by the presence of small numbers of their fossil representatives from beds immediately adjacent to the 'marine bands'.

Rhinoocypris. Recent species of *Ilyocypris*, a very closely allied, if not the same genus, are freshwater dwellers but with a certain tolerance of brackish conditions. Hartman (1964, p. 490 in discussion) mentions its occurrence in the brackish environments of the Baltic, with salinities of 5‰ or more, although the same species is usually found in fresh or nearly freshwater. In the Weald Clay *Rhinoocypris* occurs with *Cypridea* suggesting a limnic biotope generally but on the evidence of modern species from the Baltic we envisage a slight tolerance of brackish conditions.

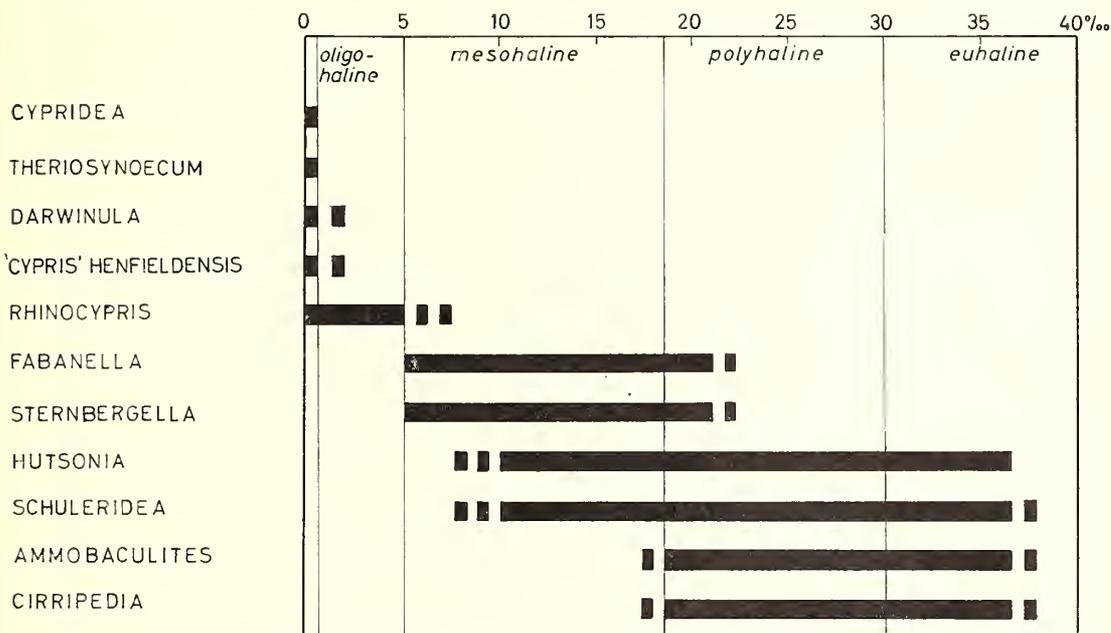
Darwinula. Recent species of *Darwinula* live in waters with salinities of 0-1‰ (Wagner 1957, Neale 1964).

'*Cypris*' *henfieldensis*. Very little can be said about this genus as it is certainly new and as yet undescribed. Anderson (1963) states this to be a 'marine or quasimarine' species. It occurs, however, right through the Weald Clay in large numbers with the usual 'freshwater' fauna. The presence of numerous valves of '*Cypris*' *henfieldensis* in certain

samples from the 'marine bands' may be explained by current transportation of the thin but large valves. Tentatively a slight tolerance of brackish conditions may, however, be assumed.

C. *Meso-polyhaline assemblage*

Fabanella is not known from fully marine deposits. Oertli (1963b) estimates its range between 5–18‰, possibly higher.



TEXT-FIG. 9. Presumed salinity tolerances of microfossils from the 'marine bands'. (Classification of brackish waters according to the 'Venice System'.)

Sternbergella (*Parasternbergella*) occurs with *Fabanella*, for this reason it is considered here brackish. Both genera are common in the brackish horizons of the German Wealden (Wolburg 1962, Martin 1961a, 1961b).

D. *Poly-euhaline assemblage*

Schuleridea (*Eoschuleridea*). Species of this subgenus have been described only from the Bathonian Upper Estuarine Series of Eastern England (Bate 1967). According to Bate (personal communication) these species come from a shallow marine environment with *Ostrea*, although the salinity may have been less than standard. *Schuleridea* s. str. has a wide tolerance of brackish conditions (Oertli 1963b, Donze 1960) although it is found predominantly in marine deposits (Morkhoven 1962).

Hutsonia is generally considered a marine/brackish form with most species described from marine deposits (Swain 1946). On the basis of its occurrence in the Weald Clay 'marine bands' we tentatively suggest the same salinity tolerance for *Hutsonia* as for *Schuleridea*. *Ammobaculites* is a typical brackish/marine arenaceous foraminifer found

in modern delta and lagoonal environments with salinities between 20–30‰ (Phleger 1960) but fossil species probably have wider tolerance.

Cirripedia. Modern barnacles are usually marine but tolerate somewhat reduced salinity.

THE AGE OF THE 'MARINE BANDS'

The described marine/brackish microfauna of the 'marine bands' gives little in the way of correlation with other Lower Cretaceous deposits outside the Weald. There is a close affinity with marine/brackish microfaunas from the higher German Wealden (4–6) but the similarity is due to the presence of such long ranging forms as *Fabanella bononiensis*, *Ammobaculites* sp., etc. Species of more marine character are, however, totally different, *Schuleridea* (*Eoschuleridea*) *wealdensis* sp. nov., *Hntsonia capelensis* sp. nov., and *Cirripedia* in the Weald Clay and species of *Pachycytheridea*, *Galliaecytheridea*, *Protocythere*, *Parexophtalmocythere*, *Schuleridea*, *Cytheropteron*, and *Haplocytheridea* in the Wealden of north-west Germany (Martin 1961a).

There is a complete lack of Boreal Lower Cretaceous marine microfauna (Neale 1960, Kaye 1963) in the 'marine bands' of the Weald Clay, indicating the presence of an effective barrier between the marine environment of Northern England and the Weald during the deposition of the 'marine bands'.

REFERENCES

- ALLEN, P. 1965. Age of the Wealden in North-West Europe. *Geol. Mag.* **92**, 265–81 and 512.
 — and KEITH, M. L. 1965. Carbon Isotope ratios and Palaeosalinities of Purbeck-Wealden Carbonates. *Nature* **208**, 1278–80.
 ANDERSON, F. W. 1939. Wealden and Purbeck Ostracoda. *Ann. Mag. natur. Hist.* **3**, 291–310.
 — 1940a. Ostracod zones of Purbeck (Abstract). *Advancement of Science*, **1**, 259.
 — 1940b. Ostracoda from the Portland and Purbeck beds at Swindon. *Proc. Geol. Ass.* **51**, 373–84.
 — 1951. Note sur quelques Ostracodes fossiles du Purbeckien du Suisse. *Arch. Sci.* **4**, 209–12.
 — 1956. In *Summ. Prog. Geol. Surv. G.B. for 1955*.
 — 1962. Correlation of the upper Purbeck beds of England with the German Wealden. *Lpool. Manchr. geol. J.* **3**, 21–32.
 — 1963. In *Geology of the Country around Maidstone. Mem. Geol. Surv. G.B.*
 — 1964. In *Summ. Prog. Geol. Surv. G.B. for 1963*.
 — and CASEY, R. 1957. in: *Summ. Prog. Geol. Surv. G.B. for 1956*, p. 51.
 — and HUGHES, N. F. 1964. The 'Wealden' of North-West Germany and its English equivalents. *Nature*, **201**, 907–8.
 ARKELL, W. J. 1947. The Geology of the Country around Weymouth, Swanage, Corfe, and Lulworth. *Mem. Geol. Surv. G.B.*
 BARKER, D. 1963. Size in relation to salinity in fossil and recent euryhaline ostracods. *J. mar. biol. Ass. U.K.* **43**, 785–95.
 BARTENSTEIN, H. and BURRI, F. 1955. Die Jura-Kreide-Grenzsichten im Schweizerischen Faltenjura und ihre Stellung im mittel-europäischen Rahmen. *Eclog. geol. Helv.* **47**, 426–43.
 BATE, R. H. 1967. The Bathonian Upper Estuarine Series of Eastern England. Part I. Ostracoda. *Bull. Brit. Mus. (Nat. Hist.)* **14**, 2.
 CASEY, R. 1961. The stratigraphical palaeontology of the Lower Greensand. *Palaeontology*, **3**, 487–621.
 CHRISTENSEN, O. B. 1963. Ostracods from the Purbeck-Wealden Beds in Bornholm. *Geol. Surv. Denmark*, II. ser., **86**.
 DINES, H. G. and EDMUNDS, F. H. 1933. The Geology of the Country around Reigate and Dorking. *Mem. Geol. Surv. G.B.*
 DONZE, P. 1960. Les formations du Jurassique terminal dans la partie NW de l'île d'Oleron (Charente-Maritime). *Trav. Lab. Géol. Lyon* (N.S.), **5**.

- DUNKER, W. 1843. Über den norddeutschen sogenannten Walderthon und dessen Versteinerungen. *Studien Göttinger Vor. Bergmann. Freunde* **5**.
- 1846. *Monographie der norddeutschen Wealdenbildung*. Braunschweig.
- GALLOIS, R. W. 1965. The Wealden District. *British Regional Geology, H.M.S.O.*
- GREKOFF, N. 1953. Sur l'utilisation des microfaunes d'Ostracodes dans la stratigraphie précise du passage Jurassique-Crétacé (facies continentaux). *Rev. Inst. franç. Petr.* **8**, 362-79.
- HARTMAN, G. 1964. The problem of polyphyletic characters in ostracods and its significance to ecology and systematics. *Pubbl. staz. Napoli*, **33**, suppl., 32-44.
- HUGHES, N. F. 1958. Palaeontological evidence for the age of the English Wealden. *Geol. Mag.* **95**, 41-49.
- JONES, T. R. 1862. A Monograph of the Fossil Estheriae. *Pal. Soc. London, Monogr.*
- 1880. Lettre sur le 'Calcaire Cypris' du Boulonnais. *Bull. Soc. Geol. France*, ser. 3, **8**, 615-16.
- 1885. On the Ostracoda of the Purbeck Formation, with notes on the Wealden Species. *Quart. J. geol. Soc. Lond.* **41**, 311-53.
- KAYE, P. 1963. Ostracoda of the subfamilies *Protocytherinae* and *Trachyleberidinae* from the British Lower Cretaceous. *Paläont. Z.* **37**, 225-38.
- 1963b. The Ostracod species *Orthonotacythere inversa* (Corneul) and its allies in the Speeton Clay of Yorkshire. *Palaeontology*, **6**, 430-9, pl. 61.
- 1966. Lower Cretaceous Palaeogeography of North-West Europe. *Geol. Mag.* **103**, 257-62.
- KLINGLER, W., MALZ, H. and MARTIN, G. P. R. 1962. Malm NW-Deutschlands. *Leitfossilien der Mikropaläontologie*, **1**, 159-90, Borntraeger, Berlin.
- KORNICKER, L. S. and WISE, C. D. 1960. Some environmental boundaries of a marine ostracod. *Micro-paleontology*, **6**, 393-8.
- LYELL, C. 1855. *Manual of Elementary Geology*.
- MARTIN, G. P. R. 1940. Ostracoden des norddeutschen Purbeck und Wealden. *Senckenbergiana*, **22**, 276-361.
- 1961a. Eine marine Mikrofauna im Wealden von Emlichheim (Emsland, N.W.-Deutschland). *Palaeontographica*, **116A**, 105-21.
- 1961b. Die Gattung *Fabanelia* n.g. (Ostracoda) im NW-deutschen Malm und Wealden. *Senck. leth.* **42**, 181-95.
- and WEILER, H. 1963. Der Wealden in der Gegend von Barnstorf (Kreis Grafschaft Diepholz, Niedersachsen). *N. Jb. Geol. Paläont. Abh.* **118**, 30-64.
- MORKHOVEN, F. P. C. M. VAN, 1962. *Post-Palaeozoic Ostracoda*. Elsevier.
- NEALE, J. W. 1960. Marine Lower Cretaceous Ostracoda from Yorkshire. *Micro-paleontology*, **6**, 203-24.
- 1964. Some factors influencing the distribution of Recent British Ostracoda. *Pubbl. staz. zool. Napoli*, **33**, suppl., 247-307.
- OERTLI, H. J. 1957. Ostracoden als Salzgehalts-Indikatoren im obern Bathonien des Boulonnais. *Eclog. geol. Helv.* **50**, 280-3.
- 1963a. Ostracodes du 'Purbeckien' du bassin Parisien. *Rev. Inst. franç. Petr.* **18**, 5-24.
- 1963b. *Mesozoic Ostracod Faunas of France*. E. J. Brill, Leiden.
- 1963c. Fossile Ostracoden als Milieuindikatoren. *Fortschr. Geol. Rheinld. u. Westf.* **10**, 53-66.
- BROTZEN, F., and BARTENSTEIN, H. 1961. Mikropaläontologisch-Feinstratigraphische Untersuchung der Jura-Kreide Grenzschichten in Südschweden. *Årsb. Sverig. Geol. Unders.* **55**, 3.
- PHLEGER, F. B. 1960. *Ecology and distribution of Recent Foraminifera*. Johns Hopkins Press, Baltimore.
- PINTO, I. D. and SANGUINETTI, Y. T. 1962. A complete revision of the Genera *Bisulco-cypris* and *Theriosynoecum* (Ostracoda) with the world geographical and stratigraphical distribution. *Esc. Geol. P. Alegre, Publ. Esp., Rio Grande do Sul*, **4**, 1-165.
- SANDBERG, P. 1964. Notes on some Tertiary and Recent brackish-water Ostracoda. *Pubbl. staz. Napoli*, **33**, suppl., 496-514.
- SCHMIDT, G. 1955. Stratigraphie und Mikrofauna des mittleren Malm im nordwestdeutschen Bergland mit einer Kartierung am Südlichen Ith. *Abh. senckenb. naturf. Ges.* **491**, 1-76.
- STEGHAUS, H. 1951. Ostracoden als Leitfossilien im Kimmeridge der Ölfelder Wietze und Fuhrberg bei Hannover. *Paläont. Z.* **24**, 201-24.
- SUNG, G. C. L. 1955. Wealden in Netherlands. *Proc. 4th World Petr. Congr. Rome*, **1**, 151-60.

- SWAIN, F. M. 1946. Upper Jurassic Ostracoda from the Cotton Valley Group in northern Louisiana; the genus *Hutsonia*. *J. Paleont.* **20**, 119–29.
- WAGNER, C. W. 1957. Sur les ostracodes du Quaternaire récent des Pays-Bas et leur utilisation dans l'étude géologique des dépôts holocènes. Mouton & Co., 's-Gravenhage. pp. 259.
- 1964. Ostracods as environmental indicators in Recent and Holocene estuarine deposits of the Netherlands. *Pubbl. staz. Napoli*, **33**, suppl., 480–95.
- WHITE, H. J. O. 1926. The Geology of the Country near Lewes. *Mem. Geol. Surv. G.B.*
- WICHER, C. A. 1940. Zur Stratigraphie der Grenzsichten Jura-Kreide Nordwestdeutschlands. *Oel und Kohle*, **36**, 263.
- WICK, W., and WOLBURG, J. 1962. Wealden in NW-Deutschland. *Leitfossilien der Mikropaläontologie*, **1**, 191–224. Borntraeger, Berlin.
- WOLBURG, J. 1959. Die Cyprideen des NW-deutschen Wealden. *Senck. leth.* **40**, 223–315.
- 1961. *Fabarella polita inflata* n. ssp., eine Leit-Ostracode im NW-deutschen Wealden. *Senck. leth.* **42**, 197–203.
- 1962. Zur Taxonomie und Nomenclatur einiger im Handbuch 'Leitfossilien der Mikropaläontologie' (1962) dargestellten Wealden-Ostracoden. *Senck. leth.* **43**, 529–32.
- WORSSAM, B. C. 1963. Geology of the Country around Maidstone. *Mem. Geol. Surv. G.B.*
- 1965. In *Summ. Progr. geol. Surv. G.B. for 1964*, 46–47.
- and THURRELL, R. G. 1967. Field meeting to an area north of Horsham, Sussex. *Proc. Geol. Ass.* **67**, 263–72.
- ZALÁNYI, B. 1959. Ostracoden-Faunen aus der Aptstufe des Nördlichen Bakony-Gebirges. *Ann. Hungarian Geol. Inst.* **47**, 2, 357–565.

T. I. KILENYI
Department of Geology,
Sir John Cass College,
Jewry Street,
London, E.C.3

NEIL W. ALLEN
American Overseas Petroleum,
P.O.B. 693
Tripoli,
Libya

Typescript received 15 December 1966

ADDENDUM

F. W. Anderson in two recent papers (1967*a, b*) describing ostracods from the Weald and Wadhurst Clays mentions a large number of 'marine' bands from these formations. These marine bands are based on the presence of the so-called 'S-phase species' (e.g. non-*Cypridea* species) and he states that the 'S' and 'C' (*Cypridea*) faunas are antipathetic in vertical distribution. In our opinion only certain genera in the 'S-phase faunas' can be considered as marine-brackish indicators. These are *Fabarella*, *Orthonotacythere*, *Eoschuleridea* (= *Haplocytheridea* of Anderson) and *Sternbergella*. Species of these genera occur together with foraminifera and cirripedes, and are antipathetic to species of *Cypridea*. The rest of the 'S-phase' species in borehole material we examined occur in varying quantities together with species of *Cypridea*, and the variation in the ratio of the *Cypridea* and non-*Cypridea* species may be a function of some other factor than salinity. Some of these 'S-phase' species have living equivalents and the salinity tolerance of these is discussed on pp. 158–9 above. Among the others *Miocytheridea henfieldensis* in our view is a cypridinid ostracod and *Mantelliana mantelli* shows affinity to *Candona* on the basis of its muscle scars. *Theriosynoecum fittoni* is in our view a non-marine ostracod. Allen and Keith (1965) indicated extremely low salinities ($\delta^{13}\text{C} = -15.33$) from near the top of the Weald Clay (sub-sample 66–382). Professor Allen kindly sent us a piece of this sample; the ostracod fauna consisted almost entirely of *T. fittoni*.

According to our interpretation of the salinity ranges of Wealden ostracod species only three brackish-marine horizons exist in the Weald Clay of Sussex and Surrey. The lowest, in the *dorsispinata* Zone, is doubtful as it only contains *Fabarella bononiensis* but no foraminifera, cirripedes or *Cassiope*, and therefore was not included in our paper. The second in the *tuberculata* Zone is described in detail above while the third horizon, not encountered in the borehole material is found in the *valdensis* Zone near the top of the Weald Clay.

REFERENCES

- ANDERSON, F. W. 1967. Ostracods from the Weald Clay of England. *Bull. geol. Surv. G.B.* **27**, 237–69.
- BAZLEY, R. A. B. and SHEPHARD-THORN, E. R. 1967. The Sedimentary and faunal sequence of the Wadhurst Clay (Wealden) in boreholes at Wadhurst Park, Sussex. *Bull. geol. Surv. G.B.* **27**, 171–235.

THE PALAEOONTOLOGICAL ASSOCIATION

COUNCIL 1967-8

President

Professor T. S. WESTOLL, The University, Newcastle upon Tyne

Vice-Presidents

Dr. W. S. MCKERROW, University Museum, Oxford
Professor F. H. T. RHODES, University College, Swansea
Professor C. H. HOLLAND, Trinity College, Dublin, Ireland

Treasurer

Dr. C. DOWNIE, Department of Geology, The University, Mappin Street, Sheffield 1

Membership Treasurer

DR. A. J. LLOYD, Department of Geology, University College, Gower Street, London, W.C.1

Secretary

Dr. J. M. HANCOCK, Department of Geology, King's College, London

Editors

Mr. N. F. HUGHES, Sedgwick Museum, Cambridge
Dr. GWYN THOMAS, Department of Geology, Imperial College, London, S.W.7
Dr. I. STRACHAN, Department of Geology, The University, Birmingham, 15
Professor M. R. HOUSE, The University, Kingston upon Hull, Yorkshire
Dr. R. GOLDRING, Department of Geology, The University, Reading

Other members of Council

Mr. M. A. CALVER, Geological Survey Office, Leeds
Dr. C. B. COX, King's College, London
Mr. D. CURRY, Eastbury Grange, Northwood, Middlesex
Dr. GRACE DUNLOP, Bedford College, London
Mr. G. F. ELLIOTT, 60 Fitzjohn Avenue, Barnet, Herts.
Dr. T. D. FORD, The University, Leicester
Dr. A. HALLAM, University Museum, Oxford
Dr. R. P. S. JEFFERIES, British Museum (Natural History), London
Dr. G. A. L. JOHNSON, The University, Durham City
Dr. W. D. I. ROLFE, Hunterian Museum, Glasgow
Dr. A. H. SMOUT, British Petroleum Company, Sunbury-on-Thames
Dr. L. B. H. TARLO, The University, Reading
Professor H. B. WHITTINGTON, Sedgwick Museum, Cambridge

Overseas Representatives

Australia: Professor DOROTHY HILL, Department of Geology, University of Queensland, Brisbane
Canada: Dr. D. J. MCLAREN, Institute of Sedimentary and Petroleum Geology, 3303-33rd Street NW., Calgary, Alberta.
India: Professor M. R. SAHNI, 98 The Mall, Lucknow (U.P.), India
New Zealand: Dr. C. A. FLEMING, New Zealand Geological Survey, P.O. Box 368, Lower Hutt
West Indies and Central America: Mr. JOHN B. SAUNDERS, Geological Laboratory, Texaco Trinidad, Inc., Pointe-à-Pierre, Trinidad, West Indies
Western U.S.A.: Professor J. WYATT DURHAM, Department of Paleontology, University of California, Berkeley 4, Calif.
Eastern U.S.A.: Professor J. W. WELLS, Department of Geology, Cornell University, Ithaca, New York

PALAEONTOLOGY

VOLUME 11 · PART 1

CONTENTS

Some new diplograptids from the Llandovery of Britain and Scandinavia. <i>By</i> O. M. B. BULMAN and R. B. RICKARDS	1
<i>Propectinatites</i> , a new Lower Kimmeridgian ammonite genus. <i>By</i> J. C. W. COPE	16
Epizoic oysters on Kimmeridgian ammonites. <i>By</i> J. C. W. COPE	19
New evidence on <i>Jaymotius kerwoodi</i> White, an important ostracoderm from the Silurian of Lanarkshire, Scotland. <i>By</i> A. RITCHIE	21
The Jurassic dinosaur <i>Scelidosaurus</i> , Owen. <i>By</i> B. H. NEWMAN	40
Tabulate corals from the Ilfracombe Beds (Middle-Upper Devonian) of North Devon. <i>By</i> the late F. J. W. HOLWILL	44
Carboniferous schizophoriid brachiopods from western Europe. <i>By</i> YVONNE P. POCOCK	64
Preserved ligaments in Australian Permian bivalves. <i>By</i> B. RUNNEGAR	94
<i>Biscalitheca</i> (Coenopteridales) from the Upper Pennsylvania of Illinois. <i>By</i> T. L. PHILLIPS and H. N. ANDREWS	104
A Tournaisian spore flora from the Cementstone Group of Ayrshire, Scotland. <i>By</i> H. J. SULLIVAN.	116
A sinus-bearing monoplacophoran and its role in the classification of primitive molluscs. <i>By</i> H. B. ROLLINS and R. L. BATTEN	132
Marine brackish bands and their microfauna from the lower part of the Weald Clay of Surrey and Sussex. <i>By</i> T. I. KILENYI and N. W. ALLEN	141

FZ.

VOLUME 11 • PART 2

Palaeontology

MARCH 1968

PUBLISHED BY THE
PALAEOLOGICAL ASSOCIATION
LONDON

Price £3

THE PALAEOONTOLOGICAL ASSOCIATION

The Association was founded in 1957 to further the study of palaeontology. It holds meetings and demonstrations, and publishes the quarterly journal *Palaeontology*. Membership is open to individuals, institutions, libraries, etc., on payment of the appropriate annual subscription:

Institute membership	£7. 0s. (U.S. \$16.00)
Ordinary membership	£5. 0s. (U.S. \$13.00)
Student membership	£3. 0s. (U.S. \$8.00)

There is no admission fee. Student members are persons receiving full-time instruction at educational institutions recognized by the Council; on first applying for membership, they should obtain an application form from the Secretary or the Treasurer. All subscriptions are due each January, and should be sent to the Membership Treasurer, Dr. A. J. Lloyd, Department of Geology, University College, Gower Street, London, W.C.1, England.

Palaeontology is devoted to the publication of papers (preferably illustrated) on all aspects of palaeontology and stratigraphical palaeontology. Four parts at least are published each year and are sent free to all members of the Association. Members who join for 1968 will receive Volume 11, Parts 1 to 5.

All back numbers are still in print and may be ordered from B. H. Blackwell, Broad Street, Oxford, England, at £3 per part (post free). A complete set, Volumes 1-10, consists of 38 parts and costs £114.

Special Papers in Palaeontology is a series of substantial separate works published by the Association. The subscription rate is £6 (U.S. \$16.00) for Institute Members and £3 (U.S. \$8.00) for Ordinary and Student Members. Subscriptions and orders by members of the Association should be placed through the Membership Treasurer.

The following *Special Papers* are available. Members may obtain them at reduced rates through the Membership Treasurer. Non-members may obtain them from B. H. Blackwell, Broad Street, Oxford, England, at the prices indicated.

Special Paper Number One (for 1967): MIOSPORES IN THE COAL SEAMS OF THE CARBONIFEROUS OF GREAT BRITAIN, by A. H. V. Smith and M. A. Butterworth. 324 pp., 72 text-figs., 27 collotype plates. Price £8 (U.S. \$22.00), post free.

Special Paper Number Two (for 1968): EVOLUTION OF THE SHELL STRUCTURE OF ARTICULATE BRACHIOPODS, by Alwyn Williams. 55 pp., 27 text-figs., 24 collotype plates. Price £5 (U.S. \$13.00).

Special Paper Number Three (for 1968): UPPER MAESTRICHTIAN RADIOLARIA OF CALIFORNIA, by Helen P. Foreman. Text with 8 collotype plates. Price £3 (U.S. \$8.00).

Typescripts on all aspects of palaeontology and stratigraphical palaeontology are invited. They should conform in style to those already published in this journal, and should be sent to Mr. N. F. Hughes, Department of Geology, Sedgwick Museum, Downing Street, Cambridge, England, who will supply detailed instructions for authors on request (these are published in *Palaeontology*, 10, pp. 707-12).

CORRIGENDA

for *Palaeontology*, Volume 3, Part 2, at Reprinting 1968

page 155, line 18: For 'GSM 7176', read 'GSM 7177'.

page 155, line 5 up: For 'GSM 87097', read 'GSM 87079'.

page 163, line 8: For 'GSM 7176', read 'GSM 7177'.

page 164, line 7: For 'Plate 26, fig. 11', read 'Plate 26, fig. 10'.

page 164, Explanation of Plate 26,

line 5 up: For 'Fig. 10', read 'Fig. 11'.

line 4 up: For 'GSM 7176', read 'GSM 7177'.

line 3 up: For 'Fig. 11', read 'Fig. 10'.

page 182, Explanation of Plate 29,

line 6 up: For 'GSM 87091', read 'GSM 87101'.

page 227, line 12 up: For 'Muscovian', read 'Moscovian'.

page 240, Explanation of Plate 41,

line 3 up: For 'partition', read 'extremity'.

CORRIGENDA

for *Palaeontology*, Volume 3, Part 3, at Reprinting 1968

page 388, Text-figure caption,

End of first line: For 'teeth or' read 'teeth of'.

End of fourth line: For 'ridge) of', read 'ridge) or'.

page 392, line 14: For 'Position', read 'Posterior'.

CORRIGENDUM

for *Palaeontology*, Volume 3, Part 4, at Reprinting 1968

page 497, Table 1, Column 8:

For 'Hopton Wood Clay', read 'Horton Wood Clay'.

ADDENDUM

page 590, line 3 up: The name *Brightonia* is preoccupied
(see Note in Volume 4, Part 2, page 312).

THE MICROSTRUCTURE AND MINERALOGY OF THE SHELL OF A JURASSIC MYTILID (BIVALVIA)

by J. D. HUDSON

ABSTRACT. Well-preserved shells of *Praemytilus strathairdensis* (Anderson and Cox) from the Great Estuarine Series (Middle Jurassic) of the Isle of Eigg, Scotland, are described with special reference to their microstructure, mineralogy, and chemical composition. Both the main calcareous shell layers are nacreous, with the crystal structure apparently identical to modern nacre. Myostracal layers are composed of prismatic aragonite; calcified traces of the periostracum have been observed. The inner layer shows sub-layers defined by variations in thickness of the nacreous laminae. These probably represent seasonal growth. Mineralogically, the shells are wholly aragonite, with a high strontium content compared to modern bivalves. The organic matrix is in part physically preserved but with altered ultrastructure; it is reduced in amount from the probable original value and the carbon-nitrogen ratio is much higher. The species is one of the earliest representatives of *Mytilus sensu lato*; the structural data agree with this. The aragonitic composition suggests warm temperatures, by comparison with modern Mytilidae; the growth pattern suggests the existence of seasons.

IN 1930 Bøggild laid the foundations for all subsequent studies of molluscan shell structure in a classic paper in which he defined the different types of structure and surveyed their distribution, and that of aragonite and calcite mineralogies, among the Mollusca. He was extremely cautious in offering interpretations of his extensive observations, but clearly showed that shell structure is of potential importance in taxonomy. The taxonomy he himself used is not entirely satisfactory and there is no doubt that some of his material, from old museum collections, was misleadingly identified (Schenck 1934, Lowenstam personal communication). Newell (1937, 1942, 1965) is one of the few authors who has critically studied shell structure in connexion with systematic palaeontology.

In recent years it has become clear that shell structure is in part ecologically, as well as taxonomically, controlled; high temperatures have been shown to favour aragonite over calcite in the molluscan shell (as well as in other phyla), so that warm-water and cold-water species of the same genus, or other taxon, differ in their mineralogy (Lowenstam 1954*a*). This mineralogical change necessarily involves also a change in shell structure, as in *Chama* (Lowenstam 1954*a*, 1963). Striking instances of this effect occur in the Mytilidae. Lowenstam (1954*a*) found that the tropical species he examined were 100% aragonite, whereas the temperate species, particularly *Mytilus californianus*, were composed of aragonite plus calcite with the aragonite percentage positively correlated with temperature. The results on the temperate species have recently been extended by Dodd (1963, 1964, 1965) who considered shell structure and trace-element concentrations as well as mineralogy, and by Hare (1963) who has studied the composition of the the organic matrix. Some tropical species have been examined in detail by Hare, Hudson, and Lowenstam (unpublished data).

The existence of this unusually good, though still incomplete, knowledge of the modern forms, together with the apparent coherence of the Mytilidae over long periods of geological time, makes investigations of fossil representatives of this family an attractive proposition. This paper is a description of some unusually well-preserved shells of the

Jurassic species *Praemytilus strathairdensis* (Anderson and Cox) with a brief discussion of the taxonomic and ecological implications.

OCCURRENCE AND PRESERVATION

Mytilus (Praemytilus) strathairdensis was described by Anderson and Cox (1948) from the Great Estuarine Series (Middle Jurassic) of Strathaird, Isle of Skye, Scotland. Their material consisted of internal and external moulds in hard shale. The species also occurs, with the shell well preserved, in the Isle of Eigg, 18 miles south of the Skye locality. Both localities are in the Mytilus Shales of the Great Estuarine Series; the species is known only from this formation and has not been found outside the Hebrides. All the material for the present study came from Bed 5 of the type locality of the Mytilus Shales in Eigg (Hudson 1963, p. 338; pl. 53, fig. 6). A detailed account of the stratigraphy and palaeoecology of the Mytilus Shales is given by Hudson (1966).

The material consists of shells preserved in shell-layers in soft silty shales; most are disarticulated but some have the valves still associated. They are translucent and have a pearly lustre, though without the brilliant iridescence shown by some fossil nacreous shells. They are unfortunately very fragile mechanically. In associated beds the shells are found in various stages of diagenetic alteration. This subject will be treated in more detail elsewhere (Hudson, 1965, abstract).

SHELL MORPHOLOGY

The species *Mytilus (Praemytilus) strathairdensis* was described by Anderson and Cox (1948) who created the monotypic subgenus *Praemytilus* for it. Their diagnoses were as follows:

Subgeneric characters. Shell much resembling *Mytilus s. str.* in shape, with a rather broad, reflected marginal area, without teeth, in the umbonal angle, and with a deep, elongate anterior adductor scar close and parallel to the antero-ventral margin. Ligament supported by a sub-internal ridge, as in *Mytilus s. str.*

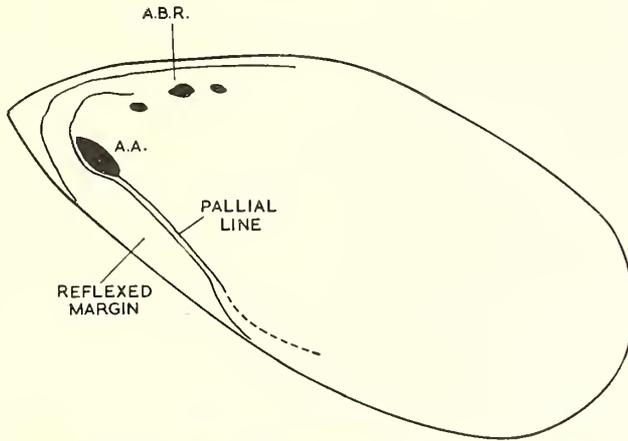
Specific characters. Medium size for a Mytilid, obliquely ovate, of slightly variable proportions; a line from the umbo to the most distant point on the posterior margin usually makes an angle of about 30° with the hinge margin. Umbo terminal. Dorsal margin feebly convex, meeting the moderately convex posterior margin in an even curve; ventral margin evenly convex; anterior lobe undeveloped. Shell evenly inflated except for a slight postero-dorsal flattening; no umbonal ridge. Surface unornamented, but with pronounced, irregular growth rugae. Anterior adductor scar deep and elongate, extending from the umbonal angle in a direction parallel to the antero-ventral margin.

The holotype measures 29.5 mm. in length and 17.5 mm. in height perpendicular to hinge margin. Anderson and Cox comment on the distinctive, for a Jurassic mytilid, evenly convex outline, and remark that the shell seems to have been very thick.

My material agrees with this diagnosis except that the growth rugae would not be described as 'pronounced' by comparison with most modern Mytilidae, and they are fairly regular in shape, although there are variations in the strength of individual rugae. The shell is thick in the umbonal region, but very thin elsewhere. At the level of taxonomic discrimination used by Soot-Ryen (1955) for recent Mytilidae there is little doubt that *Praemytilus* ranks as a full genus.

The new material enables some details to be added to the description of the internal structure of the shell. The structures are typically mytilid and, as is usual in the family, the details are somewhat variable.

Musculature. The deeply impressed and elongate anterior adductor scar was noted by Anderson and Cox (1948, p. 106). My specimens also show the anterior byssal retractor scar, in a similar dorsal position to that in modern Mytilidae (text-fig. 1, cf. Newell 1942, Soot-Ryen 1955). Both these muscle scars are striated in well-preserved specimens. Sometimes there is another scar below and anterior to the byssal retractor; possibly the termination of this muscle was bifid as shown by Newell (1942) for some Palaeozoic forms. Thus there is direct evidence that the species was byssiferous throughout life. There is no direct evidence of the emergence of the byssus, but by analogy with modern



TEXT-FIG. 1. Interior of right valve of *Praemytilus strathaird-ensis*, showing musculature. A.A., anterior adductor; A.B.R., anterior byssal retractor (with two small additional muscle scars). The posterior musculature is unknown. Anterior traced from a photograph; posterior outline reconstructed, based on a more complete specimen. $\times 2\frac{1}{2}$.

Mytilus it probably emerged just posterior to the termination of the thickened antero-ventral margin which is described below. Other small muscle scars are seen in the umbonal cavity on some specimens but they are not constant. Probably they bore mantle-attachment muscles. There is often a line of small discrete pits along the anterior part of the pallial line. The posterior musculature has not been seen on any of the specimens or moulds examined. It must have been very shallowly impressed. The shell in this region is very thin and fragile.

Hinge structure and reflexed margin. The most distinctive internal feature of the species is a broad, reflexed, and thickened margin to the antero-ventral part of the shell. It is especially thick, forming a swelling, immediately behind the deeply impressed anterior adductor muscle scar, where it is bordered internally by the pallial line (text-fig. 1). At one-quarter to one-third of the length of the shell the thickened margin fades gradually into the general margin of the shell. From the anterior adductor scar the reflexed margin continues in a smooth curve inside the umbonal region, so that the species has an internal 'platform' which is lacking in *Mytilus s. str.* or other modern mytilids. Usually this platform is quite smooth, so that the shell is edentulous, but in a few specimens

there are corrugations immediately behind the umbo. Unlike the teeth of *Mytilus s. str.*, these are not continuations of grooves across the external lunule which occurs behind the umbo in this position. Traced beneath the dorsal margin, the 'platform' decreases rather rapidly in thickness and disappears in the region of the anterior byssal retractor muscle scar.

The ligament region is marked by a thin and fragile flange, of lesser external convexity than the rest of the shell, which extends from the umbo along the dorsal margin. This easily breaks off in development. In some specimens it can be seen to bear a thin ridge between the dorsal margin and the 'platform', and this apparently continues dorsally beyond the 'platform'. There is no preserved trace of the ligamental ridge of porous, prismatic aragonite which is present in modern Mytilidae, but the thin ridge referred to could correspond to the nacreous ridge which lies below the porous ligamental ridge in the modern forms. The ligament was 'split' and non-functional in adult shells at the anterior end, in the region of the lunule, as in modern *Mytilus* (Stasek 1963, fig. 4D). This is shown by a specimen which has the valves attached where they were held by the ligament but in which they gape in the region of the lunule.

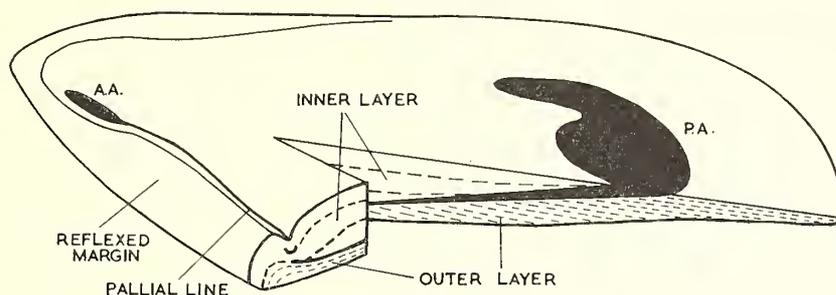
Ontogeny. Juvenile shells are abundant in the rocks studied. Like the juveniles of many other Mytilidae, they are modioliform in shape, with a distinct ventral lobe. The transformation to the mytiliform adults can be followed in the growth-lines of adult individuals. In shells greater than about 5 mm. in length, growth in the plane of the commissure was concentrated in a posterior direction, so that the umbones became effectively terminal. Beneath the umbones growth was almost entirely normal to the commissure in later ontogeny, as the shell inflation increased and the reflexed antero-ventral margin was formed. At a still later stage growth at the shell margin ceased, but the shell was still thickened by the deposition of inner layer material in the umbonal cavity. This is commonly found in modern *Mytilus*.

SHELL STRUCTURE AND MICROSTRUCTURE

The shells of bivalves are composed of structurally and sometimes mineralogically distinct layers secreted by different parts of the mantle, as described in general accounts Yonge (1960), Wilbur (1964), and Mutvei (1964). The outermost layer, the *periostracum*, is secreted by the inner surface of the outer mantle fold. It is not calcified. Inside the periostracum are two or more calcareous layers. In many bivalves two such layers are readily distinguished, an *outer layer* secreted by the outer surface of the outer mantle fold, and an *inner layer* secreted by the whole mantle surface inside the pallial line. Oberling (1964) points out, however, that there are frequently three main calcareous layers, and that these may also be divided into *sub-layers* by alternations of structure within a main layer. He also stresses the importance of structurally distinct layers secreted beneath the muscle attachments. These he terms the *myostracal layers*, differentiated into *adductor myostracum*, etc., according to the muscle concerned. The alternative term 'hypostracum' has been used in conflicting senses for both inner (main) layer and adductor myostracum (Oberling 1955, 1964). The 'Helle Schicht' of Schmidt (1924) refers to adductor myostracum. The classic account of shell microstructure (i.e. the arrangement of crystals and organic matrix within a layer, rather than

the arrangement of layers within a shell) is that by Bøggild (1930) whose terminology will be used here. The individual layers of aragonite crystals in nacreous structure will be referred to as *laminae*.

The shell structure of *Praemytilus strathairdensis* is summarized in text-fig. 2. Apart from rare preserved traces of periostracum, the shell consists of two calcareous layers, a thin outer layer of nacreous structure with fine laminae (less than 0.5μ) and a thicker inner layer, also nacreous but with coarser (1μ) laminae; the inner layer is divided into



TEXT-FIG. 2. Reconstruction to show the distribution of shell layers in *Praemytilus strathairdensis*, showing longitudinal and transverse sections. Trend of nacreous laminae schematically shown in outer layer; myostracal layers black; sub-layers schematically shown in inner layer. A.A. anterior adductor; P.A. posterior adductor, conjecturally drawn after modern Mytilidae.

sub-layers. Between the main layers is a thin layer of pallial myostracum. In the hinge region the structure is complex with traces of anterior adductor—and byssal retractor—myostracum preserved.

In thin sections the layers are not always easy to distinguish, but usually the nacreous structure of the inner layer is apparent under high power, and its division into sub-layers is best seen under crossed nicols (Pl. 35, fig. 1). The outer layer appears homogeneous in thin section but its structure is revealed by electron microscopy. Slightly altered shells are often coloured brown in thin section and are pseudopleochroic (Hudson 1962), with Y or $Z > X$, probably due to partial decomposition of the organic matrix. In these shells the outer layer is usually distinctly darker than the inner, and this helps in differentiating the layers.

In the following paragraphs the different shell layers are described in detail, and some special topics are discussed. In view of the importance of nacre in the shell, the microstructure of this material is described first. This paragraph is based mainly on the literature cited, supplemented by personal observations mainly on Mytilidae.

Crystal structure of nacre and its relationship to the organic matrix. The nacreous structure is found in the three main classes of the mollusca but is not known outside that phylum. It is the simplest and also the best-known type of molluscan microstructure. Its distribution within the mollusca is described by Bøggild (1930) and by Oberling (1964), who stress that it is particularly characteristic of the 'primitive' members of the molluscan classes (Archaeogastropods, *Nautilus*, Nuculidae, for instance). The most comprehensive optical study of nacre is by Schmidt (1924); Wada (1961) has published

a very well illustrated account of the crystal structure using electron microscopy and X-ray methods. The organic matrix has been studied, using electron microscopy, by Grégoire, Duchateau, and Florkin (1955) and by Grégoire (1957, 1959, 1962). More details of the relationship between the crystals and the matrix are revealed in an elegant study by Watabe (1965).

Nacre consists of tabular crystals of aragonite arranged in thin parallel sheets (laminae), typically 0.5–1.0 μ thick. These are separated by even thinner sheets of the proteinaceous organic matrix (conchiolin), less than 0.1 μ thick, the *interlamellar matrix*. The individual aragonite crystals within the laminae are separated by *intercrystalline matrix*, and within each single crystal are very fine sheets of *intracrystalline matrix* (Watabe 1965). The pattern formed by the interlamellar and intercrystalline matrices is responsible for the familiar brick-wall appearance of vertical sections of nacre (Pl. 31). The intracrystalline matrix is too fine to be seen with the light microscope and is only imperfectly seen on electron micrographs of surface replicas (like those used here). Its detailed distribution was revealed by Watabe (1965), who prepared diamond-knife ultramicrotome sections of the shell, and examined these by transmission electron microscopy both before and after decalcification. The structure is summarized in text-fig. 3. The continuous sheets of interlamellar matrix are a distinctive feature of nacreous structure, not found in other molluscan shell structures. If nacre is decalcified, separate sheets of organic matrix are released; if the organic matter is destroyed with sodium hypochlorite solution, sheets of aragonite (probably still containing some intercrystalline and intracrystalline matrix) are liberated. Diagenesis or weathering frequently has the same effect, and fossil nacreous shells are often 'flaky'.

Nacre has a regular crystal orientation. the *c* axis of aragonite is always normal to the laminae. On the growing surface of the shell, especially when growth is slow, euhedral crystals of aragonite may be formed (Schmidt 1924, Wada 1961). Wada showed that the commonest forms developed in the zone normal to the *c* axis in the pearl oyster *Pinctada* are (110), usually predominant, and (010), and that the orthorhombic *b* axis of the crystals are aligned in parallel growth normal to the growing edge of the mantle. Grégoire (1962) found that in *Nautilus* (010) was dominant, so that the crystals were elongated along *a* and this axis was normal to the growth-lines.

The fine structure of the interlamellar matrix has been described by Grégoire (1957, etc.). It consists of reticulated sheets of protein, the pattern of the reticulations being characteristic of the class (Gastropoda, Bivalvia, Cephalopoda). In the Bivalvia the reticulations are fine and the structure correspondingly dense. Grandjean, Grégoire, and Lutts (1964) recorded preservation of this pattern in some fossils, but in others it is

EXPLANATION OF PLATE 31

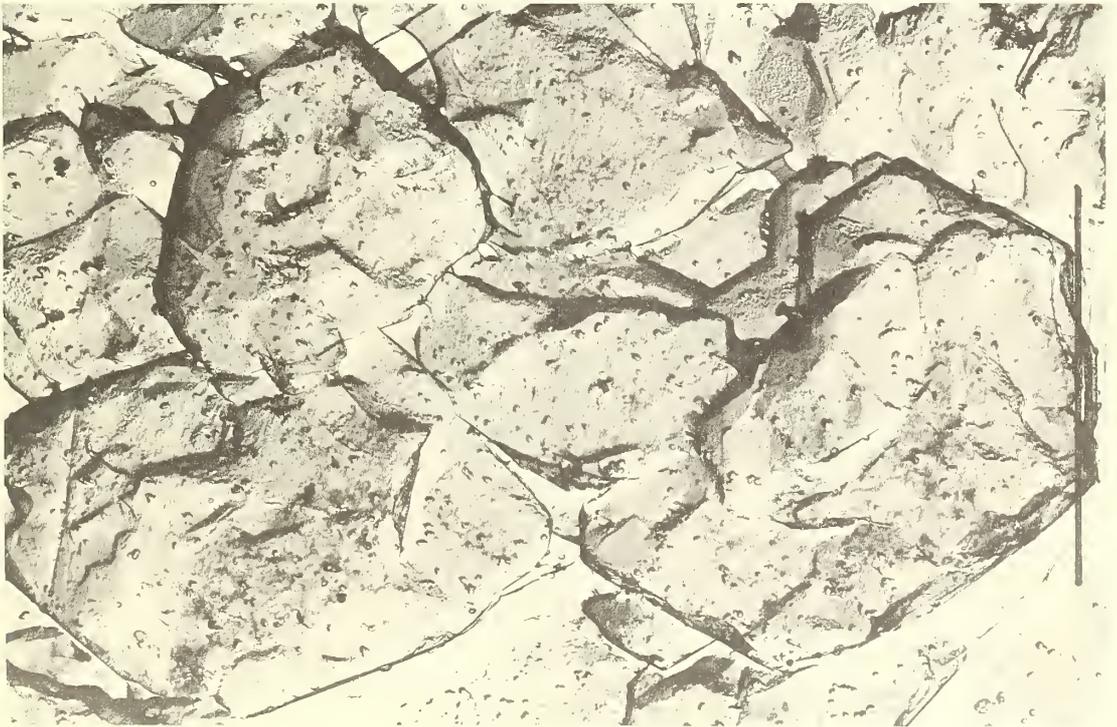
Plates 31–34 and figs. 2–4 of Plate 35 are electron micrographs of carbon replicas of broken or polished and etched sections of the shell of *Praemytilus strathairdensis*. Printed direct from film exposed in the microscope; shadows are white. Vertical sections are normal to the shell surface; horizontal sections parallel to it. Longitudinal sections are parallel, and transverse sections normal, approximately, to the axis of greatest growth of the shell.

Fig. 1. Nacreous structure. Broken vertical surface approximately normal to the laminae. Single-stage replica, $\times 6,800$ (scale measures 10 μ).

Fig. 2. Nacreous structure. Polished and etched vertical section approximately normal to the laminae. Two-stage replica, $\times 7,100$ (scale measures 10 μ).



1

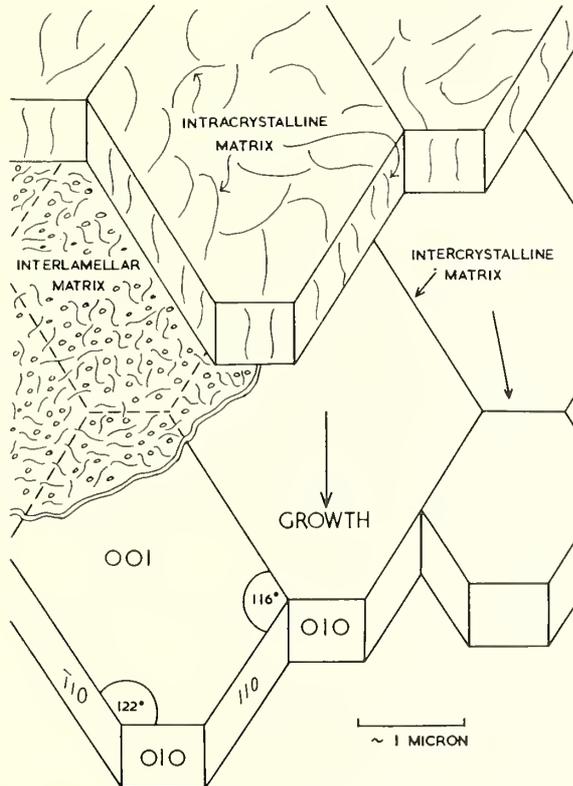


2

HUDSON, Jurassic mytilid shell microstructure

diagenetically altered to a meshwork of irregular swellings, and this change could also be produced by heating a modern shell (Grégoire 1965).

Wada (1961) studied seasonal variations in the crystal size and structure of nacre on the growing surfaces of *Pinctada* shells. He showed that when nacre deposition was fastest, in the autumn, many rather small (about 4μ) and uniform crystals were formed.



TEXT-FIG. 3. Generalized structure of bivalve nacre. Two laminae viewed obliquely in the yz plane of the constituent aragonite crystals, which are arranged in parallel growth. The laminae are separated by sheets of interlamellar matrix, of which a portion is shown with the reticulate structure drawn diagrammatically. Single crystals of aragonite are separated by intercrystalline matrix and contain intracrystalline matrix as thin sheets (shown diagrammatically in upper part of figure only). Growth in bivalves is in the direction of the y axis. The diagram shows structure only; it does not represent a stage in growth. (Based on the work of Wada, Watabe, and Grégoire.)

As growth slowed down before the winter cessation, crystals larger than 6μ were formed together with very small ones of less than 2μ . When growth started again in spring very small crystals predominated at first. Slow growth resulted in the best-formed aragonite crystals whereas fast-formed ones were rounded; during growth-halts resorption sometimes occurred resulting in corroded crystals (Wada 1961; especially table VIII, p. 758).

Structure of nacre in P. strathairdensis. The preservation of fossil nacre, including its sub-microscopic detail, has been recorded by several authors, especially Grégoire (1959) and Grandjean, Grégoire, and Lutts (1964). Similar excellent preservation has been studied in this species using the electron microscope.

Carbon replicas were used for electron microscopy. The surfaces replicated were of two kinds: (1) broken surfaces of nacre either parallel, approximately normal, or oblique to the lamination, (2) polished and etched surfaces, usually normal to the lamination and either longitudinal or transverse with respect to the shell. Various polishing techniques were used and either 1% HCl or saturated EDTA was used for etching, for times varying from 30 sec. to 3 min. Because of their lower organic content the etching times for fossil shells are less critical than with recent ones. From either broken or etched surfaces either single-stage or two-stage carbon replicas were prepared. For *single-stage replicas* carbon was evaporated *in vacuo* directly on to the prepared surface. The shell was then dissolved in very dilute HCl or dilute EDTA, and the carbon films floated free. They were transferred to distilled water before being picked up on grids for examination in the Philips 200 electron microscope. For *two-stage replicas* acetate peels were prepared of the chosen surfaces, by placing the surface on cellulose acetate with a few drops of acetone, allowing to dry, and stripping off. The peels were washed in HCl to remove adhering aragonite. The peels were then shadowed with carbon in the usual way. The area to be examined was cut out from the peels under a binocular microscope, the acetate dissolved in acetone and the carbon replicas floated off on distilled water before being picked up (from above) on parlodion-coated grids for electron microscopy. By making the cut-out areas of distinctive shape the orientation of these two-stage replicas with respect to the shell could usually be maintained. This is not possible, with the method employed, in the single-stage replicas, which also suffer from the fact that the method is destructive. However, single-stage replicas of broken surfaces are the simplest of possible replication techniques, and the most free from the danger of producing artefacts.

Vertical sections of *P. strathairdensis* nacre show the familiar brick-wall structure. In the inner layer the laminae are rather coarse (greater than $1\ \mu$) and show the structure particularly clearly (Pl. 31, fig. 1, of a broken section; Pl. 31, fig. 2, of a polished and etched section). The vertical strips of intercrystalline matrix define the individual aragonite crystals, and it can be seen despite imperfect replication of the matrix strips that many of the crystals in Plate 31 are between 5 and $10\ \mu$ across. Plate 35, fig. 4, shows indications of a structure, presumably the network of intracrystalline matrix, within the individual aragonite crystals. Observations with the light microscope show that this coarse, regular nacre has the aragonite *c* axis normal to the laminae, as in modern nacre (Pl. 35, fig. 1).

The shells of *P. strathairdensis* break easily along certain planes parallel to the lamination. These surfaces were examined mostly by single-stage replication. Some of them (Pl. 32, fig. 1) proved to bear very well preserved, sharply euhedral crystals of aragonite, showing parallel growth and development of (101) and (110) faces. They are apparently identical to the crystals on modern nacre described and figured by Wada (1961, p. 757, figs. 102–4, etc.). Their orientation with respect to the growth direction of the shell is not known. Plate 32, fig. 2, shows small rounded objects up to $0.2\ \mu$ in diameter scattered over the surface of the larger crystals. These resemble the crystal seeds described by Watabe *et al.* (1958, p. 282, fig. 1) as the early stages of the formation of

EXPLANATION OF PLATE 32

For explanation of preparation of electron micrographs see Plate 31. The scale shown measures $10\ \mu$.
Fig. 1. Nacreous structure. Horizontal broken surface parallel to laminae. Euhedral aragonite crystals.

Single-stage replica, $\times 7,350$.

Fig. 2. Preparation as fig. 1. Euhedral aragonite crystals and (?) crystal seeds. $\times 5,300$.



1



2

calcite crystals in oysters. The diameter of the large crystals is about 12–14 μ in Plate 32, fig. 2, and 6–8 μ in Plate 32, fig. 1. Other broken surfaces showed smaller and less regular polygons. Sometimes these were aggregated into apparently continuous sheets, with the crystal boundaries (defined by intercrystalline matrix) not conforming to any regular crystal shape. In other cases the polygons, although irregular, remained distinct from each other and the gaps between them were presumably filled, in life, with organic matrix, or were void. The diameter of the irregular polygons varied from about 0.5–3 μ . An acetate peel of a broken surface showed, under the light microscope, fragmentary growth-spirals similar to those described by Wada (1961, p. 767).

The variations in *P. strathairdensis* may be related to the supposedly seasonal growth variations which are also reflected in the vertical thickness of laminae (see below). It has not been possible so far to relate the two types of variation accurately, though it does seem that the crystals in the thick regular nacreous laminae are often fairly large in diameter ($> 6 \mu$).

When fragments of shell are decalcified they yield coherent but brittle sheets of brown-coloured organic matrix, representing part of the original interlamellar matrix. The chemical composition of this material is discussed below. Examined in the electron microscope by methods similar to those of Grégoire (1959) it has so far failed to show well-preserved ultrastructure of the kind figured by Grégoire from recent shells and some fossils. Instead it shows irregular swellings said to be characteristic of diagenetically altered fossil material (see Grandjean, Grégoire, and Lutts 1964, pl. II, etc.). More work is needed to see if all the *P. strathairdensis* material is similarly affected.

Vertical and horizontal sections examined by the replica techniques described above show 'sheets' corresponding positionally to the organic matrix. These may, in the case of two-stage replicas, be actual pseudo-replicas of the organic matrix itself, pulled off in making the peel (this certainly happens with recent shells), or they may be acetate which has penetrated cracks during the making of the peel. It is frequently impossible to tell the difference for certain (cf. Grégoire 1962, p. 8, footnote). On single-stage replicas folded-over carbon films can also be confused with true sheets of organic matrix, unless the matrix shows definite ultrastructure.

Thus *P. strathairdensis* nacre shows crystallographic features identical to those found in modern bivalve nacre, and some details of the relationship between the crystals and the organic matrix have been preserved. In the following paragraphs the distribution of nacre and other structures within the shell is described.

Periostracum. In thin sections of limestones, which consist largely of the aragonitic shells of *P. strathairdensis* cemented by calcite, the external surfaces of the shells are bordered by a thin sheath, about 5–15 μ thick, which is now composed of clear calcite devoid of internal structure. Usually the sheath adheres to the shell surface, but in places it has buckled and partially broken away from it. Such sheaths are only found on the external, never internal, surfaces of *Mytilus* shells, and have not been found on constituents of the limestones other than shells. Their spatial relations suggest that they are calcite-replaced periostraca. Presumably the conchiolin of the periostraca was replaced by calcite, while that of the calcareous layers was not, because it was external to the shell and not enclosed in aragonite. Also Hare (1963) shows that the amino-acid composition of the periostracum of *Mytilus californianus* differs from that of the protein matrix of the calcareous layers. Calcite has replaced a variety of minerals in these rocks,

and in the Ostracod Limestones a little higher in the succession the 'chitinous' carapaces of *Euestheria* have been replaced. No electron micrographs have been made, but similar sheaths on gastropods from the Reptile Bed of the Mytilus Shales (Hudson 1963, 1966) have been seen on micrographs. They showed no structures apart from calcite crystal boundaries.

Outer layer. This is fairly uniform in thickness over the major part of the shell. Typical values are: 80 μ at the pallial line in a small shell; 200 μ at the pallial line and 140 μ near the centre of a large shell; and several measurements of around 150 μ on apparently adult shells.

In thin sections with the light microscope the structure appears homogeneous, but on electron micrographs the structure is revealed as typically nacreous, with fine laminae. The thickness of these has been estimated by measuring groups of from 12–60 laminae and calculating the mean. Within such groups the individual lamina thickness is fairly uniform. The range of mean values for the main part of the shell is 0.32–0.51 μ , with a grand mean of 16 determinations (mostly of different parts of one shell) of 0.41 μ . This means that the outer layer, given a mean thickness of 140 μ , contains about 340 laminae in the central part of an adult shell. There is a tendency for lamina thickness to increase towards the ventral margin as the thickness of the outer layer increases. Beyond the pallial line, in the thickened reflexed margin, the distinction between inner and outer layers, in the absence of a myostracum, cannot be made on lamina thickness. In this region laminae have a mean thickness of about 0.7 μ .

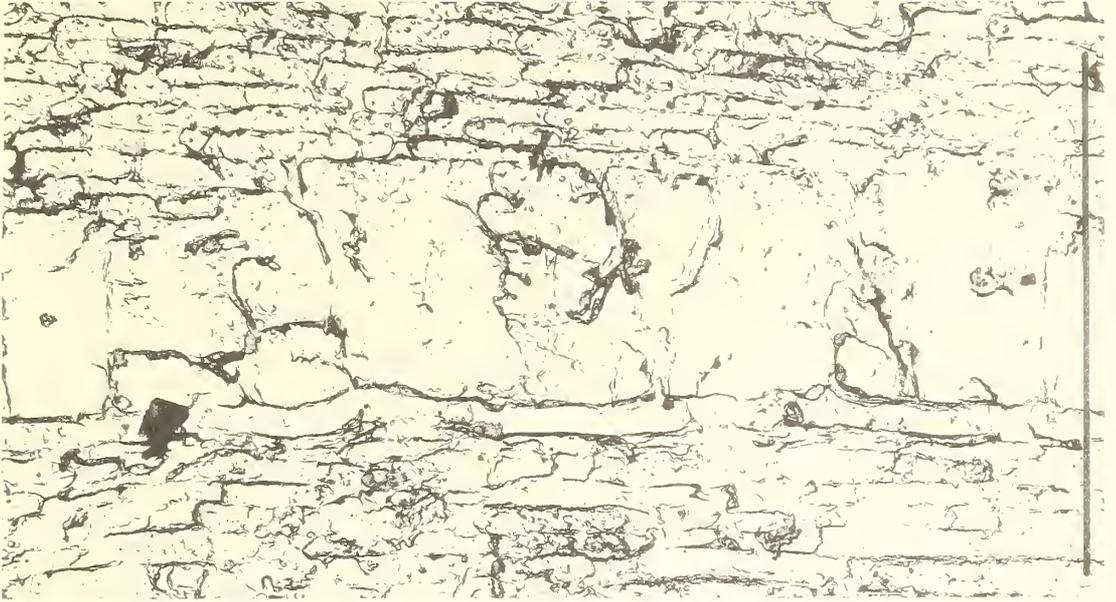
Myostracal layers. Between the inner and outer shell layers, most sections show a layer about 3 μ thick (sometimes up to 10 μ), which is not divided into nacreous laminae. Its structure, where discernible, appears to be coarsely prismatic with the columns almost as wide as they are high. By analogy with modern mytilids (Schmidt 1924; Hudson, unpublished), this is interpreted as a myostracal layer. In the main part of the shell it must represent pallial myostracum or the myostracal layers associated with the posterior musculature. It is emplaced between the main shell layers, as the shell grows, because the pallial line is the border of the area of secretion of the inner layer. In this main part of the shell the myostracum is parallel, or nearly so, to the nacreous lamination (Pl. 33, fig. 1), but towards the margin it is oblique to, and truncates, the laminae of the outer layer (Pl. 35, figs. 2, 3).

Myostracal layers, which are similar in internal structure to the pallial myostracum, occur associated with the anterior adductor muscle and the pallial line immediately posterior to it, in the trough between the main part of the shell and the reflexed ventral margin. Some of these are enclosed entirely within the inner layer. The complex structures of this region are further described below.

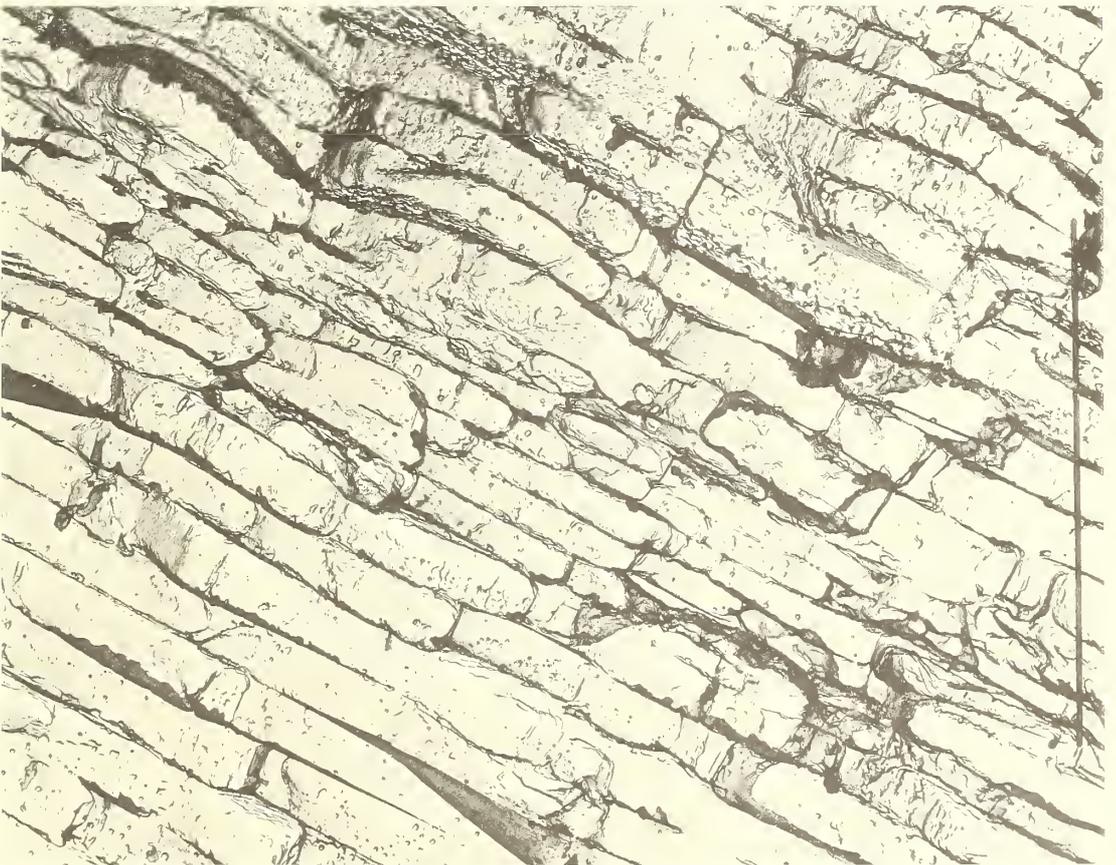
EXPLANATION OF PLATE 33

For explanation of preparation of electron micrographs see Plate 31. The scale shown measures 10 μ .
 Fig. 1. Myostracal layer in nacre; outer layer at top, inner layer beneath. Polished and etched vertical transverse section. Two-stage replica, $\times 7,000$.

Fig. 2. Sub-layer junction in inner layer nacre. Later formed sub-layer is in lower left of photograph. Polished and etched vertical transverse section. Two-stage replica, $\times 7,000$.



1



2

Inner layer. This reaches a thickness of at least 1.5 mm. in the post-umbonal region of thick adult shells, and extends to the pallial line where it forms a feather-edge. The microstructure is typically nacreous as seen by both light and electron microscopy. The most conspicuous feature is that the layer is divided into several sub-layers. As seen in vertical section, each sub-layer consists of clear, coarsely laminated nacre at its outermost (i.e. oldest) part, and for most of its thickness. The thickness of laminae decreases gradually, and at the junction with the next sub-layer there is a zone of fine laminae, not easily resolvable with the light microscope. Between crossed nicols, with the main part of the nacre in extinction, the junction zone shows up as speckles of light, apparently because the aragonite crystals are less well orientated there.

On electron micrographs, the layer junction appears as a group of from 5–20 (approx.) laminae which are much finer than the adjacent ones. They tend to grade into those above (i.e. older), and have a sharp junction with those below, but their limits may be difficult to define. Frequently the junction zone has acted as a weak zone in etching so that replication is poor. In the main part of the shell the laminae in adjacent sub-layers are parallel or nearly so (Pl. 33, fig. 2).

The maximum number of sub-layers seen in a shell is about eight, and this number or thereabouts is frequently attained. The range of thickness of sub-layers is not large (about 150–250 μ), and thick shells have more sub-layers than thin ones. This is consistent with their having been added throughout the life of the animal at a constant rate. Apparently similar sub-layers are found in the inner-layer nacre of the pearl oyster, *Pinctada*, where each sub-layer is interpreted as representing one year's growth (Wada 1961, p. 727, fig. 41).

Sub-layers and laminae. One transverse section of the post-umbonal region (E 203 D) provided particularly good replication of laminae for measurement by electron microscopy, and more detailed measurements were made on it. The number of laminae in each sub-layer was estimated and the results are summarized in text-fig. 4. It was not possible to count all the individual laminae across the sub-layers, because of interruption by grid bars and imperfect replication. Instead the thickness of each sub-layer was measured in the light microscope, and then electron micrographs were taken of each sub-layer junction and of typical nacre within each sub-layer. From these micrographs the number and thickness of laminae actually photographed could be determined, and mean thicknesses estimated for the remaining laminae. Thus the total number of laminae for each sub-layer was estimated. Obviously this method of calculation is not ideally precise. The range obtained was 120–230 laminae per sub-layer. The outer (first-formed) sub-layers have, in general, finer laminae than the inner ones (mean of 0.8–0.9 μ for the uniform central part of the outermost sub-layer, compared with 1.4–1.5 μ for several separate determinations on the inner four sub-layers). The fine laminae at sub-layer junctions have mean thicknesses around 0.5–0.7 μ . These measurements were all made on one carbon replica, but other parts of the same shell and of different shells gave similar results.

Structure of the reflexed margin. The same transverse vertical section (E 203 D) that was used to measure the laminae described in the last paragraph also gives a section through

the reflexed ventral margin, posterior to the anterior adductor muscle scar. This has been examined by means of peels and electron micrographs. Random sections of the same region, both approximately longitudinal and approximately transverse, have been studied in thin sections of limestones. The structure is complex and not fully understood. However, certain points can be established; in particular, the sharp division into two layers, characteristic of the main part of the shell, does not seem to hold.

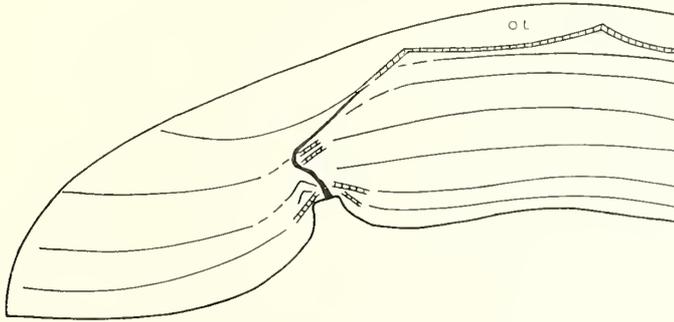
LAYER OR SUBLAYER	LAYER THICKNESS	MEAN LAMINA THICKNESS	ESTIMATED No. OF LAMINAE
OUTER LAYER	140	(0.41)	(340)
MYOSTRACUM	3	—	—
INNER LAYER: SUBLAYER 1	120	0.83 0.94 — 0.56 —	150
2	220	1.3 0.94 1.0 — 0.58 —	220
3	290	1.0 1.4 — 1.1 — 0.54 —	230
4	220	1.2 1.4 — 1.0 — 0.7 —	160
5	150	0.95 1.4 0.98 — 0.54 —	130
6	170	1.3 1.5 — 1.2 —	120
7	120	0.86 1.3	100(+ ?)

TEXT-FIG. 4. Data on laminae in a vertical section of *Praemytilus* nacre. Thicknesses are in microns. Figures in brackets extrapolated from different sections. The broken lines at the base of each sub-layer delimit the transition zone of thin laminae at sub-layer junctions. For explanation, see text.

Text-fig. 5 is based on the polished section and peels of E 203 D, incorporating some evidence from electron microscopy. Note that (1) the outer layer thickens towards the pallial line. (2) The outer sub-layers of the inner layer abut against the outer layer in this same region. (3) The myostracum separating the outer and inner layers disappears in the region of the pallial line. (4) At the pallial line the sub-layers of the inner layer are sharply curved into 'anticlines', some of which include prismatic layers identical to myostraca. Sharp angular breaks between sub-layers are present (Pl. 34). (5) Within the reflexed margin, beyond the final position of the pallial line, all laminae are more or less

parallel and there is no myostracum, so that there is no clear distinction between 'inner' and 'outer' layers. However, at least part of the thickness is probably 'inner' layer, because it includes sub-layers like those of the inner layer proper. Coloration in thin-section, and the thickening of the outer layer towards the pallial line which was mentioned above, suggest that the 'outer layer' is nevertheless rather thick, as drawn in the figure. Other, less precisely orientated, sections show similar relations.

The relationships described imply that when the first few sub-layers of the inner layer were deposited the reflexed margin consisted entirely of 'outer layer', so that the pallial



TEXT-FIG. 5. Structure of the reflexed margin in a vertical transverse section of *P. strathairdensis*. O.L., outer layer. Myostracal layers shown in brick pattern. Trend of laminae in inner layer shown by sub-layer boundaries. The black line above the pallial line represents a crack in the specimen. Structures generalized, especially in the zone of complex folds above the pallial line. For detail of part of this region, see Plate 34. Plate 35, fig. 1, corresponds approximately to the right-hand end of this figure. Drawn from an enlargement of an acetate peel.

The shell is approximately 1.5 mm. thick.

line marked the junction between the layers, as in the main part of the shell. Subsequently, the margin was formed of material identical to the inner layer, so that the pallial myostraca and the unconformities of growth associated with the deeply impressed pallial line of the adult came to lie entirely within the inner layer.

If this is the case, the simple generalization that the outer layer is deposited by the mantle edge and the inner layer by the mantle surface within the pallial line, needs to be modified as regards this part of the shell. This is not surprising when the greatly different structural requirements of the two regions are considered. Probably the apparent cessation of shell-secreting activity by the mantle edge at the reflexed ventral margin is related to the fact that, after a certain point in ontogeny, the shell ceased to grow in the plane of the commissure in this region but only became thicker. For this, the type of mantle activity represented by the deposition of 'inner-layer' is sufficient, and the mantle edge no longer needs to extend itself or to produce new epithelial cells as it does in a normal marginal region. Plate 34 shows an example of the relationship between laminae, sub-layers, and myostracal layers in the region of the pallial line. The complex geometry and particularly the sharp truncations of earlier laminae may imply that some resorption of shell is necessary during the re-positioning of the pallial muscles which produces the successive layers of myostracal material.

MINERALOGY AND CHEMISTRY OF THE SHELLS

The excellent physical preservation of the microstructure suggested that a chemical investigation of the shell carbonate and organic matter might yield results of interest for comparison with modern shells. Results obtained so far are given here.

Mineralogy. The presence of aragonite in well-preserved *P. strathairdensis* shells was first conclusively shown by powder photographs taken by Dr. P. Gay at Cambridge (Hudson 1963). Later, a series of shells was selected to range from excellently preserved to porous and 'chalky', and analysed using the X-ray diffractometer procedure of Lowenstam (1954*a*) for calcite-aragonite ratio. All were aragonite, with calcite below the limit of detection (about 1%). This agrees with the results of Hallam and O'Hara (1961) that 'chalkification' does not necessarily involve a mineralogical change, and with unpublished results of the author's on other shells from the Jurassic and from the California Pleistocene terraces. Thin sections of limestones containing *P. strathairdensis* shells, cemented and infiltrated along cracks by sparry calcite, were tested using Feigl's solution, and the shells shown to consist of aragonite. Elsewhere, sometimes in the same rock, *Mytilus* shells have recrystallized to calcite (Hudson 1965).

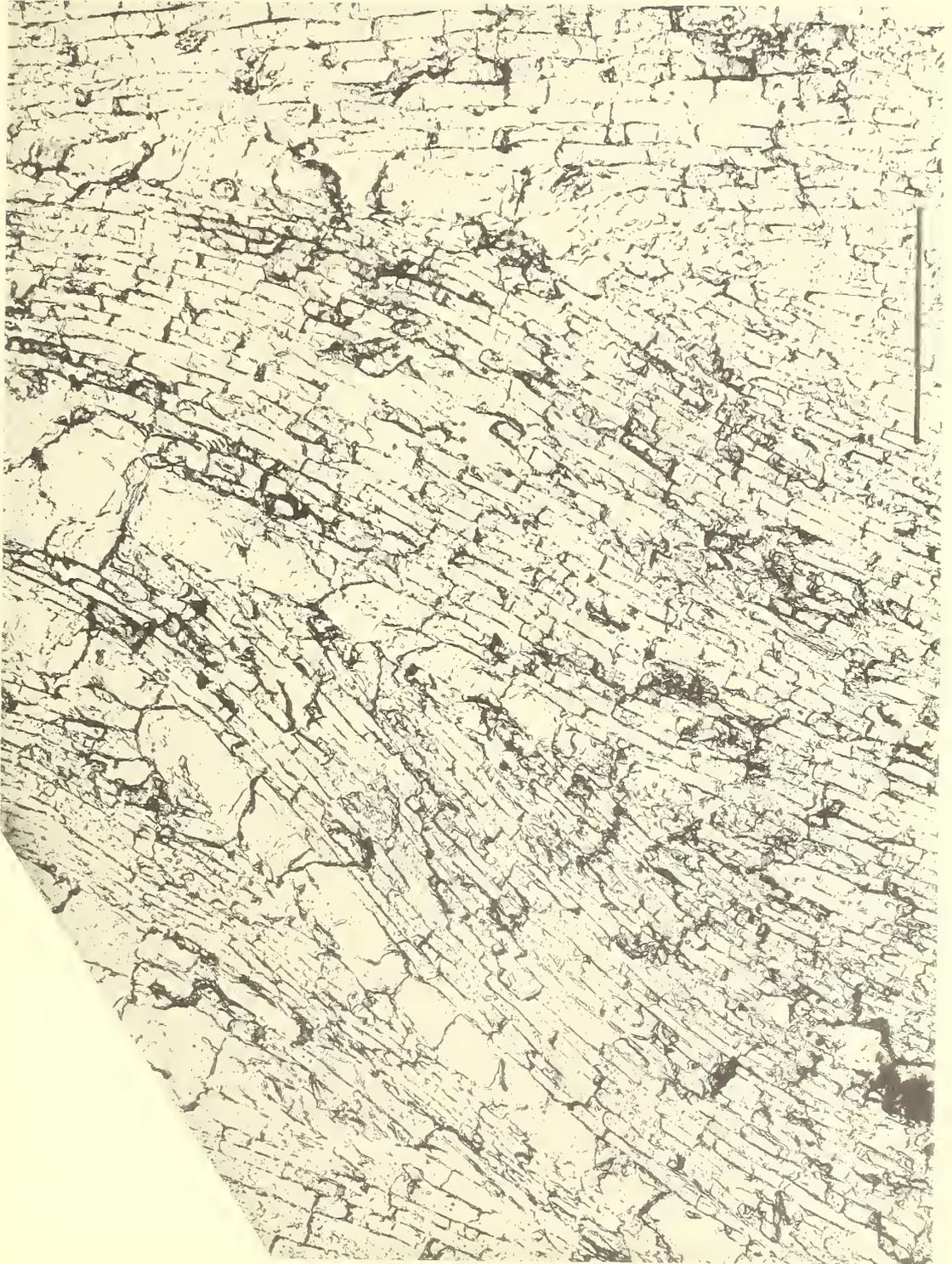
Strontium-calcium ratios. Strontium analyses of *P. strathairdensis* shells were made by optical emission spectroscopy and by the electron microprobe. A series of four shells from very well preserved to porous and 'chalky', previously shown to be aragonite as described above, were analysed spectroscopically for Sr and Mg by the methods used for brachiopod shells by Lowenstam (1961). The results are given in Table 1; each number is the mean and standard deviation of mean from three separate determinations. The apparently anomalous result (E 217) was repeated and confirmed. The results from the best-preserved shells are consistent.

Two well-preserved specimens were used for exploratory analyses by electron microprobe. Vertical transverse sections were made of the region behind the umbo where the inner layer is thick, and these were polished and coated with carbon in the usual way. Step-scan analyses of 1 μ spots were made at 10 μ intervals across the shell, Sr $L\alpha$, Ca $K\alpha$, and Mg $K\alpha$ count-rates over 20 sec. being recorded simultaneously. The Ca figures were used to make sure that the spot being analysed was aragonite (not a crack, etc.); the Mg figures were too low for estimation. The Sr figures were compared by direct proportionality to a strontianite standard containing 55% Sr. The mean Sr percentages for the two shells based on about 100 points each were 0.48% and 0.47% respectively. Clearly these figures need confirmation, using standards closer in composition to the unknown and with corrections for atomic number effect, etc., but the agreement between these first results and the emission spectroscopy results is gratifying. With the

EXPLANATION OF PLATE 34

For explanation of preparation of electron micrographs see Plate 31. The scale shown measures 10 μ .

Vertical transverse section in the region above the pallial line, between the reflexed margin and the main part of the shell. Outer layer uppermost. Shows complex folds in nacreous laminae and irregular myostracal layers. Two-stage replica, $\times 3,700$.



HUDSON, Jurassic mytilid shell microstructure

probe it will be possible to explore variations in Sr percentage between layers and sub-layers but the present data are insufficient for this. If variations can be found, this should put limits on the amount of diagenetic alteration undergone by the shells, since it is unlikely that minor variations would survive extensive trace element migration.

Interpretations of the present data are necessarily limited. The Sr figures are higher than those for modern aragonitic bivalves, though lower than those of aragonite secreted by the lower invertebrates (Lowenstam 1964). It is not possible at this stage to do more than speculate on possible biochemical evolution towards lower Sr/Ca ratios

TABLE I

Strontium contents of aragonitic Mytilid shells

Number	Specimen	Sr Wt. %	Atoms Sr/1000 Ca	Method or Reference
E 203	<i>P. strathairdensis</i> , well preserved	0.49±0.02	5.6	S
E 218-1A	" "	0.49±0.02	5.6	2
E 218-1B	" " (same shell)	0.42±0.04	4.8	2
E 217	" slightly 'chalky'	0.73±0.05	8.4	S
E 210	" very 'chalky'	0.49±0.03	5.6	S
E 220-1	" well preserved	0.48	5.5	P
E 220-2	" "	0.47	5.4	P
—	<i>Cuneolus tippiana</i> (U. Cret.), Tennessee	—	3.1	(1)
—	" " (U. Cret.), Maryland	—	3.5	(1)
—	<i>Septifer</i> sp. (Recent), Palau	—	2.2	(1)
—	<i>Mytilus californianus</i> , <i>M. edulis</i> (Recent), Calif. nacreous layer (negative temperature dependence of Sr)	—	1.5-2.5	(2)

S = optical emission spectroscopy, P = electron probe, (1) = Lowenstam (1964), (2) = Dodd (1965).
See discussion in text.

in aragonite within the Mytilidae, like that postulated by Lowenstam for certain gastropods. It is tentatively considered that the Sr figures of around 0.48% Sr (Sr/1,000 Ca = 5.5) are original and not diagenetic, but this needs more rigorous proof (cf. Turekian and Armstrong 1961). A further complication is the probable lagoonal habitat of *P. strathairdensis* (see below), so that the possible effects of abnormal salinity and water chemistry would also have to be considered. Nevertheless the figures for modern and Cretaceous Mytilidae, given in Table I for comparison, are interesting and further work should enable their significance to be assessed.

Organic matrix. Physical preservation of some organic matrix but with diagenetically altered ultrastructure has been described above in connexion with the structure of nacre. The proportion and chemical composition of this organic matrix were determined with an F & M Model 180 CHN Analyser, modified to allow the analysis of the organic fraction in the presence of shell carbonate. The organic matter is oxidized by heating in the presence of a catalyst, and the combustion gases passed over Cu and CuO. Peaks due to C (as CO₂), H (as H₂O), and N (as N₂) are separated by gas chromatography. The results were obtained as part of a more extensive investigation (Hudson, in press). Comparisons with modern Mytilidae indicate that (1) the total amount of organic carbon in the shells (mean of five specimens = 0.15%) is reduced to about 10-20% of

the probable original value (nacre of recent *M. californianus* = 0.65%, *Choromytilus palliopunctatus* = 1.0%, *M. smargdensis* = 1.9%). (2) The organic carbon/organic nitrogen ratio in the fossils (mean of five specimens = 23) is much higher than in the modern *Mytilus* nacre (range of several determinations 2.8–3.7). This indicates preferential loss of nitrogen and at least partial degradation of the original proteins, perhaps to 'kerogen-like' material. (3) High hydrogen contents beyond the H probably directly combined with the organic carbon. These amount to nearly 0.2% by weight of hydrogen, thought to be present as free water firmly trapped in the structure. It is not removed by drying at 110°. This excess water is a general feature of recent and fossil nacre (Hudson, in press.)

These data suggest extensive post-depositional alteration of the organic matrix so that it is unlikely to reveal details of its original composition.

DISCUSSION

Differences (or similarities) in microstructure, mineralogy, and chemistry between the species under discussion and other recent and fossil shells must be assessed with the following questions in mind: Are the differences original or are they the result of diagenetic alteration? If original, are they the result of taxonomic differences reflecting evolutionary history, or do they follow from the ecological habitat of the particular shells studied? Clearly the questions are linked and cannot profitably be considered separately from one another. In the following paragraphs taxonomic and ecological aspects are stressed and the question of diagenesis is dealt with as it arises.

Taxonomy and evolution. *Praemytilus strathairdensis* is distinct from any other described Jurassic species and has been found at only one stratigraphical horizon in one small basin of deposition. It is, however, morphologically closer to modern mytiliform species than most, or perhaps any, of its contemporaries and may therefore be significant in the evolution of the Mytilidae.

Cox (1937, 1940) and Newell (1942) discuss the history of the Mytilidae. *Modiolus* appears to be a long-ranging genus from which the other Mytilidae, including mytiliform species (i.e. *Mytilus sensu lato*) have evolved, perhaps several times. The Jurassic genera *Praemytilus* and *Falcimytilus* appear to be the earliest mytiliform genera which are undoubted members of the Mytilidae (i.e. excluding the Upper Palaeozoic Myalinidae,

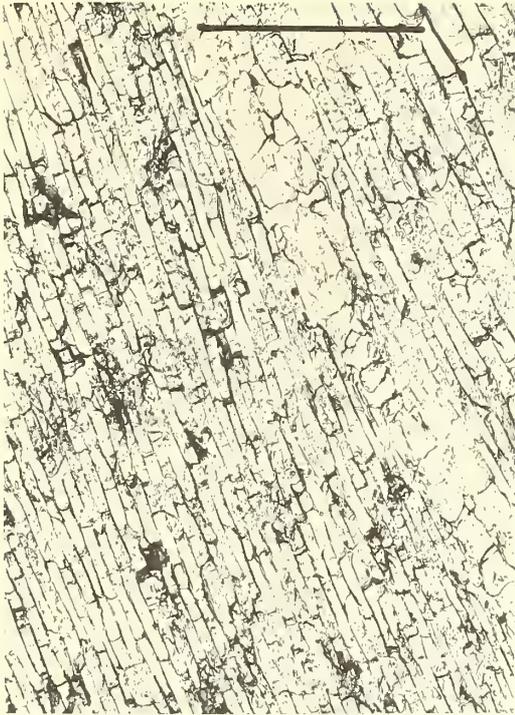
EXPLANATION OF PLATE 35

The outer shell layer will be uppermost, as in Plates 31–34, if this plate is viewed from the side.

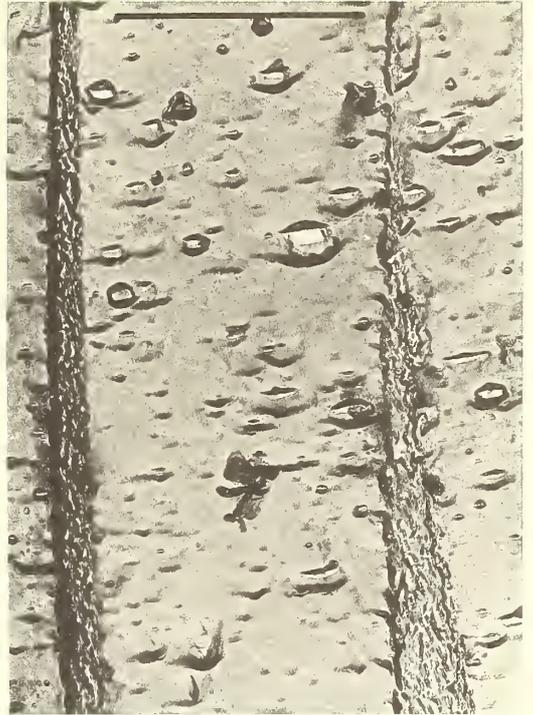
Fig. 1. Photomicrograph of vertical transverse section, crossed polarizers. Thin partially broken outer layer at top; rest is inner layer showing division into sub-layers. Thin section, $\times 50$ (scale measures 1 mm.).

Figs. 2, 3. Two figures of same electron micrograph with slight overlap between figures allowing continuity to be visualized. Junction between inner and outer shell layers in a vertical transverse section, towards the shell margin. Myostracal layer is oblique to, and truncates, the nacreous laminae of the outer layer. Inner layer laminae approximately parallel to the myostracum, which is somewhat irregularly developed. Two-stage replica, $\times 3,000$ (scale measures 10 μ).

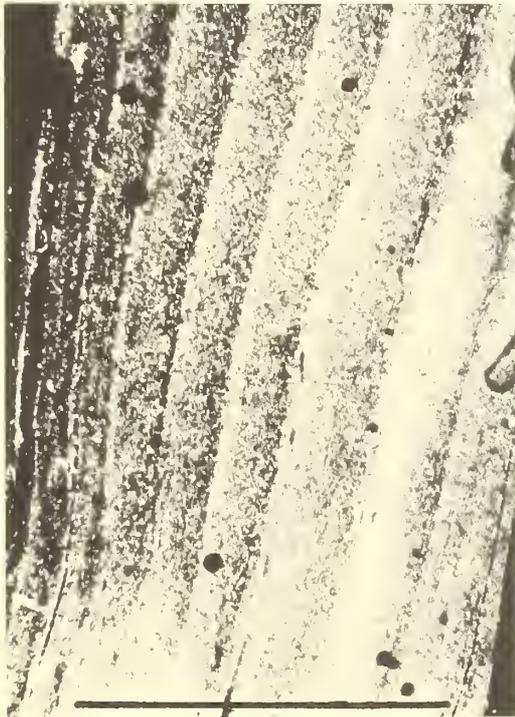
Fig. 4. Part of the same preparation as Plate 31, fig. 1. Detail of nacreous laminae, showing structure within aragonite crystals. Single-stage replica, $\times 33,000$ (scale measures 1 μ).



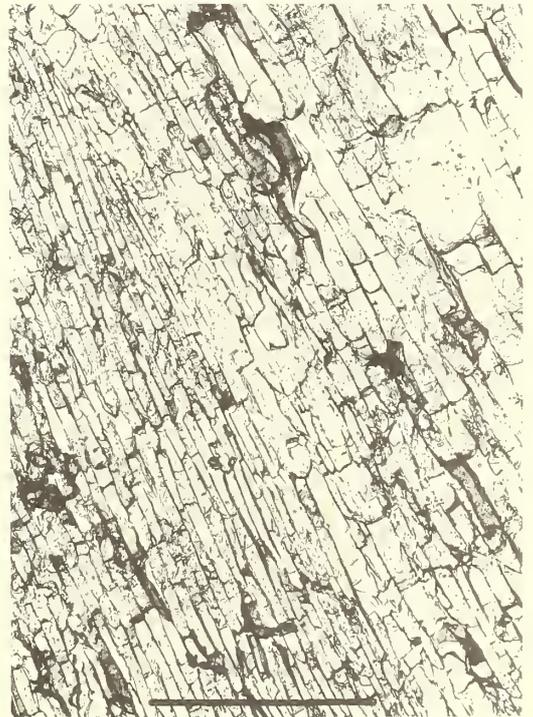
2



4



1



3

HUDSON, Jurassic mytilid shell microstructure

and such Triassic and Jurassic genera as *Lycettia* which Cox (1937) considers may be descended from them, or whose internal structure is unknown). In harmony with this, the shell structure of *P. strathairdensis* is closely similar to that of modern tropical representatives of *Mytilus sensu lato* (see below) whereas its edentulous hinge agrees with that of *Modiolus*. The shell structure of *Falcimytilus* is unknown, unless the 'Upper Jurassic *M. mirabilis*' described briefly by Bøggild (1930, p. 273) is the same species as the Liassic *M. mirabilis* (Lepsius) which Cox (1940) suggested was a *Falcimytilus*. Bøggild's description, inferred from a poorly preserved specimen, suggests a shell structure further removed from modern *Mytilus* than that of *Praemytilus*, and closer to that of some modern *Modiolus* (an unnamed species described by Bøggild 1930, p. 273; and *Volsella capax* listed by Oberling 1964, p. 37).

The modern genus *Mytilus sensu lato* (i.e. smooth Mytilidae with terminal umbones in the adult and a hinge bearing teeth) was split into two subgenera by Jukes-Brown (1906) and into at least five genera by Soot-Ryen (1955), who did not regard his genera as necessarily closely related to one another. Whether any or all of these are direct descendants of *Praemytilus*, or whether they are later offshoots from, presumably, *Modiolus*, is pure speculation at this stage owing to lack of knowledge of the intervening history of the family. In either case it would appear that edentulous forms preceded those with teeth, which is not what would be expected from a recapitulation of ontogeny.

Palaeoecology. The palaeoecology of the Mytilus Shales as deduced from lithology and from a comparison of the fauna with modern representatives of the same genera has been described by Hudson (1963, 1966). *P. strathairdensis* is the dominant member of the fauna in the main part of the succession. It was concluded that the habitat of the species was a mud or silt bottom, where it probably attached itself by its byssus to shell or 'seaweed', in lagoons whose salinity no doubt fluctuated but was normally below that of the open sea.

The present results can perhaps add to this. The wholly aragonitic mineralogy and concomitant nacreous structure in both main layers agree with modern tropical and subtropical species of *Mytilus sensu lato* (Lowenstam 1954*a, b*; Hudson unpublished data). *M. (Perna) perna* from Brazil is wholly aragonitic in a temperature range of 18.9–27.8° C with a mean of 23° C. Temperate species of *Mytilus*, on the other hand, have a calcitic outer layer, and show an aragonite/calcite ratio which increases approximately linearly with temperature to the limit of their range at a mean temperature of about 20° C (Lowenstam 1954*a*). The Upper Cretaceous Mytilid *Cuneolus tippiana* from the Coon Creek Formation of Tennessee is wholly aragonitic and wholly nacreous (Bøggild 1930; Lowenstam 1954*a*); it gave an isotopic palaeotemperature of 23° C whereas the range of palaeotemperatures of other members of the Coon Creek fauna was closely similar to the modern temperature range of *M. (P.) perna* quoted above (Lowenstam and Epstein 1954). This suggests a similar temperature response in Cretaceous Mytilidae as in modern ones, and extension to the Jurassic would predict high temperatures for the aragonitic *P. strathairdensis*. There is, however, a pronounced species effect in modern Mytilidae as shown, for instance, in the much higher aragonite percentages in temperate species of *Modiolus* ('*Volsella*') compared to *Mytilus* from the same temperature range (Lowenstam 1954*a*). The fact that *P. strathairdensis* probably lived in brackish water may also be relevant, since Lowenstam (1954*a*) and Dodd (1964) concluded that

reduced salinity probably favours increased aragonite percentage in *M. edulis*, though this has subsequently been disputed (Eisma 1966, Dodd 1966). Despite these complications, the fact that *wholly* aragonitic *Mytilus* and *Modiolus* are exclusively tropical to subtropical today is probably significant for the life-temperature of *P. strathairdensis*.

It has been shown above that the inner layer of *P. strathairdensis* shows sub-layers which are very similar to those interpreted as annual growth-layers in the nacre of modern pearl oysters by Wada (1961). This suggests seasonal growth. The pearl oysters stop depositing shell when the temperature falls below 13° C. In their isotopic study of the Bermuda fauna Epstein and Lowenstam (1953) concluded that many bivalves showed such a temperature threshold; in *Channa macerophylla* it was as high as 21° C. These results were not related to visible structures in the shell, however. The evidence for seasonal growth in *P. strathairdensis* may thus imply seasonal temperature fluctuations in the environment. The belemnite analysed in detail by Urey *et al.* (1951) came from the Upper Jurassic of Skye. It showed a mean temperature of 20·8° C (corrected to the new palaeotemperature scale) and an annual temperature-range of 6° C. Whereas the temperature need not have been similar in the Middle Jurassic, it is likely that the implied tendency to fairly marked seasonal temperature variations would already have been established in the same area.

The regular aragonite-organic matrix lamination in nacre suggests some small-scale rhythmic control which might be external. There is, however, no evidence at present on this. It does not appear to be a circadian rhythm. Wada's (1961) data on pearl oysters give (by calculation) over 500 laminae per growth season. The number per supposed season in *P. strathairdensis* is less than 250.

Many of the doubts expressed about quantitative conclusions from the data presented come from uncertainty about the salinity régime of the Great Estuarine Series lagoons. It is hoped (1) to obtain isotopic palaeotemperatures and trace-element data for fully marine faunas of the same general horizon and region, (2) to obtain carbon and oxygen isotopic data on apparently unaltered shells from the Great Estuarine Series and try to relate these to palaeosalinities. Combined chemical and structural studies, preferably on several members of the same fauna, may enable much more precise interpretations of temperature, seasonality, etc., to be drawn, as well as contributing data to evolutionary palaeontology.

Acknowledgements. This work was carried out during the tenure of a Research Fellowship at the California Institute of Technology, Pasadena, financed by the Ford Foundation, for which I am very grateful. I wish to thank Professor H. A. Lowenstam for discussions, Dr. A. Hodge for the use of the electron microscope, and Dr. K. Towe and the late Mr. A. Lielausis for advice on techniques. The spectrographic analyses were made by Mrs. E. Bingham. Mr. A. A. Chodos advised on the use of the electron microprobe. Dr. M. R. House kindly criticized an earlier version of the manuscript.

REFERENCES

- ANDERSON, F. W. and COX, L. R. 1948. The 'Loch Staffin Beds' of Skye; with notes on the molluscan fauna of the Great Estuarine Series. *Proc. roy. Phys. Soc. Edinb.* **23**, 103–22.
- BÖGGILD, O. B. 1930. The shell structure of the molluscs. *K. danske vidensk. Selsk. Skr., Natur. og Math.* 9th ser. **2**, 233–326.
- COX, L. R. 1937. Notes on Jurassic lamellibranchia. V. On a new subgenus of *Mytilus* and a new *Mytilus*-like genus. *Proc. malac. Soc. Lond.* **22**, 339–48.

- COX, L. R. 1940. The Jurassic lamellibranch fauna of Kachh (Cutch). *Mem. geol. Surv. India Palaeont. indica*, ser. 9, 3 pt. 3, 1-157.
- DODD, J. R. 1963. Palaeoecological implications of shell mineralogy in two pelecypod species. *J. Geol.* **71**, 1-11.
- 1964. Environmentally controlled variation in the shell structure of a pelecypod species. *J. Paleont.* **38**, 1065-71.
- 1965. Environmental control of strontium and magnesium in *Mytilus*. *Geochim. cosmoch. Acta*, **29**, 385-98.
- 1966. The influence of salinity on mollusk shell mineralogy: a discussion. *J. Geol.* **74**, 85-89.
- EISMA, D. 1966. The influence of salinity on mollusk shell mineralogy: a discussion. *Ibid.* **74**, 89-94.
- EPSTEIN, S. and LOWENSTAM, H. A. 1953. Temperature-shell growth relations of Recent and Interglacial Pleistocene shoal water biota from Bermuda. *Ibid.* **61**, 424-38.
- GRANDJEAN, J. C., GRÉGOIRE, C., and LUTTS, A. 1964. On the mineral components and the remnants of organic structures in shells of fossil mollusca. *Bull. Acad. r. Belg. Cl. Sci.* 5th ser. **50**, 562-95.
- GRÉGOIRE, C. 1957. Topography of the organic components in mother-of-pearl. *J. biophys. biochem. Cytol.* **3**, 797-808.
- 1959. A study on the remains of organic components in fossil mother-of-pearl. *Bull. Inst. r. Sci. nat. Belg.* **35**, 1-14.
- 1962. On submicroscopic structure of the *Nautilus* shell. *Ibid.* **38**, 1-71.
- 1965. Thermal changes in the *Nautilus* shell. *Nature*, **203**, 868-9.
- DUCHATEAU, G., and FLORKIN, M. 1955. La trame protidique des nacrés et des perles. *Annl. Inst. océanogr., Monaco*, **31**, 1-36.
- HALLAM, A. and O'HARA, M. J. 1961. Aragonitic fossils in the Lower Carboniferous of Scotland. *Nature*, **195**, 273-4.
- HARE, P. E. 1963. Amino-acids in the proteins from aragonite and calcite in the shells of *Mytilus californianus*. *Science*, **139**, 216-17.
- HUDSON, J. D. 1962. Pseudo-pleochroic calcite in recrystallized shell limestones. *Geol. Mag.* **99**, 492-500.
- 1963. The ecology and stratigraphical distribution of the invertebrate fauna of the Great Estuarine Series. *Palaeontology*, **6**, 327-48.
- 1965. (Abstract.) Preservation and recrystallization in some Jurassic mollusc shells from Scotland. *Spec. Pap. geol. Soc. Am.* **82**, 98.
- 1966. Hugh Miller's Reptile Bed and the *Mytilus* Shales, Middle Jurassic, Isle of Eigg, Scotland. *Scot. J. Geol.* **2**, 265-81.
- The elemental composition of the organic matrix and the water content of recent and fossil mollusc shells. *Geochim. cosmoch. Acta* (in press).
- JUKES-BROWN, A. J. 1906. A review of the family Mytilidae. *Proc. malac. Soc. Lond.* **6**, 211-24.
- LOWENSTAM, H. A. 1954a. Factors affecting the aragonite-calcite ratios in carbonate-secreting marine organisms. *J. Geol.* **62**, 284-322.
- 1954b. Systematics, palaeoecologic and evolutionary aspects of skeletal-building materials. *in Status of invertebrate paleontology. Bull. Mus. comp. Zool. Harv.* **112**, 287-317.
- 1961. Mineralogy, O¹⁸/O¹⁶ ratios, and strontium and magnesium contents of recent and fossil brachiopods and their bearing on the history of the oceans. *J. Geol.* **69**, 241-60.
- 1963. Biologic problems relating to the composition and diagenesis of sediments. *In: The Earth Sciences: problems and progress in current research.* Ed. T. W. DONNELLY, Rice University.
- 1964. Sr/Ca ratio of skeletal aragonites from the recent marine biota at Palau, and from fossil gastropods. *In: Isotopic and Cosmic Chemistry.* Ed. H. CRAIG, S. L. MILLER, and G. J. WASSERBURG, Amsterdam.
- and EPSTEIN, S. 1954. Paleotemperatures of the post-Aptian Cretaceous as determined by the oxygen-isotope method. *J. Geol.* **62**, 207-48.
- MUTVEL, H. 1964. On the shells of *Nautilus* and *Spirula* with notes on the shell secretion in non-cephalopod molluscs. *Ark. Zool.* **16**, 221-77.
- NEWELL, N. D. 1937. Late Paleozoic pelecypods: Pectinacea. *Kansas State geol. Surv.* **10** (1), 1-123.
- 1942. Late Paleozoic pelecypods: Mytilacea. *Ibid.* **10** (2), 1-115.
- 1965. Classification of the Bivalvia. *Am. Mus. Novit.* **2206**, 1-25.
- OBERLING, J. J. 1955. Shell structure of west American pelecypods. *J. Wash. Acad. Sci.* **45**, 128-30.

- OBERLING, J. J. 1964. Observations on some structural features of the pelecypod shell. *Mitt. naturf. Ges. Bern*, N.F. **20**, 1-60.
- SCHENK, H. G. 1934. Literature on the shell structure of pelecypods, *Bull. Mus. r. Hist. nat. Belg.* **10**, 1-20.
- SCHMIDT, W. J. 1924. Bau und Bildung der Perlmuttermasse. *Zool. Jb. (Abt. Anat. u. Ontog. d. Tiere)* **45**, 1-148.
- SOOT-RYEN, T. 1955. A report on the family Mytilidae (Pelecypoda). *Allan Hancock Pacif. Exped.* **20**, 1-176.
- STASEK, C. R. 1963. Geometrical form and gnomonic growth in the bivalved Mollusca. *J. Morph.* **112**, 215-31.
- TUREKIAN, K. K. and ARMSTRONG, R. L. 1961. Chemical and mineralogical composition of fossil molluscan shells from the Fox Hills Formation, South Dakota. *Bull. geol. Soc. Am.* **72**, 1817-28.
- UREY, H. C., LOWENSTAM, H. A., EPSTEIN, S., and MCKINNEY, C. R. 1951. Measurements of paleotemperatures and temperatures of the Upper Cretaceous of England, Denmark, and the south-eastern United States. *Ibid.* **62**, 399-416.
- WADA, K. 1961. Crystal growth of molluscan shells. *Bull. National Pearl Research Lab. Japan*, **7**, 703-828.
- WATABE, N. 1965. Studies on shell formation XI. Crystal-matrix relationships in the inner layers of mollusk shells. *J. Ultrastruct. Res.* **12**, 351-70.
- SHARP, D. G., and WILBUR, K. M. 1958. Studies on shell formation VIII. Electron microscopy of crystal growth of the nacreous layer of the oyster *Crassostrea virginica*. *J. biophys. biochem. Cytol.* **4**, 281-6.
- WILBUR, K. M. 1964. Shell formation and regeneration. in *Physiology of Mollusca*. Ed. K. M. WILBUR and C. M. YONGE, New York.
- YONGE, C. M. 1960. in *Treatise on invertebrate paleontology (I) Mollusca 1*. Ed. R. C. MOORE, Univ. Kansas Press, 121-8.

JOHN D. HUDSON
Department of Geology
The University
Leicester

Typescript received 28 April 1967

LOWER AND EARLY MIDDLE CAMBRIAN TRILOBITES FROM THE PIOCHE SHALE, EAST-CENTRAL NEVADA, U.S.A.

by W. H. FRITZ

ABSTRACT. Trilobites belonging to the Upper *Olenellus* Faunizone (Lower Cambrian) and to the late *Albertella* and *Glossopleura* Faunizones (Middle Cambrian) are described from a single stratigraphic section that spans the Pioche Shale. Trilobites representing the oldest Middle Cambrian, the *Plagiura-Poliella* Faunizone, and the early *Albertella* Faunizone were not found. The interval in which the latter trilobites might be expected contains 260 ft. of barren strata. Four established, two undetermined, and three new species are described from the Upper *Olenellus* Faunizone. Fourteen established, five undetermined, and seventeen new species are described from the late *Albertella* Faunizone and *Glossopleura* Faunizone. Some of these latter species are placed in two new genera, *Achlysopsis* and *Albertelloides*. Seven undetermined and seven new species are described from the *Glossopleura* Faunizone.

The Pioche Shale is locally 1,280 ft. thick and is exposed in an 8,800-ft. section containing Lower, Middle, and Upper Cambrian strata.

MOST of the trilobites described in this paper are from the *Albertella* Faunizone, and all are from the Pioche Shale of the Campbell Ranch section. The approximate limits of the *Albertella* Faunizone are demonstrated by presenting some trilobites from the older Upper *Olenellus* Faunizone and younger *Glossopleura* Faunizone. A few collections contained brachiopods which are not described.

The use of the term faunizone and the zonation framework employed is essentially consistent with that described by Lochman-Balk and Wilson (1958).

At present there is almost no geological information published on the area in which the collections were made. As collecting involved understanding the stratigraphy and structure, considerable data had to be gathered pertaining to these subjects. These data are being compiled on a geologic map and a facing sheet of written description which will be published in 1968 as Nevada Bureau of Mines Map 35.

Geographical location. The Campbell Ranch section is in White Pine County, Nevada. It is located at approximately 114° 56' W. and 39° 33' N. and is within Township 20N near the mutual boundary of Ranges 62 and 63E. The section is exposed on the east flank of the Northern Egan Range and 20 miles north of the town of Ely. It can be approached by automobile along a graded road that parallels the range to the east and passes through the Campbell Ranch. From the ranch the section lies 2½ miles to the northwest. No permanent road leads to the section, however, and it is necessary to turn west just north of the ranch on to the road leading to the Cuba Mine. In one mile this road takes the observer across valley alluvium and close to the Palaeozoic outcrops of the Egan Range. Parking here and looking half a mile northward, one can see a spur sloping eastward that terminates with pink Prospect Mountain Quartzite against valley alluvium. After walking to the quartzite outcrop, the less resistant Pioche Shale can be easily located as the basal Pioche beds overlie the quartzite and are immediately to the west. By continuing northward along the quartzite-shale contact for one mile, one crosses the toe of three spurs, the latter two being similar to the first. The collecting and measuring site for the Pioche Shale is along the crest of the third spur, and the over- and underlying formations were measured on the crest of the second.

Acknowledgements. The writer wishes to thank Drs. Peter Misch, Christina Lochman-Balk, and A. R. Palmer for time spent discussing the research and for reading the manuscript. He is also grateful for financial support received from the U.S. National Science Foundation through Postdoctoral Fellowship 40146 and Grant G19406.

STRATIGRAPHY

Five formations of Lower to early Upper Cambrian age were measured at the Campbell Ranch section. They have a total thickness exceeding 8,800 ft. and can be correlated with type outcrops near Pioche and Eureka, Nevada. In ascending order the formations are Prospect Mountain Quartzite (2,000 ft. +), Pioche Shale (1,280 ft.), Eldorado Limestone (1,385 ft.), Secret Canyon Shale (1,775 ft.), and Hamburg Formation (2,350 ft.). Because the Pioche Shale contains the trilobites to be described, this formation will be discussed in greater detail. The only other formations discussed are those immediately over- and underlying the Pioche Shale.

Prospect Mountain Quartzite

The oldest formation in the Campbell Ranch section is the Prospect Mountain Quartzite which was first described by Hague (1883) from outcrops near Eureka, Nevada. There the formation is considered to be Lower Cambrian in age (Nolan *et al.* 1956, p. 7). To the southeast, in the Grand Canyon region of Arizona, the Prospect Mountain (Tapeats) Quartzite locally contains Middle Cambrian beds in its uppermost part (Wheeler 1948, p. 1796; McKee 1945, p. 36). To the east, in the Wasatch Range, Utah, the Prospect Mountain (Tintic) Quartzite also may contain younger beds of Middle Cambrian age (Walcott 1908*a*, p. 9). Other Prospect Mountain sections in the northern Wasatch may not be younger than Lower Cambrian (Oriel 1964, p. 341). Regional studies by Wheeler (1948) and McKee (1945) have shown that the formation represents near-shore sands deposited by an eastwardly transgressing sea.

At the site of the Campbell Ranch section, approximately 2,000 ft. of the Prospect Mountain Quartzite is exposed between the valley alluvium and the overlying Pioche Shale. As it is typically found elsewhere, the Prospect Mountain is here barren of fossils and is composed of clean, medium- to coarse-grained, cross-bedded quartzite that parts uniformly at intervals averaging 1 ft. in thickness. At the Campbell Ranch section the Prospect Mountain cannot be younger than late Lower Cambrian since a faunule belonging to the Upper *Olenellus* Faunizone is present in the overlying Pioche Shale.

Pioche Shale

This formation was named by Walcott (1908*a*, pp. 9–12) to describe outcrops near Pioche, Nevada. There the formation consists of micaceous siltstone with some interbedded quartzite and limestone. Identifications by Palmer (1964*a*, pp. 25–27) of fossils collected near the type area clearly indicate the Lower Cambrian Upper *Olenellus* Faunizone, give some suggestion of the early Middle Cambrian *Plagiura–Poliella* Faunizone, and adequate evidence of the Middle Cambrian *Albertella* Faunizone.

West of the present area, near Eureka, Nevada, the Pioche has yielded only Lower Cambrian fossils (Nolan *et al.* 1956, p. 8). To the east, in the House Range, Utah, the Pioche contains Lower Cambrian fossils and is immediately overlain by the Tatow (Busby?) Quartzite containing Middle Cambrian trilobites (Wheeler 1948, text-fig. 5).

In the Grand Canyon region, Arizona, the Pioche (Bright Angel) Shale is Lower and Middle Cambrian in age (McKee 1945, text-fig. 1), and the formation is shown to represent a later phase of an eastward Cambrian transgression that began with the deposition of the Prospect Mountain (Tapeats) Quartzite.

At the site of the Campbell Ranch section the Pioche Shale has a lithology which is generally similar to that found near Pioche, Nevada. Two members (text-fig. 1) are recognized at the Campbell Ranch section, a lower siltstone member (420 ft.) and an upper interbedded limestone and siltstone member (860 ft.).

In the lower member the basal 150 ft. consist of brown micaceous siltstone that is exposed at nearby outcrops and weathers to brown dirt on the section. Half a dozen resistant quartzite interbeds averaging $2\frac{1}{2}$ in. in thickness are present within the siltstone unit. The lithology of the quartzite resembles that of the Prospect Mountain Quartzite below.

In the interval 150–160 ft. above the base is a thick-bedded, medium-grey weathering limestone unit (shown as thin-bedded in text-fig. 1 because of scale). The limestone surface is mottled by irregular lenses of siltstone that average 1 in. in thickness. Both a lighter colour and a slightly higher relief distinguish the siltstone from the enclosing limestone. Fossils are common in the uppermost foot of the limestone unit (collection locality 2). Typical fossils in this interval are olenellid fragments, *Onchocephalus papulus*, and *Bonnia copia*.

Strata in the interval 160–420 ft. above the base of the lower member weather to brown dirt and contain a few quartzite interbeds. These strata differ from those of the lower siltstone unit in that they include at least three thin to medium interbeds of limestone. Olenellid fragments and *Bonnia copia* are common in the first interbed 15 ft. above the base and in the second interbed known from float and located at a slightly higher horizon. The third limestone interbed 150 ft. above the base is barren.

The upper member, consisting partly of shale and possibly some siltstone that weathers to brown dirt, constitutes between a half and two-thirds of the member's thickness. Throughout most of the member are medium to thin interbeds of medium- to dark-grey weathering limestone. Fresh surfaces of the limestone are finely crystalline and nearly black.

At the base of this member is a 2-ft. bed of limestone containing a considerable amount of quartz silt. Abundant specimens of *Girvanella sp.* are conspicuous here and in beds 80 ft. higher in the section. Approximately 65 ft. above the base are beds containing *Albertella judithi* in abundance, and in the lower portion of the member, a few distinctive light-grey bioclastic limestone beds are present. The uppermost 130 ft. is the least resistant portion of the member as it contains almost no limestone. A sharp upper contact of the Pioche Shale is present at the top of this unit and immediately below thick-bedded, very light-grey limestone beds of the Eldorado Formation.

The age of the Pioche Shale at the site of the Campbell Ranch section will be discussed in more detail later in this paper. It will suffice here to state that the oldest two units in the lower member are late Lower Cambrian. It is debatable whether the third, barren unit should be assigned in part or all to the Lower or to the Middle Cambrian. The upper member is probably entirely Middle Cambrian with only the lower 65 ft. being in question. Most of this member can definitely be assigned to the Middle Cambrian *Albertella* and *Glossopleura* Faunizones.

Eldorado Limestone

Walcott (1908b) gave this name to a thick succession of limestone and dolomite between the Pioche Shale and Secret Canyon Shale, near Eureka, Nevada. This original broad usage is followed here, and the Geddes Limestone is not differentiated from the Eldorado, as was later proposed by Wheeler and Lemmon (1939, pp. 20–22).

The Eldorado at the Campbell Ranch section is 1,385 ft. thick, and it contains four members that are briefly described in ascending order as follows: white to very light grey, dense limestone, 260 ft.; dark blue-grey limestone with abundant rod-like structures that are approximately 2 mm. in diameter, 160 ft.; light-grey to cream-coloured dolomite, 200 ft.; and medium-grey limestone, 765 ft. The local age of the Eldorado is Middle Cambrian since *Glossopleura* is present below the formation and a faunule belonging to the *Batlyuriscus-Elrathina* Faunizone was collected a short distance above the top.

Localities and repository. All the trilobites described in this paper are from the Pioche Shale. The approximate stratigraphic position of each locality is shown on text-fig. 1. In order to be more precise, the stratigraphic position above the base of the Pioche is given here for each locality as follows: Loc. 2, 162 ft.; loc. 3, 177 ft.; loc. 1085, \pm 223 ft.; loc. 8, 485 ft.; loc. 9, 495 ft.; loc. 10, 510 ft.; loc. 71, 536 ft.; loc. 72, 570 ft.; loc. 11, 623 ft.; loc. 12, 668 ft.; loc. 14, 711 ft.; loc. 15, 742 ft.; loc. 16, 779 ft.; loc. 17, \pm 823 ft.; loc. 18, 838 ft.; loc. 74, 1,125 ft. Localities 1085 and 17 are pieces of float thought to have been collected near their sources, but their positions must be questioned. All the trilobites collected are in a limestone matrix.

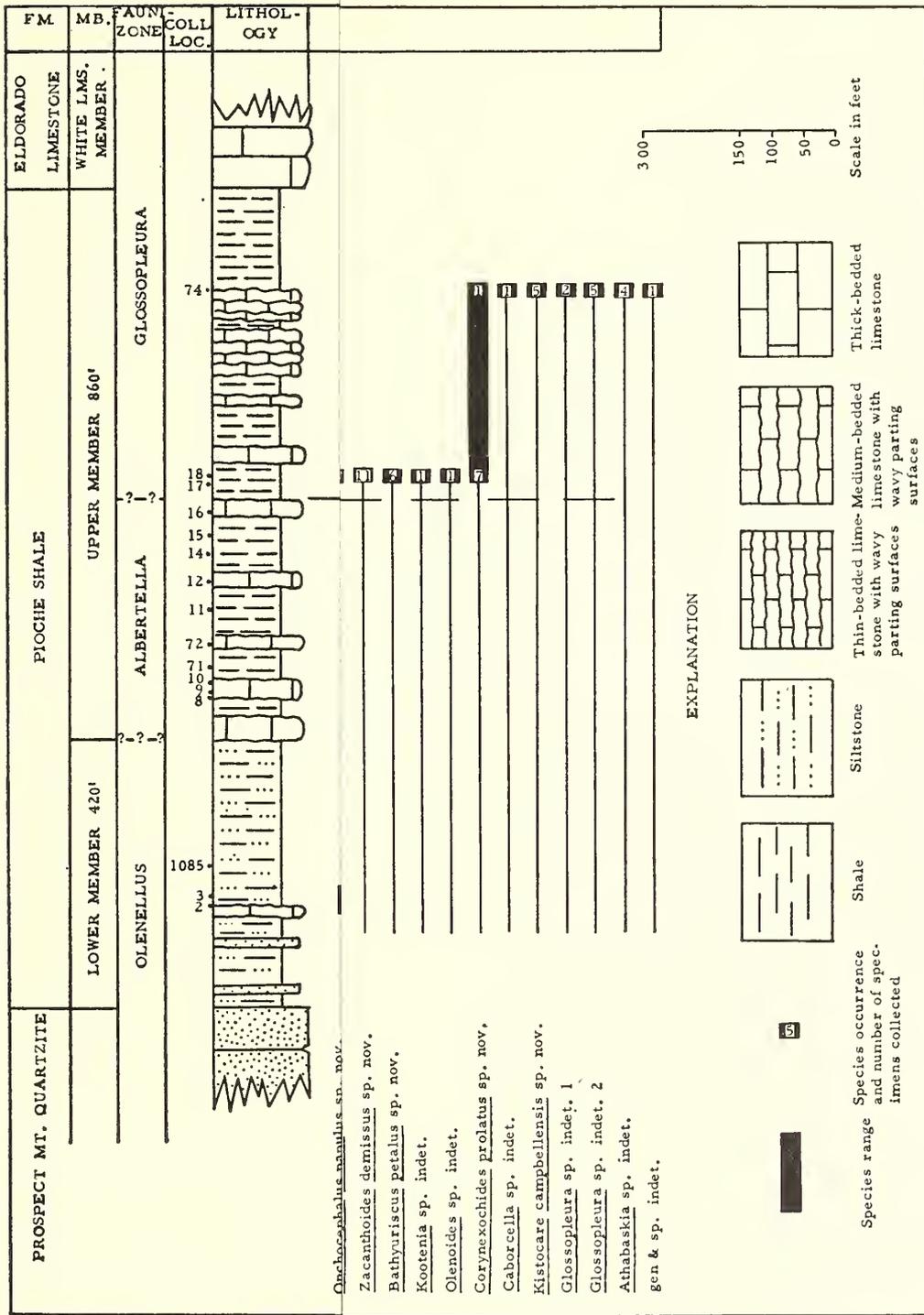
The trilobites are stored at the U.S. National Museum, Washington, D.C. Museum numbers are given in the plate explanations.

BIOSTRATIGRAPHY

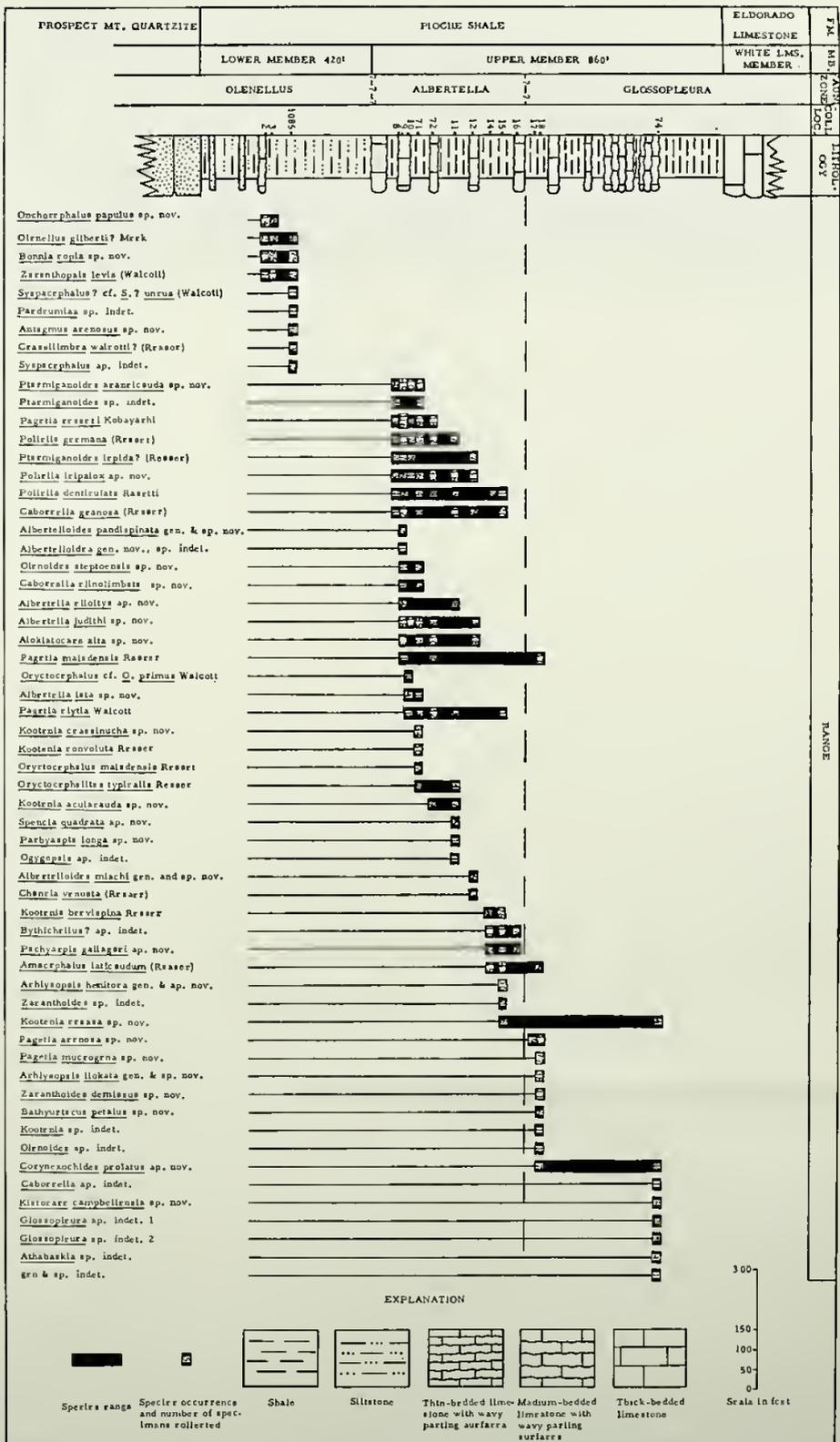
Trilobites from the three localities in the lower member of the Pioche Shale belong to the Upper *Olenellus* Faunizone. *Olenellus gilberti*?, *Bonnia copia*, and *Zacanthopsis levis* are common to all three collections. *Onchocephalus papulus* was found only at the lowest two localities and *Antagmus arenosus*, *Crassifunbra walcotti*?, *Paedeunnias sp.*, *Syspacephalus*? cf. *S.?* *uncus*, and *Syspacephalus sp. indet.* were found only at the upper locality. All three collections bear a close resemblance to the *Bonnia fieldensis* faunule from the top of the St. Piran Sandstone of British Columbia (Rasetti 1951, p. 82). Essentially the same faunule has been reported from the Combined Metals Member of the Pioche Shale near Pioche, Nevada by Palmer (1964a, p. 26). A faunule from the Buelna Limestone in Sonora, Mexico (Lochman 1952, p. 71) bears a likeness to the faunule in the three Campbell Ranch collections, but the closest resemblance is to the two former faunules.

The upper member of the Pioche Shale contains trilobites belonging to two faunizones. The oldest, the *Albertella* Faunizone, is represented by collections 8–12, 14–16, 71, and 72. Nineteen genera and twelve species from these localities are common to the 'Ptermigania fauna' described by Resser (1939a) from northwestern Utah. The localities containing the 'Ptermigania fauna' were later mapped by Williams and Maxey (1941) who found the fossils to be in the Langston Limestone and to be associated with *Albertella*. Their work demonstrated the validity of the *Albertella* Faunizone and its position immediately below the *Glossopleura* Faunizone.

In reviewing the *Albertella* collections from the Campbell Ranch section, it is difficult to believe that they represent the entire *Albertella* Faunizone. Only the lower collections



TEXT-FIG. 1. Chart showing the local range of trilobite species in the Pioche Shale, Campbell Ranch Section, East-Central Nevada, U.S.A.



TEXT-FIG. 1. Chart showing the local range of trilobite species in the Pioche Shale, Campbell Ranch Section, East-Central Nevada, U.S.A.

(see text-fig. 1) contain the more characteristic trilobites of the faunizone in abundance, such as three species of *Poliella*, two of *Albertella*, and three of *Caborcella*. Thus the Campbell Ranch collections may represent a time interval past the peak of the zone. The 262-ft. interval between the lowest *Albertella* collection and the uppermost Upper *Olenellus* collection is barren and, therefore, the possibility that the *Albertella* Faunizone may extend downward cannot be tested locally.

The close correlation between the *Albertella* collections from the Campbell Ranch section and the 'Ptarmigania fauna' of Utah does not help to position the former collections within the *Albertella* Faunizone. Like the Campbell Ranch collections, the 'Ptarmigania fauna' is underlain by barren beds, and is immediately overlain by the *Glossopleura* Faunizone. Lochman (1952, p. 75) previously concluded that the 'Ptarmigania fauna' represents only the later portion of the *Albertella* Faunizone.

Near the top of the *Albertella* Faunizone there is a definite pattern of transition toward the overlying *Glossopleura* Faunizone (see text-fig. 1). Unfortunately, no fossils were found in the 287-ft. interval between locality 18 and the only *Glossopleura*-bearing locality, locality 74. This lack of data detracts from the reliability of a local horizon chosen to represent the mutual boundary of the *Albertella* and *Glossopleura* Faunizones. Enough data are present, however, to tentatively locate this boundary pending the finding of more fossil localities or more fossiliferous sections elsewhere. The tentative boundary selected is between localities 16 and 17 where a significant faunal change occurs. Near or just below this boundary the teilzone terminates for the following characteristic trilobites in the Campbell Ranch section: *Bythicheilus?* sp., *Caborcella granosa*, *Kootenia brevispina*, *Pachyaspis gallagari*, *Pagetia clytia*, and *Poliella denticulata*. Common to the *Albertella* and *Glossopleura* Faunizones are *Amecephalus laticaudum*, *Kootenia crassa*, and *Pagetia maladensis*. The genus *Caborcella* is represented in both faunizones, but by different species.

The *Glossopleura* Faunizone is unquestionably represented at locality 74. Two species of *Glossopleura* and one of *Kistocare* are considered reliable faunizone indicators. Less weight is given to *Athabaskia* as its range may possibly extend downward into the *Albertella* Faunizone in British Columbia (Rasetti 1951, p. 96). The age of *Corynexochides* has thus far been uncertain, although Rasetti (1963, p. 576) does suggest that two species found in boulders near Metis, Quebec, may belong to the *Glossopleura* Faunizone. The species from the Campbell Ranch section is definitely from the *Glossopleura* Faunizone and is the first to be reported from the North American Cordillera.

Below locality 74 and above the tentative base of the *Glossopleura* Faunizone are localities 17 and 18. As they are closely spaced, and as the single species present at 17 is also present at 18, the two localities can be discussed together. Here there is an early occurrence of *Bathyriscus*. A second early occurrence of the genus was reported by Rasetti (1951, p. 96) from British Columbia where it may extend downward into the *Albertella* Faunizone. A third is known from one small pygidium, *Bathyriscus politus*, which Resser (1939a, p. 30) described from northwestern Utah. As this pygidium is associated with the 'Ptarmigania fauna', it can be assumed to belong to the *Albertella* Faunizone.

Except for *Pagetia maladensis*, the more abundant species just above the tentative base of the *Glossopleura* Faunizone (loc. 17-18) are new. These are *Achlysopsis liokata*, *Pagetia arenosa*, *Pagetia mucrogena*, and *Zacanthoides demissus*. As Resser (1939a, p. 25)

has described *P. maladensis* from the 'Ptarmigania fauna' of northwestern Utah, the species can be said to range down into the upper portion of the *Albertella* Faunizone in that region, as it does here.

Between the localities bearing fossils from the Upper *Olenellus* and late *Albertella* Faunizones is a barren interval in which no representatives of the intermediate *Plagiura-Poliella* and early *Albertella* Faunizones were found. The stratigraphic interval within which the apparent break occurs is the barren 262 ft. between localities 1085 and 8. Four hypotheses that might explain the missing faunules are as follows: (1) fossils are only locally missing because they have been faulted from the section; (2) strata in the barren interval were deposited during a time when the *Plagiura-Poliella* and early *Albertella* faunas were locally evolving, but no fossil record was preserved; (3) an unconformity is present within the interval in question; (4) representatives of the late Upper *Olenellus* Faunizone (Lower Cambrian) in the Campbell Ranch section lived here at a time when a laterally equivalent *Plagiura-Poliella* fauna ('Middle Cambrian') and possibly part of the *Albertella* fauna lived in what is now British Columbia, the type area for the *Plagiura-Poliella* Faunizone.

The first hypothesis seems unlikely, as a considerable area was mapped surrounding the Campbell Ranch section to ensure that a fault would not be overlooked.

The second hypothesis can best be approached by considering the fossils immediately under and overlying the barren interval in question. The three underlying localities contain a typical late Lower Cambrian faunule, but there are no 'transition' elements to suggest that Middle Cambrian strata are just above the highest of the three localities. The first locality above the barren interval contains fossils that can be placed in the later part of the *Albertella* Faunizone or, in other words, well into the Middle Cambrian. As the thickness of the barren interval is less than that occupied by the later part of the *Albertella* Faunizone, either slow deposition or rapid evolution must have taken place if the second hypothesis is correct.

The third hypothesis is similar to one considered by Rasetti (1951, p. 87) who concluded that a regional unconformity may exist in the North American Cordillera between strata of Lower and Middle Cambrian age. He has mentioned that published data from various areas in the Cordillera indicate a sharp faunal break at this horizon, and he has presented evidence that a physical and faunal break exists at this boundary in British Columbia. Regional studies by Wheeler (1948) and McKee (1945) give no clue of such an unconformity and, indeed, contain data that could be used to counter Rasetti's conclusion. Should regional investigations be made to pursue the unconformity question in the future, early attention will undoubtedly focus on the Busby Quartzite. This or similar clastic units are present at the top or overlying the Pioche Shale in various sections in eastern Nevada and western Utah. At the Campbell Ranch section no physical evidence of an unconformity was noted nor is the Busby Quartzite present.

The fourth hypothesis entertains the possibility that the top of the Lower Cambrian, locally a horizon immediately overlying the youngest olenellids, may not be a 'time' plane even in the geologic sense. It may transgress time as do boundaries of an ecozone as visualized by Vella (1964). Locally an ecozone boundary is a record of an abrupt faunal change that occurred due to a sudden change in environment. At the Lower-Middle Cambrian boundary in what is now the Great Basin such a displacement of faunas may have occurred, as here the Lower Cambrian consists predominantly of sandstone and siltstone and the Middle Cambrian of limestone and shale.

Furthermore, the bulk of the immediate ancestors to the Middle Cambrian faunas have not been found here. We can assume that these ancestors did intermix with olenellids in a more seaward environment during late Lower Cambrian time because in rare localities, such as near Goldfield, Nevada (Palmer 1964b), a record of this intermixing has been found. If, at the same time and slightly further seaward, Middle Cambrian stocks completely displaced the olenellids, we would not recognize this fauna as being Lower Cambrian. The 'Middle Cambrian' *Plagiura-Poliella* Faunizone in British Columbia might represent such a seaward displacement. To pursue this hypothesis to what is admittedly

an extreme position, we might suppose the faunal displacement proposed above existed and remained effective for a considerable length of time. Still pressing towards the extreme, we might assign only a short amount of time to the deposition of the barren strata in question. Having done this, we could then equate a post-olenellid *Plagiura-Poliella* and lower *Albertella* Faunizone in British Columbia to a latest Upper *Olenellus* Faunizone in the Campbell Ranch section.

None of the last three hypotheses can be favoured without overemphasizing the meagre data available. However, these three hypotheses do serve to illustrate the gaps in our understanding of late Lower and early Middle Cambrian faunas, and they may suggest an approach preferable to describing random collections of that age. To the writer, they suggest a need to emphasize the study of stratigraphically allocated collections that demonstrate the crossing of at least one zonal boundary. The first hypothesis suggests that collecting be done only after the local geology is understood by the collector.

SYSTEMATIC PALAEOLOGY

Class TRILOBITA Walch 1771
 Order AGNOSTIDA Kobayashi 1935
 Family PAGETIIDAE Kobayashi 1935
 Genus PAGETIA Walcott 1916

Pagetia arenosa sp. nov.¹

Plate 43, figs. 10, 11

Material. Seven cranidia 0.8–2.1 mm. long and fifteen pygidia 0.4–2.3 mm. long.

Description. Cranidium wider than long by ratios ranging from approximately 2:2 to 3:4. Glabella small, tapered forward, front portion even with or slightly below level of fixigenae and terminating well back of border furrow. Three faint sets of glabellar furrows, anterior two sets transversely directed, anterior set joining, posterior set inclined toward rear. Postglabellar spine tapers uniformly back to a node, remaining spine is narrow, total length at least equalling and probably exceeding that of glabella. Fixigenae convex in both directions. Eye ridges thin but distinct. Palpebral lobes thin, broadly curved; palpebral furrow narrow but well impressed. Anterior border wider than border furrow; radial marking well impressed but irregular in spacing and depth.

Pygidium has length–width ratios that are approximately the same as those of cranidium. Axis narrower than pleural field, composed of four distinct rings bearing nodes, one poorly defined ring, and a terminal piece with spine. Pleural field exhibits weak pleural furrows. Some pygidia show faint interpleural furrows paralleled by a row of very small granules. Border uniformly narrow and horizontal. Pygidial surface rough but not distinctly granular, cranidium obviously granular, especially palpebral areas.

Remarks. *Pagetia arenosa* most resembles *Pagetia clytia* Walcott 1916, but differs in having lower fixigenae, a locally swollen palpebral area, well-defined eye ridges and palpebral lobes, a narrower pygidial axis, and a rough to granular test.

Occurrence. *Glossopleura* (?) Faunizone, upper member, localities 17 and 18.

¹ This species was preoccupied by *Pagetia rugosa* Rasetti 1966 (p. 509) after submission of this paper. (See RASETTI, F., 1966. Revision of the North American species of the Cambrian trilobite genus *Pagetia*. *J. Paleont.* **40**, 502–11, pl. 59, 60.)

Pagetia clytia Walcott

Plate 38, figs. 10, 11

- 1916b *Pagetia clytia* Walcott, p. 408, pl. 67, figs. 2, 2 a-e.
 1920 *Pagetia clytia* Walcott; Raymond, p. 145, fig. 37.
 ? 1935 *Pagetia clytia* Walcott; Mason, pp. 114, 115.
 non 1939a *Pagetia clytia* Walcott; Resser, pp. 25, 26, pl. 2, figs. 5-8.
 1939b *Pagetia clytia* Walcott; Resser, p. 8, pl. 2, figs. 30-32.
 1943 *Pagetia (Mesopagetia) clytia* Walcott; Kobayashi, p. 40.
 1944 *Pagetia (Mesopagetia) clytia* Walcott; Kobayashi, p. 64, pl. 1, fig. 14.
 1944 *Pagetia clytia* Walcott; Shimer and Shrock, p. 615, pl. 252, figs. 13-15.

Material. Twenty cranidia 1.3-2.5 mm. long and twenty pygidia 1.0-2.0 mm. long.

Description. Cranidium as wide or slightly wider than long. Axial furrow deep and wide, abruptly changes to moderate width opposite and anterior to eye ridges. Glabella uniform in width except for anterior third which tapers forward; glabella lightly furrowed, anterior set transverse and joining, median set directed forward, posterior set directed back, latter two sets closely spaced and visible only as small indentations on most specimens. Fixigena plump, top surface broadly curved (exsag.) and dips uniformly inward; palpebral area well rounded near outer margin and almost vertical near facial suture; postero-lateral region of fixigena has a steep, almost facet-like surface on some specimens. Anterior border defined by wide furrow, radial markings deep, alternate markings deeper and longer. Eye ridges located just forward of anterior pair of glabellar furrows, visible only near dorsal furrow. Palpebral lobes very weakly outlined by a narrow furrow. Postglabellar spine thick.

Pygidial length approximately three-quarters width. Axis narrow, composed of a rather long (sag.) articulating half ring, five axial rings, and terminal piece with spine; anterior axial ring short (sag.), remaining rings of uniform size, last ring poorly defined from terminal piece. Up to three pleural furrows barely visible on pleural field. Border uniformly narrow except for being very narrow at back. Outer surface of test nearly smooth.

Remarks. *Pagetia clytia* resembles *Pagetia bootes* Walcott 1916, but has a stronger postglabellar spine, weaker eye ridges, and a glabella that extends closer to the border furrow.

Occurrence. *Albertella* Faunizone, upper member, localities 10, 71, 72, 11, and 15.

Pagetia maladensis Resser

Plate 43, figs. 14-16

- 1939a *Pagetia maladensis* Resser, p. 25, pl. 2, figs. 4 (cranidium only) and 5 (cranidium in upper right only).
 ? 1943 *Pagetia (Mesopagetia) maladensis* Resser; Kobayashi, p. 40.
 1944 *Pagetia (Mesopagetia) maladensis* Resser; Kobayashi, pp. 64-66, pl. 2, fig. 4a (non fig. 4b).

Material. Four cranidia 1.2-1.5 mm. long and ten pygidia 0.9-1.7 mm. long.

Description. Cranidium wider than long. Glabella narrow, front half level with fixigenae, back half rises above locally back-sloping fixigenae, sides straight and slightly converging, front abruptly pointed. One set of glabellar furrows visible as slight indentations

on anterior sides of glabella. Palpebral area convex in both directions; eye ridges broad and low. Palpebral lobes defined by very shallow furrow. Anterior border furrow shallow, deepening medially where it connects back to axial furrow. Border of fairly uniform width, radial markings narrow, some markings inclined considerably off a truly radial course. Postglabellar spine long, thin, and bearing a node.

Pygidial length-width ratio approximately 3:4. Axis narrow, sides parallel, posterior relief high above pleural field, extending slightly beyond posterior margin of border; axis composed of two node-bearing rings followed by one or two faintly defined rings and long terminal piece. Spine present on postero-dorsal surface of terminal piece is uptilted and uniformly thin. Border furrow shallow and of uniform depth. Border downsloping, convex, widening at postero-lateral positions. Outer surface of test nearly smooth.

Remarks. In describing this species Resser assigned the wrong pygidia to his holotype cranidium. His assigned pygidia are on average larger than those of *P. maladensis*, are punctate, and belong to unnamed cranidia which Resser (1939a, p. 65, pl. 2, fig. 5) misidentified as *Pagetia clytia* Walcott 1916. Unmentioned pygidia of *P. maladensis* are visible in one of Resser's figures (pl. 2, fig. 4), and others are present in material from the same collection. *Pagetia maladensis*, as here defined, closely resembles *Pagetia ferox* Lermontova 1940. Poor figures of *P. ferox* plus the lack of access to comparative material preclude a detailed comparison of the two species.

Occurrence. *Albertella* and *Glossopleura* (?) Faunizone, upper member, localities 9, 18, and 72.

Pagetia mucrogena sp. nov.

Plate 43, figs. 12, 13

Material. Forty-seven cranidia 0.9–1.8 mm. long and thirty pygidia 0.7–1.5 mm. long.

Description. Cranidium with length-width ratio ranging between 4:5 and 7:8. Glabella tapers gradually forward, anterior one-fifth tapers rapidly to a point touching or nearly reaching border furrow. Three faint sets of evenly spaced glabellar furrows, all sets transversely directed, forward set joining, second set weakest, posterior set with branch directed back. Axial furrow of uniform width and depth. Fixigenae slope moderately inward, palpebral areas distally extended into blunt points. Palpebral lobes uniformly narrow, outlined on points by a very faint furrow, neither furrows nor lobes visible on most specimens. Eye ridges weak and visible on only a few specimens. Anterior border and border furrows uniform in width and sharply defined. Postglabellar spine thick at base, uniformly tapered; spine on numerous specimens has a thin medial ridge on dorsal surface that extends across union of spine and glabella.

Pygidium with length-width ratios ranging from 2:3 (small pygidia) to 7:8 (large pygidia). Axis composed of five distinct rings and a terminal piece, each bearing a spine or large node; axis narrower than pleural field on small pygidia, equal in width on larger. Pleural furrows of medium depth near axis, shallow near border; interpleural furrows faint on smaller specimens, not visible on others. Border uniformly narrow, downsloping, not as wide as border furrow. Ornamentation on cranidium consists of radial markings only; pygidium has single rows of small granules located between and parallel

to pleural furrows. Granules visible on most small pygidia, visible on some medium to large pygidia.

Remarks. *Pagetia fossula* Resser 1938a resembles this species in many respects, but differs by having (1) palpebral areas with less lateral distension, (2) palpebral lobes that are clearly defined, (3) a narrower pygidial axis with less longitudinal curvature, (4) only four well-defined axial rings, and (5) shallower furrows on the pleural field.

Occurrence. *Glossopleura* (?) Faunizone, upper member, locality 18.

Pagetia resseri Kobayashi

Plate 38, figs. 8, 9

1939a *Pagetia clytia* Walcott; Resser, p. 25, pl. 2, figs. 6–8 (*non* fig. 5).

1943 *Pagetia (Eopagetia) resseri* Kobayashi, p. 40.

1944 *Pagetia (Eopagetia) resseri* Kobayashi; Kobayashi, pp. 64–66, pl. 2, figs. 2 a, b.

Material. Fifty-four cranidia 0.9–2.0 mm. long and 104 pygidia 0.8–1.8 mm. long.

Description. Cranidium as wide as long or slightly wider. Axial furrow of medium depth and width. Glabella rises above fixigenae along entire length, sides parallel at back, forward two-thirds converges to a point which touches or almost reaches border furrow. Three shallow sets of glabellar furrows, all sets directed transversely, posterior two sets closely spaced, rear set has posteriorly directed branch. Fixigenae low, broadly curved (*exsag.*), and nearly horizontal in transverse profile. Palpebral lobes uniformly narrow, parallel to axial furrow, length approximately one-third cranidial length. Palpebral furrow narrow, well impressed, paralleled at inner edge by a sharp ridge that is more pronounced on smaller cranidia. Eye ridges faint or not visible. Anterior border narrower than border furrow, border–border furrow contact gradational, radial markings short. Postglabellar spine initially strong, rapidly tapering, thin prolongation continues back for a distance equalling length of strong portion plus length of glabella. Surface of well-preserved cranidia exhibit very sparse granules, most fixigenae exhibit a pair of granules opposite posterior margin of glabella.

Pygidial length–width ratios range from 2:3 to slightly greater than 4:5. Axis considerably wider than pleural field, consisting of five rings with prominent nodes or spines and terminal piece bearing a node or spine. Pleural field marked by moderately impressed pleural furrows, weak interpleural furrows, and two closely spaced rows of granules on either side of interpleural furrows. Border not as wide as border furrow, tilted outward, and marked with granules.

Remarks. Resser (1939a) described two pygidia and a cranidium of this species with two cranidia of an unnamed species. He wrongly placed all under the name *Pagetia clytia* Walcott 1916. *Pagetia resseri*, as here interpreted, differs from other species of *Pagetia* at present known from North America in having a pygidium with a very broad axis, a well-furrowed pleural field, and abundant ornamentation.

Occurrence. *Albertella* Faunizone, upper member, localities 8–10, 71, and 72.

Order REDLICHIIIDA Richter 1933
 Family OLENELLIDAE Vodges 1893
 Genus OLENELLUS Billings 1861

Type species. *Olenus thompsoni* Hall 1859.

Olenellus gilberti? Meek

Plate 36, figs. 26–28

- 1874 *Olenellus gilberti* Meek *in* White, p. 7.
 1910 *Olenellus gilberti* Meek; Walcott, pp. 324–30, pl. 36, figs. 1–17, pl. 43, figs. 5, 6 (synonymy to date).
 1916b *Mesonacis gilberti* (Meek); Walcott, pp. 406–7, pl. 45, fig. 3.
 1944 *Olenellus gilberti* Meek; Shimer and Shrock, p. 613, pl. 253, figs. 2, 3.
 1952 *Olenellus gilberti* Meek; Best, pp. 17, 18, pl. 1, figs. 13–17.
 1962 *Olenellus gilberti* Meek; Norford, p. 6, pl. 1, figs. 8, 9.

Material. Fifteen incomplete glabellae 1.3–24.0 mm. long and various other cephalic parts.

Description. Glabella moderately raised, parallel-sided, front rounded and nearly reaching border. Three sets of glabellar furrows, all straight, all inclined toward rear, each pair inclined less strongly than pair in front, median pair shortest, anterior and median pairs do not reach glabellar margin. Occipital ring approximately the same size as adjacent glabellar lobe and bearing a small spine. Ocular lobes abruptly elevated at margins, long and narrow, terminating well posterior to occipital furrow.

Remarks. Most of the material resembles like parts of *Olenellus gilberti* Meek, but the collection is too incomplete for definite identification.

Occurrence. Upper *Olenellus* Faunizone, lower member, localities 2, 3, and 1085.

Genus PAEDEUMIAS Walcott 1910

Type species. *Paedeumias transitans* Walcott 1910.

Paedeumias sp. indet.

Plate 36, fig. 25

Material. One incomplete internal mould of a cephalon approximately 25 mm. long.

Description. Cephalon broadly convex, length–width ratio approximately 2:3. Glabella slightly concave along sides, widest at posterior end, anterior lobe pointed and terminating well posterior to border. Ocular lobes long and narrow, uniformly curved along outer margin, directed strongly back, terminating close to posterior border and to postero-lateral corner of occipital ring. Border uniformly narrow.

Remarks. A narrow border and a considerable distance between the border and the anterior lobe of the glabella serve to differentiate this specimen from other olenellids in

the Campbell Ranch section. These two features are considered diagnostic of the genus *Paedeumias*.

Occurrence. Upper *Olenellus* Faunizone, lower member, locality 1085.

Order CORYNEXOCHIDA Kobayashi 1935
Family DORYPYGIDAE Kobayashi 1935
Genus BONNIA Walcott 1916

Type species. *Bathyurus parvulus* Billings 1861.

Bonnia copia sp. nov.

Plate 36, figs. 17–24

Material. Eighty-nine cranidia 2.0–11.0 mm. long and sixty-eight pygidia 3.2–13.0 mm. long.

Description. Cranidium moderately convex, slightly wider across palpebral lobes than long. Glabella expands forward, strongly so on small cranidia, moderately so on large; all sizes broadly curved across front. Glabellar furrows weak, posterior set short and wide, remaining three sets faintly visible on internal moulds only, all sets probably branch. Axial furrow broadly convex outwards to nearly straight, of medium depth and width, considerably deeper and wider on internal moulds. Fixigenae downsloping, broadly curved in both directions. Palpebral lobes and furrows narrow, furrows much stronger on peeled specimens. Eye ridges visible only on internal moulds; they are low and located just posterior to border furrow. Anterior border narrow and slightly up-warped in front view. Posterior border furrow wide and expanding distally. Occipital ring bears a node on some specimens, a very small spine on others.

EXPLANATION OF PLATE 36

Upper *Olenellus* Faunizone.

- Figs. 1–5. *Onchocephalus papulus* sp. nov. (p. 224). 1–3, Holotype cranidium, plan, side, and front view, $\times 6.2$, USNM 153529. 4, Paratype cranidium, $\times 7.6$, USNM 153530. 5, Tentatively assigned pygidium with one attached thoracic segment, $\times 27.0$, USNM 153531. All specimens from loc. 2.
- Figs. 6–10. *Antagmus arenosus* sp. nov. (p. 220). 6–8, Holotype cranidium, plan, front, and side view, $\times 3.1$, USNM 153532. 9, Paratype cranidium, partially peeled, $\times 3.1$, USNM 153533. 10, Paratype cranidium, mostly peeled, $\times 3.3$, USNM 153534. All specimens from loc. 1085.
- Figs. 11–14. *Zacanthopsis levis* (Walcott) (p. 217). 11, 12, Cranidium, plan and side view, $\times 3.5$, USNM 153535, loc. 3. 13, Cranidium, mostly peeled, $\times 4.7$, USNM 153536, loc. 3. 14, Cranidium, $\times 4.1$, USNM 153537, loc. 1085.
- Figs. 15, 16. *Syspacephalus*? cf. *S. ? uncus* (Walcott) (p. 225). Cranidium, plan and side view, $\times 11.6$, USNM 153538, loc. 1085.
- Figs. 17–24. *Bonnia copia* sp. nov. (p. 194). 17, Paratype cranidium, small, $\times 4.5$, USNM 153539, loc. 3. 18, Paratype pygidium, small, $\times 4.5$, USNM 153540, loc. 3. 19–21, Holotype cranidium, plan, side, and front view, $\times 3.5$, USNM 153541, loc. 2. 22, 23, Paratype pygidium, plan and side view, $\times 4.3$, USNM 153542, loc. 2. 24, Paratype pygidium, mostly peeled, $\times 5.4$, USNM 153543, loc. 3.
- Fig. 25. *Paedeumias* sp. indet. (p. 193). Partial cephalon, mostly peeled, $\times 0.6$, USNM 153544, loc. 1085.
- Figs. 26–28. *Olenellus gilberti*? Meek (p. 193). 26. Partial glabella and ocular lobe, partially peeled, $\times 0.6$, USNM 153545. 27, Glabella and ocular lobes, partially peeled, $\times 0.5$, USNM 153546. 28, Gena, partially peeled, $\times 0.6$, USNM 153547. All specimens from loc. 1085.



1



2



3



4



5



6



7



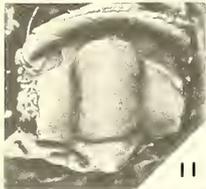
8



9



10



11



13



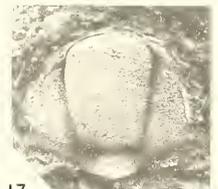
14



15



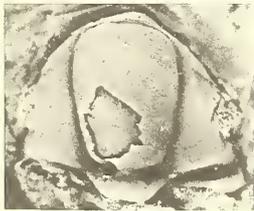
16



17



18



19



20



22



21



23



24



25



26



27



28

Pygidium has length-width ratio of approximately 2:3. Axis consists of one well-defined ring, one poorly defined ring, and terminal piece; internal moulds exhibit four rings and terminal piece. Pleural field lightly marked by pleural furrows; peeled specimens show three strong pleural furrows and their faint continuations across border furrow and border. Border fairly uniform except for slight reduction of width and broadening of curvature posterior to axis. Test nearly smooth, terrace lines present on anterior border and on front of glabella.

Remarks. Cranidia of *Bonnia copia* resemble those of *Bonnia fieldensis* (Walcott) 1916. However, the anterior border is not directed as strongly back along its distal portions on *B. fieldensis*. Pygidia of *B. fieldensis* are lower, relatively longer, and have lateral margins that trend more strongly rearward before curving abruptly into a broadly arcuate rear margin. Thus the pygidial outline of *B. fieldensis* has a more 'squared' appearance than does that of *B. copia*. *Bonnia sonora* Lochman 1952 is similar to the above two species, but is represented by only one small cranidium and seven poorly preserved pygidia and thus is difficult to compare at the specific level.

Occurrence. Upper *Olenellus* Faunizone, lower member, localities 2, 3, and 1085.

Genus KOOTENIA Walcott 1889

Type species. *Bathyriscus (Kootenia) dawsoni* Walcott 1889.

Kootenia acnlaecauda sp. nov.

Plate 41, figs. 1-8

Material. Twelve cranidia 1.8-11.2 mm. long and four pygidia 3.1-6.9 mm. long.

Description. Cranidium convex, length approximately three-quarters width across palpebral lobes. Glabella of medium height, sides parallel, front broadly curved. Glabellar furrows not visible except for three shallow sets on smallest cranidium, all sets fork, anterior two have one branch inclined forward and one inclined back, posterior set has transverse branch and branch inclined back. Palpebral area wide, convex, average slope is outward. Eye ridges broad and low. Palpebral furrows very wide and of moderate depth. Palpebral lobes narrow, centred posterior to glabellar midpoint, set well below level of axial furrow, nearly one-third as long as glabella. Border narrow in front of glabella, broadens considerably and then narrows near ends. Posterior area as wide (tr.) as occipital ring and traversed by a deep, broad furrow. Occipital furrow of medium depth near ends, shallow medially. Occipital ring very short (sag.), bearing a thin, uptilted spine.

Pygidium moderately convex, length-width ratio slightly less than 2:3. Axis nearly cylindrical, tapered slightly toward rear, consisting of three rings and rather long terminal piece. Pleural field of medium convexity, steep near border furrow, marked by three prominent and one weak pleural furrow and three faint interpleural furrows. Border narrow, bearing six sets of short, thin spines, anterior four sets slightly divergent. Surface of cranidium marked by terrace lines on anterior border and on part of occipital

ring; irregular granules of medium size locally fuse on large areas of cranidium and pygidium to give pitted as well as granular appearance.

Remarks. Cranidia and pygidia of *Kootenia germana* Resser 1939a most closely resemble those of this species. Cranidia of *K. germana* have a higher glabella, an anterior border of more uniform breadth, and a much narrower palpebral area. Pygidia have pleural areas that are less convex and a posterior set of spines that are more closely spaced. Three species of *Kootenia* from the Campbell Ranch section have six-spined pygidia as does *K. aculacauda*. Of these, *K. brevispina* and *K. sp. indet.* have short, rapidly tapering pygidial spines that are obviously different from those of *K. aculacauda*. Pygidial spines of *K. crassa* superficially resemble the narrow spines of *K. aculacauda*, but they are longer and somewhat flattened. The area occupied by the spines of *K. crassa* approximately equal the interspaces between, while the interspaces between spines of *K. aculacauda* are proportionately far wider.

Occurrence. *Albertella* Faunizone, upper member, localities 72 and 11.

Kootenia brevispina Resser

Plate 40, figs. 1-6

1939a *Kootenia brevispina* Resser, p. 50, pl. 11, figs. 1-4.

Material. Fifty-seven cranidia 5.0-14.5 mm. long, twenty-seven pygidia 2.6-11.4 mm. long, and five hypostomata.

Description. Cranidium moderately convex, length almost equals width across palpebral lobes. Glabella of medium height, sides parallel, curvature broad to medium in front. Two faint, broad sets of glabellar furrows visible on some specimens. Palpebral area narrow and downsloping. Palpebral furrows of medium depth and width; palpebral lobes centred posterior to glabellar midpoint, length between one-quarter and one-third that of glabella. Ocular ridge low and broad. Anterior border furrow shallow. Posterior area narrower (tr.) than occipital ring, distal margin rounded. Occipital furrow of moderate depth and width. Occipital ring bears a short spine. Hypostoma has elongate medial body with sides converging only slightly toward rear. Maculae shallow and steeply inclined toward rear. Lateral border furrows broad and of medium depth; anterior and posterior border furrows narrow. Anterior margin of hypostoma sharply downwarped near axial line.

Pygidium of medium convexity, length two-thirds width. Axis consists of three rings and a terminal piece. Pleural area marked by three medium pleural furrows and two weak interpleural furrows. Border flat, rather wide, downsloping. Six sets of flat, short, marginal spines, posterior three closely spaced, anterior three more widely spaced, posterior five shaped like teeth on a saw. Surface of cranidium and pygidium covered with fine granules, moderately worn areas appear pitted, strongly worn, smooth.

Remarks. Resser (1939a) erected three additional species from material that resembles *Kootenia brevispina*, but lacks the necessary detail for adequate comparison at specific level. Represented by this poor material are *Kootenia venusta* (cranidium only), *Kootenia*

mendosa, and *Kootenia pectenoides*. Another species, *Kootenia serrata* (Meek) 1873 resembles *K. brevispina*, but has a wider palpebral area and narrower, inwardly directed pygidial spines. *Kootenia brevispina* can be readily distinguished from other species of *Kootenia* in the Campbell Ranch collections by its six sets of broad, short, pygidial spines.

Occurrence. *Albertella* Faunizone, upper member, localities 14 and 15.

Kootenia convoluta Resser

Plate 41, figs. 17–24

1939a *Kootenia convoluta* Resser, p. 46, pl. 10, figs. 1–3, 7–11 (*non* figs. 4–6).

1939a *Kootenia maladensis* Resser, p. 47, pl. 10, figs. 12–15.

1939a *Kootenia gramulosa* Resser, p. 47, pl. 10, figs. 16–20.

1939a *Kootenia nitida* Resser, p. 47, pl. 10, fig. 21.

1944 *Kootenia convoluta* Resser; Shimer and Shrock, p. 613, pl. 257, figs. 1–4.

Material. Six cranidia 9·4–13·8 mm. long and four pygidia 4·9–10·3 mm. long.

Description. Cranium moderately convex, length somewhat less than width across palpebral lobes. Glabella low for genus, parallel-sided, front broadly curved. Two sets of faint, broad glabellar furrows, both sets transverse. Palpebral area broadly convex, slightly downsloping. Palpebral lobes centred well posterior to glabellar midpoint, length approximately one-third that of glabella. Anterior border furrow shallow, very narrow and shallow in front of glabella; anterior border rolled downward and under cranium producing rounded appearance in side view. Posterior area as wide (tr.) as occipital ring. Occipital furrow rather narrow and of moderate depth. Occipital ring bears a spine.

Pygidium moderately convex, length–width ratio slightly less than 2:3. Axis consists of three rings and a rather long terminal piece. Pleural field broadly convex, marked by three distinct sets of pleural and two sets of interpleural furrows. Border gives rise to five sets of round, slightly uptilted spines. Entire surface of smallest pygidium and border and spines of all pygidia are granular. Surface of anterior border marked by terrace lines, front of glabella marked by short, irregular ridges. Remaining portions of medium-sized cranidia, pygidia, and of librigena, have definite pitted appearance.

Remarks. In describing specimens similar to these, Resser (1939a) recognized four species (see synonymy) from a single locality, based upon slight differences in ornamentation, relief, depth of furrows, and width of anterior border. The writer believes these differences should have been attributed to differences in preservation—with one exception. That is a cranium which Resser (pl. 10, figs. 4–6) placed under *Kootenia convoluta* and which more closely resembles *Kootenia crassinucha* sp. nov. Among the Campbell Ranch collections of *Kootenia*, only *K. convoluta* and *K. crassinucha* have pygidia bearing five sets of spines. The spines of *K. crassinucha* have a more swollen base and terminate in sharper, thorn-like points. Cranidia of *K. crassinucha* have glabellae that are more oval shaped in plan view and palpebral areas that are more strongly downsloping.

Occurrence. *Albertella* Faunizone, upper member, locality 71.

Kootenia crassa sp. nov.

Plate 42, figs. 23–27

1952 *Kootenia exilaxata* Deiss; Lochman, p. 125, pl. 26, figs. 1–20.*Material.* Four cranidia 1·8–6·9 mm. long and six pygidia 1·0–3·2 mm. long.

Description. Cranidium moderately convex, length approximately equal to width across palpebral lobes. Glabella rather low for genus, sides parallel to slightly divergent in forward direction, front broadly curved. Glabella marked by one short, shallow set of glabellar furrows that are inclined moderately toward rear. Palpebral area broadly curved and downsloping. Palpebral lobes one-third as long as glabella, centred opposite posterior one-third point on glabella. Anterior border flat, rather broad (exsag.) in front of anterior area, horizontal except for slight downwarp near ends. Posterior area not as wide (tr.) as occipital ring and traversed by a furrow of uniform depth and width. Occipital furrow deep at sides, shallow near axial midline; occipital ring narrow near ends, rapidly broadening (exsag.) toward axial midline.

Pygidium two-thirds as long as wide. Axis consists of three rings, a faint fourth, and terminal piece. Pleural field marked by three clear sets of pleural furrows and two faint sets of interpleural furrows. Border furrow wide and shallow; border weakly developed and bearing six sets of spines. All sets slightly divergent and flattened in cross-section, anterior set shorter than rest. Width of spines equals or slightly exceeds width of inter-spaces between. Surface of specimens worn, ornamentation indistinct except for terrace lines on anterior border of cranidium.

Remarks. A species described by Lochman (1952) from Sonora, Mexico as *Kootenia exilaxata* Deiss 1939 is considered to be conspecific with *K. crassa*. The only difference noted between the Sonora and Campbell Ranch material is that the pygidial spines of the Sonora specimens tilt less strongly upwards. Pygidia in both collections differ from the paratype of *K. exilaxata* Deiss in having a narrower axis and pygidial spines that are flat rather than round in cross-section. In the Campbell Ranch collections, *Kootenia aculacauda* sp. nov. is the only species that might be confused with *K. crassa*. *Kootenia aculacauda* differs from *K. crassa* in that its pygidium is less triangular in outline and the pygidial spines are shorter, narrower, and round in cross-section.

Occurrence. *Albertella* and *Glossopleura* Faunizones, upper member, localities 15 and 74.

Kootenia crassimucha sp. nov.

Plate 41, figs. 12–16

Material. Thirty-one cranidia 13·1–18·5 mm. long and three pygidia 11·5–12·3 mm. long.

Description. Cranidium moderately convex, length approximately four-fifths width across palpebral lobes. Glabella of moderate height, subparallel to slightly convex along sides, curvature medium at front and broad at back. One set of faint glabellar furrows located posteriorly on glabella and inclined back. Palpebral area convex and downsloping. Eye ridges broad and low. Palpebral lobes centred posterior to glabellar

midpoint, defined by a shallow furrow, length is between one-quarter and one-fifth that of glabella. Border furrow shallow; border narrow in front of glabella, wider and having a flat upper surface at sides. Posterior area rounded at distal end, width (tr.) considerably less than that of occipital ring. Margin of occipital furrow steep bordering glabella, moderate bordering occipital ring. Medial portion (sag.) of occipital ring tilted gently forward as does small occipital spine.

Pygidium moderately convex, length approximately three-quarters width. Axis composed of three rings and a rather long terminal piece. Pleural field marked by three pleural furrows and three low, narrow ridges; anterior two ridges originate between anterior and second axial ring, posterior ridge between second and third ring. Border moderately downsloping, bearing five sets of spines, swollen near base of each spine; spines taper rapidly and then extend into thin points. Surface of cranidium is worn and thus appears to be rather smooth; fine pits are sparsely scattered on palpebral area and pleural area of pygidium.

Remarks. These cranidia most resemble those of *Kootenia germana* Resser 1939a. However, they have palpebral areas which are not as wide, longer (sag.) occipital rings, and shorter occipital spines. Pygidia of *K. crassinucha* have five sets of spines while those of *K. germana* have six. *Kootenia convoluta* Resser 1939a, the only other five-spined *Kootenia* in the Campbell Ranch collections, differs from *K. crassinucha* in having a glabella that is more rectangular in outline and less rapidly tapering pygidial spines. The spines of *K. convoluta* do not produce a swelling on the border of the pygidium.

Occurrence. *Albertella* Faunizone, upper member, locality 71.

Kootenia sp. indet.

Plate 43, figs. 31, 32

Material. One damaged pygidium approximately 11·8 mm. long.

Description. Pygidium moderately convex; axis composed of three rings and a terminal piece. Pleural field of medium convexity, crossed by three pleural furrows. Border of average width, swollen near base of each marginal spine. Six sets of spines, size and spacing of posterior five is uniform. Surface of internal mould nearly smooth.

Remarks. Marginal spines of this species resemble those of *Kootenia crassinucha* sp. nov. in that they are of medium length and their base is associated with a swelling on the border. They differ from those of *K. crassinucha* in that they number six rather than five, and do not extend into slender points.

Occurrence. *Glossopleura* (?) Faunizone, upper member, locality 18.

Genus *OLENOIDES* Meek 1877

Type species. *Paradoxides? nevadensis* Meek 1877.

Olenoides steptoensis sp. nov.

Plate 39, figs. 1-8

Material. Four cranidia 5·8-19·4 mm. long and four pygidia 3·8-15·4 mm. long.

Description. Cranium convex, slightly wider across palpebral lobes than long. Glabella parallel sided, curvature medium across front, length-width ratio a bit less than 4:3. Two weak sets of glabellar furrows, anterior set short, transverse, and located opposite glabellar midpoint, posterior set forked, one branch transverse and one inclined toward rear. Palpebral area convex, average slope slightly outward. Palpebral lobes centred posterior to glabellar midpoint. Anterior border back-sloping, width in front of glabella half that at sides. Posterior area nearly as wide (tr.) as axial ring, traversed by a wide furrow of medium depth. Occipital ring of moderate length (sag.) and bearing a spine.

Pygidium moderately convex, length-width ratio almost 2:3. Axis consists of four rings with nodes and terminal piece. Pleural field marked by three pleural furrows and a fourth (?) positioned almost against axis, three narrow interpleural furrows (third is bounded by sharp ridges), and one narrow ridge located against terminal piece. Border bears four sets of spines, posterior set directed straight back, other sets slightly divergent. Test covered with medium-size granules.

Remarks. Pygidia of *Olenoides maladensis* Resser 1939a most resemble these, but have smaller spines with the posterior pair spaced further apart. In the type lot containing *O. maladensis* are five unfigured cranidia of that species. Compared with *O. steptoensis*, they have a broader glabella, a narrower anterior border, and a shorter (sag.) occipital ring. In addition, the second set of glabellar furrows from the rear are situated further forward than on *O. steptoensis*. The five unfigured cranidia agree in every respect with a cranidium figured by Resser (1939a, pl. 14, fig. 3) as his holotype for *Taxioura magna* and are from the same locality. Palmer (1964b, pp. 6, 7) has correctly suggested that this cranidium belongs to *O. maladensis*.

Occurrence. Albertella Faunizone, upper member, localities 9 and 71.

Olenoides sp. indet.

Plate 43, figs. 20-23

Material. One cranidium 16.6 mm. long and one tentatively assigned hypostoma.

Description. Cranium convex, length somewhat less than width across palpebral lobes. Glabella parallel sided, curvature medium in front. Two sets of glabellar furrows, anterior set short, transverse, and located opposite midpoint; posterior set forked with one branch inclined forward and one back. Palpebral area convex and downsloping. Eye ridges strong. Palpebral lobes start approximately opposite glabellar midpoint, length less than one-third that of glabella. Posterior area not as wide (tr.) as occipital ring, broadly pointed. Occipital ring short (sag.) and bearing a small spine. Tentatively assigned hypostoma strongly convex, median body ovoid in plan view, marked by very shallow maculae, border furrow narrow, posterior and postero-lateral border much wider than antero-lateral and anterior border, anterior wings small. Cranium covered by granules of medium size; irregular ridges present on forward portion of glabella and on most of hypostoma.

Remarks. A wider glabella, more steeply dipping palpebral area, and a shorter (sag.) occipital ring distinguish this cranidium from those of *Olenoides steptoensis* sp. nov. The hypostoma tentatively placed with this large cranidium is also large and has a similar ornamentation. However, the anterior wings are relatively small for a dorypygid hypostoma.

Occurrence. *Glossopleura* (?) Faunizone, upper member, locality 18.

Family OGYGOPSIDAE Rasetti 1951

Genus OGYGOPSIS Walcott 1889

Type species. *Ogygia klotzi* Rominger 1888.

Ogygopsis sp. indet.

Plate 40, fig. 30

Material. One pygidial fragment 15.4 mm. long.

Description. Pygidial axis narrow, nearly cylindrical, sides slightly converging toward rear. Axis composed of at least seven rings, terminal piece, and short postaxial ridge fused to border. Each axial ring marked by a very shallow, transverse furrow that does not extend to axial furrow. Pleural field composed of six or more fused pleurae. Pleural furrows of medium width and depth; no interpleural furrows visible. Border narrow, well rounded in cross-section, curved posteriorly except for almost straight portion behind axis. Surface of pygidium nearly smooth except for faint, undulating ridges on border.

Remarks. This pygidium differs from that of *Ogygopsis typicalis* (Resser) 1939a [= *O. magna* (Resser) 1939a] in having narrower and shallower axial furrows, a wider terminal piece, and by lacking a medial notch on the posterior margin.

Occurrence. *Albertella* Faunizone, upper member, locality 11.

Family ORYCTOCEPHALIDAE Beecher 1897

Genus ORYCTOCEPHALUS Walcott 1886

Type species. *Oryctocephalus primus* Walcott 1886.

Oryctocephalus cf. *O. primus* Walcott

Plate 40, figs. 14-16

1886 *Oryctocephalus primus* Walcott, p. 210, pl. 29, figs. 3, 3a

1890 *Oryctophalus primus* Walcott; Walcott, p. 653, pl. 95, figs. 4, 4a.

1889 *Oryctocephalus primus* Walcott; Miller, p. 558, figs. 1036, 1037.

non 1935 *Oryctocephalus primus* Walcott; Kobayashi, pl. 15, fig. 1.

1954 *Oryctocephalus primus* Walcott; Palmer, p. 68, pl. 15, figs. 1, 2.

Material. One damaged cranidium.

Remarks. The cranidium that Walcott designated as a cotype for *Oryctocephalus primus* agrees closely with this one. Assignment of the present cranidium is questioned only because of its incompleteness. A slightly higher, more parallel-sided glabella and a narrower palpebral area served to distinguish the cranidium of *O. primus* from that of *Oryctocephalus maladensis* Resser 1939a.

Occurrence. Albertella Faunizone, upper member, locality 10.

Oryctocephalus maladensis Resser

Plate 41, figs. 25-27

1939a *Oryctocephalus maladensis* Resser, p. 45, pl. 3, figs. 7-9.

Material. Seven cranidia 3·1-4·1 mm. long.

Description. Cranidium low, longitudinal profile broadly convex, transverse profile averages horizontal, length-width ratio 3:4. Glabella subrectangular, low along margins and along transverse depressions between pits, slightly higher along remaining portion near axial midline. One set of short glabellar furrows located opposite origin of ocular ridge. Three sets of glabellar pits, longitudinal interspace distance equal between sets, same distance separates posterior set from two pits in occipital furrow, transverse interspace distance wider but likewise equal for glabellar and occipital pits. Axial furrow has uniformly moderate depth and width. Palpebral area wide, flat, and up-sloping. Ocular ridge low, outlined by a shallow furrow on either side. Palpebral lobes originate opposite anterior set of pits, length slightly exceeds half that of glabella. Anterior border narrow; anterior border furrow narrow and shallow. Posterior area half again as wide (tr.) as occipital ring, traversed by a furrow that broadens and deepens distally. Occipital ring bears a node located anterior to midpoint. Surface of cranidium nearly smooth, faint venation present on palpebral area.

Remarks. Cranidia of this species in the Campbell Ranch collections are nearly identical to the original types described by Resser from the 'Ptarmigania strata' of southern Idaho.

Occurrence. Albertella Faunizone, upper member, locality 71.

GENUS ORYCTOCEPHALITES Resser 1939

Type species. *Oryctocephalites typicalis* Resser 1939a.

Oryctocephalites typicalis Resser

Plate 41, figs. 9-11

1939a *Oryctocephalites typicalis* Resser, p. 45, pl. 3, figs. 1-6.

Material. Six cranidia 1·6-3·9 mm. long.

Description. Cranidium moderately convex in side view, broadly convex in front view, length approximately three-quarters width. Glabella moderately low, sides convex, narrowest at posterior margin, widest at midlength, broadly curved across front. Three

sets of glabellar pits, longitudinal spacing equal between sets, transverse spacing equal between anterior two sets, posterior set more closely spaced and joined by a furrow. Axial, anterior border, posterior border, and occipital furrows all moderately narrow and of medium depth. Eye ridges barely visible. Palpebral lobes upsloping, half as long as glabella, and terminating just ahead of occipital furrow. Anterior border of uniform width, bearing a node located slightly anterior to midpoint.

Occurrence. *Albertella* Faunizone, upper member, localities 71 and 11.

Family DOLICHOMETOPIDAE Walcott 1916
Genus ATHABASKIA Raymond 1928

Type species. *Athabaskia ostheimeri* Raymond 1928.

Athabaskia sp. indet.

Plate 43, figs. 1, 2

Material. Four broken pygidia estimated to be 1.9–4.3 mm. long and three tentatively assigned librigenae.

Description. Pygidium probably twice as wide as long. Axis consists of three rings bearing large nodes or spines, an indistinct fourth ring, and terminal piece. Pleural region convex across inner three-fifths, outer two-fifths concave. Pleural region marked by four pleural and interpleural furrows, all are of equal strength, all shallow abruptly and vanish before reaching margin of pygidium. Librigena with long eye platform, lateral border furrows deep and very broad, lateral border consists of turned up edge of test. Librigena and pygidium nearly smooth.

Remarks. The above material is too fragmentary for comparison with other species. It is figured and briefly described only to document the presence of the genus.

Occurrence. *Glossopleura* Faunizone, upper member, locality 74.

Genus BATHYURISCUS Meek 1873

Type species. *Bathyurus? haydeni* Meek 1873.

Bathyuriscus petalus sp. nov.

Plate 43, figs. 27–30

Material. Three cranidia 4.5–8.5 mm. long and three pygidia 5.1–6.9 mm. long.

Description. Cranidium moderately convex, length slightly greater than width across palpebral lobes. Glabella approximately twice as long as wide, sides parallel along posterior half, only slightly divergent along anterior half, broadly curved across front. Anterior three sets of glabellar furrows barely visible, posterior set shallow and inclined toward rear. Axial furrow shallow. Palpebral area moderately convex and downsloping. Palpebral furrow uniformly wide and shallow; palpebral lobes uniformly narrow, half

as long as glabella, terminating just ahead of occipital furrow. Fixigena immediately anterior to palpebral lobe much wider (tr.) than frontal area (sag.). Posterior area exceeds occipital ring in width (tr.). Occipital furrow broad and shallow; occipital ring bears a small spine on posterior margin.

Pygidium nearly twice as wide as long. Axis consists of four rings, terminal piece, and short postaxial ridge; a transverse ridge or node is present on each of the anterior three rings. Pleural field only slightly convex, marked by four strong pleural and four narrow interpleural furrows. Border upsloping, width uniform except for constriction near shallow posterior cusp and local extension into a set of short, antero-lateral spines. Scattered puncti present on occipital ring, remainder of test smooth.

Remarks. The combination of a long, narrow glabella and a wide pygidium with antero-lateral spines differentiates this species from others in the genus *Bathyriscus*. A single, small (2 mm.) pygidium, *Bathyriscus politus* Resser 1939a, resembles this species in many respects, but has a subtriangular outline and one less set of pleural and interpleural furrows. It is impossible to ascertain whether or not specific features are fully developed on this small pygidium.

Occurrence. *Glossopleura* (?) Faunizone, upper member, locality 18.

Genus CORYNEXOCHIDES Rasetti 1948

Type species. *Corynexochides gregarius* Rasetti 1948.

Corynexochides prolatus sp. nov.

Plate 42, figs. 7-11

Material. Seven cranidia 1.6-4.5 mm. long and one pygidium 0.9 mm. long.

Description. Cranidium convex, length approximately equal to width across palpebral lobes. Glabella cylindrical except for moderate expansion along anterior one-third, broadly curved across front. Two weak sets of glabellar furrows, anterior set short, transverse, located opposite glabellar midpoint, posterior set inclined toward rear. Palpebral area convex, downsloping. Palpebral lobes narrow, broadly curved along anterior half, extending nearly straight back along posterior half, terminating slightly forward of occipital furrow. Anterior area of fixigena uniformly narrow, width (tr.) approximately equals breadth (exsag.) of anterior border. Anterior border furrow of medium depth, deeper than axial furrow. Posterior area not as wide (tr.) as occipital ring, distal end rounded, furrow occupies nearly half of area. Occipital furrow straight and of medium depth, broadening near ends. Occipital ring expanded medially and bears an elongate (sag.) node.

Pygidium over twice as wide as long, lateral margins converge to points. Axis consists of one distinct ring, one faint ring, and terminal piece, latter two portions have a flattish surface on top. Pleural area moderately downsloping, marked by two pleural furrows. Border has same slope as pleural field, two sets of cusps present on postero-lateral margin. Test punctate.

Remarks. A close resemblance exists between this species and *Corynexochides bicensis* Rasetti 1948. The latter species differs in having a lower, broader glabella, a narrower anterior border, and broader palpebral lobes. Pygidia of *C. bicensis* are smaller, but in other respects similar to the one here assigned to *C. prolatus*.

Occurrence. *Glossopleura* Faunizone, upper member, localities 18 and 74.

Genus GLOSSOPLEURA Poulsen 1927

Type species. *Dolichometopus boccar* Walcott 1916.

Glossopleura sp. indet. 1

Plate 43, figs. 3, 4

Material. Two damaged pygidia estimated to be 8.5 and 10.8 mm. long and two tentatively assigned librigenae.

Description. Pygidium moderately convex. Axis probably consists of three to four faintly defined rings and terminal piece. Pleural field marked by one pleural furrow and two low ridges that are near first (anterior) interpleural position. Contact between pleural field and border poorly defined; border broadly convex, narrowing posteriorly, maximum width exceeds that of pleural field. Librigena has wide border that expands slightly in posterior direction. Anterior inner edge of lateral border nearly converges with eye platform. Genal spine drawn into a slender point. Surface of pygidium and librigena nearly smooth except for medium-spaced, thin, irregular terrace lines.

Remarks. Pygidia and librigena of this species and of *Glossopleura* sp. indet. 2 occur together in a single locality. Parts have been tentatively assigned using similarities in the strength and pattern of terrace lines as a principal guide. As the differences in this ornamentation are not pronounced, there is some possibility that the natural association of parts has been reversed.

Occurrence. *Glossopleura* Faunizone, upper member, locality 74.

Glossopleura sp. indet. 2

Plate 43, figs. 5, 6

Material. Five damaged pygidia estimated to be 1.8 to 9.2 mm. long and seven tentatively assigned librigenae.

Description. Pygidium low; axis wider than pleural field, consisting of approximately five poorly defined rings and terminal piece. Pleural field broadly convex, crossed by four broad, shallow, pleural furrows. Border concave, width expands in posterior direction. Librigena has wide border of uniform width and a broad, evenly tapering spine. Surface of pygidium and librigena slightly rough, border marked by closely spaced, thin, irregular ridges.

Remarks. Pygidia of this species differ from those of *Glossopleura* sp. indet. 1, in having a border that broadens (tr.) in the posterior rather than the anterior direction. The

pleural field of *G. sp. indet.* 1 is less deeply furrowed, the upper surface is smoother, and the border is ornamented by terrace lines which are spaced further apart.

Occurrence. *Glossopleura* Faunizone, upper member, locality 74.

Genus POLIELLA Walcott 1916

Type species. *Bathyriscus (Poliella) anteros* Walcott 1916.

Remarks. *Poliella* is a genus which needs reviewing and a clearer definition. At present it is being used for similar forms found in the *Plagiura-Poliella*, *Albertella*, and *Glossopleura* Faunizones. The holotype is the youngest known species and, unlike most of the other species assigned to *Poliella*, it is small (1.5 cm.), bears an occipital spine, and axial spines on each thoracic segment.

Poliella denticulata Rasetti

Plate 38, figs. 14-18

1951 *Poliella denticulata* Rasetti, p. 173, pl. 12, figs. 6-9.

1951 *Poliella* cf. *P. denticulata* Rasetti, p. 174, pl. 9, figs. 7, 8.

Material. Eighteen cranidia 1.3-5.1 mm. long and seven pygidia 1.3-4.0 mm. long.

Description. Cranidium moderately convex, length equal to width measured across palpebral lobes. Glabellar length nearly twice minimum width, sides almost parallel along posterior half, slightly expanding along anterior half, front broadly curved and nearly reaching front margin of cranidium. Glabellar furrows indistinct, all four sets probably branched, posterior branch on fourth set deepest and strongly inclined toward rear. Palpebral area downsloping, maximum width nearly two-thirds that of glabella. Frontal area very narrow. Posterior area of fixigena nearly parallel-sided along most of width (tr.), width exceeds that of occipital ring. Palpebral lobes and furrows narrow and well defined, lobes terminate opposite or slightly anterior to occipital furrow. Occipital ring bears a short spine.

Pygidium twice as wide as long. Axis consists of anterior ring with transverse ridge rather than node, second ring bearing small node, poorly defined third ring, and terminal piece. Pleural field marked by three pleural furrows and one weak interpleural furrow. Border of moderate width, bearing a short, flat spine on antero-lateral margins, three sets of small lobes, and a medial cusp. Test punctate.

Remarks. There is close agreement between these pygidia and those in the type collection of *Poliella denticulata* Rasetti 1951. Cranidia in the latter collection are distorted, but cranidia in a second collection, which Rasetti (1951) has identified as *Poliella* cf. *P. denticulata*, are not; these closely resemble cranidia from the Campbell Ranch section.

Occurrence. *Albertella* Faunizone, upper member, localities 8, 9, 71, 72, 11, 14, and 15.

Poliella germana (Resser)

Plate 37, figs. 1-9

- 1939a *Dolichometopsis comis* Resser, p. 33, pl. 4, fig. 24 lower left cranidium only (*non* figs. 22, 23).
1939a *Dolichometopsis potens* Resser, p. 36, pl. 6, figs. 17-20 (*non* figs. 21-23).
1939a *Ptarmigania agrestis* Resser, p. 39, pl. 7, figs. 1, 2.
1939a *Ptarmigania altilis* Resser, p. 40, pl. 7, figs. 3, 4 (*non* fig. 5).
1939a *Ptarmigania sobrina* Resser, p. 40, pl. 7, figs. 13 pygidium only, 14, 15 (*non* fig. 12).
1939a *Ptarmigania germana* Resser, p. 41, pl. 7, figs. 16-20.
1939a *Ptarmigania dignata* Resser, pl. 41, pl. 8, figs. 1, 2, 4-7 (*non* fig. 3).

Material. Twenty-seven cranidia 0.9-26.0 mm. long, thirty-five pygidia 2.3-10.0 mm. long, four librigenae, and three hypostomata.

Description. Cranidium low, length somewhat less than width across palpebral lobes. Glabella nearly parallel sided along posterior third, expanding forward along anterior two-thirds, front broadly curved and almost reaching forward edge of cranidium. Four sets of broad, shallow glabellar furrows, anterior two sets inclined forward, third set inclined back, fourth with short transverse branch and long posteriorly inclined branch. Palpebral area nearly flat to slightly convex, sloped moderately downward, width equals two-thirds minimum width of glabella. Palpebral lobes set somewhat below adjoining palpebral area, broad and flat, nearly horizontal, and terminating opposite front margin of occipital furrow; palpebral furrow shallow and poorly defined. Anterior border very narrow in front of glabella, wider and more obvious along antero-lateral margin of cranidium. Posterior area expands distally, width (tr.) approximately equals that of occipital ring. Occipital furrow shallow; occipital ring bears a small node. Librigena has border that is approximately two-thirds as wide as area between border furrow and eye platform. Hypostoma with medium body that is traversed by deep furrow, posterior lobe small, anterior lobe uniformly convex, border furrow locally wide on strong anterior wings.

Pygidium approximately twice as wide as long, anterior margin directed out from axis and slightly back, posterior margin broadly curved except for medial cusp. Axis consists of three rings, terminal piece, and postaxial ridge extending to margin; anterior ring has a low, transverse ridge rather than node. Pleural field marked by three distinct and one faint pleural furrow, all extend across weak border furrow and on to wide border. Test punctate, transverse ridges visible on occipital ring, venation present on librigenae.

Remarks. In the above synonymy are listed seven of Resser's species that the writer believes have been based upon differences in preservation and upon artificially mixed parts from other species. Here the foreign parts are removed and the remainder placed under *Poliella germana*. The present species concept is focused upon the holotype of *P. germana*, which is the best preserved cranidium among the types representing Resser's seven species. The cranidia in this case are considered more distinctive than the equally well-preserved pygidia.

Occurrence. *Albertella* Faunizone, upper member, localities 8-11, 71, and 72.

Poliella leipalox sp. nov.

Plate 38, figs. 22–28

Material. Sixty-one cranidia 2.4–15.4 mm. long, thirty-seven pygidia 1.5–8.5 mm. long, sixteen librigenae, nineteen hypostomata, and two incomplete thoracic regions.

Description. Cranidium very low, somewhat wider across palpebral lobes than long. Glabella nearly rectangular, slightly concave along sides, very slightly expanded anteriorly, front broadly curved. Pattern of glabellar furrows similar to that on *Poliella germana* (Resser) 1939a. Palpebral area broadly convex, gently downsloping, width a bit more to slightly less than two-thirds minimum glabellar width. Palpebral lobes set a little lower than adjacent area and terminating opposite anterior margin of occipital furrow. Palpebral furrow shallow. Fixigena anterior to eye ridge wide (tr.) for a dolicho-metopid and downsloping. Border and border furrow poorly differentiated on frontal area; area dips gently forward, more strongly so near axial midline. Posterior area expanded distally; occipital ring has a small node. Librigena has border half to less than half as wide as area between border furrow and eye platform. Hypostoma with medial body traversed by deep furrow, posterior lobe small, anterior lobe has strong medial (sag.) keel with steep flanks, antero-lateral border furrow wide, anterior border furrow slightly narrower and much deeper, anterior wings strong.

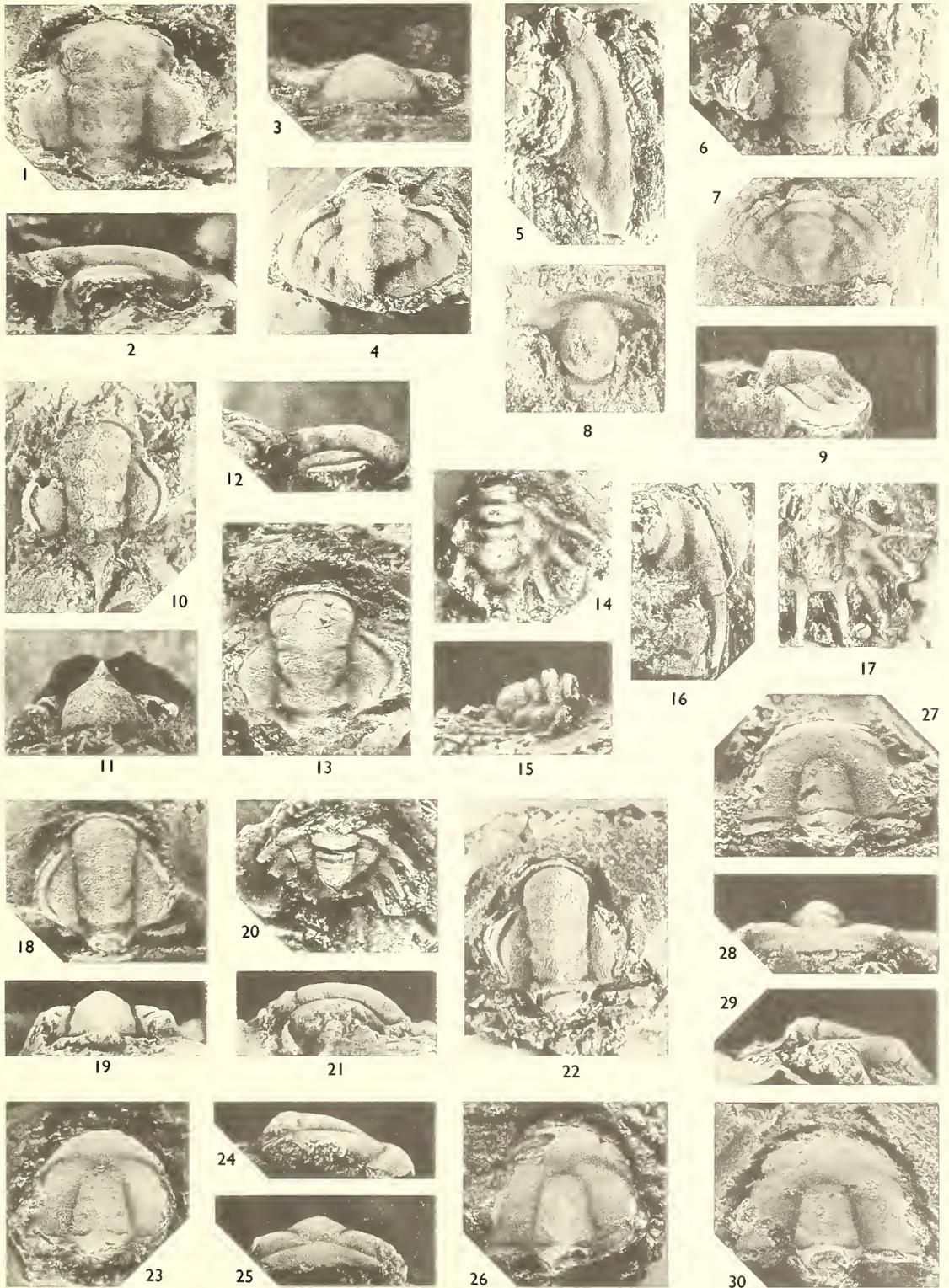
Pygidial width less than twice length. Axis consists of one ring with transverse ridge, terminal piece, and postaxial ridge. Anterior margin of pygidium begins to curve strongly back a short distance from axis, sides very strongly inclined toward rear, posterior margin broadly curved except for a medial cusp. Pleural field marked by three pleural furrows and one faint interpleural furrow. Border broad and poorly defined from pleural field. Test punctate, venation visible on librigenae, pygidium, and hypostoma.

Remarks. The most complete of two damaged thoracic regions in the above material shows a minimum of ten thoracic segments. *Poliella prima* (Walcott) 1916 resembles this species but has at least two less thoracic segments and a narrower palpebral area.

EXPLANATION OF PLATE 37

Olenellus and *Albertella* Faunizones.

- Figs. 1–9. *Poliella germana* (Resser) (p. 207). 1–3, Cranidium, plan, side, and front view, $\times 2.4$, USNM 153548, loc. 71. 4, 9, Pygidium, plan and side view, $\times 1.9$, USNM 153549, loc. 71. 5, Librigena, $\times 4.8$, USNM 153550, loc. 71. 6, Cranidium, small, $\times 7.2$, USNM 153551, loc. 71. 7, Pygidium, small, $\times 5.8$, USNM 153552, loc. 71. 8, Hypostoma, $\times 6.2$, USNM 153553, loc. 72.
- Figs. 10–17. *Ptarmiganoides araneicauda* sp. nov. (p. 209). 10–12, Paratype cranidium, plan, front, and side view, $\times 4.4$, USNM 153554, loc. 71. 13, Paratype cranidium, $\times 3.2$, USNM 153555, loc. 71. 14, 15, Holotype pygidium, plan and side view, $\times 3.5$, USNM 153556, loc. 9. 16, Paratype librigena, $\times 3.0$, USNM 153557, loc. 9. 17, Latex cast of paratype pygidium, $\times 1.9$, USNM 153558, loc. 71.
- Figs. 18–22. *Ptarmiganoides lepida*? (Resser) (p. 209). 18, 19, 21, Cranidium, plan, front, and side view, $\times 5.3$, USNM 153559, loc. 10. 20, Pygidium, partially peeled, $\times 3.9$, USNM 153560, loc. 12. 22, Cranidium, $\times 5.5$, USNM 153561, loc. 9.
- Figs. 23–26. *Crassifimbria walcotti*? (Resser) (p. 223). 23–25, Cranidium, plan, side, and front view, $\times 5.3$, USNM 153562, loc. 1085. 26, Cranidium, $\times 5.5$, USNM 153563, loc. 1085.
- Figs. 27–30. *Syspacephalus* sp. indet. (p. 226). 27–29, Cranidium, peeled, plan, front, and side view, $\times 6.2$, USNM 153564, loc. 1085. 30, Cranidium, peeled, $\times 6.2$, USNM 153565, loc. 1085.



FRITZ, Cambrian trilobites, Pioche Shale, Nevada

Poliella germana (Resser) 1939a has a more rapidly expanding glabella, a narrower (sag.) frontal area, and a wider pygidium.

Occurrence. *Albertella* Faunizone, upper member, localities 8–12, 71, 72.

Genus PTARMIGANOIDES Rasetti 1951

Type species. *Ptarmiganoides bowensis* Rasetti 1951.

Ptarmiganoides araneicauda sp. nov.

Plate 37, figs. 10–17

Material. Sixty-eight cranidia 1·8–16·0 mm. long and twenty-eight pygidia 1·8–7·4 mm. long.

Description. Cranidium as wide or wider across palpebral lobes than long. Glabella moderately low, posterior half sub-parallel and somewhat concave along sides, anterior half expanded, front broadly curved. Four sets of glabellar furrows, anterior two sets inclined forward, third set curved back, last set with transverse branch and deep branch inclined back. Palpebral area upsloping, width exceeds half that of glabella at mid-length. Fixigena anterior to eye ridge narrow (tr.) but not as narrow (sag.) as anterior border. Posterior border broadens and flattens distally, bearing metafixigenal spine. Palpebral lobes strongly curved, positioned below level of adjacent fixigena and paralleled by a wide, deep palpebral furrow. Occipital ring tapers back for a considerable distance and extends into a spine. Librigena with spine wider than area between border furrow and eye platform.

Pygidium has high, wide axis consisting of three rings and terminal piece. Anterior ring tapers upward to form large spine. Pleural area downsloping, marked by one wide and two narrower pleural furrows. Border furrow nearly absent except for alignment of three sets of pits opposite interspaces between four sets of border spines. Spines approximately equal in size, widely spaced, nearly round in cross-section, anterior set almost normal to pygidial axis, posterior set almost parallel to axis. Test covered by granules of variable size.

Remarks. Pygidia of this species differ from those of *Ptarmiganoides lepida?* (Resser) 1939a, in having more widely spaced, round spines and deeper pits near the border. Cranidia differ in having a broader glabella that is less convex in cross-section.

Occurrence. *Albertella* Faunizone, upper member, localities 8–10, and 71.

Ptarmiganoides lepida? (Resser)

Plate 37, figs. 18–22

1939a *Dolichometopsis lepida* Resser, p. 31, pl. 3, figs. 31[?], 32, 33.

Material. Seventeen cranidia 0·9–8·0 mm. long and four pygidia 2·5–4·9 mm. long.

Description. Cranidium convex, length equal to or slightly greater than width across palpebral lobes. Glabella somewhat cylindrical, sides nearly parallel along posterior half, slightly expanded along anterior half, broadly curved across front, minimum width is approximately half glabellar length. Glabellar furrows arranged as on *Ptarmiganoides*

araneicauda sp. nov. Palpebral area slightly upsloping to horizontal, width approximately three-quarters minimum glabellar width. Palpebral lobes strongly curved, curvature along anterior half nearly as strong as along posterior half, elevation equals or is slightly less than that of area immediately across deep palpebral furrow. Posterior area almost as broad (tr.) as occipital ring and bearing a metafixigenal spine. Occipital ring drawn back into a spine that is inclined moderately upward.

Pygidium considerably wider than long. Axis moderately high, composed of an anterior ring bearing a large spine, two additional rings, and terminal piece. Pleural field marked by one wide and two narrower pleural furrows and set of faint ridges near anterior and near second interpleural position. Three sets of shallow pits on poorly defined border furrow. Four sets of flattened border spines, each set slightly larger than next anterior set. Area between spines nearly uniform except wider between posterior two. Test covered with medium to coarse granules.

Remarks. The holotype cranidium of *Dolichometopsis lepida* Resser 1939a agrees closely with cranidia in the present collection. Unfortunately, no associated pygidia were found in the type collection for comparison. Because many dolichometopid cranidia, and zacanthoidid cranidia as well, are known to be similar, the present assignment must be questioned.

Occurrence. *Albertella* Faunizone, upper member, localities 8–10 and 12.

Ptarmiganoides sp. indet.

Plate 38, figs. 19–21

Material. Five cranidia 7.2–13.1 mm. long.

Description. Cranial length slightly exceeds width measured across palpebral lobes. Glabella nearly parallel-sided, very slightly concave along posterior two-thirds, slightly

EXPLANATION OF PLATE 38

Albertella Faunizone.

Figs. 1–7. *Albertelloides mischi* gen. et sp. nov. (p. 215). 1–3, Paratype cranidium, small, plan, front, and side view, $\times 7.2$, USNM 153566. 4, Paratype pygidium, small, $\times 2.5$, USNM 153567. 5, 7, Holotype pygidium, side and plan view, $\times 1.6$, USNM 153568. 6, Paratype cranidium, $\times 1.1$, USNM 153569. All specimens from loc. 12.

Figs. 8, 9. *Pagetia resseri* Kobayashi (p. 192). 8, Cranidium, $\times 11.6$, USNM 153570, loc. 72. 9, Pygidium, $\times 11.6$, USNM 153571, loc. 9.

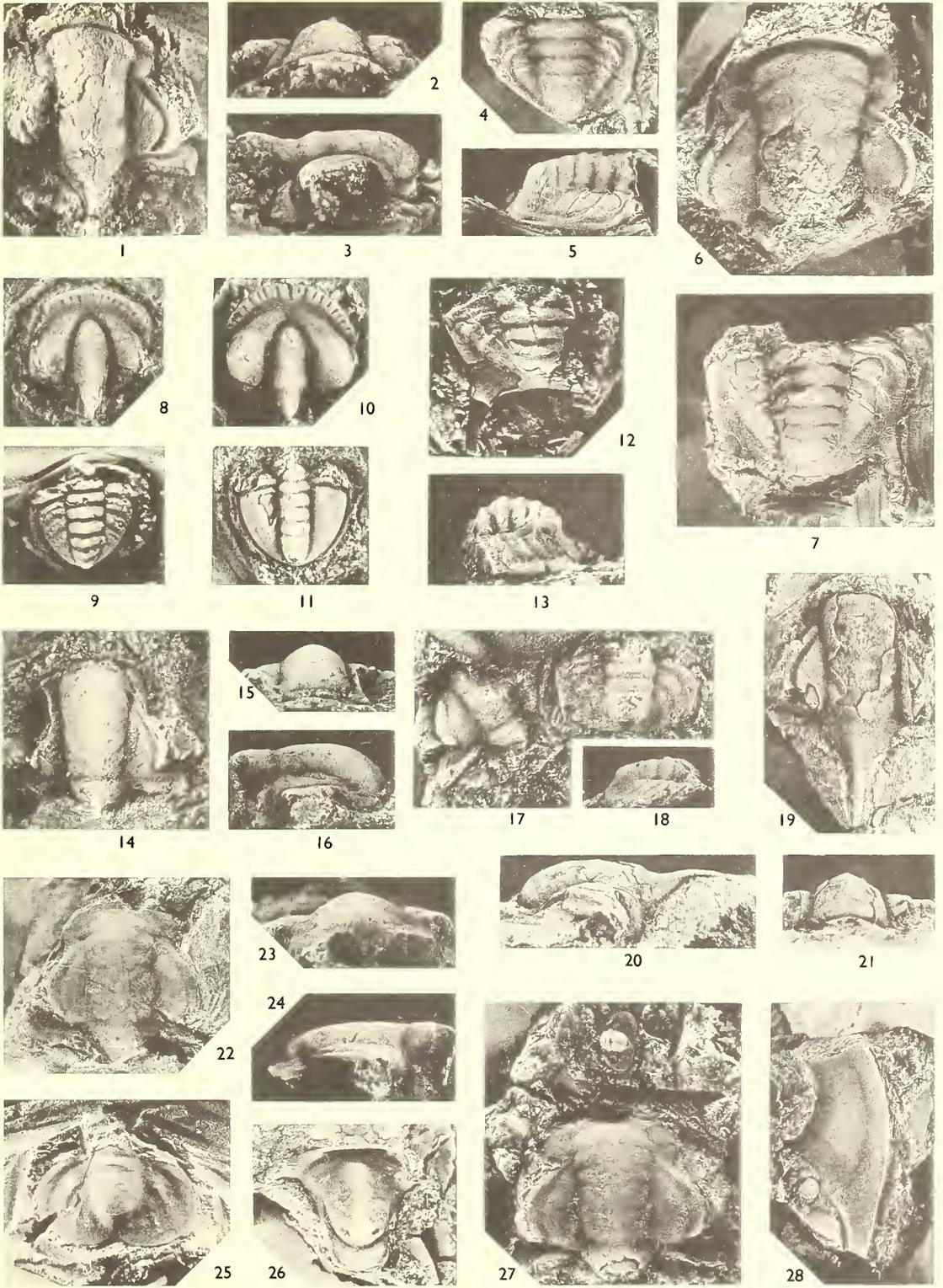
Figs. 10, 11. *Pagetia clytia* Walcott (p. 189). 10, Cranidium, $\times 9.7$, USNM 153572, loc. 72. 11, Pygidium, $\times 9.7$, USNM 153573, loc. 72.

Figs. 12, 13. *Albertelloides* sp. indet., gen. nov. (p. 217). Pygidium, partially peeled, plan and side view, $\times 3.1$, USNM 153574, loc. 9.

Figs. 14–18. *Poliella denticulata* Rasetti (p. 206). 14–16, Cranidium, plan, front, and side view, $\times 5.1$, USNM 153575, loc. 72. 17, 18, Pygidium, plan and side view; note partial cranidium in 17, $\times 4.5$, USNM 153576, loc. 71.

Figs. 19–21. *Ptarmiganoides* sp. indet. (p. 210), Cranidium, partially peeled, plan, side, and front view, $\times 3.4$, USNM 153577, loc. 8.

Figs. 22–28. *Poliella leipalox* sp. nov. (p. 208). 22–24. Paratype cranidium, plan, front, and side view, $\times 2.4$, USNM 153578, loc. 11. 25, Paratype pygidium, $\times 2.8$, USNM 153579, loc. 72. 26, Paratype hypostoma, $\times 2.9$, USNM 153580, loc. 11. 27, Holotype cranidium; note small pygidium, $\times 3.1$, USNM 153581, loc. 72. 28, Paratype librigena, $\times 2.5$, USNM 152582, loc. 72.



FRITZ, Cambrian trilobites, Pioche Shale, Nevada

expanded along anterior third, front broadly rounded, length twice minimum width. Glabellar furrows have pattern as on *Ptarmiganoides araneicauda* sp. nov. except posterior set does not branch and is more strongly inclined toward rear. Palpebral area upsloping, a little less than two-thirds as wide as minimum width of glabella. Palpebral lobes moderately curved and terminating slightly anterior to point opposite occipital furrow. Occipital ring tapers back for a considerable distance before forming a spine. Cranidia covered with granules of varying sizes.

Remarks. These cranidia differ from those of *Ptarmiganoides araneicauda* sp. nov. and *Ptarmiganoides lepida?* (Resser) 1939a in having glabellae with less forward expansion, unbranched and strongly inclined posterior glabellar furrows, narrower palpebral areas, longer (sag.) occipital rings, and palpebral lobes that terminate ahead of the occipital furrow.

Occurrence. *Albertella* Faunizone, upper member, localities 8 and 71.

Family ZACANTHOIDIDAE Swinnerton 1915

Genus ZACANTHOIDES Walcott 1888

Type species. *Olenoides typicalis* Walcott 1886.

Zacanthoides demissus sp. nov.

Plate 42, figs. 1-6

Material. Six cranidia 4.6-12.3 mm. long and five pygidia 2.5-6.6 mm. long.

Description. Cranidium moderately convex, length equals width across palpebral lobes. Glabella rather low, parallel-sided, broadly curved across front. Anterior two sets of glabellar furrows indistinct; posterior two sets angle back, third set does not reach shallow axial furrow. Palpebral area flat and nearly horizontal. Palpebral lobes upsloping, originating against axial furrow, length exceeds three-quarters that of glabella. Facial suture strongly divergent from palpebral lobes forward; anterior limb wide and long. Posterior area narrow, width (tr.) exceeds that of occipital ring. Occipital furrow deep near ends, shallows and widens one-quarter furrow length in from ends, very shallow medially. Occipital ring bears a small spine.

Pygidial length slightly exceeds three-quarters width. Axis high, consisting of three rings, terminal piece, and steep postaxial ridge extending to margin. Pleural region flat and horizontal, marked by one faint interpleural and two pleural furrows. Three sets of broad, flat spines on posterior margin, sets decrease rapidly in size inward, all spines point slightly inward and are tilted gently downward. Test covered by small granules.

Remarks. Combined features that serve to differentiate this species from others in the genus *Zacanthoides* are a very wide and long (tr. and sag.) anterior limb on the cranidium and three sets of broad, flat, pygidial spines.

Occurrence. *Glossopleura* (?) Faunizone, upper member, locality 18.

Zacanthoides sp. indet.

Plate 40, figs. 7-10

Material. One cranium and one pygidium estimated to be 13.1 mm. and 4.6 mm. long respectively.

Description. Cranium slightly longer than wide across palpebral lobes. Glabella parallel-sided, front has medium curvature. Two sets of glabellar furrows, both sets angle back. Palpebral area moderately convex, averaging horizontal. Palpebral lobes originate at axial furrow, terminate opposite occipital furrow, length approximately three-quarters that of glabella. Facial suture strongly divergent from palpebral lobes forward. Occipital ring probably bears a spine.

Pygidium approximately two-thirds as long as wide. Axis consists of four rings and a terminal piece. Pleural field marked by three sets of furrows which terminate between four sets of spines. Spines round to elliptical in cross-section, directed slightly inward and downward; very small additional spines may be present behind axis. Test covered by small granules.

Remarks. This material is too poorly preserved for specific identification. There is little question, however, that it represents a species different from *Zacanthoides demissus* sp. nov., as the cranium has a narrower (tr.) palpebral area and the pygidium has more numerous, round spines.

Occurrence. *Albertella* Faunizone, upper member, locality 15.

Genus ALBERTELLA Walcott 1908

Type species. *Albertella helena* Walcott 1908.

Albertella judithi sp. nov.

Plate 39, figs. 22-30

Material. Seventy crania 2.3-10.0 mm. long and seventy-two pygidia 1.5-13.1 mm. long.

Description. Cranium as wide or slightly wider across palpebral lobes than long. Glabella nearly cylindrical, sides straight and slightly converging, front well rounded. Four sets of glabellar furrows, anterior and second set inclined moderately forward, third set inclined back, posterior set forks into nearly obsolete anterior branch and posterior branch that is inclined toward rear. Palpebral area flat, slightly upsloping, maximum width nearly four-fifths width of glabella at base. Palpebral lobes raised above adjacent palpebral area and terminating well posterior to occipital furrow; palpebral furrow narrow. Anterior limb tilted moderately upward along forward edge of cranium. In addition to ocular ridge, a second, weaker ridge originates in depression near antero-lateral margin of glabella; the latter ridge curves forward and outward to terminate at antero-lateral margin of cranium. Posterior area narrow and as wide (tr.) as occipital ring. Occipital ring has medial (sag.) ridge terminating in a short spine. Librigena has ridge originating on posterior portion of border and continuing along genal spine. Hypostoma with small, abrupt swelling paralleling and just posterior to maculae, antero-lateral and anterior border furrows shallow.

Pygidial length equal to width at base of spines. Axis consists of six rings and a terminal piece. Rings uniformly decrease in size except for relatively short (sag.) posterior ring; each bears a spine with a round basal cross-section. Anterior half of pleural field marked by two sharp ridges just behind anterior and second interpleural position, and two weaker ridges just ahead of these positions; posterior half of field marked by four weak ridges. Border posterior to spines is uniform in width and drops slightly in elevation near terminal piece. Border spines are uniformly narrow, horizontal, slightly divergent, and at least three-quarters as long as pygidium. Test covered by small granules; venation present on pygidium, particularly apparent on and near terminal piece.

Remarks. This species resembles *Albertella limbata* Rasetti 1951. It differs in having a glabella that converges rather than expands forward, an anterior border that slopes backward rather than forward, and glabellar furrows that are shallower. The pygidium differs by having one less axial ring, and border spines that are directed slightly outward rather than straight back.

Occurrence. *Albertella* Faunizone, upper member, localities 9, 10, 12, 71, and 72.

Albertella eiloitys sp. nov.

Plate 39, figs. 16–18

Material. Twelve pygidia 3.2–6.3 mm. long.

Description. Cranidium probably similar to that of *Albertella judithi* sp. nov.

Pygidial length exceeds width measured just anterior to border spines; entire pygidium posterior to spines slopes moderately toward rear. Axis consists of six rings and terminal piece, five rings bear spines with transversely ovate cross-sections at base, posterior ring has smaller spine or node. Pleural field narrow, marked by two sharp ridges near anterior and second interpleural position and by two or three similar but weaker ridges further back. Border tilted inward along postero-lateral margin of pygidium giving an 'upcurled' appearance. Border spines inclined upward and slightly outward, length unknown. Cranidium probably covered by small granules, pygidium nearly smooth except for venation on and near base of terminal piece.

Remarks. Cranidia of this species are thought to resemble those of *Albertella judithi* sp. nov. so closely that they cannot be differentiated. A second possibility, considered less likely, is that only cranidia of *A. judithi* are in the collections. Pygidial borders of *A. eiloitys* from two localities tilt inward, and therefore this feature cannot be attributed to distortion. In other respects, pygidia of *A. eiloitys* resemble those of *Albertella bosworthi* Walcott 1908 and *Albertella declavis* Rasetti 1951. If the first of the assumptions concerning the cranidia of *A. eiloitys* is correct, they differ from those of *A. bosworthi* and *A. declavis* in having a wider (tr.) anterior limb.

Occurrence. *Albertella* Faunizone, upper member, localities 9 and 11.

Albertella lata sp. nov.

Plate 39, figs. 19–21

Material. Five pygidia 3·1–7·5 mm. long.

Description. Pygidium low, wider than long. Axis strongly tapered, consisting of six rings and terminal piece, anterior five rings bear spines with round basal cross-sections. Pleural field low but slightly higher than border, traversed by two sharp ridges originating between anterior three rings and by several very weak ridges further back. Border flat and nearly horizontal, tilted moderately outward and broadly curved across rear of pygidium. Border spines located far back, horizontal and slightly divergent. Pygidium may be granular (surface preservation poor).

Remarks. A low relief, posteriorly located spines, and a broad curvature of the border between spines differentiate these pygidia from those of other species in this genus.

Occurrence. Pioche Shale, upper member, localities 10 and 71.

Genus ALBERTELLOIDES gen. nov.

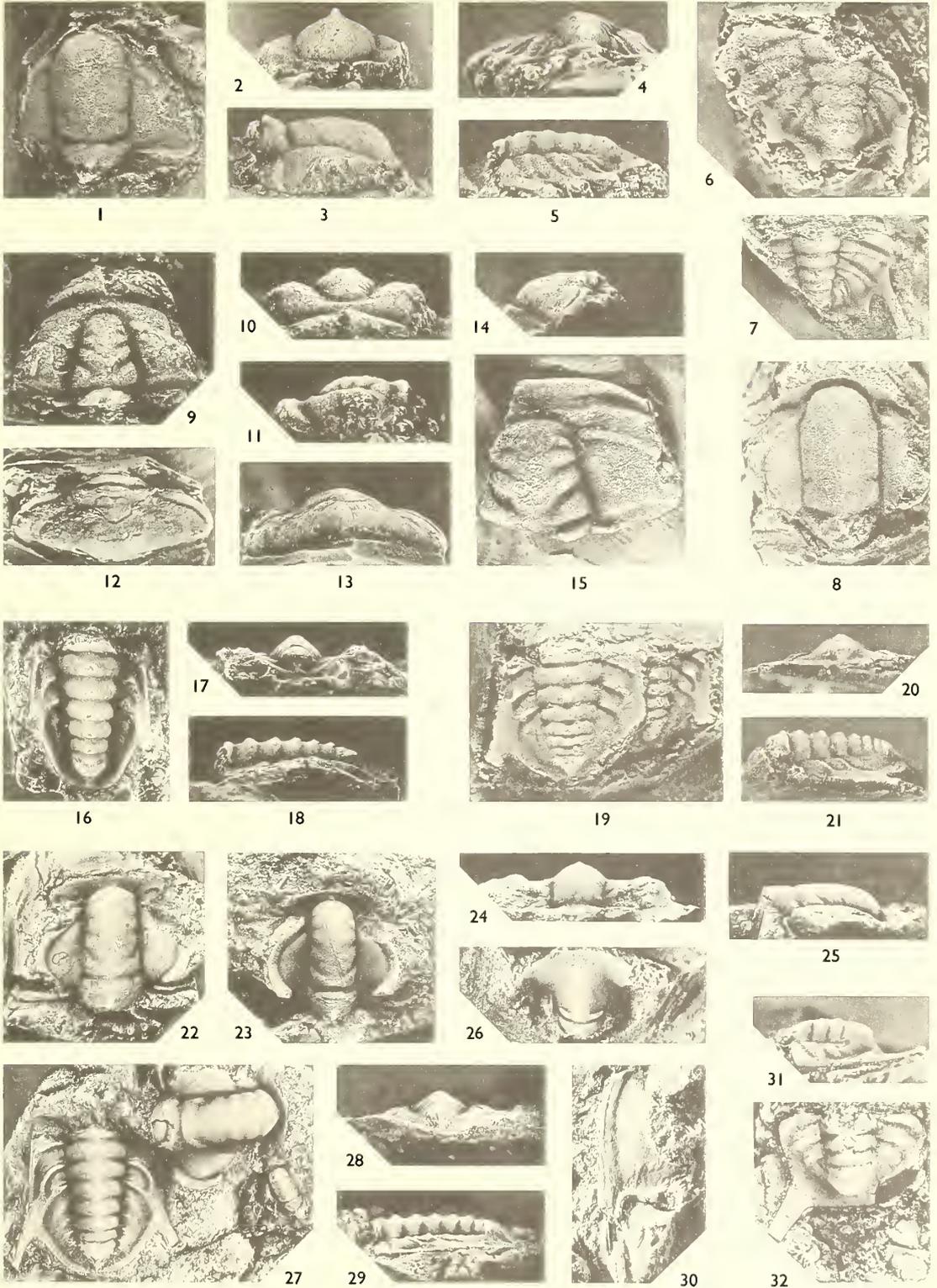
Type species. *Albertelloides mischli* gen. et sp. nov.

Description. Cranium convex, approximately as wide across palpebral lobes as long. Glabella expands anteriorly, broadly curved across front, marked by four sets of glabellar furrows. Anterior border uniformly narrow. Palpebral area convex, at least half as wide as minimum glabellar width. Palpebral lobes narrow, set below level of adjacent palpebral area, length approximately half that of glabella. Eye ridges prominent and narrow. Posterior area narrow (exsag.) and bearing a metafixigenal spine. Occipital ring triangular in plan view and terminating in a spine. Thoracic section unknown.

EXPLANATION OF PLATE 39

Albertella Faunizone.

- Figs. 1–8, *Olenoides steptoensis* sp. nov. (p. 199). 1–3, Paratype cranium, small, plan, front, and side view, $\times 3\cdot7$, USNM 153583. 4–6, Holotype pygidium, rear, side, and plan view, $\times 3\cdot3$, USNM 153584. 7, Paratype pygidium, $\times 3\cdot8$, USNM 153585. 8, Paratype cranium, $\times 2\cdot5$, USNM 153586. All specimens from loc. 71.
- Figs. 9–15, *Caborcella granulosa* (Resser) (p. 221). 9–11, Cranium, plan, front, and side view, $\times 4\cdot0$, USNM 153587, loc. 9. 12–14, Pygidium, plan, rear, and side view, $\times 4\cdot5$, USNM 153588, loc. 11. 15, Partial cranium, large, $\times 1\cdot7$, USNM 153589, loc. 12.
- Figs. 16–18, *Albertella eiloitys* sp. nov. (p. 213). Holotype pygidium, plan, rear, and side view, $\times 4\cdot2$, USNM 153590, loc. 11.
- Figs. 19–21, *Albertella lata* sp. nov. (p. 214). Holotype pygidium, plan, rear, and side view; note second pygidium under holotype in fig. 19; $\times 3\cdot7$, USNM 153591, loc. 10.
- Figs. 22–30, *Albertella judithi* sp. nov. (p. 212). 22, 24, 25, Paratype cranium, plan, front, and side view, $\times 2\cdot3$, USNM 153592. 23, Paratype cranium, $\times 3\cdot9$, USNM 153593. 26, Paratype hypostoma, $\times 4\cdot5$, USNM 153594. 27–29, Holotype pygidium, plan, rear, and side view; note two cranidia of the species in fig. 27; $\times 2\cdot2$, USNM 153595. 30, Paratype librigena, $\times 2\cdot5$, USNM 153596. All specimens from loc. 71.
- Figs. 31, 32, *Albertelloides pandispinata* gen. et sp. nov. (p. 216). Holotype pygidium, side and plan view; note two pygidia of *Pagetia resseri* in fig. 32; $\times 5\cdot0$, USNM 153597, loc. 9.



FRITZ, Cambrian trilobites, Pioche Shale, Nevada

Pygidium considerably wider than long, highly convex. Axis well elevated, extending back to border, consisting of approximately four or five rings and terminal piece. Pleural field convex, traversed by at least several sets of narrow ridges located near interpleural position. Border of medium width, giving rise to two marginal spines in postero-lateral position. Posterior margin between spines is moderately convex to nearly straight.

Remarks. *Albertella* is the genus which most closely resembles *Albertelloides*. Cranidia of most, but by no means all, specimens of *Albertella* differ from the three cranidia thus far assigned to the new genus by having (1) a narrower (tr.) anterior limb, (2) a glabella with less expansion along the anterior half and a more rounded front, (3) palpebral areas that are less convex in cross-section (tr.), and (4) palpebral lobes that are broader. Pygidia of most specimens of *Albertella* differ from those of *Albertelloides* in having (1) a lower axis, (2) pleural fields that are less convex, (3) axial rings that bear spines, and (4) marginal spines that are located further forward. No species of *Albertella* is known to have attained as large a size as *Albertelloides mischi* or to possess metafixigenal spines. Nearly all species of *Albertella* have a granular test while those belonging to *Albertelloides* do not.

Of the five species known to belong to *Albertelloides*, three, *A. mischi*, *A. pandispinata*, and *A. sp. indet.* are described in this paper. The fourth and fifth are known from pygidia described by Resser (1919a) as *Kochaspis dispar* and *Kochaspis maladensis*. Cranidia which Resser wrongly assigned to *K. dispar* probably belong to the genus *Caborcella*.

Occurrence. Upper member of the Pioche Shale in the Campbell Ranch section, and 'Ptarmigania strata' of southern Idaho. Both localities are believed to be in the later portion of the *Albertella* Faunizone.

Albertelloides mischi gen. et sp. nov.

Plate 38, figs. 1-7

Material. Three cranidia 4.2-21.2 mm. long and three pygidia 7.2-13.5 mm. long.

Description. Cranidium convex, length approximately equal to width across palpebral lobes. Glabellar sides straight and parallel along posterior half, diverging along anterior half, front broadly curved, crest outlined in side view is evenly curved from front to back. Four sets of shallow glabellar furrows, anterior two sets inclined forward, third set inclined back, fourth set branched with both limbs inclined back. Axial furrow of uniform depth and width except for set of small pits just anterior to eye ridges and small swellings ahead of pits. Palpebral area moderately convex, tilted slightly inward. Eye ridges swept strongly back, width approximately same as that of palpebral lobes. Palpebral lobes narrow, set below level of adjacent palpebral area, terminating opposite or just posterior to occipital furrow. Anterior area of fixigena wider (tr.) than anterior border is long (sag.); facial suture slightly divergent from palpebral lobes to anterior border furrow. Anterior border of uniformly narrow width and tilted back. Posterior area broadens distally and bears metafixigenal spine. Occipital furrow of uniform width and depth; occipital ring drawn back into a spine.

Pygidium convex, much wider than long, greatest width just posterior to strongly curved antero-lateral margins, from these points lateral margins are nearly straight and slightly

converging until reaching marginal spines, posterior margin broadly and evenly curved. Axis high, extending to border, composed of five or six rings and terminal piece. Pleural field convex, downsloping, marked by four narrow ridges, anterior two closely spaced near first (anterior) interpleural position, posterior two similarly spaced near second position and weaker. Border furrow shallow; border moderately downsloping at sides of pygidium, steeply downsloping along back. Spines located postero-laterally, slightly divergent, and tilted moderately upward. Surface of test nearly smooth except for venation that is most noticeable on border of pygidium and on palpebral area.

Remarks. Pygidia of *Albertelloides dispar* (Resser) 1939a resemble those of this species but have a wider pleural field and only three to four distinct axial rings.

Occurrence. *Albertella* Faunizone, upper member, locality 12.

Albertelloides pandispinata gen. et sp. nov.

Plate 39, figs. 31, 32

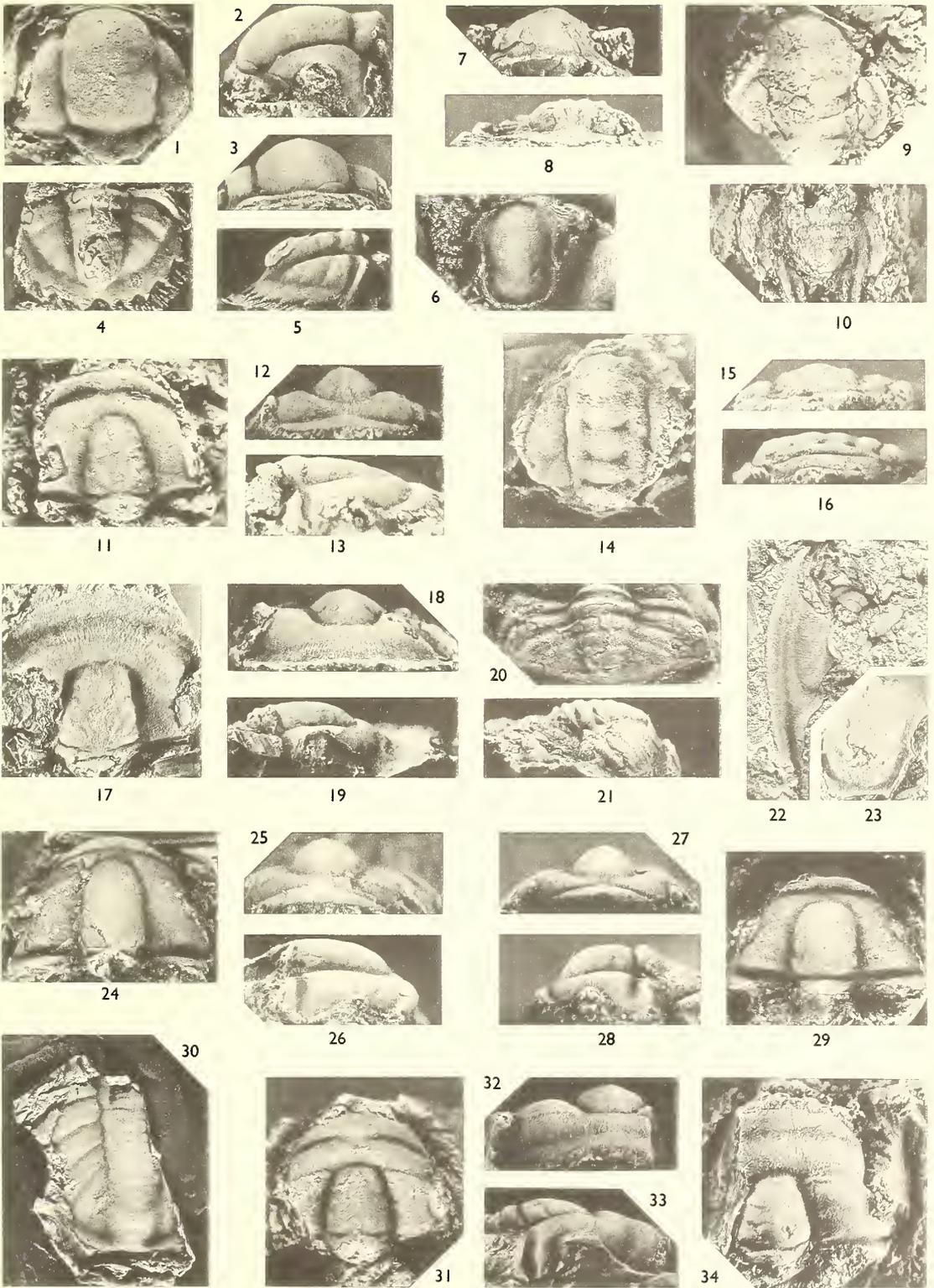
Material. Two pygidia, each 9.0 mm. long.

Description. Pygidium approximately two-thirds as long as wide. Axis nearly cylindrical, slightly tapered toward rear, composed of four rings and terminal piece, furrows between rings widen near middle. Pleural field slopes moderately outward, abruptly steepens near border, marked by two sets of sharp ridges near first (anterior) and second interpleural position. Border widest and locally horizontal near spines, steeply downsloping between spines, posterior margin straight. Spines flattish, strongly divergent, tilted slightly upward. Ornamentation unknown (pygidium is worn).

EXPLANATION OF PLATE 40

Albertella Faunizone.

- Figs. 1–6. *Kootenia brevispina* Resser (p. 196). 1–3, Paratype cranium, plan, side, and front view, $\times 2.3$, USNM 153598, loc. 14. 4, 5, Holotype pygidium, plan and side view, $\times 2.2$, USNM 153599, loc. 14. 6, Paratype hypostoma, $\times 2.7$, USNM 153600, loc. 15.
- Figs. 7–10. *Zacanthoides* sp. indet. (p. 212). 7, 9, Cranium, front and plan view, $\times 2.8$, USNM 153601, loc. 15. 8, 10, Pygidium, side and plan view, $\times 3.6$, USNM 153602, loc. 15.
- Figs. 11–13. *Pachyaspsis gallagari* sp. nov. (p. 231). Holotype cranium, plan, front, and side view, $\times 6.0$, USNM 153603, loc. 14.
- Figs. 14–16. *Oryctocephalus* cf. *O. primms* Walcott (p. 201). Cranium, plan, front, and side view, $\times 6.5$, USNM 153604, loc. 10.
- Figs. 17–23. *Amecephalus laticandum* (Resser) (p. 227). 17–19, Cranium, plan, front, and side view, $\times 2.3$, USNM 153605, loc. 14. 20, 21, Pygidium, plan and side view, $\times 3.7$, USNM 153606, loc. 15. 22, Librigena, $\times 2.9$, USNM 153607, loc. 18. 23, Partial hypostoma, $\times 2.9$, USNM 153608, loc. 15.
- Figs. 24–26. *Pachyaspsis longa* sp. nov. (p. 231). Holotype cranium, plan, front, and side view, $\times 6.5$, USNM 153609, loc. 11.
- Figs. 27–29. *Spencia quadrata* sp. nov. (p. 232). Holotype cranium, front, side, and plan view, $\times 7.9$, USNM 153610, loc. 11.
- Fig. 30. *Ogygopsis* sp. indet. (p. 201). Latex cast of partial pygidium, $\times 1.8$, USNM 153611, loc. 11.
- Figs. 31–34. *Chancia venusta* (Resser) (p. 230). 31, Cranium, small, peeled, $\times 5.0$, USNM 153612, loc. 12. 32–34, Cranium, peeled, front, side, and plan view, $\times 2.3$, USNM 153613, loc. 12.



FRITZ, Cambrian trilobites, Pioche Shale, Nevada

Remarks. This species most resembles *Albertelloides unaladensis* (Resser) 1939a, but has four rather than three axial rings, a straight rather than broadly curved posterior margin, and marginal spines that are more strongly divergent.

Occurrence. *Albertella* Faunizone, upper member, locality 9.

Albertelloides sp. indet.

Plate 38, figs. 12, 13

Material. One pygidial fragment estimated to be 6.2 mm. long.

Description. Pygidium very convex. Axis high, consisting of four rings and terminal piece, furrows between rings widen near axial midline. Pleural field convex, steeply down-sloping, marked by four narrow ridges, anterior two closely spaced near first (anterior) interpleural position, posterior two weaker and similarly arranged near second position. Border slopes gently outward. Spines horizontal, elliptical in cross-section, slightly divergent near base, gently curved and less divergent further out. Posterior margin of pygidium slightly concave inward. Surface of pygidium poorly preserved, ornamentation unknown.

Remarks. Compared to *Albertelloides paudispinata* sp. nov., this species has a higher axis, more steeply sloped pleural field, and spines which are less divergent.

Occurrence. *Albertella* Faunizone, upper member, locality 9.

Genus ZACANTHOPSIS Resser 1938

Type species. *Olenoides levis* Walcott 1886.

Zacanthopsis levis (Walcott)

Plate 36, figs. 11–14

- 1886 *Olenoides levis* Walcott, p. 187, pl. 25, figs. 3, 3a.
- 1888 *Zacanthoides levis* Walcott; Walcott, p. 165.
- 1891 *Zacanthoides levis* Walcott; Walcott, p. 646, pl. 94, figs. 5, 5a.
- 1906 *Zacanthoides?* *levis* Walcott; Lorenz, p. 72, 1 text-fig.
- 1938b *Zacanthopsis levis* (Walcott); Resser, p. 106, pl. 3, figs. 40, 41.
- 1964b *Zacanthopsis levis* (Walcott); Palmer, pl. 3, figs. 1–3.

Material. Thirty-six cranidia 3.1–6.7 mm. long.

Description. Glabella nearly cylindrical, anterior portion slightly expanded, front broadly rounded. Three sets of shallow glabellar furrows, anterior set short, second and third sets inclined back, third set joining. Palpebral area horizontal, nearly flat, as wide or wider than glabella at midpoint. Anterior border furrow broad; anterior border steeply back-sloping. Eye ridges of weak to medium strength; palpebral furrows narrow; palpebral lobes raised above adjacent area and slightly longer than half glabellar length. Posterior border nearly normal to axis, bends abruptly forward and downward at point just posterior to palpebral lobe. Occipital furrow expands near ends, otherwise of

medium width and depth. Occipital ring set below level of glabella, triangular in plan view, drawn back into spine that has small node at base. Top and undersurface of cranium covered by fine granules.

Occurrence. Upper *Olenellus* Faunizone, lower member, localities 2, 3, and 1085.

Order PTYCHOPARIIDA Swinnerton 1915

Family PTYCHOPARIIDAE Matthew 1887

Genus ACHLYSOPSIS gen. nov.

Type species. *Achlysopsis liokata* gen. et sp. nov.

Description. Cranium moderately low, very lightly furrowed, broadly curved in both directions, length approximately equal to width across palpebral lobes. Glabella low, particularly so in front, length and width about equal, sides converge forward, front moderately rounded. Glabellar front and preglabellar field slope forward at approximately same angle, forward slope of flat anterior border is less steep. Length (sag.) of preglabellar field slightly greater than that of anterior border. Palpebral area broadly curved, averages horizontal to slightly downsloping, approximately half as wide as maximum glabellar width. Palpebral lobes narrow, centred posterior to glabellar midpoint, approximately half as long as glabella. Posterior area not as wide (tr.) as occipital ring, rounded at distal end. Occipital ring short (sag.), low, bearing a node.

Tentatively assigned pygidium is small, transverse, and convex. Axis low, narrow, composed of approximately six rings and terminal piece. Pleural region comprised of six or seven fused segments that slope gently outward near axis and rather steeply outward near margin, both pleural and interpleural furrows visible.

Remarks. Cranidia of this genus closely resemble those in the genus *Mexicella*. They differ from the type species, *Mexicella mexicana* Lochman 1952, in having a lower glabella, shallower dorsal furrow, larger and more posteriorly located palpebral lobes, and by lacking a boss on the preglabellar field. *Mexicella stator* (Walcott) 1916 occupies a more intermediate position between the two genera as it has a low glabella and lacks a boss. Pygidia tentatively assigned to *Achlysopsis* have a narrower axis with far more segments than those belonging to *Mexicella*. A second genus, *Onchocephalites* Rasetti 1957, resembles *Achlysopsis* in its general appearance and in having very shallow cranial furrows. *Onchocephalites* differs from *Achlysopsis* in having a glabella with convex lateral margins, facial sutures that turn sharply inward after crossing the anterior border furrow, and an anterior border that slopes more steeply forward. *Nanogia* Poulsen 1964 also resembles *Achlysopsis*, but has a glabella with concave lateral margins, palpebral lobes that are located in a more posterior position, and facial sutures that are strongly divergent from the palpebral lobes forward. The only known species of *Achlysopsis* are the two described in the present paper. If the pygidium tentatively assigned to the type species proves to be the correct one, then a similar pygidium described as *Tonkinella idahoensis* Resser 1939a may represent a third species.

Occurrence. Upper member of the Pioche Shale, Campbell Ranch section. In this section the genus ranges from the late *Albertella* into the early *Glossopleura* (?) Faunizone.

Achlysopsis liokata gen. et sp. nov.

Plate 42, figs. 17-22

Material. Thirty-eight cranidia 1·8-9·2 mm. long and two tentatively assigned pygidia 1·5 and 3·8 mm. long.

Description. Cranidium moderately low, length somewhat less than width across palpebral lobes. Glabella very low, anterior half flush with fixigenae, posterior half rises slightly above. Axial furrow narrow and shallow, converging forward at sides of glabella, curvature medium across front. Four very shallow sets of glabellar furrows visible only on internal moulds, anterior two closely spaced and inclined slightly forward, third set transverse, posterior set transverse and then forked with one branch inclined forward and other back. Palpebral lobes narrow and downsloping, centred slightly posterior to glabellar midpoint, nearly half as long as glabella. Preglabellar field longer (sag.) than border, side view shows forward slope continuous with that of glabella. Anterior border furrow shallow; border flat, slopes forward less steeply than preglabellar field. Facial suture slightly divergent from palpebral lobes to anterior border furrow. Posterior area not as wide (tr.) as occipital ring. Occipital furrow narrow and shallow near ends, very shallow and wider near middle. Occipital ring short (sag.) and bearing a node.

Pygidium tentatively assigned to this species has shape of half dome, curvature across top broad, becoming steep near margin. Axis low in front, flush with pleural region in back, consisting of six rings and a terminal piece; anterior two rings each exhibit two faint, transverse ridges. Pleural region marked by six pleural furrows of medium depth and five narrow and shallow interpleural furrows. Surface of cranidium and tentatively assigned pygidium nearly smooth.

Remarks. A single pygidium that may be congeneric with these has been described by Resser (1939a) as *Tonkinella idahoensis*. It differs from the present pygidia in having shallower furrows on the pleural region and a lower axis.

Occurrence. *Glossopleura* (?) Faunizone, upper member, locality 18.

Achlysopsis hemitora gen. et sp. nov.

Plate 42, figs. 12-16

Material. Thirty cranidia 1·8-10·0 mm. long.

Description. Cranidium low, length slightly less than width across palpebral lobes. Glabella moderately low, sides straight, curvature broad to medium across front. Four sets of shallow glabellar furrows visible on internal mould; anterior two weak and inclined forward; third normal and then forks into two branches, one inclined forward and the second back; posterior set forks into two branches, one directed slightly back and the other strongly back. Axial furrow shallow. Palpebral area nearly flat, slightly downsloping. Eye ridges well developed on internal mould and swept strongly back. Palpebral lobes slightly downsloping, half as long as glabella, terminating just ahead of occipital furrow. Preglabellar field slopes moderately forward, slightly longer (sag.) than

border. Facial suture directed straight forward from palpebral lobe to border furrow, slightly divergent on flattened cranidia, slightly convergent on those that are transversely compressed. Anterior border furrow shallow and uniform except near middle where it shallows because of very small swelling which extends a short distance on to border. Posterior area nearly as wide (tr.) as occipital ring, distal ends rounded. Occipital furrow narrow and deep near ends, shallow and bowed forward near middle. Occipital ring short (sag.) and bearing a node. Test covered with small granules, preglabellar field and adjacent fixigena marked by longitudinal venation.

Remarks. Cranidia of this species differ from those of *Achlysopsis liokata* sp. nov. by having a higher glabella, wider palpebral area, and more posteriorly located palpebral lobes.

Occurrence. *Albertella* Faunizone, upper member, locality 15.

Genus ANTAGMUS Resser 1936

Type species. *Antagmus typicalis* Resser 1937 [= *Ptychoparia teucer* (Billings) Walcott 1886; non *Conocephalites teucer* Billings 1861].

Antagmus arenosus sp. nov.

Plate 36, figs. 6-10

Material. Six cranidia 6.7-8.3 mm. long.

Description. Cranidium broadly convex in both directions. Glabella low, sides straight to very slightly concave and converging forward, front broadly curved. Posterior two sets of glabellar furrows visible on outer surface of test; four sets visible on internal mould, anterior two sets short and faint, third set has transverse and posteriorly inclined branch, posterior set has two branches inclined back. Facial suture divergent between palpebral lobes and anterior border furrow. Palpebral area broadly curved (tr.), average slope is outward; front of anterior area slopes steeply toward anterior furrow; medial portion of preglabellar field nearly horizontal. Anterior border furrow wide and deep distally, shallow near axial midline. Anterior border upwarped in front view; in plan view rear margin evenly curved on upper surface of test, but exhibiting slight medial recurvature on internal moulds. Eye ridges of medium strength; palpebral lobes located slightly posterior to glabellar midpoint, length approximately one-third that of glabella. Width (tr.) of posterior area approximately equal to that of occipital ring. Posterior and occipital furrows narrow; occipital ring narrow (exsag.), only slightly broader medially (sag.), and bearing a node. Both upper and lower surfaces of cranidium are covered by medium-sized, closely spaced granules.

Remarks. A very wide palpebral area serves to distinguish this species from others in the genus *Antagmus*.

Occurrence. Upper *Olenellus* Faunizone, lower member, locality 1085.

Genus CABORCELLA Lochman 1948

Type species. *Caborcella arrojensis* Lochman 1948.

Caborcella granosa (Resser)

Plate 39, figs. 9–15

1939a *Poulsenia granosa* Resser, p. 59, pl. 13, figs. 19, 22–30 (non figs. 20, 21).

? 1939a *Poulsenia bearensis* Resser, p. 60, pl. 13, figs. 5–8.

1944 *Poulsenia granosa* Resser; Shimer and Shrock, p. 615, pl. 259, figs. 6, 7.

1951 *Caborcella granosa* (Resser); Rasetti, p. 211.

Material. Fifty-two cranidia 1.7–12.6 mm. long and two pygidia 2.3 and 3.1 mm. long.

Description. Cranium considerably wider across palpebral lobes than long, convex, and deeply furrowed. Glabella cone-shaped, sides slightly concave, front medium to strongly curved. Four sets of glabellar furrows, anterior two sets inclined forward, posterior two inclined back, posterior set somewhat arcuate. Palpebral area convex; eye ridges strong. Palpebral lobes centred well posterior to glabellar midpoint, tilted inward, and approximately one-third as long as glabella. Preglabellar field narrow (sag.); adjacent anterior area of fixigenae slopes steeply forward. Border rounded in side view, broadly uparched in front view with locally stronger arch near middle. Facial suture directed nearly straight forward for first half of distance from palpebral lobe to border furrow, then curved slightly inward. Posterior limb considerably wider (tr.) than occipital ring. Occipital ring short (sag.); occipital node, if present, is very small.

Pygidium short, width more than twice length, antero-lateral margins broadly curved, postero-lateral margins straight and rapidly converging toward broad curvature behind axis. Axis wide and low, articulating half ring very short (sag.), one well-defined axial ring, remaining rings fused to a terminal piece which reaches posterior edge of pygidium. Pleural region marked by one pleural and one interpleural furrow, sloped steeply downward along postero-lateral margin of pygidium. Test ornamented with large tubercles and small granules, tubercles are best developed near edges of furrows.

Remarks. Resser (1939a) correctly assigned one pygidium (pl. 13, fig. 19) to this species, but also assigned to it pygidia (pl. 13, figs. 20, 21) belonging to *Amecephalus laticaudum* (Resser) 1939b. In addition, two incomplete cranidia described as *Poulsenia bearensis* Resser 1939a may belong to this species. These cranidia cannot at present be placed under *C. granosa* with certainty as they have a slightly longer preglabellar field and obvious venation on the forward portion of the anterior area. These features may be within the limits of interspecific variation and would be considered to be so if more parts of *C. bearensis* are located and found to match like parts of *C. granosa*.

Occurrence. *Albertella* Faunizone, upper member, localities 8, 9, 71, 11, 12, and 15.

Caborcella clinolimbata sp. nov.

Plate 41, figs. 33–35

Material. Four cranidia 3.1–4.1 mm. long.

Description. Cranium convex, length less than width across palpebral lobes, furrows shallow to moderately impressed. Glabella is of medium height, sides straight and slightly

converging, front well rounded. Two sets of transverse glabellar furrows, anterior set weak, posterior set forks with branches inclined forward and back. Palpebral area nearly flat, slightly upsloping. Eye ridges broad and low. Palpebral lobes set off by a broad, shallow furrow, centred opposite glabellar midpoint, nearly half as long as glabella. Pre-glabellar field narrow laterally, absent medially where dorsal and border furrows converge. Facial suture slightly divergent from palpebral lobe to border furrow. Anterior border slopes back along posterior third, slopes uniformly and steeply forward along anterior two-thirds. Posterior area considerably wider (tr.) than occipital ring. Occipital ring of uniform width and bearing a node. Crania marked by sparse tubercles.

Remarks. Shallower furrows and an anterior border with a uniformly steep forward slope in front serve to differentiate this species from *Caborcella granosa* and others in the genus *Caborcella*.

Occurrence. *Albertella* Faunizone, upper member, locality 9 and 71.

Caborcella sp. indet.

Plate 43, figs. 17–19

Material. One cranium 2.5 mm. long.

Description. Cranium wider across palpebral lobes than long, moderately convex. Glabella subquadrate, sides straight and slightly converging, front broadly curved. Four sets of glabellar furrows, anterior three sets shallow, anterior two inclined forward, third set transverse and possibly bifurcating, posterior set inclined toward rear. Axial furrow of uniformly moderate depth and width. Palpebral area convex, averaging horizontal; eye ridges low but distinct. Palpebral lobes centred posterior to glabellar

EXPLANATION OF PLATE 41

Albertella Faunizone.

Figs. 1–8. *Kootenia aculacauda* sp. nov. (p. 195). 1. Paratype cranium, small, $\times 4.5$, USNM 153614, loc. 11. 2–4, Paratype cranium, plan, front, and side view, $\times 2.7$, USNM 153615, loc. 11. 5, 6, 8, Holotype pygidium, plan, side, and rear view, $\times 4.9$, USNM 153616, loc. 72. 7. Paratype pygidium, $\times 4.9$, USNM 153617, loc. 72.

Figs. 9–11. *Oryctocephalites typicalis* Resser (p. 202). Cranium, plan, front, and side view, $\times 3.9$, USNM 153618, loc. 11.

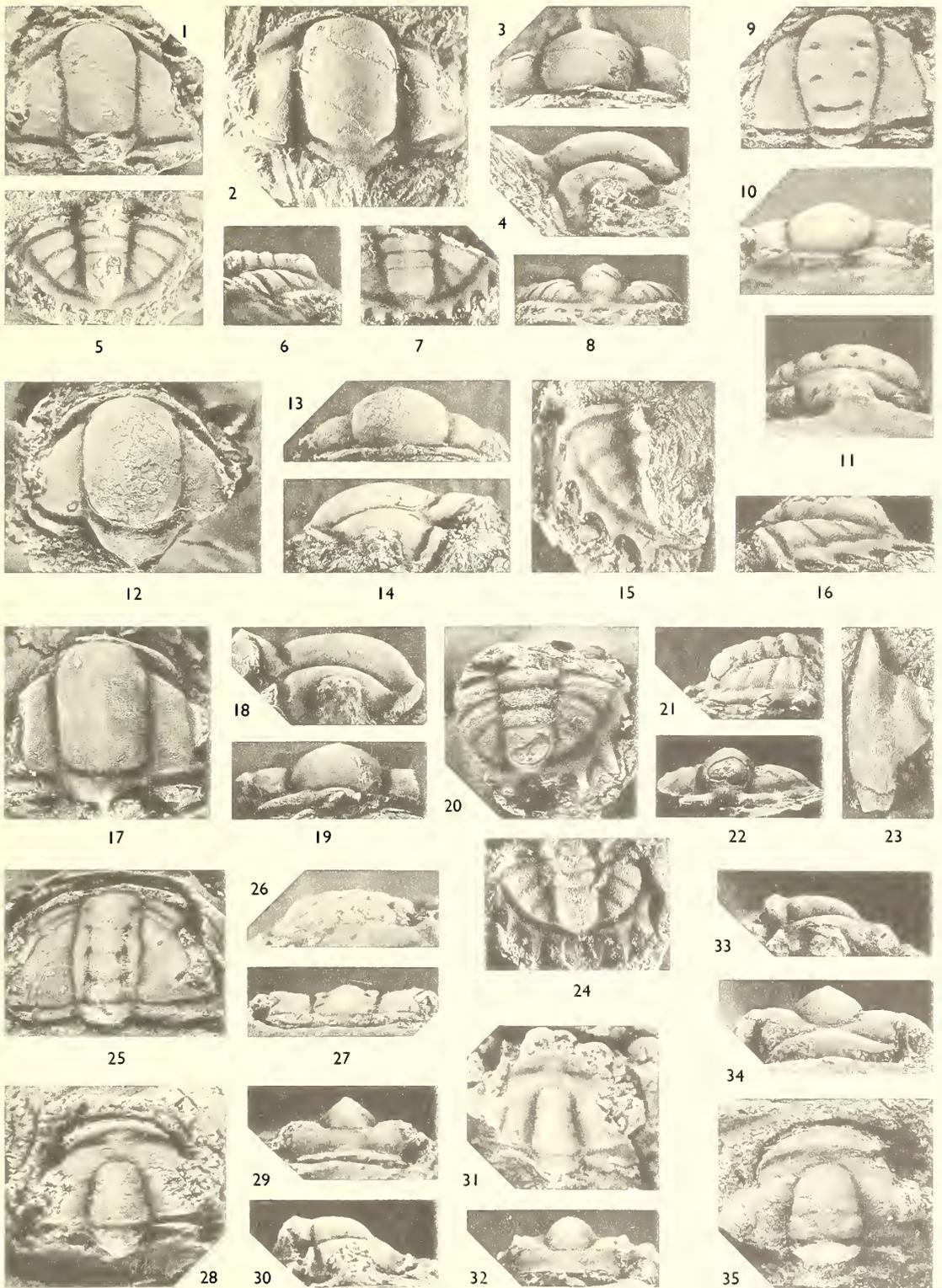
Figs. 12–16. *Kootenia crassinucha* sp. nov. (p. 198). 12–14, Paratype cranium, plan, front, and side view, $\times 1.8$, USNM 153619, loc. 71. 15, 16, Holotype pygidium, plan and side view, $\times 2.1$, USNM 153620, loc. 71.

Figs. 17–24. *Kootenia convoluta* Resser (p. 197). 17–19, Cranium, plan, side, and front view, $\times 2.6$, USNM 153621. 20–22, Pygidium, plan, side, and rear view, $\times 1.8$, USNM 153622. 23, Librigena, $\times 1.9$, USNM 153623. 24, Latex cast of small pygidium, $\times 3.3$, USNM 153624. All specimens from loc. 71.

Figs. 25–27. *Oryctocephalus maladensis* Resser (p. 202). Cranium, plan, side, and front view, $\times 5.0$, USNM 153625, loc. 71.

Figs. 28–32. *Alokistocare alta* sp. nov. (p. 226). 28–30, Holotype cranium, plan, front, and side view, $\times 5.2$, USNM 153626, loc. 71. 31, 32, Paratype cranium, small, plan and front view, $\times 10.5$, USNM 153627, loc. 9.

Figs. 33–35. *Caborcella clinolinbata* sp. nov. (p. 221). Holotype cranium, side, front, and plan view, $\times 5.1$, USNM 153628, loc. 9.



midpoint and half as long as glabella. Preglabellar field narrow laterally, absent medially where dorsal and border furrows meet. Anterior border furrow of moderate depth, slightly recurved medially. Anterior border uniformly rounded in side view. Posterior area damaged, probably not as wide (tr.) as occipital ring. Occipital furrow narrow, deep near ends. Occipital ring thickens medially; node, if present, is small. Cranium covered with granules of small to large size.

Remarks. As this cranium is small, adult features may not be fully developed and hence the specific assignment is uncertain. The cranium most resembles *Caborcella columbiana* (Rasetti) 1957, but has narrower (tr.) palpebral areas and larger palpebral lobes.

Occurrence. *Glossopleura* Faunizone, upper member, locality 74.

Genus CRASSIFIMBRA Lochman 1947

Type species. *Onchocephalus walcotti* Resser 1937.

Crassifimbria walcotti? (Resser)

Plate 37, figs. 23–26

- 1886 *Crepicephalus augusta* Walcott, pp. 208, 209, pl. 28, fig. 2*b* (*non* figs. 2, 2*a*).
 1890 *Crepicephalus augusta* Walcott; Walcott, p. 653, pl. 96, fig. 9 (*non* figs. 9*a*, 9*b*).
 1916*a* *Crepicephalus augusta* Walcott; Walcott, pp. 204, 205, pl. 29, fig. 6 (*non* figs. 6*a*, 6*b*).
 1937 *Onchocephalus walcotti* Resser, p. 21.
 1947 *Crassifimbria walcotti* (Resser); Lochman, p. 64, 71, text-figs. 1–3.
 1958 *Crassifimbria walcotti* (Resser); Palmer, pp. 157–70, pl. 25, figs. 1–3 (*non* pl. 25, figs. 7–25; pl. 26, figs. 1–24).
 1962 *Antagmus (Antagmus) walcotti* (Resser); Shaw, pp. 334, 335.

Material. Three cranidia 3·8–4·2 mm. long.

Description. Cranium has length–width ratio of 2:3. Glabella low, exceptionally low posteriorly for a ptychoparioid, sides straight, converging forward, front truncated. Glabellar furrows shallow, anterior set inclined forward, second set transverse, third and fourth transverse with branch inclined toward rear. Axial furrow shallow. Fixigena downsloping, broadly curved in both directions. Facial sutures diverge from front of palpebral lobe to just beyond anterior border furrow, inclined strongly back from palpebral lobes to posterior margin of cranium. Anterior border of medium breadth (exsag.) near ends, broad medially, sloped forward, posterior margin slightly recurved near axial midline. Eye ridges narrow and low; palpebral furrow weak posteriorly, remaining furrow barely visible. Palpebral lobes low and narrow. Posterior border furrow thin and moderately impressed; occipital furrow narrow, shallowing and broadening near middle. Occipital ring low and bearing a node. Test nearly smooth.

Remarks. This small collection from the Campbell Ranch section shows some variations that are probably interspecific. All the specimens are smaller than the holotype of *Crassifimbria walcotti* (Resser) and, although they closely resemble the holotype, they

can only questionably be considered conspecific with it. Silicified trilobites described by Palmer (1958) as *C. walcotti* were compared with the holotype, original topotypes, and the present three cranidia. The writer believes the silicified specimens definitely belong to a different species and probably to a different genus. The silicified cranidia differ from those of *C. walcotti* as follows: (1) cranidial width greater, (2) smaller glabella with far more posterior relief, (3) larger and more highly raised palpebral lobes, (4) narrower (sag.) anterior borders, and (5) posterior areas extend into distinct limbs rather than wedge-shaped areas.

Occurrence. Upper *Olenellus* Faunizone, upper member, locality 1085.

Genus ONCHOCEPHALUS Resser 1937

Onchocephalus papulus sp. nov.

Plate 36, figs. 1-5

Material. Twenty-two cranidia 1.2-4.3 mm. long and one tentatively assigned pygidium 0.5 mm. long.

Description. Cranidium moderately convex; side profile of large specimens are forward sloping and nearly straight from mid-occipital ring to anterior border furrow; profile of medium and small cranidia are slightly to moderately convex. Glabella rather low, sides straight and slightly converging, broadly curved across front. Three sets of glabellar furrows faintly visible on outer surface; internal mould shows four sets, anterior set opposite eye ridges and inclined forward, second transverse, third with transverse (?) branch and branch inclined back, fourth with branches inclined forward and back. Axial furrows wide and deep, connected by narrow furrow to border furrow. Connecting

EXPLANATION OF PLATE 42

Albertella and *Glossopleura* Faunizones.

Figs. 1-6. *Zacanthoides demissus* sp. nov. (p. 211). 1-3, Paratype cranidium, plan, front, and side view, $\times 4.0$, USNM 153629, loc. 18. 4-6, Holotype pygidium, plan, rear, and side view, $\times 5.1$, USNM 153630, loc. 18.

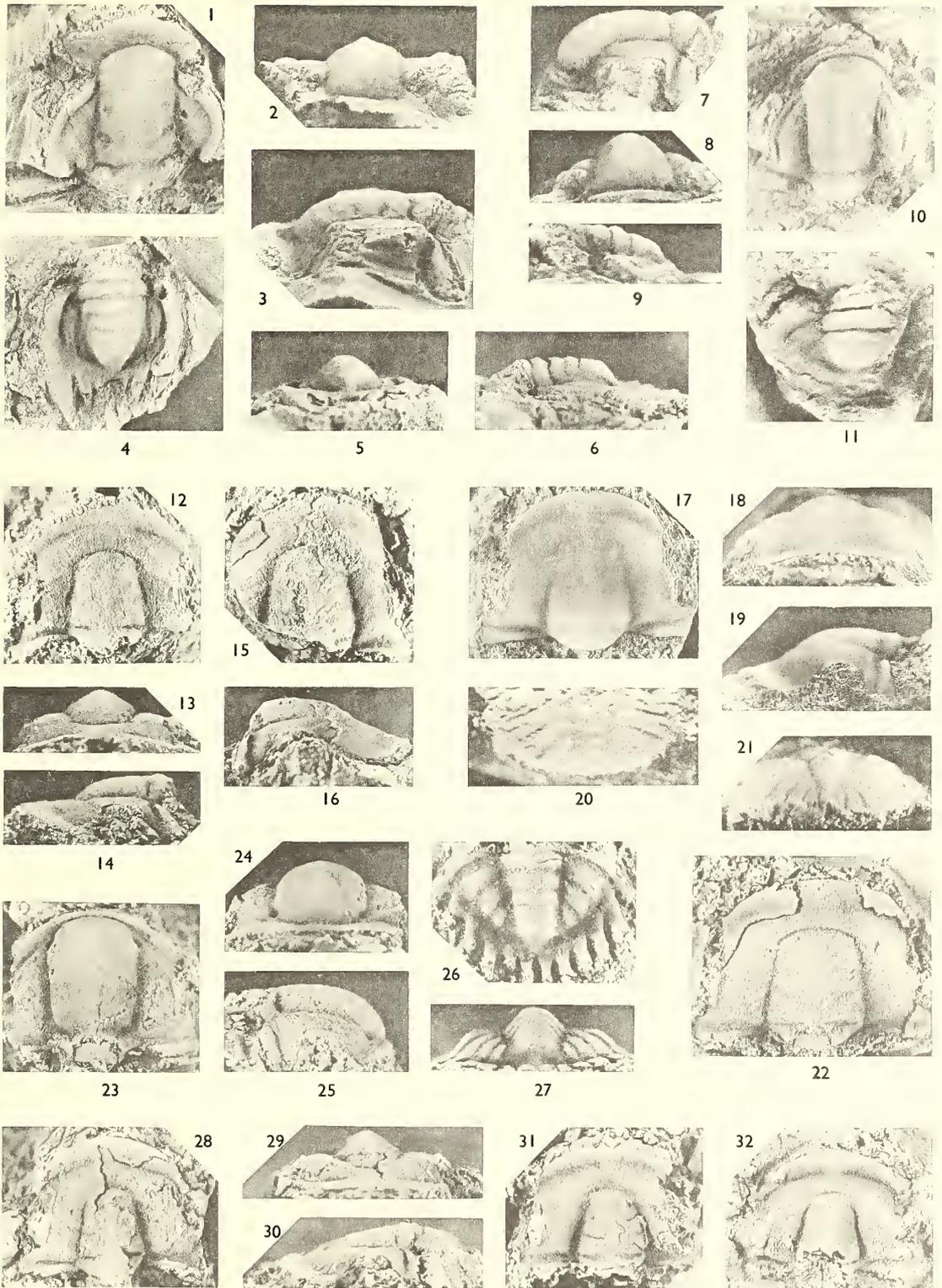
Figs. 7-11. *Corynexochides prolatus* sp. nov. (p. 204). 7, 8, 10, Holotype cranidium, side, front, and plan view, $\times 10.0$, USNM 153631, loc. 18. 9, 11, Paratype pygidium, side and plan view, $\times 14.3$, USNM 153632, loc. 18.

Figs. 12-16. *Achlysopsis hemitora* gen. et sp. nov. (p. 219). 12-14, Holotype cranidium, plan, front, and side view, $\times 3.5$, USNM 153633, loc. 15. 15, 16, Paratype cranidium, partially peeled, plan and side view, $\times 2.6$, USNM 153634, loc. 15.

Figs. 17-22. *Achlysopsis liokata* gen. et sp. nov. (p. 219). 17-19, Holotype cranidium, plan, front, and side view, $\times 4.8$, USNM 153635. 20, 21, Tentatively assigned pygidium, plan and rear view, $\times 10.0$, USNM 153636. 22, Paratype cranidium, mostly peeled, $\times 4.4$, USNM 153637. All specimens from loc. 18.

Figs. 23-27. *Kootenia crassa* sp. nov. (p. 198). 23-25, Paratype cranidium, partially peeled, plan, front, and side view, $\times 3.8$, USNM 153638, loc. 15. 26, 27, Holotype pygidium, plan and rear view, $\times 6.5$, USNM 153639, loc. 15.

Figs. 28-32. *Bythelcheilus?* sp. indet. (p. 229). 28-30, Cranidium, partially peeled, plan, front, and side view, $\times 4.9$, USNM 153640, loc. 14. 31, Cranidium, mostly peeled, $\times 5.1$, USNM 153641, loc. 16. 32, Cranidium, small, $\times 7.0$, USNM 153642, loc. 15.



FRITZ, Cambrian trilobites, Pioche Shale, Nevada

furrow visible on most, but not all specimens. Palpebral area rather flat, gently down-sloping. Eye ridges faint; palpebral furrows well impressed. Palpebral lobes centred opposite glabellar midpoint, length three-fifths that of glabella. Anterior border furrow narrow and deep; anterior border wide, convex, has slight reverse bend near mid-posterior margin. Occipital ring has forward curvature along anterior margin and bears a small node. Posterior area rounded distally, traversed by a deep furrow of moderate width. Test noticeably pitted on glabella and on fixigena between eye ridges and posterior border furrows. Pits coalesce on palpebral area to give granular appearance.

Tentatively assigned pygidium has length equal to two-thirds width. Axis straight sided, converging slightly toward rear, composed of five rings and very small terminal piece. Axial furrow between anterior and second ring is broad. Pleural region exhibits three sets of interpleural furrows.

Remarks. This species can be distinguished from other ptychoparioids by its low glabella, exceptionally wide and deep axial furrow, large palpebral lobes, and medial furrow crossing the preglabellar field.

Occurrence. Upper *Olenellus* Faunizone, lower member, localities 2 and 3.

Genus SYSPACEPHALUS Resser 1936

Type species. *Agraulos charops* Walcott 1917.

Syspacephalus? cf. *S.? uncus* (Walcott)

Plate 36, figs. 15, 16

1917 *Agraulos? unca* Walcott, p. 73, 74, pl. 13, figs. 1, 1a.

1936 *Syspacephalus unca* (Walcott); Resser, p. 28.

Material. One cranidium 1.3 mm. long.

Description. Cranidium nearly twice as wide as long, side profile uniformly curved from mid-occipital ring to front of anterior border. Glabella unfurrowed, sides nearly straight to slightly convex, converging forward, front well rounded. Axial furrow uniformly narrow and shallow. Facial sutures fairly straight and converging along length of cranidium, deviation at palpebral lobes is slight. Fixigenae uniformly convex, down-sloping; anterior border furrow faint; anterior border slopes forward. Posterior border furrow well impressed near axis, shallows distally; posterior border widens distally. Eye ridges faint. Palpebral lobes small, centred slightly anterior to glabellar midpoint, and set well below level of axial furrow. Occipital ring narrow (sag.) and bearing a node. Surface nearly smooth.

Remarks. A close resemblance exists between this poorly preserved specimen and *Syspacephalus? uncus* (Walcott) 1917. Unlike most species now included in the genus, *S.? uncus* has neither a truncated glabella nor a relatively flat, horizontal region on the fixigena bordering the glabella.

Occurrence. Upper *Olenellus* Faunizone, lower member, locality 1085.

Syspacephalus sp. indet.

Plate 37, figs. 27-30

Material. Two internal moulds of crania 3.0-3.5 mm. long.

Description. Cranidium low and broad. Glabella small, sides straight and converging forward, front truncated; side profile straight and forward sloping from mid-occipital ring to glabella front. Three sets of shallow glabellar furrows, anterior set short and transverse, remaining sets have two branches, one inclined forward and one back. Surface of fixigenae and preglabellar field surrounding glabella is flat and horizontal. Axial and anterior border furrows are narrow and shallow; anterior border furrow indistinct near axial midline. Facial sutures converge forward from palpebral lobes. Eye ridges faint; palpebral lobes approximately half as long as glabella and centred opposite glabellar midpoint. Posterior border furrow narrow and of medium depth. Ornamentation on upper surface of cranidium unknown, internal mould is smooth.

Remarks. These specimens have most of the generic characters of *Syspacephalus* as listed by Lochman (1947, p. 64). They differ from her description in having larger and more posteriorly located palpebral lobes. The writer knows of no species that resemble these, but is reluctant to base a new species on only two internal moulds.

Occurrence. Upper *Olenellus* Faunizone, lower member, locality 1085.

Family ALOKISTOCARIDAE Resser 1939

Genus ALOKISTOCARE Lorenz 1906

Type species. *Conocephalites subcoronatus* Hall and Whitfield 1877.*Alokistocare alta* sp. nov.

Plate 41, figs. 28-32

Material. Forty-two crania 1.5-4.0 mm. long.

Description. Cranidium has high relief, length approximately equals width across palpebral lobes. Glabella high, sides straight and converging moderately forward, front truncated. Axial furrow shallow in front of glabella, moderate at sides, deep at sides on small crania. Three sets of glabellar furrows, anterior set inclined forward, median and posterior inclined back. Palpebral area flat and tilted slightly inward. Anterior area of fixigena and preglabellar field inclined steeply forward. Facial sutures divergent from palpebral lobe to posterior margin of broad border furrow. Anterior border consists of narrow, upturned edge of cephalon. Medial boss present on preglabellar field and extending forward across border furrow. Ocular ridge strong. Palpebral lobes centred opposite glabellar midpoint, half as long as glabella, inclined steeply inward and attaining considerable height. Posterior area wider (tr.) than occipital ring; posterior border furrow wide and deep. Occipital ring triangular in plan view, posterior margin bears spine that tilts upward and is at least as long (sag.) as occipital ring. Cranidium marked by small, closely spaced granules and sparse, large granules.

Remarks. A rather short (sag. and exsag.) frontal area and anterior area distinguish cranidia of this species from others in the genus.

Occurrence. *Albertella* Faunizone, upper member, localities 9, 12, 71, and 72.

Genus AMECEPHALUS Walcott 1924

Type species. *Ptychoparia piochensis* Walcott 1886.

Remarks. *Amecephalus* is a genus which has been suppressed by some writers (Resser 1935; Palmer 1954; Howell 1959) in favour of *Alokistocare* and deliberately retained by others (Rasetti 1951; Stoyanow 1952; Kobayashi 1962; Poulsen 1958, 1964). Of the forms that the writer would place in *Alokistocare*, only the cranidia are well known. For this reason, criteria used for separating the two genera are based upon this portion of the test. Cranidia of *Amecephalus* are low and of medium size (average length 1.5–2.0 cm.). The anterior margin is broadly curved; anterior border flat, tilted slightly back, intergrades with shallow anterior border furrow. The preglabellar field is long, slopes gently forward, and is ornamented by longitudinal striae as is the adjacent anterior area. Glabellae are of low relief and marked by three to four sets of broad, shallow furrows. Palpebral areas nearly horizontal and wide; palpebral lobes centred well posterior to glabellar midpoint, defined by a shallow furrow, and raised only moderately above the adjacent area. Occipital ring short (sag.), of uniform breadth (exsag.), and bearing a node. Posterior areas on most species not nearly as wide (tr.) as occipital ring, tilted only slightly downward at distal ends, and traversed by a furrow of medium width and depth.

By contrast, cranidia of *Alokistocare* are somewhat convex and small (length usually less than 1 cm.). The anterior margin is moderately to strongly curved; anterior border slopes moderately to steeply back and is of medium to narrow breadth (sag.). Anterior border furrow moderate to deep except for shallowing near a preglabellar boss. Anterior area long (sag.) and inclined steeply forward. Glabella of medium to high relief. Palpebral area of medium width; palpebral lobes centred posterior to glabellar midpoint, abruptly raised above adjacent area, defined by a furrow of medium depth. Posterior area inclined rather steeply downward, traversed by a deep, broad furrow. Occipital ring triangular in plan view and marked by a node or terminating in a small spine.

Amecephalus laticaudum (Resser)

Plate 40, figs. 17–23

1939a *Alokistocare euchare* Resser, p. 51, pl. 2, figs. 11, 12.

1939a *Poulsenia granosa* Resser, p. 59, pl. 13, figs. 20, 21 (*non* figs. 19, 22–30).

1939b *Alokistocare laticaudum* Resser, p. 17, pl. 4, figs. 15–19.

Material. Fifty-two cranidia 5.7–14.6 mm. long, fifteen pygidia 2.9–4.6 mm. long, four librigenae, and four hypostomata.

Description. Cranidium low to moderately convex, length slightly greater than width measured across palpebral lobes. Glabella low, length a bit less than half that of cranidium, sides straight to slightly convex, converging forward, front truncated.

Glabellar furrows shallow and broad, anterior set very faint, median set angles back, posterior set forked with both branches inclined toward rear. Palpebral area nearly flat and horizontal, eye ridges low and angling back. Palpebral lobes centred well posterior to glabellar mid-point, tilted inward, and slightly longer than one-third glabellar length. Preglabellar field longer (sag.) than border furrow plus border, convex, and marked anteriorly by a transverse swelling. Border furrow a broad depression between forward-sloping pre-glabellar field and a flat, back-sloping border. Facial sutures divergent and straight from palpebral lobes to posterior margin of anterior border. Posterior area nearly horizontal from glabella outward to position behind palpebral lobes, then inclined downward, width (tr.) less than that of occipital ring. Occipital furrow and ring fairly uniform in breadth, ring bears a node. Hypostoma has set of short spines on lateral and postero-lateral margin of border. Librigena border marked by furrow that continues on to genal spine.

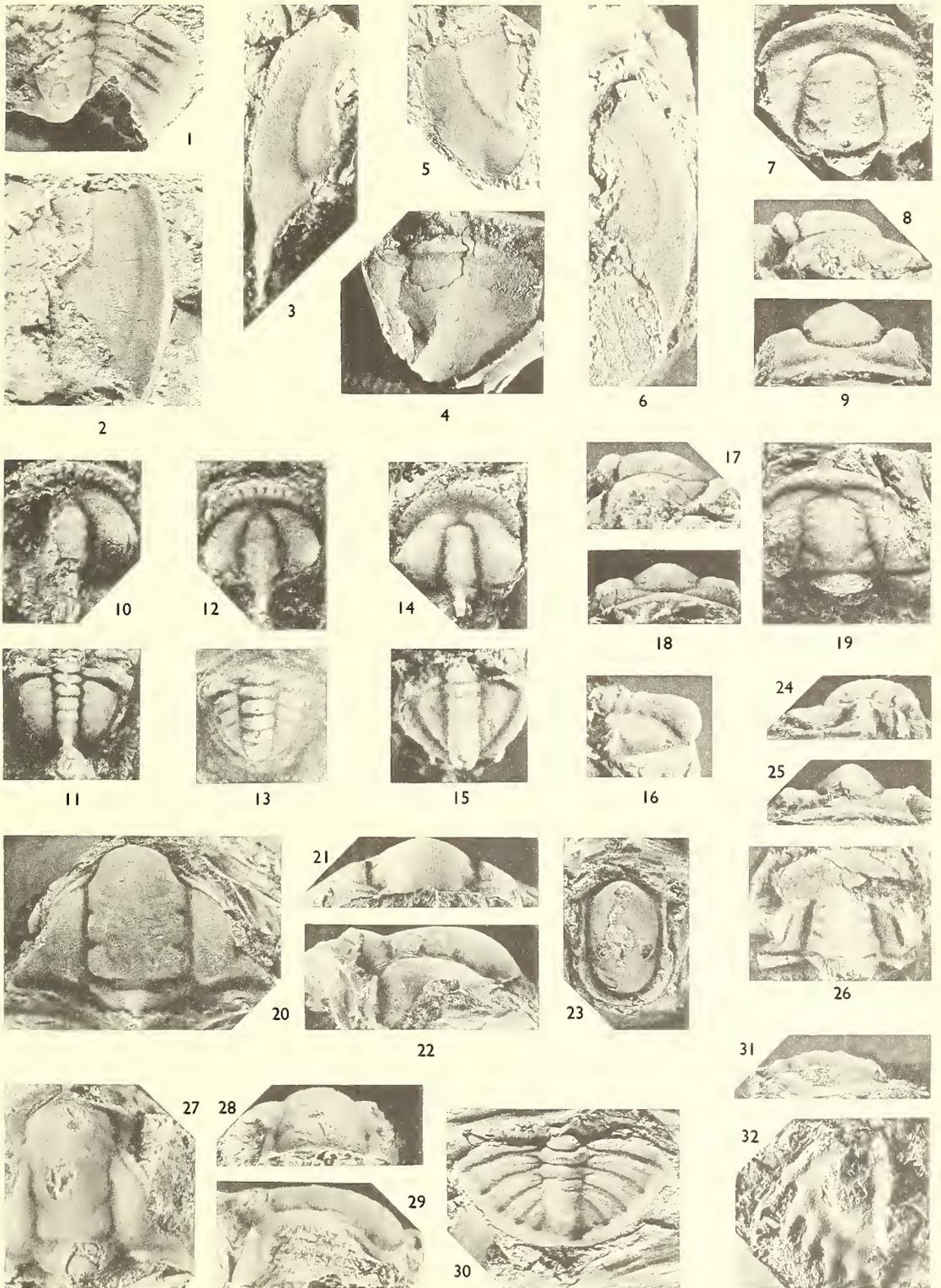
Pygidium short and very broad. Axis consists of three well-defined rings, several more faint rings, and terminal piece. Pleural region convex, steeply turned down along posterior and postero-lateral margin. Two prominent sets of pleural furrows and two narrow sets of interpleural furrows visible. Test covered by small granules, venation runs down preglabellar field.

Remarks. Resser (1939a, pl. 13, figs. 20, 21) assigned two *A. laticaudum* pygidia to *Poulsenia granosa* Resser 1939a and a cranidium of *A. laticaudum* from the same

EXPLANATION OF PLATE 43

Glossopleura Faunizone.

- Figs. 1, 2. *Athabaskia* sp. indet. (p. 203). 1, Pygidium, $\times 5.3$, USNM 153643, loc. 74. 2, Librigena, $\times 5.1$, USNM 153644, loc. 74.
- Figs. 3, 4. *Glossopleura* sp. indet. 1 (p. 205). 3, Tentatively assigned librigena, $\times 3.8$, USNM 153645, loc. 74. 4, Latex cast of pygidium, $\times 3.2$, USNM 153646, loc. 74.
- Figs. 5, 6. *Glossopleura* sp. indet. 2 (p. 205). 5, Latex cast of pygidium, $\times 2.8$, USNM 153647, loc. 74. 6, Tentatively assigned librigena, $\times 6.7$, USNM 153648, loc. 74.
- Figs. 7–9. Gen. et sp. indet. (p. 232). Cranidium, peeled, plan, side, and front view, $\times 4.6$, USNM 153649, loc. 74.
- Figs. 10, 11. *Pagetia arenosa* sp. nov. (p. 189). 10, Holotype cranidium, $\times 9.5$, USNM 153650, loc. 18. 11, Paratype pygidium, $\times 10.6$, USNM 153651, loc. 18.
- Figs. 12, 13. *Pagetia mucrogena* sp. nov. (p. 191). 12, Holotype cranidium, $\times 12.5$, USNM 153652, loc. 18. 13, Paratype pygidium, $\times 11.4$, USNM 153653, loc. 18.
- Figs. 14–16. *Pagetia maladensis* Resser (p. 190). 14, Cranidium, $\times 12.0$, USNM 153654, loc. 18. 15, 16, Pygidium, plan and side view, $\times 13.0$, USNM 153655, loc. 18.
- Figs. 17–19. *Caborcella* sp. indet. (p. 222). Cranidium, side, front, and plan view, $\times 8.1$, USNM 153656, loc. 74.
- Figs. 20–23. *Olenoides* sp. indet. (p. 200). 20–22, Cranidium, plan, front, and side view, $\times 1.7$, USNM 153657, loc. 18. 23, Hypostoma, $\times 1.7$, USNM 153658, loc. 18.
- Figs. 24–26. *Kistocare campbellensis* sp. nov. (p. 230). Holotype cranidium, side, front, and plan view, $\times 6.2$, USNM 153659, loc. 74.
- Figs. 27–30. *Bathyriscus petalus* sp. nov. (p. 203). 27–29, Paratype cranidium, plan, front, and side view, $\times 3.5$, USNM 153660, loc. 18. 30, Holotype pygidium, $\times 3.5$, USNM 153661, loc. 18.
- Figs. 31, 32. *Kootenia* sp. indet. (p. 199). Pygidium, peeled, side and plan view, $\times 1.9$, USNM 153662, loc. 18.



FRITZ, Cambrian trilobites, Pioche Shale, Nevada

locality to *Alokistocare euchare* Resser 1939a. As the holotype and a paratype of *A. laticaudum* consist of tests with both pygidia and cranidia attached, the correct association of parts has been clearly demonstrated. Cranidia of *A. laticaudum* closely resemble those of *Anecephalus idahoense* (Resser) 1939b [= *Anecephalus spencense* (Resser) 1939b]. The present species has 17 thoracic segments and a wide pygidium while *A. idahoense* has 23 or 24 thoracic segments and a very small and relatively narrower pygidium.

Occurrence. *Albertella* and *Glossopleura* (?) Faunizones, upper member, localities 14, 15, and 18.

Genus BYTHICHEILUS Resser

Type species. *Bythicheilus typicum* Resser 1939b.

Bythicheilus? sp. indet.

Plate 42, figs. 28–32

Material. Thirty-one cranidia 1.7–5.2 mm. long.

Description. Cranidium of medium convexity, length slightly less than width across palpebral lobes. Glabella low, sides straight, front broadly curved. Three sets of weak, transverse glabellar furrows, posterior two probably branch. Axial furrow of medium and uniform depth. Palpebral area rather flat to slightly convex, averages horizontal. Eye ridges well defined and inclined back. Palpebral lobes located well posterior to glabellar midpoint, half as long as glabella. Facial sutures divergent from palpebral lobes to anterior border furrow. Preglabellar field and border have approximately equal (sag.) length, border slopes moderately back. Border furrow narrow and deep laterally, shallow near middle. Posterior limb not as wide (tr.) as occipital ring, traversed by a furrow that expands distally. Occipital ring fairly uniform in breadth and bearing a node; occipital furrow narrow near ends and expanded medially. Test covered with granules of medium size.

Remarks. The generic importance of a depression on the preglabellar field of *Bythicheilus* is difficult to assess because the type species, *Bythicheilus typicum* Resser 1939b and associated material, have been deformed. This is also true of *Bythicheilus alveatum* Resser 1939b from the same locality and which may be conspecific with *B. typicum*. Although the depressions are variable, and obviously emphasized on some specimens due to crushing, they are visible on a majority of the cranidia. In the present collection a slight depression is visible on only several of thirty-one cranidia. In other respects the present cranidia differ from *B. typicum* in having a greater relative length and a smaller glabella. Another species having the cranidial proportions of *Bythicheilus* but no preglabellar depression is *Alokistocare nothum* Resser 1938. That species differs from *Bythicheilus?* sp. indet. in having a wider cranidium, a straighter anterior border and border furrow, and more posteriorly located palpebral lobes.

Occurrence. *Albertella* Faunizone, upper member, localities 14, 15, and 16.

Genus *CHANCIA* Walcott 1924

Type species. *Chancia ebdome* Walcott 1924.

Chancia venusta (Resser)

Plate 40, figs. 31-34

1939a *Kochina venusta* Resser, p. 53, pl. 6, figs. 9, 10.

Material. Three cranidia 4.5-10.1 mm. long.

Description. Cranidium moderately convex, subrectangular in plan view except for protruding limbs of posterior area. Glabella low, sides straight to slightly convex and converging forward, front truncated. Three sets of glabellar furrows, anterior two sets inclined slightly toward rear, posterior set branched with limbs inclined forward and back. Dorsal furrow very deep and wide at sides of glabella, shallower and narrower in front. Palpebral area swollen, particularly so just posterior to well-defined eye ridge. Palpebral lobes centred opposite glabellar midpoint, length slightly exceeds half that of glabella. Preglabellar field convex in side view, both field and anterior border slope forward at approximately same angle. Border furrow shallow, broad, only slightly curved in plan view of large cranidia. Facial sutures divergent and straight from palpebral lobe to anterior border furrow. Posterior area considerably wider (tr.) than occipital ring; posterior border furrow broad and deep. Occipital furrow and ring are fairly uniform in breadth (exsag.), ring bears a small node. Cranidium covered by fine granules; preglabellar field and adjacent anterior area marked by venation.

Remarks. The assignment of this species to the genus *Kochina* by Resser (1939a, p. 53) is not followed here, as the long preglabellar field and short, quadrate glabella are considered more diagnostic of the genus *Chancia*.

Occurrence. *Albertella* Faunizone, upper member, locality 12.

Genus *KISTOCARE* Lochman 1948

Type species. *Kistocare corbini* Lochman 1948.

Kistocare campbellensis sp. nov.

Plate 43, figs. 24-26

Material. Five cranidia 1.3-3.1 mm. long.

Description. Cranidium convex, length slightly less than width across palpebral lobes. Glabella large, lateral flanks flat and steep, sides straight and converging, front broadly curved. Four sets of glabellar furrows, anterior two inclined forward, posterior two inclined back. Axial furrow of medium depth at sides of glabella, shallow at front. Palpebral area narrow, flat, and nearly horizontal. Eye ridges very strong. Palpebral lobes high and steeply upsloping, half as long as glabella, terminating well ahead of occipital furrow. Preglabellar field and anterior border of approximately equal length

(sag.); border furrow shallow and narrow. Facial sutures divergent from palpebral lobes to anterior border furrow. Posterior area considerably narrower (tr.) than occipital ring, horizontal from glabella to point behind palpebral lobe, then tilted steeply downward. Posterior border furrow narrow and deep. Occipital ring short (sag.). Occipital furrow narrow and deep near ends, shallowing near axial midline. Surface of cranidium covered by granules of medium size.

Remarks. *Kistocare corbini* Lochman 1948 resembles this species but has a lower glabella, wider palpebral areas, and longer palpebral lobes that terminate just ahead of the occipital furrow.

Occurrence. *Glossopleura* Faunizone, upper member, locality 74.

Genus *PACHYASPIS* Resser 1939a

Type species. *Pachyaspis typicalis* Resser 1939a.

Pachyaspis gallagari sp. nov.

Plate 40, figs. 11–13

Material. Eight cranidia 1.7–4.3 mm. long.

Description. Cranidium moderately convex in both directions, length slightly less than width across palpebral lobes. Glabella of moderate height, lower on large cranidia, sides straight, converging forward, well rounded across front. Four glabellar furrows barely visible, best developed on small specimens, anterior set short, second set inclined forward, posterior two sets branch with one limb inclined forward and other back. Axial furrow of moderate depth throughout. Palpebral area downsloping; eye ridge very faint. Palpebral lobes narrow, centred well posterior to glabellar midpoint, half as long as glabella. Facial sutures directed nearly straight forward from palpebral lobe to border furrow, then inward. Preglabellar field slightly longer (sag.) than anterior border. Border slopes moderately forward, posterior margin has slight raise and recurvature near axial midline. Posterior limb traversed by wide, deep furrow. Occipital ring narrow near ends, considerably expanded medially. Occipital furrow narrow and deep distally, shallow near middle. Cranidium marked by medium-sized granules on anterior border and occipital ring, some cranidia are completely covered by granules.

Remarks. Long palpebral lobes centred posterior to the glabellar midpoint differentiate this species from others in the genus *Pachyaspis*.

Occurrence. *Albertella* Faunizone, upper member, localities 14, 15, and 16.

Pachyaspis longa sp. nov.

Plate 40, figs. 24–26

Material. One cranidium 3.4 mm. long.

Description. Cranidium has high relief, length–width ratio approximately 2:3. Glabella high, nearly cylindrical, tapered slightly forward, well rounded in front. Two very weak glabellar furrows visible in posterior and next adjacent furrow position. Axial furrow shallow and narrow. Palpebral area convex (tr.) and downsloping. Eye ridges faint.

Palpebral lobes centred anterior to glabellar midpoint, length slightly exceeds one-quarter that of glabella. Preglabellar field and anterior border are of approximately equal length (sag.) and slope forward at nearly same angle. Border furrow of moderate depth and width throughout. Facial suture converges moderately forward along posterior segment, deviates only slightly at palpebral lobes, and converges slightly from lobes to anterior border furrow. Posterior area wider (tr.) than occipital ring, traversed by a furrow of uniform width and depth. Surface of cranium worn, appears to be nearly smooth.

Remarks. *Pachyaspis attenuata* Rasetti 1951 has an unusually long narrow glabella, such as the one in this species. *P. attenuata* differs from *P. longa* in having a longer prelabellar field and an anterior border that slopes back rather than forward.

Occurrence. *Albertella* Faunizone, upper member, locality 11.

Genus SPENCIA Resser 1939

Type species. *Spencia typicalis* Resser 1939b.

Spencia quadrata sp. nov.

Plate 40, figs. 27-29

Material. Five cranidia 2.0-3.8 mm. long.

Description. Cranium convex, length slightly greater than three-quarters width across palpebral lobes. Glabella high, subquadrate, slightly convex along sides, front broadly curved. Axial furrow of moderate depth, shallow in front of glabella. Palpebral area convex, steeply downsloping. Palpebral lobes set well ahead of glabellar midpoint and far below level of axial furrow, length one-third that of glabella. Preglabellar field and anterior border are approximately equal in length (sag.), border slopes less steeply forward than field. Anterior border furrow of uniformly moderate depth, straight in plan view except for curvature near ends. Facial sutures converge forward from palpebral lobes. Posterior area wider (tr.) than occipital ring, rounded distally, traversed by a furrow that is very deep near glabella and shallow distally. Occipital furrow uniform in width and depth. Occipital ring short (sag.) and bearing a large node. Surface of test appears smooth but is worn.

Remarks. *Spencia typicalis* Resser 1939b is similar to this species but differs as follows: palpebral lobes located farther back but ahead of glabellar midpoint, glabella more pointed, occipital ring longer (sag.), fixigenae not as convex or as steeply downsloping.

Occurrence. *Albertella* Faunizone, upper member, locality 11.

Gen. et sp. indet.

Plate 43, figs. 7-9

Material. One damaged internal mould of cranium 5.7 mm. long.

Description. Cranium convex, width across palpebral lobes probably greater than or equal to length. Glabella large, of medium height, sides straight and slightly converging,

broadly curved across front. Three sets of glabellar furrows, anterior set angles forward, median set transverse before branching into limbs inclined forward and back, posterior set branching into transverse limb and limb inclined toward rear. Palpebral area narrow (tr.), convex, and downsloping. Eye ridges of medium strength. Palpebral lobes centred far posterior to glabellar midpoint and nearly half as long as glabella. Preglabellar field considerably shorter (sag.) than anterior border. Anterior border of uniform width, sloped forward at low angle; border furrow of moderate depth except for medial rise at low boss which extends on to posterior edge of border. Posterior limb unknown. Occipital furrow and ring broaden (exsag.) near middle. Rough surface of internal mould suggests test may have been granular.

Remarks. The writer knows of no established genus to which this cranidium could be assigned, and it is judged inadequate to serve as a holotype for a new genus.

Occurrence. *Glossopleura* Faunizone, upper member, locality 74.

REFERENCES

- BEST, R. V. 1952. Two new species of *Olenellus* from British Columbia. *Trans. R. Soc. Can.* (ser. 3), **46** (4), 13–22, pl. 1.
- FRITZ, W. H. 1960. Structure and stratigraphy of the Northern Egan Range, White Pine County, Nevada. Unpublished Ph.D. thesis, Univ. Washington.
- HAGUE, A. 1883. Abstract of report on geology of the Eureka District, Nevada. *3rd. Ann. Rep. U.S. geol. Surv.* 237–90, pl. 24, 25.
- 1892. Geology of the Eureka District, Nevada. *Monogr. U.S. geol. Surv.* **20**, i–xvii+1–419, pl. 1–8.
- HALL, J. 1858. Palaeontology of New York; being some of the results of investigations made during the years 1855, '56, '57, and '58. *12th Ann. Rep. N.Y. St. Cab. nat. Hist.* 110 pp.
- HOWELL, B. F. in MOORE, R. C. (ed.) 1959. *Treatise on invertebrate paleontology, Part O—Arthropoda* 1. Geol. Soc. Am. and Univ. Kansas Press.
- KOBAYASHI, T. 1935. The Cambro-Ordovician formations and faunas of South Chosen: Palaeontology, Part III, Cambrian faunas of South Chosen with a special study on the Cambrian trilobite genera and families. *J. Fac. Sci. Tokyo Univ.* (sec. 2), **4**, 49–344, pl. 1–24.
- 1943. Brief notes on the eodiscids. 1, Their classification with a description of a new species and a new variety. *Proc. Imp. Acad. Tokyo*, **19** (1), 37–42.
- 1944. On the eodiscids. *J. Fac. Sci. Tokyo Univ.* (sec. 2), **7** (1), 1–74, pl. 1, 2.
- 1962. The Cambro-Ordovician formations and faunas of South Korea. Part IX, Palaeontology XIII, The Machari fauna. *Ibid.* (sec. 2), **13** (1), 1–152, pl. 1–12.
- LERMONTOVA, E. in VOLOGDIN, A. (ed.) 1940. *Atlas of the leading forms of the fossil faunas of the USSR, Vol. 1, Cambrian; Type 6—Arthropoda*. 112–57, pl. 35–49, Moscow. [In Russian.]
- LOCHMAN, C. 1947. Analysis and revision of eleven Lower Cambrian trilobite genera. *J. Paleont.* **21**, 59–71.
- 1948. New Cambrian trilobite genera from northwest Sonora, Mexico. *Ibid.* **22**, 451–4, pl. 69, 70.
- in COOPER, G. A. *et al.* 1952. Cambrian stratigraphy and paleontology near Caborca, northwestern Sonora, Mexico. *Smithson. misc. Collns.* **119** (1), 60–161, pl. 15–31.
- LOCHMAN-BALK, C. and WILSON, J. L. 1958. Cambrian biostratigraphy in North America. *J. Paleont.* **32**, 312–50.
- LORENZ, T. 1906. Contribution to the geology and palaeontology of East Asia with especial consideration of the Province of Shantung in China. *Z. dt. geol. Ges.* **58**, 53–108, pl. 4–6. [In German.]
- MASON, J. F. 1935. Fauna of the Cambrian Cadiz Formation, Marble Mountains, California. *Bull. St. Calif. Acad. Sci.* **34**, 97–119, pl. 15.
- MCKEE, E. D. in MCKEE E. D. and RESSER, C. E. 1945. Cambrian history of the Grand Canyon region. *Publs. Carnegie Instn.* **563**, i–viii+1–231, pl. 1–27.

- MEEK, F. B. 1873. Preliminary paleontological report, consisting of lists and descriptions of fossils, with remarks on the ages of the rocks in which they were found. *U.S. geol. Surv. Terr. 6th Ann. Rep.* 429-518.
- MERRIAM, C. W. 1964. Cambrian rocks of the Pioche Mining District, Nevada. *Prof. Pap. U.S. geol. Surv.* **469**, i-iv+1-59, pl. 1-6.
- MILLER, S. A. 1889. *North American geology and palaeontology for the use of amateurs, students, and scientists*. Western Methodist Book Concern, Cincinnati.
- NOLAN, T. B., MERRIAM, C. W., and WILLIAMS, J. S. 1956. The stratigraphic section in the vicinity of Eureka, Nevada. *Prof. Pap. U.S. geol. Surv.* **276**, i-iii+1-77, pl. 1-2.
- NORFORD, B. S. 1962. Illustrations of Canadian fossils, Cambrian, Ordovician and Silurian of the western Cordillera. *Geol. Surv. Pap. Can.* **62-14**, 1-24, pl. 1-10.
- ORIEL, S. S. 1964. Brigham, Langston, and Ute Formations in Protneuf Range, southeastern Idaho. *Spec. Pap. geol. Soc. Am.* **82**, 341.
- PALMER, A. R. 1954. An appraisal of the Great Basin Middle Cambrian trilobites described before 1900. *Prof. Pap. U.S. geol. Surv.* **264-D**, i-iii+55-86, pl. 13-17.
- 1958. Morphology and ontogeny of a Lower Cambrian ptychoparioid trilobite from Nevada. *J. Paleont.* **32**, 154-70, pl. 25, 26.
- in MERRIAM, C. W. 1964a. Cambrian rocks of the Pioche Mining District, Nevada. *Prof. Pap. U.S. geol. Surv.* **469**, i-iv+1-59, pl. 1-6.
- 1964b. An unusual Lower Cambrian trilobite fauna from Nevada. *Ibid.* **483-F**, i-iii+1-13, pl. 1-3.
- POULSEN, V. 1958. Contributions to the Middle Cambrian paleontology and stratigraphy of Argentina. *Mat.-fys. Meddr.* **31** (8), 1-22, pl. 1.
- 1964. Contribution to the Lower and Middle Cambrian paleontology and stratigraphy of north-west Greenland. *Meddr. Gronland*, **164** (6), 1-105, pl. 1-3.
- RASETTI, F. 1948. Middle Cambrian trilobites from the conglomerates of Quebec (exclusive of the Ptychopariidea). *J. Paleont.* **22**, 315-39, pl. 45-52.
- 1951. Middle Cambrian stratigraphy and faunas of the Canadian Rocky Mountains. *Smithson. misc. Collns.* **116** (5), i-v+1-277, pl. 1-34.
- 1957. Additional fossils from the Middle Cambrian Mt. Whyte Formation of the Canadian Rocky Mountains. *J. Paleont.* **31**, 955-72, pl. 118-22.
- 1963. Middle Cambrian ptychoparioid trilobites from the conglomerates of Quebec. *Ibid.* **37**, 575-94, pl. 66-70.
- RAYMOND, P. E. 1920. The appendages, anatomy, and relationships of trilobites. *Mem. Com. Acad. Arts Sci.* **7**, 169 pp., pl. 1-11.
- 1928. The ontogenies of trilobites, and their significance. *Am. J. Sci.* **15**, 168-70.
- RESSER, C. E. 1935. Nomenclature of some Cambrian trilobites. *Smithson. misc. Collns.* **93** (5), 1-46.
- 1936. Second contribution to nomenclature of Cambrian trilobites. *Ibid.* **95** (4), 1-29.
- 1937. Third contribution to nomenclature of Cambrian trilobites. *Ibid.* **95** (22), 1-29.
- 1938a. Middle Cambrian fossils from Pende Oreille Lake, Idaho. *Ibid.* **97** (3), 1-12, pl. 1.
- 1938b. Cambrian System (restricted) of the Southern Appalachians. *Special Pap. Geol. Soc. Am.* **15**, 1+vii+1-140, pl. 1-16.
- 1938c. Fourth contribution to nomenclature of Cambrian fossils. *Smithson. misc. Collns.* **97** (10), 1-43.
- 1939a. The *Ptarmigania* strata of the northern Wasatch Mountains. *Ibid.* **98** (24), 1-72, pl. 1-14.
- 1939b. The Spence Shale and its fauna. *Ibid.* **97** (12), 1-29, pl. 1-6.
- SHAW, A. B. 1962. Paleontology of northwestern Vermont IX. Fauna of the Monkton Quartzite. *J. Paleont.* **36**, 322-45.
- SHIMER, H. W. and SHROCK, R. R. 1944. *Index fossils of North America*. John Wiley and Sons, Inc., New York.
- STOYANOW, A. in COOPER, G. A. 1952. Cambrian stratigraphy and paleontology near Caborca, northwestern Sonora, Mexico. *Smithson. misc. Collns.* **119**, 49-59, pl. 14.
- VELLA, P. 1964. Biostratigraphic units. *N.Z. J. Geol. Geophys.* **7**, 615-25.
- WALCOTT, C. D. 1886. Second contribution to the studies on the Cambrian faunas of North America. *Bull. U.S. geol. Surv.* **30**, 1-369, pl. 1-33.

- WALCOTT, C.D. 1890. The fauna of the Lower Cambrian or *Olenellus* zone. *10th Ann. Rep. U.S. geol. Surv.* 509-774, pl. 49-98.
- 1908a. Cambrian geology and paleontology no. 1.—Nomenclature of some Cambrian Cordilleran formations. *Smithson. misc. Collns.* 53, pp. 1-12.
- 1908b. Cambrian geology and paleontology no. 5.—Cambrian sections of the Cordilleran area. *Ibid.* 53, pp. 167-230, pl. 13-22.
- 1910. Cambrian geology and paleontology no. 6.—*Olenellus* and other genera of the Mesonacidae. *Ibid.* 53, 231-422, pl. 23-44.
- 1916a. Cambrian geology and paleontology III, no. 5. Cambrian trilobites. *Ibid.* 64 (5), 303-570, pl. 45-67.
- 1916b. Cambrian geology and paleontology III, no. 3—Cambrian trilobites. *Ibid.* 64 (3), 157-258, pl. 24-38.
- 1917. Fauna of the Mount Whyte Formation. *Ibid.* 67 (3), 61-114, pl. 8-13.
- WHEELER, H. E. 1948. Late Pre-Cambrian-Cambrian stratigraphic cross section through southern Nevada. *Univ. Nev. Bull. Geol. Min. Ser.* 47, 1-61.
- and LEMMON, D. M. 1939. Cambrian formations of the Eureka and Pioche Districts, Nevada. *Ibid.* 31, 1-60.
- WHITE, C. A. 1874. Preliminary report upon invertebrate fossils collected by the expeditions of 1871, 1872, and 1873, with descriptions of new species. *U.S. Geog. and Geol. Surveys W. 100th Mer. Rept.* 5-27.
- WILLIAMS, J. S. and MAXEY, G. B. 1941. The Cambrian section in the Logan Quadrangle, Utah and vicinity. *Am. J. Sci.* 239, 276-85.

W. H. FRITZ
 Palaeontology Section
 Geological Survey of Canada
 601 Bootle Street
 Ottawa 4
 Ontario, Canada

Typescript received 7 March 1966

STUDIES ON TRIASSIC FOSSIL PLANTS FROM ARGENTINA III. THE TRUNK OF *RHEXOXYLON*

by DONALD W. BRETT

ABSTRACT. The occurrence of plant fossils in the Ischigualasto region in north-west Argentina is discussed in relation to the geology of the area. Specimens of large trunks of *Rhexoxylon piatnitzkyi* from the Ischigualasto formation are described and the peculiar secondary growth processes of the plant are discussed with reference to this new material.

THE Triassic fossiliferous beds of north-western Argentina have long been known as a source of fossil plants, many of which have been described by the Argentine palaeobotanist J. Frenguelli and others. A full bibliography is given in Archangelsky 1965.

Extensive exposures occur in Mendoza and San Juan provinces and over an area of some 1,750 km.² centred on Ischigualasto in the Sierra del Valle Fertil along the boundary between the provinces of San Juan and La Rioja (approximately lat. 30° S., long. 68° W.).

In the two preceding papers of this series, petrified stems of *Rhexoxylon* and *Michelil-*loa**, a cycad, were described from Ischigualasto (Archangelsky and Brett 1961, 1963). The occurrence of *Rhexoxylon* in Argentina is of special interest since along with recent finds of vertebrate remains in the same beds (Reig 1959, Romer and Cox 1962, Cox 1965) it suggests a correlation of the Ischigualasto formation with the Molteno and Red Beds of the Stormberg Series in Africa from which *Rhexoxylon* had been described previously (Archangelsky and Brett 1961). In 1961 the present author accompanied Drs. Sergio Archangelsky and Rafael Herbst on expeditions to the several Triassic exposures and collected additional material of both petrified and carbonized plants. At Ischigualasto a detailed record was kept of localities and stratigraphical position of the fossils and some relevant data is included in the present report.

Fossiliferous localities at Ischigualasto

The concordant series of Triassic sediments exposed in the Ischigualasto region has been referred to as the 'Ischichuca-Ischigualasto Series'. Since both these names are used separately for formations it is proposed to call the series the Agua de la Peña series, and so avoid possibility of confusion (Archangelsky, personal communication).

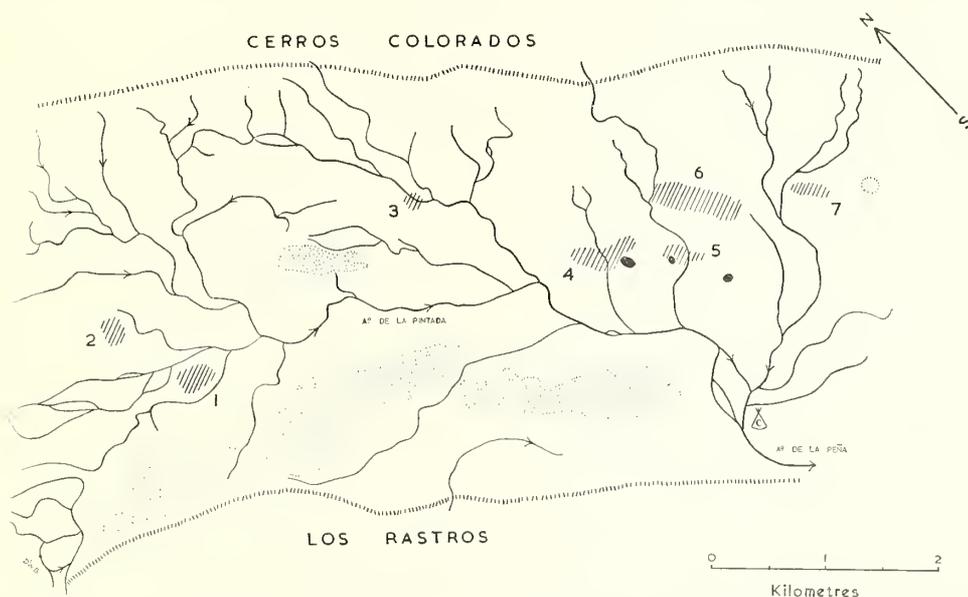
The Agua de la Peña series comprises four formations attaining a total thickness of some 1,300 m. (Groeber and Stipanovic 1953).

Los Colorados	150 m.
Ischigualasto	550 m.
Los Rastros	400 m.
Ischichuca	200 m.

The strata have been little affected by tectonic movements. Over the whole area they dip 7–10° to the north-east. All four formations are fossiliferous but only in Los Rastros and the Ischigualasto are the fossils abundant and reasonably well preserved.

The Ischigualasto formation consists mostly of sandstones, fine conglomerates, and tuffs in rhythmic successions. It is separated from Los Rastros formation in the Agua de la Peña region by a thick bed of coarse conglomerate (La Peña Conglomerate), but this bed thins out westwards until the two formations intergrade. There is likewise an insensible transition between the uppermost Ischigualasto beds and the red sandstones of Los Colorados formation.

The Ischigualasto sediments are exposed in a desert basin (map) dominated by the cliffs of the more resistant strata of Los Rastros and Los Colorados formations. The fossil



MAP. Part of the Ischigualasto basin showing the main fossiliferous areas in the Ischigualasto formation numbered 1 to 7. For further account of these see text. Stippled areas indicate the major terraces, and the smaller black areas sand dunes. The camp site near the Agua de la Peña is indicated by the wigwam symbol. (Map based on plane table survey prepared under the direction of Rogelio Bellman.)

plants occur in a medium- to coarse-grained limonitic sandstone, and in a soft grey shale which usually underlies the sandstone. These facies are lenticular and do not always contain many fossils. The fossil vertebrates are not confined to these facies.

Seven localities where fossil plants are abundant are shown on the map of the Ischigualasto basin. The localities are numbered according to their stratigraphical succession from the lowest upwards.

In the lower beds only carbonized leaves were found, but these are plentiful. At 1 the fossiliferous beds attain a thickness of over one metre. At both 1 and 2 they consist of compact layers of black plant compressions in a sandstone matrix and are conspicuous from a distance because where they outcrop they show as dark and yellowish bands across the grey detritus.

At the remaining localities 3, 4, 6, and 7, both compressions and petrifications occur, often closely associated. No great differences have been found in the assemblages of carbonized remains (compressions) at any locality except 5 where they are exclusively

equisetalean. The carbonized leaves will be described by S. Archangelsky in the following paper in this series.

Many large trunks occur at locality 4 and fewer at 3, 6, and 7. Most of the trunks are of *Rhexoxylon* and, usually, it is the broad basal part which is exposed on the surface, the rest of the trunk being buried owing to the dip of the rock.

At 4, 6, and 7 some of the trunks were found on microscopic examination to be of a conifer-type, though *not* araucarioid. (Similar trunks occur at Uspallata near Mendoza in the Potrerillos formation.)

At locality 6, along with the large specimens of *Rhexoxylon*, were found additional fragments of *Rhexoxylon piatnitzkyi* Arch. and Brett and of the cycad *Michelilloa waltonii* Arch. and Brett.

Los Rastros and Los Colorados formations appear to be of less importance as sources of petrified plants, although carbonized leaves have been described from Los Rastros by Frenguelli. These are found in grey shales, in sandstones, and in thin coaly layers exposed in the gorge of the Río de la Peña. They are mostly fragmentary, however, and a few petrifications that I have seen are too poorly preserved for adequate description.

Los Colorados formation is almost barren and no plant fossils have previously been recorded from these strata. There are several large silicified trunks, some reaching a length of 12 m., on the plateau overlooking the Ischigualasto basin. The wood, although not well preserved, is seen on microscopic examination of flakes to be araucarioid. Bonaparte (1960) has described fossil vertebrates from this formation.

The trunk of Rhexoxylon

Although the peculiar arrangement of the woody tissue in *Rhexoxylon* resembles that of certain extant lianes (Walton 1923) the size of some of the African specimens has made it clear that the adult plants had large upright trunks which could not have belonged to climbing plants (Walton 1956). Some of the largest fragments of *R. africanum* that have been described have a woody cylinder about 50 cm. across while the wood of *R. tetrapteridoides* is known to have attained a diameter of 16 cm. in the largest specimen figured by Walton (1923, text-fig. II, 3). The general features of these large stems are shown in text-fig. 1.

The numerous trunks at Ischigualasto amply confirm Walton's conclusion that *Rhexoxylon* was a tree. Partial excavation of one specimen revealed 5–6 m. of trunk that was still about 30 cm. across at the upper end. *Rhexoxylon* is thus proved to have been a large tree and it was obviously an important if not dominant plant in the vegetation of an extensive swampy area in mid-Triassic times.

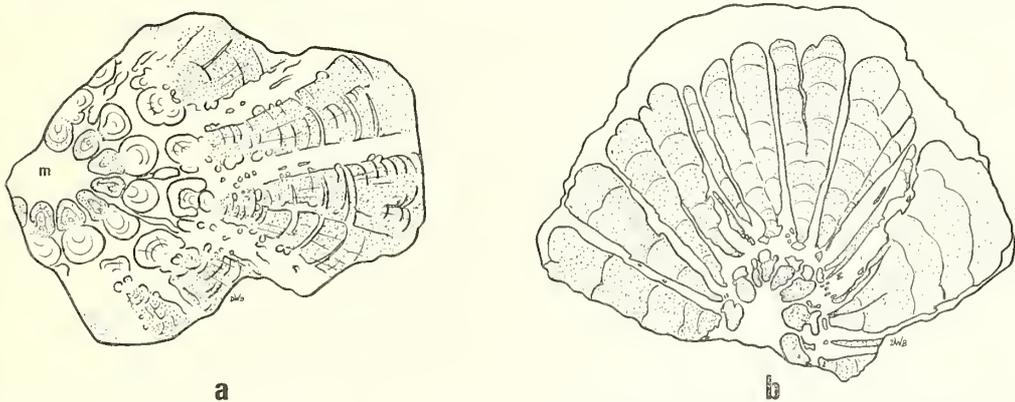
The separation of the sectors of woody tissue in the stem by broad rays of softer tissue has resulted in the fossils acquiring a fluted shape. The fossil trunks have lost most of the tissues external to the woody cylinder so there is no firm evidence that they were not terete in life. Nevertheless the trunk splayed out at the base where the woody sectors become more widely separated and it is possible that the tree was buttressed as are many present day trees.

The trunk base described below has a maximum width of about 48 cm. but this represents little more than half the full width of the woody cylinder. In life the trunk must have been at least one metre wide at a height above ground level of about a metre.

Veins of gypsum in the Ischigualasto fossils give them a tendency to fragment on

cutting so the specimen was embedded in a concrete mix with a 1-cm. aggregate before cutting was attempted. The approximate positions of the cuts are indicated on the photograph of the specimen before embedding reproduced as Plate 44, fig. 1.

The original slices are deposited in the Hunterian Museum (University of Glasgow) no. Pb 3906a-f. Cellulose acetate 'peel' sections prepared from the surfaces are in the Museo de La Plata, Argentina. Text-figs. 2-6 were prepared from the surfaces a-e in Plate 44, fig. 1 and the drawings are labelled accordingly. There is a great similarity between the arrangement of wood in the sections illustrated in text-figs. 4-6 and in the section of *R. africanum* (text-fig. 1). Comparison with sections taken from close to the



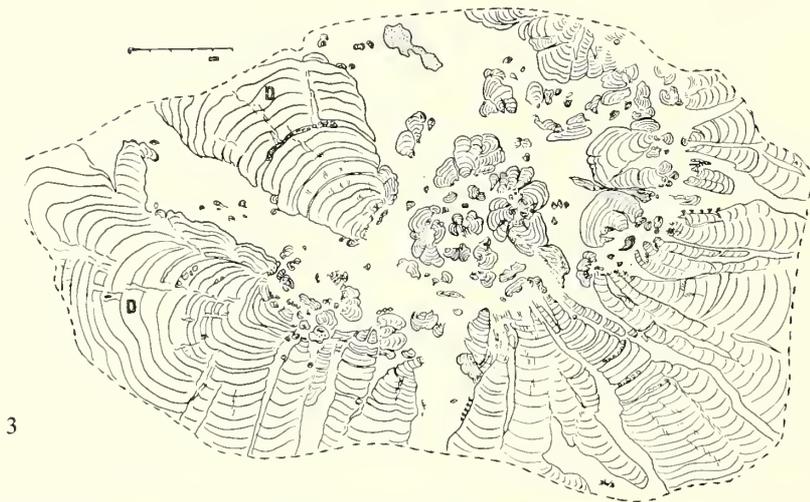
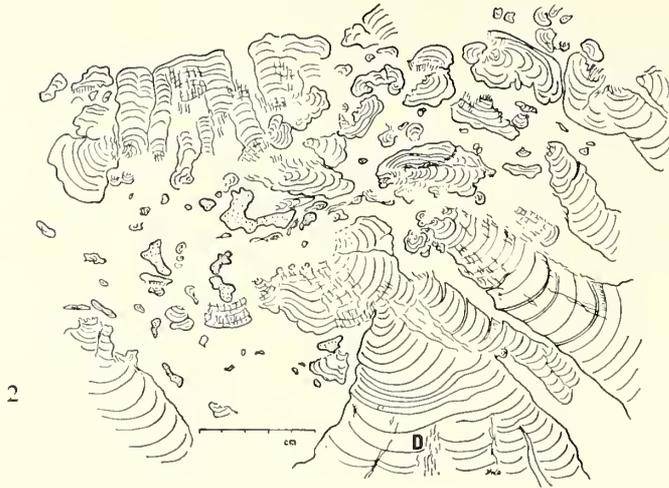
TEXT-FIG. 1. Disposition of xylem in adult stems; the separated centrifugal and centripetal xylem sectors are stippled. Both from Archangelsky and Brett 1961. (a) *Rhexoxyylon africanum* ($\times 0.2$), m, medulla. (b) *R. tetrapteridoides* ($\times 0.5$).

trunk base (text-figs. 2 and 3), which show a very confused distribution of wood, makes it clear that the regular arrangement of xylem sectors around the medulla is a feature of the upper parts of the trunk.

The major outer sectors of wood in these lower sections (labelled D in text-figs. 2 and 3) probably indicate the position of buttresses or the tops of large divergent roots. Text-fig. 2 shows very little of the outer xylem. This lowest section passes through the centre of the base of the stem in between the diverging roots or buttresses.

The structure of the trunk base leads one to expect higher levels of the trunk to have a regular arrangement of xylem sectors, not complicated by the root connexions, and, of course, in a condition in which much less secondary growth has taken place. The section shown in text-fig. 7 was taken from the narrower part of the trunk of a different specimen (Peel sections Pb 3908 in Hunterian Museum, from specimen deposited in the Museo de La Plata). The outer (centrifugal) wood sectors are here much more compact yet are quite distinctly separated from one another by the parenchyma rays. In one place (marked r in text-fig. 7) the characteristic radial splitting of the centrifugal xylem has occurred; this is brought about by local cessation of regular cambial activity. In other places (t in text-fig. 7) tangential bands of parenchyma have developed between the growth rings in the centrifugal wood. These secondary growth processes are discussed in more detail later on.

The medulla of this specimen is narrower than the medulla in the lower part of the trunk and is in fact not much broader than the medulla in the very small stem *Rhexoxyylon*

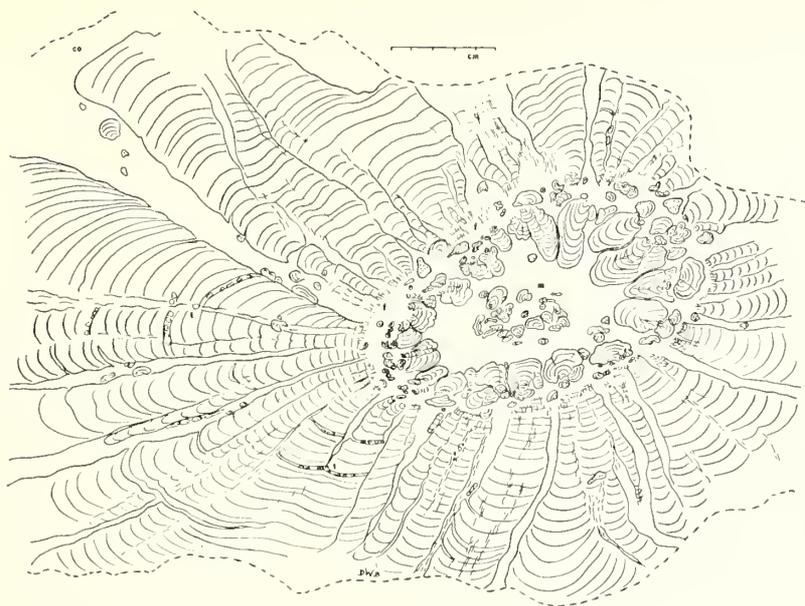


TEXT-FIGS. 2-6. *R. piatnitzkyi*. Disposition of xylem in transverse sections of trunk. Figs. 2-6 prepared from sections *a-e* of trunk base. (Fig. 7 is from the upper region of another trunk.) 5-cm. scale on each figure. Only a few of the well-defined growth rings are represented; these indicate the changes in the cambial arc that have occurred during development. Likewise many of the smaller fragments of vascular tissue and adventitious strands have been omitted for the sake of clarity. Where much frayed xylem occurs among dilatation parenchyma this is indicated by short radial lines.

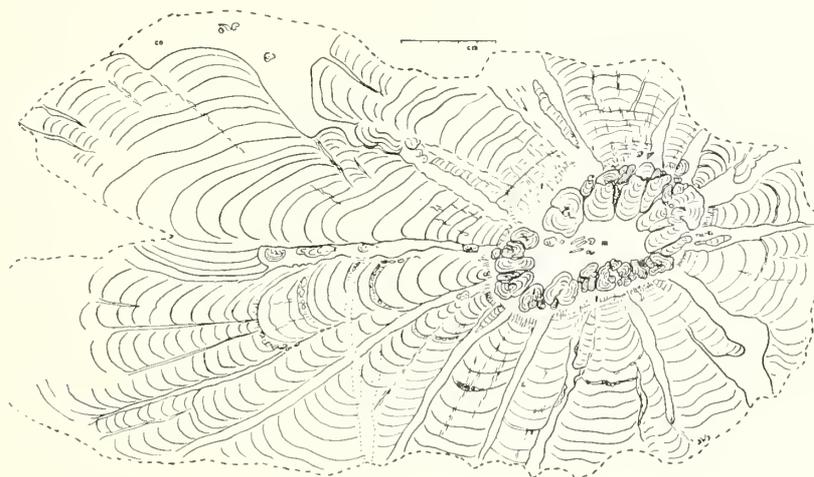
The expanded mass of centrifugal xylem at top left of fig. 2 corresponds to the innermost part of the sector labelled *D* in that position in fig. 3. Most of the large sector labelled *D* at bottom left of fig. 3 is not represented in the lower section. Stippling in these lower sections indicates the corky bodies.

co, cortex; f, frayed xylem, especially the inner fringe ('Fransxylem'); m, medulla; r, radial splitting of centrifugal xylem; t, tangential splitting of centrifugal xylem. *D*, centrifugal xylem diverging at trunk base into roots or buttresses.

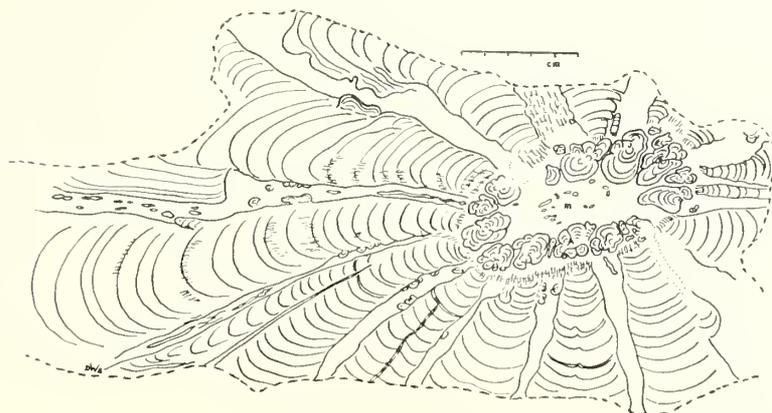
Explanation of the secondary growth processes is given in the text.



4



5



6

piatnitzkyi Archangelsky & Brett (1961). The inner (centripetal) xylem sectors are small and regularly disposed around the medulla on the same radii as their centrifugal counterparts. They are, however, separated from the latter by additional small patches of xylem. These appear to have developed centripetally, that is with their cambiums away from the protoxylems of the outer sectors.

The small fragments described by Archangelsky and Brett (1961) as '*Rhexoxylon* sp. A' are from the large trunks. Histological details were given in that account (loc. cit., pp. 6-9) so there is no need to repeat them here. There are no anatomical differences between the material described by Archangelsky and Brett and the trunks described in the present contribution to suggest that the Ischigualasto *Rhexoxylon* is not a single species. The material is therefore referred to *Rhexoxylon piatnitzkyi*. This species now comprises both the small stem and the adult trunks: an emended diagnosis follows.

Emended diagnosis of R. piatnitzkyi Archangelsky and Brett 1961. Small stem 7-8 cm. diameter: surface with rhomboidal leaf bases and branch scars or buds surrounded by small scale leaves; medulla, 2-3 cm. diameter, containing anastomosing system of vascular strands and spherical cysts (250-300 μ); cysts also abundant in cortex. Vascular cylinder dissected by gaps associated with origin of leaf traces; vascular strands 7-8 mm. in radial extent. Xylem of vascular cylinder comprising centrifugal and centripetal parts separated by narrow zone of parenchyma. Leaf traces connected to both margins of gaps, dividing in inner cortex; leaf supply of traces from several gaps; 7-8 vascular strands in leaf base arranged in semicircle, each strand comprising two or more bundles concentrically disposed.

Trunk of adult plant. Woody cylinder attaining 80 cm. diameter, medulla 8 cm., towards base of stem. Sclerotic nests and irregular secondary bodies in medulla and secondary parenchyma; centrifugal and centripetal xylem sectors separated by adventitious vascular developments and secondary parenchyma, and fragmented by proliferation of parenchyma and adventitious vascular tissue. Regular arrangement of centrifugal and centripetal xylem lost in lowest parts of trunk; broad wedges of centrifugal xylem diverge into large roots or buttresses; centre of stem occupied by confused mixture of vascular strands and secondary parenchyma.

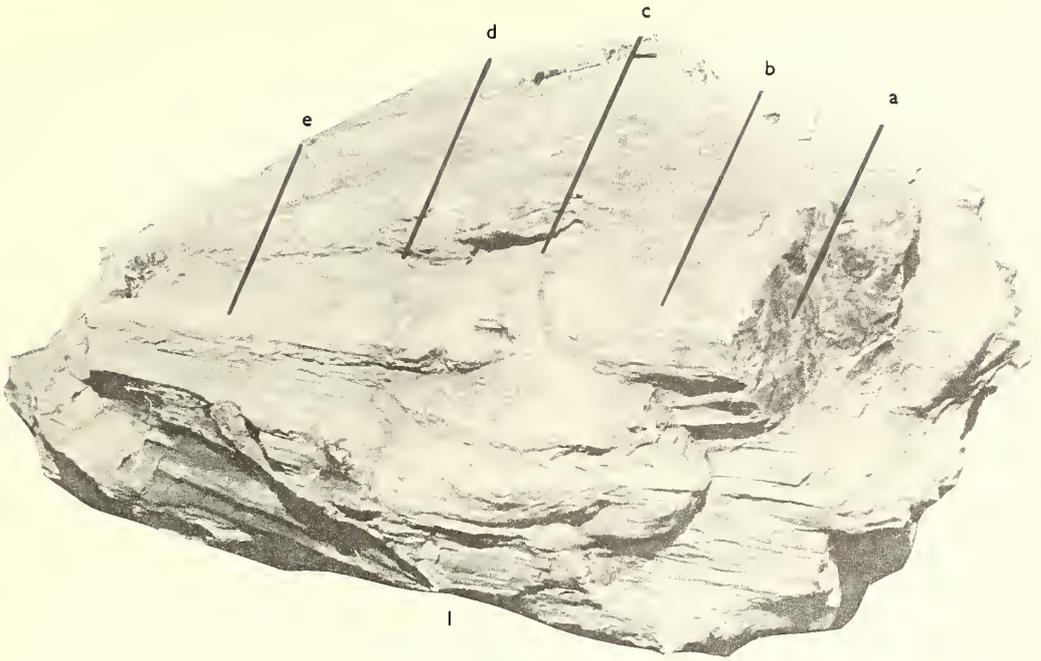
The secondary development of Rhexoxylon stems

Archangelsky and Brett (1961) suggested a course of development that could lead from the structure seen in the young stem (*R. piatnitzkyi*) to the complex structure of *R. africanum*. The xylem of the vascular cylinder in *R. piatnitzkyi*, as seen in transverse section was shown to consist of a centrifugal and a centripetal part separated by a narrow parenchyma zone and dissected by leaf gaps into about fifteen bundles. A similar arrangement was also demonstrated in the younger stems of *R. tetrapteridoides* and in an unidentified stem from Africa which was taken to be a young *R. africanum*.

EXPLANATION OF PLATE 44

Fig. 1. The trunk base before embedding in concrete. This view includes the 'upper' and 'right-hand' sides of the sections and their approximate locations are shown a-e (text-figs. 2-6); the base of the specimen is to the right of the photograph.

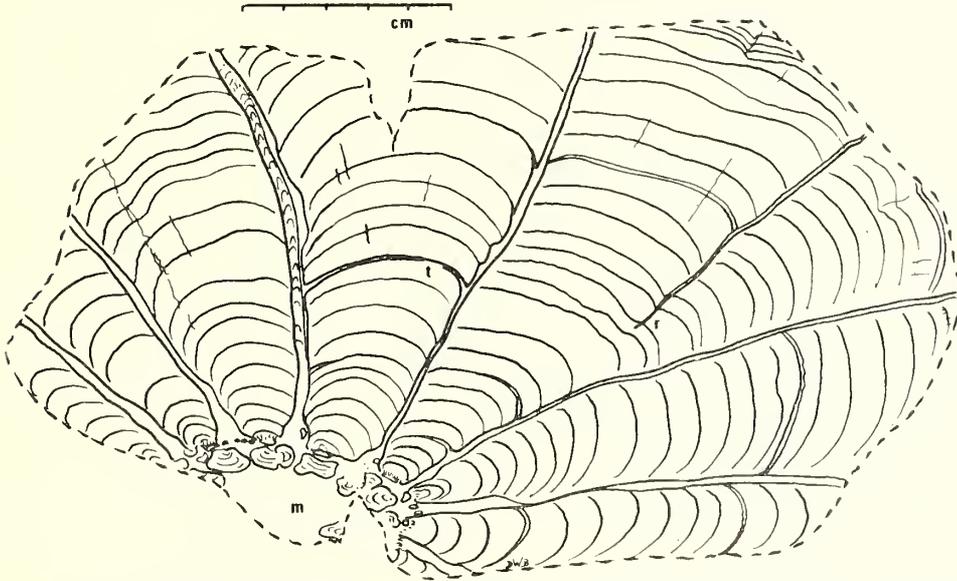
Fig. 2. Part of section from cut surface opposite that shown in text-fig. 5. Natural size. The photograph is thus a mirror image of the diagram.



2

BRETT, Trunk of *Rhexoxylon*

Secondary development in *R. africanum* and *R. tetrapteridoides*, according to their interpretation, results in the separation of the two parts of the double bundles: the outer (centrifugal) parts form the main bulk of the wood of the trunk and become split up due to the proliferation of parenchyma and growth of adventitious vascular tissue; the inner (centripetal) parts remain as a ring around the medulla. The separated parts are indicated by the stippling in text-fig. 1, the new vascular tissue formed from extra cambiums is left clear in the drawing.



TEXT-FIG. 7. *R. piatnitzkyi*. Transverse section of trunk. Peel section HM Pb 3908. Full explanation in text.

It is now possible to consider the secondary development of *Rhexoxylon* with reference to young and mature specimens of *R. piatnitzkyi* from the one locality. The present investigations have confirmed the general interpretation put forward by Archangelsky and Brett.

Centrifugal xylem. Within the individual sectors the radial extent of the secondary xylem is increased through the regular activity of the cambium in the normal manner. The tangential width of the sectors is increased through the normal broadening of the cambial arcs but this is associated with a 'splitting' of the cambium in places. This results in the formation of new broad rays of mixed tissue, mainly parenchyma. These rays are not formed by the cambium which ceases regular activity at this point (r in text-fig. 7). Some residual cambial activity occurs intermittently in the rays, however, and radially arranged groups of cells and patches of xylem occur frequently in the rays. This xylem does not appear to have been 'detached' from the margins of the xylem sectors.

In addition to the xylem arising along with the parenchyma in these rays, renewed meristematic activity at a later stage produces the characteristic fan-shaped adventitious growths of vascular tissue which develop from small cambiums along the margins of

the xylem sectors in the broad rays. Similar adventitious growths also arise within the xylem sectors but probably only after the appearance there of dilatation parenchyma in which the new vascular tissue then develops. Dilatation parenchyma proliferates along certain of the growth-ring boundaries attaining in some places a radial extent of 2–3 mm. separating adjacent growth rings (t in text-figs. 4, 7). Usually adventitious vascular tissue is seen only in the broader bands of parenchyma (t in text-fig. 4).

At a late stage of secondary thickening such as that represented by the sections from the trunk base (text-figs. 2–6), a considerable amount of dilatation parenchyma proliferates from the vascular rays in the xylem sectors. This splits the wood and gives rise to irregular tracts of mixed tissue containing many short radial strings of tracheids detached from the main masses of xylem (f in text-figs. 4 and 5). This occurs especially as a fringe along the inner margins of the centrifugal xylem sectors and corresponds to the 'Fransenxylem' of Kräusel (Kräusel 1956, Archangelsky and Brett 1961). There is no essential difference between the frayed xylem of the inner zone and that appearing further out in the secondary xylem.

Centripetal xylem and the separation zone. The variation in the appearance of the vascular bundles of the small stem is related to the origin of the leaf traces (Archangelsky and Brett 1961). This variation no doubt accounts for much of the variation seen in the bundles of the inner ring in the adult stems. Only where the cambium of the primary bundle was continuous around both centrifugal and centripetal xylem (i.e. the bundle was concentric) will the eventual separation of the two parts have involved actual rupture of the primary xylem and innermost secondary xylem. The point of separation is presumably determined by the location of production of dilatation parenchyma.

Adventitious cambiums arise in the parenchyma between the separated primary xylems and also along the newly exposed margins of the secondary xylem of the inner sectors. These new cambiums may be orientated so as to produce xylem either centripetally or centrifugally. In the former case the new tissue appears as fan-shaped developments along the frayed xylem of the outer sectors. Activity of both the original and the new cambiums soon closes up the primary faces of the inner xylem sectors resulting in the irregular, more or less concentric, bundles of the inner ring surrounding the medulla (text-figs. 4–6). The orientation of the first adventitious vascular tissue to arise during the separation process seems to be variable or at least to differ according to the region of the trunk. In the section from the upper region of the trunk (text-fig. 7) the first adventitious xylem is centripetal. In the base of the trunk however there is little evidence of centripetal adventitious xylem in the zone of separation although the bundles of the inner ring are all completely closed. Archangelsky and Brett (1961) noted the variation in the orientation of the adventitious vascular tissue of this zone in *R. africanum* in which centripetal xylem may also be lacking in some specimens. There is evidence that the first growth may be centrifugal in *R. africanum* (loc. cit., fig. 6A). In sections of *R. tetrapteridoides* (Kidston Coll., Univ. Glasgow, 2780–81) the first adventitious cambiums in some sectors have produced centripetal xylem, in other sectors both centripetal and centrifugal fan-shaped masses are equally well developed.

The extent of the centripetal development of the inner ring bordering the medulla is variable in the base of the trunk: there is a much greater development of xylem on one side of the medulla (text-figs. 3–5). The opposite side of the trunk however has the clearly defined outer sectors of wood which diverge into the large roots or buttresses and are

separated by very broad parenchyma rays. The differences between the two sides of the trunk are particularly shown in text-fig. 3. I infer from this that the tree was inclined at an angle to the vertical in life and that this resulted in the centripetal reaction wood on one side and the buttresses on the opposite side.

Medulla. The small spherical cysts present in the medulla and cortex are a primary feature. In the medulla of the small stem they occur at about 150/cm.² but their frequency is reduced to 10/cm.² in the expanded medulla of the adult trunk (Archangelsky and Brett 1961); a maximum count of 22/cm.² was obtained in the section of the new material shown in text-fig. 6. The additional tissue of the enlarged medulla is secondary in origin and consists of dilatation parenchyma and adventitious vascular tissue. Sclerotic nests are developed in all the secondary parenchyma of *Rhexoxylon* and are common in the medulla. At the very base of the trunk the primary medulla loses its identity and in the large areas of parenchyma secondary bodies of cork-like tissue develop. These are seen in text-figs. 2 and 3, and were first described by Bancroft (1913) in her original account of *R. africanum*.

Acknowledgements. My participation in the expedition to Ischigualasto was made possible through a Grant-in-Aid from the Royal Society of London. I should like to record the appreciation of all members of the expedition for the cooperation of the Comisión Nacional de Energía Atómica (Chilecito) who generously provided additional transport and camping equipment. The expedition was organized from the Universidad Nacional de Tucuman and it is a pleasure to acknowledge the help given us by Dr. A. Willink, Director of the Instituto Lillo, Tucuman.

REFERENCES

- ARCHANGELSKY, S. 1965. Tafofloras Paleozoicas y Eomesozoicas de Argentina. *Boln. Soc. argent. Bot.* **10**, 247–91.
- and BRETT, D. W. 1961. Studies on Triassic fossil plants from Argentina I. *Rhexoxylon* from the Ischigualasto Formation. *Phil. Trans. R. Soc. Lond. B*, **244**, 1–19, pl. 1, 2.
- — 1963. do. II. *Michelilloa waltonii* nov. gen. et spec. *Ann. Bot.*, N.S. **27**, 147–54, pl. 1, 2.
- BANCROFT, N. 1913. *Rhexoxylon africanum*, a new medullosean stem. *Trans. Linn. Soc. Lond.*, Bot. **8**, 87–103.
- BONAPARTE, J. 1960. Noticia sobre la presencia de restos fósiles de tetrapodos triásicos en los estratos de Los Colorados (Prov. de San Juan). *Acta Geol. lilloana* **3**, 181–6.
- COX, C. B. 1965. New Triassic dicynodonts from South America, their origins and relationships. *Phil. Trans. R. Soc. Lond. B*, **248**, 457–514.
- GROEBER, P. and STIPANICIC, P. N. 1953. *Geografía de la República Argentina*. 2 (1), Mesozoico i. Triásico. GAEA (Sociedad Argentina de Estudios Geográficos), Buenos Aires.
- KRÄUSEL, R. 1956. Lianen aus den Karru-Schichten Süd-Afrikas. *Senckenberg leth.* **37**, 1–14.
- REIG, O. 1959. Primeros datos descriptivos sobre nuevos reptiles arcosaurios del Triásico de Ischigualasto (S. Juan) Argentina. *Revta Asoc. geol. argent.* **13**, 257–70.
- ROMER, A. S. and COX, C. B. 1962. The fossiliferous Triassic deposits of Ischigualasto, Argentina, and preliminary description of *Ischigualastia*, a new genus of dicynodont. *Breviora*, **156**, 9 pp.
- WALTON, J. 1923. On *Rhexoxylon* Bancroft, a Triassic genus of plants exhibiting a liane-type of vascular organization. *Phil. Trans. R. Soc. Lond. B*, **212**, 79–109, 2 pl.
- 1956. *Rhexoxylon* and *Dadoxylon* from the Lower Shire Region of Nyasaland and Portuguese E. Africa. *Colon. Geol. Miner. Resour.* **6**, 159–68, pl. 1.

D. W. BRETT
Botany Department
Bedford College
University of London

FISH OTOLITHS FROM THE BATHONIAN OF SOUTHERN ENGLAND

by F. C. STINTON and H. S. TORRENS

ABSTRACT. The occurrence of fish otoliths in the English Bathonian is recorded, some ten undescribed forms being represented. These are described together with details of the stratigraphy at the sections yielding them.

THE fragmentary skeletal and dental fish remains which occur sporadically in the English Middle Jurassic have appeared to indicate that true Fishes other than sharks, are rare in these strata. However, the discovery of numerous otoliths by one of us (H.S.T.) suggests that they were much commoner than was formerly supposed although limited in the number of species. The otoliths were obtained (by H.S.T.) during the compilation of the stratigraphical data which follows. The relationship of the otoliths to other skeletal remains is obscure as none have been demonstrated *in situ* in skulls in this country.

STRATIGRAPHY (H. S. T.)

The two Bathonian localities at which otoliths were found are exposed respectively in Wiltshire and in Dorset. The stage name 'Bathonian' is used in the sense recommended by the Jurassic Colloquium held in Luxembourg in 1962 (published 1964, p. 78).

The first locality is the well-known section beside the eastern bank of the Kennet and Avon canal, Bradford on Avon (Nat. Grid ST 826600) described by Cox (1941, 33) among others. The actual succession at this pit has never appeared in print and the following section is reproduced, somewhat modified, by kind permission of Dr. C. E. Periam, from his unpublished Ph.D. thesis (1956, p. 32):

Descending section measured at the eastern end of the clay pit:

	ft.	ins.
FOREST MARBLE		
h. Grey-brown clay passing into clay soil		6
g. Shelly limestone		6
f. Grey clay	8	0
e. Shelly flaggy limestones separated by a 6-in. clay band	2	0
BRADFORD CLAY		
d. Grey clay	2	0
c. Impersistent fine-grained platy, shelly limestone full of fossil wood in places, <i>Clydoniceras in situ</i>	1	0
b. Grey clay	9	0
GREAT OOLITE		
a. Floor of hard shelly, oolitic limestone with adherent oysters etc.		seen

Bed *a* shows the topmost surface of the Great Oolite limestone while beds *b*, *c*, *d* together comprise the Bradford Clay—some 12 ft. thick. It is not often possible to draw

a sharp boundary between the Bradford Clay and the Forest Marble but bed *e* is probably best referred to the Forest Marble.

The Bradford Clay was assigned by Arkell (1959, p. 237) to the *Hollandi* zone of the Upper Bathonian but it is best (Torrens 1965, p. 49) to follow Tintant (1963, p. 55) in regarding this 'zone' as a subzone of the *Discus* zone. Bed *c* at this locality yielded a specimen of *Clydoniceras in situ* (H. S. Torrens coll. 997). This is only the third ammonite (all *Clydoniceras*) so far recorded from the Bradford Clay.

The rich fauna of the Bradford Clay (see Cunnington 1860 and Periam 1956, p. 33, locality 40) is best collected from the base of bed *b*. Periam noted the same assemblage to occur at the top of bed *c* as well. This was due to his failure to recognize the existence of a small fault, first pointed out by Dr. G. Green of the Geological Survey, which causes the Great Oolite Limestone (bed *a*) to form a second higher platform in the western part of the pit, nearest to the canal. This second platform on which the basal highly fossiliferous Bradford Clay is bedded, corresponds at first glance with the higher bed *c* and caused Periam to record the Bradford Clay fauna at two horizons i.e. on the top of beds *a* and *c*. In fact, the apparent recurrence of the same fauna at two different horizons is due to repetition by this fault. There may also be some horizontal displacement between the sections on either side of the fault.

The otoliths were obtained by washing the clayey oolite-rich marl collected *in situ* at the base of bed *b* through a sieve (mesh 20) and handpicking the residue under a lens. They occurred only infrequently here, approximately one specimen being obtained from every 2 lb. of original sample.

A much larger fish otolith fauna was collected from the 3–4 ft. of blue-grey clay immediately underlying the *Ostrea (Liostrea) hebridica* Forbes lumachelle exposed at Rodden Hive Point, south-west of Langton Herring, Dorset (SY 569823). This locality is recorded in the *Directory of British Fossiliferous Localities* (1954, p. 25) and the horizon, together with its fauna, has been fully described by Arkell (1940, pp. 42–9; 1947, pp. 17–18).

The otoliths were obtained by the method detailed above and are extraordinarily abundant here, a pound of clay yielding as many as five otoliths. Many of the specimens are encrusted with microfaunal bryozoa and serpulids, suggesting that the deposition of these clays was extremely slow. Macrofossils, especially the ammonites and Trigoniac, are similarly encrusted with large serpulids and must have lain on the sea-floor for a considerable period before burial.

Arkell (1959, p. 239) assigned this horizon to a level above the *Wattonensis* beds of Dorset. Further investigation of the relevant faunas confirms the suggestion of House (1957, p. 69) that it can be more accurately correlated with the upper part of the *Wattonensis* beds themselves.

An interesting brachiopod, *Acanthothiris powerstockensis* Buckman and Walker, occurs rarely at this exposure. It has not previously been recorded here but its presence, together with *Rugitela*, at the same horizon, indicates that the fauna here may be somewhat condensed in relation to that of the type locality at Watton Cliff, Dorset, where the two genera occupy different beds (Muir-Wood 1936, p. 22).

The zonal affinities of this horizon are controversial but it can be placed in an intermediate zone between the *Aspidoides* and *Morrisi* zones, at the base of the Upper Bathonian, for which no entirely suitable zonal index can yet be proposed. This is the unnamed zone of Torrens (1965, p. 50).

THE OTOLITHS (F. C. S.)

The determination of mesozoic otoliths presents problems not encountered with Tertiary forms which may be compared directly with those of living teleosts. The situation is further complicated by the fact that, with the exception of one entire specimen of the fish *Lycoptera middendorfi* Müller, from the NW. German Dogger, no otoliths have been demonstrated *in situ* in the skulls of whole fishes so far discovered. Furthermore these *in situ* otoliths, being lagenoliths (asterisci), are valueless in the present circumstances for the suite under investigation are all sacculiths (sagittae) apart from one possible utriculith (lapillus).

The circular or subcircular type of sacculith in Recent teleosts is always found in deep-bodied, compressed, circular fishes although, conversely, this type of fish does not necessarily possess a round sacculith. Thus one may look to fishes of similar morphology which occur in the Bathonian for it may be that the contours of the skulls regulate the shapes of the otoliths in some cases. It must be noted, however, that the very circular chaetodonts have quite dissimilar percoid sacculiths although those of the majority of other round fishes conform to the usual pattern.

A number of morphologically similar Jurassic fish genera occur in the Bathonian as well as the Lias and Kimmeridgian. They are included in the Semionotidae and Pycnodontidae but those with the former order are virtually excluded, for the modern *Lepiosteus* Lacépède, is presumed to have evolved from the Semionotidae. The sacculiths of *Lepiosteus* are quite insignificant while the utriculith is the major otolith so that these circular sacculiths could not be related to the semionotids. In any case, it is probable that those forms described as *incertae sedis curvatus* Frost (1926, p. 85, pl. 4, fig. 14) and as Lapilli types A & B Schröder (1956, p. 150, pl. 7, figs. 41-46) originate from semionotid skulls for they show much similarity to utriculiths of *Lepiosteus*.

With the elimination of the semionotids one is left with the pycnodonts and it is proposed to refer these otoliths to this group of fishes. There is no evidence to indicate which of the known Bathonian pycnodonts might have furnished these specimens so it is proposed to establish a new genus to embrace them.

Pokorny (1965, p. 384) has quoted Weiler as saying that modern teleosts are derived from a small group of related ganoids but these otoliths indicate an independent ancestry for a number of modern teleost groups whose otoliths have similar characters to these fossil forms. There is little or no supporting evidence, osteologically, but it might well be that evolutionary changes have obscured their relationship.

The commonest otoliths from these strata exhibit morphological features consistent with some of those seen among modern clupeids and, for this reason these are referred to the Leptolepidae for *Leptolepis* s.s. may well be the precursor of the true clupeids while *Pholidophorus* is possibly ancestral to the elopine fishes. Until recent times this group have been considered to be teleosts and Frost (1924) referred his otolith species of *Leptolepidarum* from the Upper Kimmeridgian to the Teleostei, remarking 'This earliest form yet described of a teleostean pointed saccular otolith . . .' when discussing the affinity of his species *Otolithus (Leptolepidarum) simplex*. Saint-Seine (1949) placed *Elops* in the Halecostomi and this arrangement was supported by Nybelin (1957) who considered *Elops* to be as much an holostean as *Annia* or *Lepiosteus*. Gosline (1960, p. 356) retained *Elops* in the Clupeiformes, remarking on the controversial structure of

the group, for all have certain characters relating them to the isospondylous fishes to a greater or lesser degree.

The present Systematics follow Saint-Seine in placing the Leptolepidae in the subclass Holostei, Division Halecostomes, the pholidophorids being separated at ordinal level. However, although these elopine otoliths almost certainly derive from *Pholidophorus* and *Leptolepis*, thus placing them among the Halecostomes in the present system, it must be realized that their obvious clupeoid characters prove them to be the parent stock for this group.

A forerunner of the engraulids may also be represented and a new genus, *Archengraulis* is proposed to embrace those otoliths which show some resemblance to those of *Engraulis* Cuvier.

Finally, this suite may include an ancestral form of the salmonoids but evidence is insufficient to be dogmatic on this point.

SYSTEMATIC DESCRIPTIONS

Superclass PISCES

Class ACTINOPTERYGII

Subclass CHONDROSTEI

Order CHONDROSTEIFORMES

Family CHONDROSTEIDAE

Genus GYROSTEUS (Agassiz) Egerton 1858, p. 883

Type species. *Gyrosteus mirabilis* Agassiz.

Gyrosteus subdeltoideus sp. nov.

Text-fig. 1a, b

Holotype. BM P47394. Bradford on Avon.

Paratypes and localities. Bradford on Avon, Leicester University Museum, 22725 (6 specimens).

Dimensions of holotype. Length 3.25 mm. Width 2.48 mm.

Description. A roughly triangular, left sacculith which is truncated dorsally. Dorsal rim short, horizontal, crenulate; posterior rim rounded, slightly crenulate; ventral rim long and rounded; anterior rim long and diagonal. Outer face smooth, nearly flat, with indistinct radial ribs from the dorsal area to the ventral rim. Inner face nearly flat, with a slightly arcuate sulcus opening widely on the anterior rim and narrowly on the posterior rim. It is set somewhat above the mid-line of the otolith. The sulcus consists of a very short, wide ostium, rather triangular in shape, with a long, somewhat concave lower rim with a downward trend. A long, narrower, slightly shallower cauda with parallel sides. Crista superior undivided and recurving at the ostial junction to coalesce with the upper part of the anterior rim. A very slight obtuse lower angle at the junction of ostium and cauda. A shallow depression above the crista superior, accentuating it. A moderate rostrum and excisura present but no antirostrum or colliculi. A rather wide, smooth, semicircular lower area present.

This otolith has a distinct affinity with those of the living *Acipenser* Linnaeus, both in

outline, sulcus characteristics and the features of the outer face, despite the slight amount of erosion from which it has suffered. The only relative in Jurassic times is *Gyrosteus* Agassiz, represented by skeletal remains named *G. mirabilis* Agassiz, which closely resembles the modern *Acipenser* and is recorded from the Upper Lias. It is possible that this fish had an extended range into the higher strata and this otolith is referred to this genus.

Subclass HOLOSTEI
(Division Holosteans)
Order PYCNODONTIFORMES
Family PYCNODONTIDAE
Genus SPHAERONCHUS gen. nov.

Type species. Sphaeronchus dorsetensis sp. nov.

Sacculiths with short, horizontal dorsal rims; rounded posterior rims which are continuous with the rounded ventral rims; oblique anterior rims which are slightly to moderately notched. Outer faces smooth and slightly convex. Convex inner faces with an arcuate sulcus opening widely on the anterior rim and just touching the posterior rim. Sulcus consisting of a somewhat semicircular, obliquely placed, deep, short ostium and a straight or slightly arcuate parallel-sided cauda which just reaches the posterior rim. Moderate rostrum and excisura but no antirostrum or colliculi. Osteological characters unknown.

Sphaeronchus dorsetensis sp. nov.

Text-fig. 2a, b

Holotype. BM P47395. Rodden Hive Point.

Paratypes and localities. Rodden Hive Point. Leicester University Museum 22718 (8 specimens). Bradford on Avon. Leicester University Museum 22727 (47 specimens).

Dimensions of holotype. Length 5.00 mm. Width 4.76 mm.

Description. A somewhat eroded, roughly circular, right sacculith. Dorsal rim short, horizontal, crenulate; posterior rim short, rounded, continuous with the rather deep, regularly rounded ventral rim; anterior rim obtuse and moderately notched. Outer face smooth, slightly convex. Inner face convex with an arcuate sulcus opening widely on the anterior rim and just touching the posterior rim. Sulcus consisting of a short, wide, deep, somewhat semicircular, obliquely placed ostium and a moderately wide, long, arcuate cauda which tapers towards the posterior rim. A rounded, lower right-angle and a slightly rounded upper angle are present at the junction of ostium and cauda. A depression above the crista superior, accentuating it. The sulcus is set a little above the mid-line and there is a wide, smooth, semicircular lower area. A moderate rostrum and excisura present but no antirostrum or collicula.

Pycnodont teeth referred to the genus *Gyronchus* Agassiz, occur in the Bathonian and it may be that these are congeneric with these otoliths.

Sphaeronchus circularis sp. nov.

Text-figs. 3a, b; 4

Holotype. BM P47396 (text-fig. 3a, b). Rodden Hive Point.*Paratypes and localities*. Rodden Hive Point. BM P47397 (text-fig. 4) and Leicester University Museum 22719 (111 specimens).*Dimensions of holotype*. Length 2.71 mm. Width 1.98 mm.

Description. An almost circular right sacculith, pointed anteriorly. Dorsal rim short, nearly horizontal, crenulate; posterior rim short, nearly vertical and continuous with the rather deeply rounded ventral rim; anterior rim oblique. Outer face smooth, convex, with an indistinct central umbo. Inner face slightly convex with a horizontal sulcus set slightly above the mid-line, opening obliquely on the anterior rim and terminating immediately adjacent to the posterior rim. Sulcus consisting of a short, rather deep ostium which is somewhat spatulate, and a narrower, slightly sinuous cauda which tapers to a point posteriorly. Crista superior recurving at the ostial end to form an acute angle and coalescing with the dorsal rim. A depression below the crista inferior accentuating it, while there is an obtuse lower angle at the junction of ostium and cauda. A moderate rostrum and excisura present but no anti-rostrum or collicula. Text-fig. 4 (BM P47397) represents a left sacculith.

This otolith generally resembles that of *Sphaeronchus dorsetensis* sp. nov., but differs in the sinuous cauda and the relatively shallower ventral area.

(Division Halecostomes)

Order PHOLIDIFORMES

Family PHOLIDOPHORIDAE

Genus PHOLIDOPHORUS Agassiz 1832, p. 145

Type Species. *Pholidophorus bechei* Agassiz.*Pholidophorus paradoxicus* sp. nov.

Text-fig. 5a, b

Holotype. BM P47401. Rodden Hive Point.*Paratypes and locality*. Rodden Hive Point. Leicester University Museum 22723 (6 specimens).*Dimensions of holotype*. Length 2.40 mm. Width 1.56 mm.

Description. An ovate, thin right sacculith, pointed anteriorly. Dorsal rim horizontal, coarsely denticulate; posterior rim nearly vertical, crenulate; ventral rim rounded, crenulate; anterior rim oblique, obtuse-angled. Slightly concave outer face with three small tuberculations on the dorsal periphery and radial ribbing traversing the otolith laterally to the ventral rim. Slightly convex inner face with a median sulcus opening obliquely on the anterior rim and terminating adjacent to the postero-ventral corner of the otolith. Sulcus consisting of a moderately deep, somewhat semicircular, obliquely placed ostium and a long, narrower cauda which curves downwards slightly as it approaches the posterior rim. Crista superior undivided and recurving at the ostial end

to coalesce with the dorsal rim. A moderate, obtuse lower angle at the junction of ostium and cauda. Both crista superior and crista inferior slightly accentuated by depressions above and below them respectively. A marked rostrum and moderate excisura present but no antirostrum or collicula.

This otolith is elopine in character and may perhaps be from a precursor of *Megalops* Lacépède, for the species of *Pholidophorus* represented by remains of entire fishes show a distinct resemblance to this genus.

Pholidophorus prae-elops sp. nov.

Text-figs. 6a, b; 7a, b

Holotype. BM P47402 (text-fig. 6a, b). Rodden Hive Point.

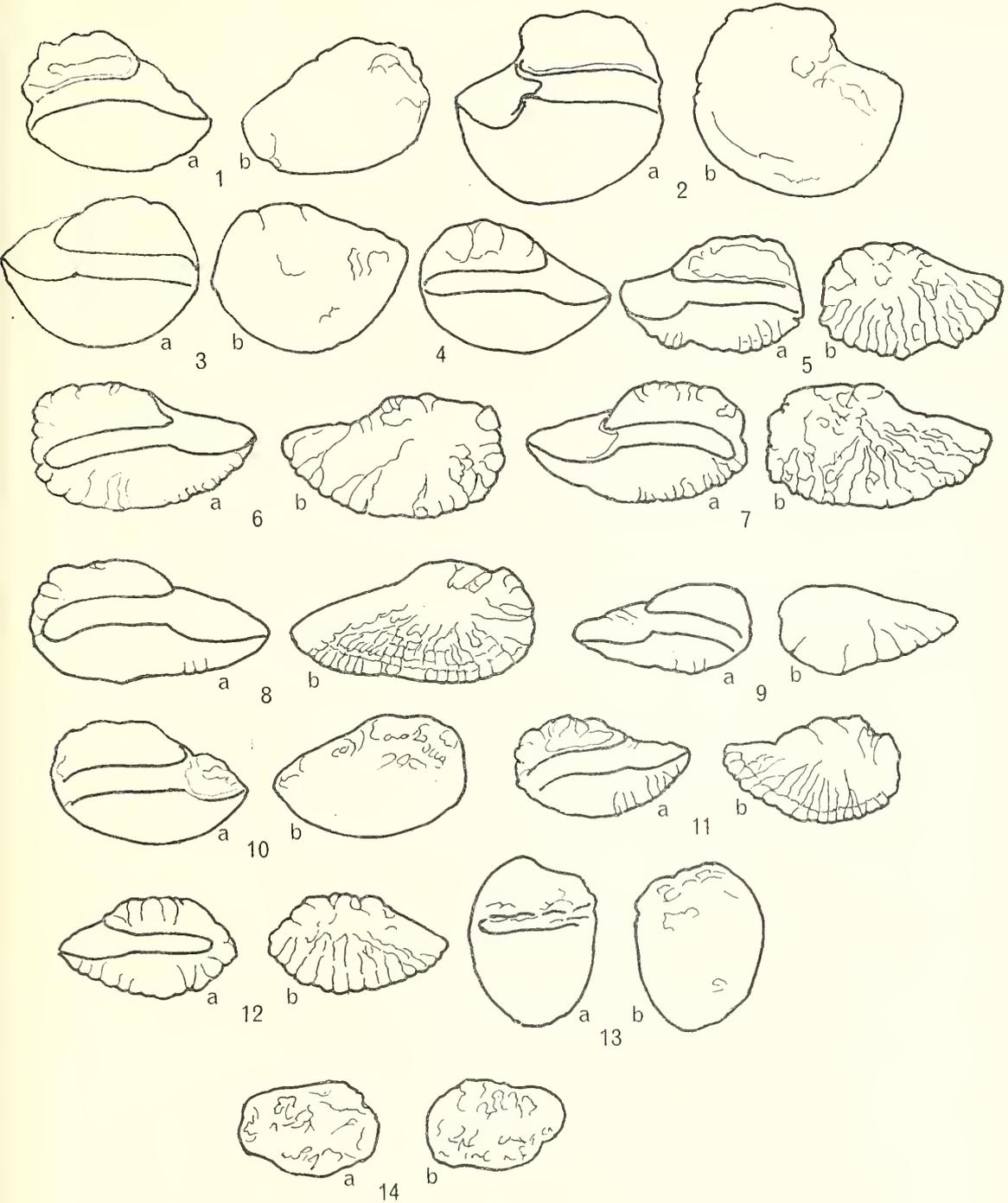
Paratypes and localities. Rodden Hive Point. BM P47403 (text-fig. 7a, b) and Leicester University Museum 22722 (20 specimens). Bradford on Avon. Leicester University Museum, 22726.

Dimensions of holotype. Length 5.01 mm. Width 2.27 mm.

Description. Slightly biconvex left sacculith, truncated posteriorly and pointed anteriorly. Dorsal rim horizontal, faintly crenulate; posterior rim short, vertical, faintly crenulate; ventral rim long, rounded, faintly crenulate; anterior rim oblique with an angulated notch. Outer face ornamented with transverse irregular ridges which radiate from the dorsal periphery to the ventral periphery. Inner face slightly convex with a median sulcus opening obliquely on the anterior rim and extending to the posterior rim. Sulcus consisting of a short, moderately deep, deltoid ostium which has a concave lower rim and a long, rather wide cauda curving slightly downwards near its posterior end which is open. Crista superior undivided and accentuated by a shallow depression above it. An obtuse lower angle present at the junction of ostium and cauda, prominent rostrum and excisura but no antirostrum or collicula.

These otoliths show a similarity to those of existing Elopidae and it seems very likely that they represent the precursors of this family.

TEXT-FIGS. 1-14. All of the figured specimens are contained in the collections of the British Museum (Natural History), Department of Palaeontology, and bear the registration numbers of this Institution. 1a, b. *Gyrosteus subdeltoideus* sp. nov. Holotype P47394. Left sacculith, inner and outer faces. $\times 10$. 2a, b. *Sphaeronchus dorsetensis* sp. nov. Holotype P47395. Right sacculith, inner and outer faces. $\times 8$. 3a, b. *Sphaeronchus circularis* sp. nov. Holotype P47396. Right sacculith, inner and outer faces. $\times 14$. 4. *Sphaeronchus circularis* sp. nov. P47397. Left sacculith, inner face. $\times 14$. 5a, b. *Pholidophorus paradoxicus* sp. nov. Holotype P47401. Right sacculith, inner and outer faces. $\times 15$. 6a, b. *Pholidophorus prae-elops* sp. nov. Holotype P47402. Left sacculith, inner and outer faces. $\times 8$. 7a, b. *Pholidophorus prae-elops* sp. nov. P47403. Right sacculith, inner and outer faces. $\times 10$. 8a, b. *Leptolepis tenuirostris* sp. nov. Holotype P47398. Left sacculith, inner and outer faces. $\times 10$. 9a, b. *Leptolepis tenuirostris* sp. nov. P47399. Right sacculith, inner and outer faces. $\times 10$. 10a, b. *Leptolepis densus* sp. nov. Holotype P47400. Left sacculith, inner and outer faces. $\times 10$. 11a, b. *Leptolepis roddenensis* sp. nov. Holotype P47405. Left sacculith, inner and outer faces. $\times 12$. 12a, b. *Archengranlis productus* sp. nov. Holotype P47404. Right sacculith, inner and outer faces. $\times 14$. 13a, b. *Cleidogonia antiqua* sp. nov. Holotype P47406. Left sacculith, inner and outer faces. $\times 18$. 14a, b. ? Utriculith. sp. indeterminate. P47800. Inner and outer faces. $\times 16$.



TEXT-FIGS. 1-14.

Order LEPTOLEPIDIFORMES
Family LEPTOLEPIDAE
Genus LEPTOLEPIS Agassiz 1832, p. 146

Type species. Leptolepis coryphaenoides (Bronn).

Leptolepis tenuirostris sp. nov.

Text-figs. 8a, b; 9a, b

Holotype. BM P47398 (text-fig. 8a, b). Rodden Hive Point.

Paratypes and locality. Rodden Hive Point BM P47399 (text-fig. 9a, b) and Leicester University Museum 22720 (147 specimens).

Dimensions of holotype. Length 4.60 mm. Width 2.31 mm.

Description. Relatively elongate, thin left sacculith, prominently pointed anteriorly and rounded posteriorly. Dorsal rim short, slightly concave; posterior rim rounded, crenulate; ventral rim long, horizontal, finely denticulate; anterior rim oblique, long and slightly sinuous. Outer face convex with a slight central umbo and radiating ribs on the ventral, dorsal and posterior areas. Indistinct concentric grooves surround the umbo on the ventral area. Inner face slightly convex with a median sulcus opening widely on the anterior rim and terminating very near to the posterior rim. Sulcus consisting of a wide, obliquely placed, short, semicircular ostium of moderate depth and a rather wide, somewhat shallower, long cauda which curves somewhat towards the posterior end. The crista superior recurves sharply to form an acute angle at the junction of ostium and cauda and there is also a moderate lower angle. A depression above the crista superior accentuating it. Marked rostrum and excisura but no antirostrum or collicula.

These otoliths almost certainly represent precursors of the modern clupeoids and their abundance in these beds may, perhaps, indicate that these fishes were gregarious by nature, as in the modern herrings. The outline and characters of the outer face are typically clupeoid while the sulcus is also rather similar although the cauda has not developed the characteristically greater width seen in the Recent forms.

Leptolepis densus sp. nov.

Text-fig. 10a, b

Holotype. BM P47400. Rodden Hive Point.

Paratypes and locality. Bradford on Avon. Leicester University Museum (3 specimens).

Dimensions of holotype. Length 3.63 mm. Width 2.17 mm.

Description. A rather thick, left sacculith. Dorsal rim horizontal, slightly undulant by virtue of two feeble lobes; nearly vertical, slightly rounded posterior rim; ventral rim rounded; anterior rim oblique and slightly undulant. Outer face smooth and slightly convex. Inner face smooth, almost flat with a median sulcus opening widely on the anterior rim and just touching the posterior rim. Sulcus consisting of a rather wide, short, deltoid ostium and a long, rather wide cauda which is open at its posterior

extremity. Crista superior recurving at its anterior end, forming an acute angle and coalescing with the anterior rim. A prominent lower angle present at junction of ostium and cauda. Crista superior accentuated by a shallow depression above it. A rostrum and excisura present but no antirostrum or collicula.

This otolith, although included here among the *Leptolepidae*, differs in being much thicker than those of the other species and its outline is more rounded. It shows some affinity with otoliths of the living *Gonorhynchus* Gronow, and also, in some degree, to the salmonoid fishes, in the characters of the sulcus.

Leptolepis roddenensis sp. nov.

Text-fig. 11a, b

Holotype. BM P47405. Rodden Hive Point.

Paratypes and locality. Rodden Hive Point. Leicester University Museum 22724 (8 specimens).

Dimensions of holotype. Length 2.68 mm. Width 1.56 mm.

Description. A thin, rather elliptical left sacculith which is pointed anteriorly. Dorsal rim irregularly denticulate, horizontal; posterior rim vertical, slightly crenulate; ventral rim rounded, finely denticulate; anterior rim oblique, slightly obtuse-angled. Outer face nearly flat with a row of indistinct, small tuberculations on the dorsal periphery and faint radial ribbing to the ventral rim. Slightly convex inner face with a median sulcus opening almost horizontally on the anterior rim and terminating adjacent to the postero-dorsal corner of the otolith. Sulcus consisting of a rather deltoid ostium with a concave lower rim and a long, slightly narrower, moderately deep cauda which is horizontal throughout its length but curving slightly downwards immediately before its posterior end which is open. Crista superior sinuous, undivided and accentuated by a depression above it. A slight, rounded, obtuse lower angle at the junction of ostium and cauda. Prominent rostrum and moderate excisura but no antirostrum or collicula. Smooth, semicircular lower area which is keeled at the ventral periphery.

This otolith differs from other described species of *Leptolepis* in its more horizontal anterior rim and straight, open-ended cauda.

Genus *ARCHENGRAULIS* nov. gen.

Elliptical sacculiths, pointed anteriorly and bluntly pointed posteriorly; irregularly crenulated dorsal, posterior and, ventral rims. Slightly convex outer face with irregular dorsal umbo and radial ribs to the ventral periphery, the posterior ones being tuberculate. Slightly convex inner face with a median sulcus opening obliquely on the anterior rim and terminating near the postero-ventral corner. Sulcus consisting of a short, rather deltoid, shallow, wide ostium and a long, rather wide, straight cauda. The crista superior is undivided, accentuated by a depression above it and, at its ostial end, recurving to coalesce with the dorsal rim. Marked rostrum and excisura. Osteological characters unknown.

Type species. *Archengraulis productus* sp. nov.

Archengraulis productus sp. nov.

Text-fig. 12a, b

Holotype. BM P47404. Rodden Hive Point.*Paratypes and locality*. Rodden Hive Point. Leicester University Museum 22721 (2 specimens).*Dimensions of holotype*. Length 2.48 mm. Width 1.38 mm.

Description. An elliptical right sacculith with the features described for the genotype. Dorsal rim slightly rounded and crenulate; posterior rim oblique, short, crenulate; ventral rim long, rounded, finely denticulate; anterior rim oblique, slightly concave. There is a very slight, rounded, obtuse lower angle at the junction of ostium and cauda. No antirostrum or collicula.

The produced posterior end of this otolith and its straight cauda distinguish it from other otoliths of the Leptolepidae and there is a similarity to otoliths of modern engraulids in several of its features.

Subclass TELEOSTEI

Superorder ACANTHOPTERYGII

Order BERYCIFORMES

Suborder ? BERYCOIDEI

Genus CLEIDOGONIA gen. nov.

Type species. *Cleidogonia antiqua* sp. nov.

Sacculiths very short, high, and elliptical in outline. Sulcus a little above the mid-line consisting of a relatively wide ostium and an horizontal cauda. The features suggest affinities with berycoid otoliths and this genus is tentatively referred to the Berycoidei. Osteological characters of genus unknown.

Cleidogonia antiqua sp. nov.

Text-fig. 13a, b

Holotype. BM P47406. Bradford on Avon.*Dimensions of holotype*. Length 1.30 mm. Width 1.71 mm.

Description. A rather eroded, ovate left sacculith. Dorsal rim somewhat broken away but probably short, rounded and continuous with the short, rounded posterior rim; ventral rim deeply rounded; anterior rim straight, vertical. Outer face smooth, slightly convex. Inner face flat, with a horizontal sulcus set a little above the mid-line, opening narrowly on the anterior rim and terminating near the postero-ventral rim. Sulcus rather indistinct but appears to consist of a short, relatively wide ostium and a narrow, horizontal cauda. A slight rounded lower angle and a moderate rounded upper angle are present at the junction of ostium and cauda while the crista superior is accentuated by a shallow depression above it. No rostrum, excisura or collicula, but there appears to be a slight antirostrum. A deep, smooth lower area is present.

This otolith has the general shape of those seen in the Monocentridae, especially that seen in *Cleidopus* De Vis, but there is also a possible affinity with *Antigonia* Lowe and

perhaps this may represent an intermediate form between these two genera. Certainly the otoliths of *Antigonia* exhibit marked berycoid characteristics and it is probable that this fish should be included within the order Berycoidei. No skeletal remains identified as berycoids have been recorded from Jurassic strata.

? Utriculith

Text-fig. 14a, b

Material. BM P48700. Bradford on Avon.

Dimensions. Length 2.18 mm. Width 1.49 mm.

An indeterminate utriculith which is rather oval and biconvex. The absence of distinguishing features makes its identification impossible.

CONCLUSIONS

The very numerous otoliths in these strata indicate a much larger fish population than the skeletal remains suggest. It is probable that littoral conditions prevailed but of moderate depth in view of the colonization of many of the specimens by serpulids and bryozoans.

Fishes and their otoliths derived from the underlying Liassic and superimposed Oxford and Kimmeridge Clays appear to be generically similar but the Bathonian specimens are specifically distinct and neither do they conform to the numerous species described by Neth and Weiler (1953, pp. 114–21), Martin and Weiler (1954, pp. 119–92; 1957, pp. 211–49) and Schröder (1956, pp. 128–53) from partly synchronous German strata. This may result from ecological differences in the various areas concerned when these beds were deposited.

The otoliths of the Jurassic fishes suggest that they are intermediary between the ganoids of the Trias and the teleosts of the Tertiary. Typically teleost features are seen in them and at least three potential groups ancestral to the modern true fishes can be demonstrated despite the absence of supporting evidence from Cretaceous strata. This latter fact may result from two causes, the Wealden fishes being ecologically different in that they were brackish or fluviatile forms and the absence of otoliths in the Chalk through their chemical composition. Otoliths do occur in the Gault but appear to be uncommon and those seen by the author were all referable to the albulid-pterothrissid lineage, a group not yet recognized in the Mesozoic. However, this may again result from an unsuitable environment during the deposition of the British Jurassic strata rather than that they had not evolved at this time.

Certainly the conflicting interpretations of the available osteological materials indicate the need for further data to resolve these problems and the otoliths offer suitable confirmatory evidence. Undoubtedly these support the views of Gosline (1960), in his definition of the limits of the Clupeiformes.

REFERENCES

- AGASSIZ, L. 1832. Untersuchungen über die fossilen Fische der Lias-Formation. *Jb. Miner., Heidelberg*, 3, 139–49.
 ——— 1833–44. *Recherches sur les poissons fossiles*. Neuchâtel.
 ARKELL, W. J. 1940. Fossils from the Fuller's Earth of the Weymouth anticline. *Geol. Mag.* 77, 42–49, 1 pl.

- ARKELL, W. J. 1947. The geology of the country around Weymouth, Swanage, Corfe and Lulworth. *Mem. geol. Surv. U.K.* xii+386 pp. 19 pl.
- 1959. *A Monograph of the English Bathonian Anononities*. Palaeontogr. Soc. [Monogr.], **8**, i-viii+209-64, pl. 30-33.
- CONGRÈS GÉOLOGIQUE INTERNATIONAL. 1964. Colloque du Jurassique à Luxembourg 1962. 948 pp. Ed. P. L. Maubeuge.
- COX, L. R. 1941. Easter Field Meeting, 1940. *Proc. Geol. Ass.* **52**, 16-35, 3 pl.
- CUNNINGTON, W. 1860. On the Bradford Clay and its fossils. *Wilts. archaeol. nat. Hist. Mag.* **6**, 1-10.
- EGERTON, P. DE M. G. 1858. On *Chondrosteus*, an extinct genus of the Sturionidae, found in the Lias Formation at Lyme Regis. *Philos. Trans. R. Soc.* **148**, 871-86, pl. 67-70.
- FROST, G. A. 1924. Otoliths of fishes from the Upper Kimmeridgian of Buckinghamshire and Wiltshire. *Aun. Mag. nat. Hist.*, (9), **14**, 139-43. 1 pl.
- 1926. Otoliths of fishes from the Jurassic of Buckinghamshire and Dorset. *Ibid.* (9), **18**, 81-5, pl. 4.
- GOSLINE, W. A. 1960. Contributions toward a classification of modern isospondylous fishes. *Bull. Brit. Mus. (Nat. Hist.)*, Lond. **6**, 325-65. 15 text-figs.
- HOUSE, M. R. 1957. The Fuller's Earth outcrop in South Dorset. *Proc. Dorset nat. Hist. Archaeol. Soc.* **78**, 64-70.
- JORDAN, D. S. 1963. *The Genera of Fishes and a Classification of Fishes*. Stanford University Press, Stanford, California. (Reprint.) i-xvi+1-800.
- MARTIN, G. P. R. and WEILER, W. 1954. Fisch-otolithen aus dem deutschen Mesozoikum (Dogger bis Wealden). *Senckenberg. leth.* **35**, 119-92.
- 1957. Das Aldorfer Otolithen-‘Pflaster’ und seine Fauna. *Senckenberg. leth.* **38**, 211-49. 3 pl.
- MIUR-WOOD, H. M. 1936. *A Monograph of the Brachiopods of the British Great Oolite Series*. Part 1. *The Brachiopods of the Fuller's Earth*. Palaeontogr. Soc. [Monogr.], pp. 1-144, 4 pl.
- NETH, U. and WEILER, W. 1953. Untersuchungen an Fisch-otolithen aus dem deutschen Dogger. *Paläont. Z.* **27**, 113-21, 1 pl.
- NYBELIN, O. 1957. Les canaux sensoriels du museau chez *Elops saurus* (L.). Notice préliminaire. *Ark. Zool.* **10**, 453-8, 3 figs.
- PALAEONTOGRAPHICAL SOCIETY. 1954. *Directory of British Fossiliferous Localities*. London. 268 pp.
- PERIAM, C. E. 1956. The Jurassic Rocks of Mid-Wiltshire. Unpublished Ph.D. Thesis, University of Reading. 1-264 pp.
- POKORNÝ, V. 1965. *Principles of Zoological Micropalaeontology*. 2 vols. 1-465 pp. Pergamon Press.
- QUENSTEDT, F. A. VON. 1858. *Der Jura*. Tübingen. vi+842, 103 pl.
- SAINT-SEINE, P. DE. 1949. Les poissons des calcaires lithographiques de Cerin (Ain). *Nouv. Arch. Mus. Hist. nat. Lyon*, **2**, 1-357, 26 pl.
- SCHRÖDER, G. 1956. Otolithen aus dem Lias und Dogger des Frankischen Jura. *Geol. Blätter No.-Bayern*, **6**, 128-53, 4 Abb., 3 taf. Erlangen.
- TINTANT, H. 1963. Les Kosmocératidés du Callovien inférieur et moyen d'Europe occidentale. *Publ. Univ. Dijon*, **29**, 1-500, 58 pl.
- TORRENS, H. S. 1965. Revised Zonal Scheme for the Bathonian Stage of Europe. *Reports of the VIIth Carpatho-Balkan Geol. Cong.*, Sofia. Pt. 2, **1**, 47-55.
- WAGNER, J. A. 1851. Beiträge zur Kenntniss der in dem lithographischen Schieferen abgelagerten urweltlichen Fische. *Abh. Akad. Wiss. München*, **6**, 1-80.

F. C. STINTON
51 Craigmoor Avenue,
Stonden Park
Bournemouth
Hampshire
H. C. TORRENS
Department of Geology
The University
Leicester

THE FIRST NON-MARINE LOWER CRETACEOUS OSTRACODS FROM GHANA, WEST AFRICA

by K. KRÖMMELBEIN

ABSTRACT. The first ostracods from the non-marine Lower Cretaceous ('West African Wealden') of Ghana are described and figured. Three species belong to the genus *Cypridea*, two are referred to '*Metacypris*', and one species might belong to *Cyclocypris* (?). All species appear to be new; they are left under open nomenclature because of scarcity of material. The ostracod assemblage shows closer affinities to the European Wealden than to the 'West African Wealden' in other occurrences.

A NUMBER of sedimentary basins with non-marine Lower Cretaceous formations ('West African Wealden') are known along the West African coast from Nigeria in the north to Angola in the south. Recently, evidence of an occurrence outside that region came to light when ostracods of Wealden appearance and age were found in Ghana in the Kobnaswaso-1 borehole put down by the Gulf Oil Corporation. As far as the writer is aware, this is the first record of non-marine Cretaceous in Ghana. There is no known surface outcrop of such formations.

The small fauna contains species of the genera *Cypridea*, '*Metacypris*', and a species whose affinities are not quite clear (*Cyclocypris*?). At present, only a few specimens of each species are available for description, and it is considered that they do not provide a sufficiently good basis for detailed description and for comparisons. Because of this scarcity of material, and also because of the poor state of preservation in most cases, description in open nomenclature is preferred. However, the uniqueness of the fauna, the first of its kind from Ghana, justifies publication.

Stratigraphic position. The ostracod-bearing non-marine strata in the Kobnaswaso-1 well-section are overlain by marine Albian at a depth of around 1,200 m.; they are therefore of Lower Cretaceous, pre-Albian age. This fits well with the general stratigraphic situation of the 'West African Wealden' of Gabon and Angola.

The ostracod fauna seems to consist of two separate faunules occurring at different depths. The lower (older) Faunule 1, from around 3,000-m. depth, includes the species:

- Cypridea* sp. A
- Cypridea* sp. B
- Faunule 1 *Cypridea* sp. C
- '*Metacypris*' sp. A
- Cyclocypris?* sp. A
- and some further species which are too poorly preserved to deserve description

The higher (younger) Faunule 2, from around 2,100-m. depth, includes the species:

- '*Metacypris*' sp. B
- '*Metacypris*' sp. (different from B, fragments only, not described)
- Faunule 2 '*Metacypris*' sp. (different from all other species, preservation too poor for description)

SYSTEMATIC DESCRIPTIONS

Order OSTRACODA Latreille 1802
 Family CYPRIDIDAE Baird 1845
 Subfamily CYPRIDEINAE Martin 1940
 Genus CYPRIDEA Bosquet 1852

Cypridea sp. A

Plate 45, fig. 1a-c

Description. Carapace in lateral view rather elongate, in dorsal view with both ends well rounded. Greatest height at about one-third to one-quarter of length. Right valve larger than left valve. Beak relatively small, not very pointed, strongly curved. Each valve with two very shallow depressions, one in an antero-dorsal position, another in a postero-median/mid-posterior/postero-dorsal position. Surface of shell rather smooth, not visibly pitted or provided with spines.

Affinities. *Cypridea* sp. A seems very like an undescribed species found in the English Wealden by Dr. F. W. Anderson (*in litt.*). There is also some similarity to *Cypridea fracta* Ljubimova 1956, from the Upper Cretaceous of Mongolia, but the latter seems to be much larger than *Cypridea* sp. A.

Occurrence. Borehole Kobnaswaso-1, Ghana. Species belongs to Faunule 1.

Dimensions of figured specimen, SMF Xe 5482: Length 0.85 mm., height 0.51 mm., breadth 0.39 mm.

Cypridea sp. B

Plate 45, fig. 2a-c

Description. Carapace in lateral view elongate, dorsal angles rounded but fairly distinct; carapace in dorsal view with both ends rounded, anterior end tapering. Greatest height of carapace at about one-quarter of length. Beak well rounded, strongly curved. Right valve larger than left valve. Surface of shell coarsely pitted. Blunt spines on both valves, apparently more strongly developed on the smaller left valve. Two of the spines are more prominent than the others, one in an antero-dorsal position, another in a dorso-median position. Some minor spines along the lower part of anterior margin of the valves, as well as immediately behind the beak-furrow, within the postero-ventral region, and especially in the postero-dorsal region immediately above and slightly behind the posterior strong spine.

EXPLANATION OF PLATE 45

All specimens figured are from borehole Kobnaswaso-1, Ghana, West Africa; non-marine Lower Cretaceous, older than Albian. Specimens deposited in the Senckenberg-Museum, Frankfurt am Main, Germany: (SMF), numbers refer to catalogue Xe. Magnifications are all about $\times 68$.

Fig. 1a-c. *Cypridea* sp. A. Carapace, SMF Xe 5482. a, right side; b, left side; c dorsal view.

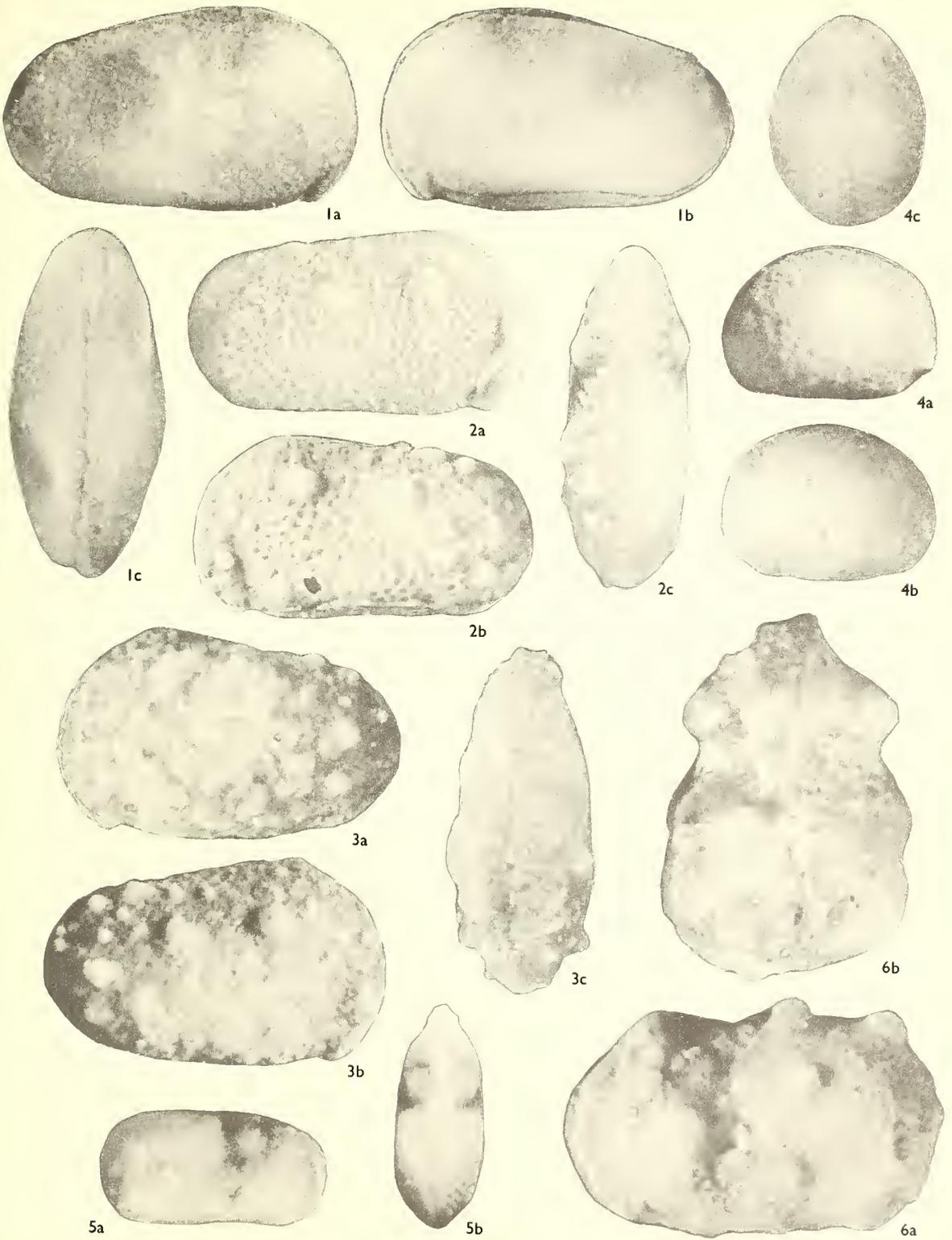
Fig. 2a-c. *Cypridea* sp. B. Carapace, SMF Xe 5483. a, right side; b, left side; c dorsal view.

Fig. 3a-c. *Cypridea* sp. C. Carapace, SMF Xe 5484. a, left side; b, right side; c, dorsal view.

Fig. 4a-c. *Cyclocypris?* sp. A. Carapace, SMF Xe 5485. a, left side; b, right side; c, dorsal view.

Fig. 5a, b. '*Metacypris*' sp. A. Carapace, SMF Xe 5486. a, right side; b, dorsal view.

Fig. 6a, b. '*Metacypris*' sp. B. Carapace, SMF Xe 5487. a, left side; b, dorsal view.



KRÖMMELBEIN, Non-marine Lower Cretaceous ostracods from Ghana

Affinities. According to Dr. F. W. Anderson (*in litt.*), *Cypridea* sp. B (and also C) compare closely with some of the subspecies of *C. clavata* (Anderson) found in the English Weald Clay. *Cypridea* sp. B shows some features of the species *Cypridea (Morinina) maringaensis* (Grekoff 1957), from the Wealden of the Congo basin, but the two species are not identical in all respects.

Occurrence. Borehole Kobnaswaso-1, Ghana. Species belongs to Faunule 1.

Dimensions of figured specimen, SMF Xe 5483: Length 0.81 mm., height 0.46 mm., breadth 0.30 mm.

Cypridea sp. C

Plate 45, fig. 3a-c

Description. In general outline somewhat similar to *Cypridea* sp. B. Anterior dorsal angle however at about one-quarter to one-third length of carapace, triangular. Dorsum rather steeply inclined. Right valve larger than left. Surface of shell coarsely pitted, and covered with numerous, more or less strongly developed spines, their arrangement apparently similar to *Cypridea* sp. B.

Remarks. The surface of the shell could not be cleaned properly. Sediment particles were still cemented to the shell substance and obscured certain ornamental features.

Affinities. The spinose surface ornamentation seems to follow the same general pattern as in *Cypridea* sp. B, from which sp. C differs in the more pronounced development and also the higher position of the anterior dorsal angle, and in the more spiny surface. See also under *Cypridea* sp. B.

Occurrence. Borehole Kobnaswaso-1, Ghana. The species belongs to Faunule 1.

Dimensions of figured specimen, SMF Xe 5484: Length 0.82 mm., height 0.46 mm.

Subfamily CYCLOCYPRIDINAE Kaufmann 1900

Genus CYCLOCYPRIS Brady and Norman 1889

Cyclocypris? sp. A

Plate 45, fig. 4a-c

Description. Carapace extremely inflated, egg-shaped in lateral and in dorsal view. Dorsum strongly convex. Greatest height at about one-half of length of carapace. Right valve slightly larger than left. Surface of shell smooth.

Affinities. The species is referred very doubtfully to *Cyclocypris*, only because of the shape of carapace and its small size. No internal details are known, and its resemblance to species of *Cyclocypris* might be completely superficial. The species 'Ostracode D 65', from the 'Wealden' of the Congo basin, figured by Grekoff 1960, shows some similarity.

Occurrence. Borehole Kobnaswaso-1, Ghana. Species belongs to Faunule 1.

Dimensions of figured specimen, SMF Xe 5485: Length 0.52 mm., height 0.44 mm., breadth 0.45 mm.

Subfamily LIMNOCYTHERINAE Sars 1925
Genus METACYPRIS Brady and Robertson 1870

'*Metacypris*' sp. A

Plate 45, fig. 5a-b

Description. Carapace in lateral view elongate, both ends well rounded, in dorsal view posterior end rounded but not blunt, anterior end tapering. Two sulci are developed: median sulcus rather narrow, not very deep, reaching down to three-quarters of carapace height; anterior sulcus small, shallow, length about one-third of carapace height. Between the two sulci a knoblike, rather circular lobe. Surface of shell densely pitted or reticulate, apparently no other ornamentation.

Affinities. '*Metacypris*' sp. A seems to be different from all remaining species of '*Metacypris*' (and similar genera) so far described.

Remarks. The species described here under '*Metacypris*' probably belong to *Theriosynoecum* Branson 1936. There is no information on internal structures (especially the hinge), however, and so it is very difficult to make reference to any particular one of the superficially similar genera in the *Metacypris*-*Gomphocythere*-*Theriosynoecum*-*Bisulco-cypris* group. It therefore seems best to leave these species under '*Metacypris*', as has been done in previous cases (Krömmelbein 1965).

Occurrence. Borehole Kobnaswaso-1, Ghana. Species belongs to Faunule 1.

Dimensions of figured specimen, SMF Xe 5486: Length 0.55 mm., breadth 0.22 mm.

'*Metacypris*' sp. B

Plate 45, fig. 6a-b

Description. Carapace in lateral view more or less rectangular, both ends broadly rounded; in dorsal view carapace with blunt posterior end, anterior end rather pointed. Median sulcus relatively deep and broad, anterior sulcus short and rather shallow. Surface of shell pitted and bearing blunt nodes forming a distinct pattern of five nodes on the posterior part of valves. The lobe between the sulci bears nodes also, of which the strongest is situated in a low antero-median position. Some weaker nodes on the shell in front of the anterior sulcus.

Affinities. The large, broad carapace shows a pattern of nodes similar to the European Wealden species *Theriosynoecum fittoni* (Mantell 1844); for comparison see Pinto and Sanguinetti 1962 (pl. 11, figs. 4, 5), and Sohn and Anderson 1964. The poor preservation of the material available for study unfortunately does not allow clarification of the question of the possible specific identity of the two species under consideration. This question is of some importance in tracing the palaeogeographic relationship between the West African and the European Wealden.

Occurrence. Borehole Kobnaswaso-1, Ghana. The species belongs to Faunule 2, together with some other species of '*Metacypris*', which are represented in the samples only by poorly preserved fragments and do not deserve description.

Dimensions of figured specimen, SMF Xe 5487: Length 0.90 mm.

CONCLUSIONS

The few ostracod species from the 'West African Wealden' of Ghana show a relatively poor preservation. They offer, therefore, only a slight basis for fully systematic description. However, it can be said that on the whole the species encountered show no close affinities to those described from other occurrences of the 'West African Wealden' as could have been expected. Surprisingly enough, the Ghana assemblage is strikingly similar to that of the English Weald Clay of Barremian age. This is especially true for the *Cypridea* species and for *Theriosynoecum* sp. A.

It is hoped that further material from Ghana will help to clarify these most interesting palaeogeographic relations between two distant regions.

Acknowledgements. I would like to express my gratitude to the Gulf Oil Corporation for granting permission to publish this paper; Dr. H. H. Renz (Exploration representative, Gulf Oil Corporation, Corseaux, Switzerland), who made available the fauna, and provided all necessary data; Dr. F. W. Anderson (Institute of Geological Sciences, London), who compared the Ghana species with those of the English Wealden, and who drew my attention to the close similarities between the two faunas; and Dr. S. C. Matthews (University of Bristol), who revised the English manuscript.

The specimens figured are deposited in the collections of the Senckenberg-Museum, Frankfurt/M., Germany.

REFERENCES

- GREKOFF, N. 1957. Ostracodes du Bassin du Congo. I. Jurassique supérieur et Crétacé inférieur du nord du bassin. *Annls Mus. r. Congo belge, Sér 8vo, Sci. géol.* **19**, 97 pp., 6 pl.
 — 1960. Ibid. II. Crétacé. Ibid. **35**, 70 pp., 10 pl.
 KRÖMMELBEIN, K. 1965a. Neue, für Vergleiche mit West-Afrika wichtige Ostracoden-Arten der brasilianischen Bahia-Serie (Ober-Jura?/Unter-Kreide in Wealden-Fazies). *Senckenberg. leth.* **46a**, 177–213, 5 pl.
 — 1965b. Ostracoden aus der nicht-marinen Unter-Kreide ('Westafrikanischer Wealden') des Congo-Küstenbeckens. *Meyniana*, **15**, 59–74, 4 pl.
 PINTO, J. D. and SANGUINETTI, Y. T. 1962. A complete revision of the genera *Bisulcoocypris* and *Theriosynoecum* (Ostracoda) with the world geographical and stratigraphical distribution (including *Metacypris*, *Elpidium*, *Gomphocythere*, and *Cytheridella*). *Publções esp. Esc. Geol., Pôrto Alegre*, **4**, 1–165, 17 pl.
 SOHN, I. G. and ANDERSON, F. W. 1964. The ontogeny of *Theriosynoecum fittoni* (Mantell). *Palaeontology*, **7**, 72–84.

KARL KRÖMMELBEIN
 Geologisch-Paläontologisches Institut
 und Museum der Universität Kiel
 Olshausenstrasse 40/60
 23 Kiel
 Germany

Typescript received 10 August 1966

A GONIATITE FAUNA FROM THE VISÉAN/NAMURIAN BOUNDARY

by KLAUS FIGGE

ABSTRACT. A section spanning the Viséan/Namurian boundary is described from the eastern part of the Rheinisches Schiefergebirge, Germany. The goniatites, mostly belonging to the genus *Eumorphoceras*, have enabled the boundary between Upper and Lower Carboniferous strata to be positioned within 50 cm.

IN 1960 the stratigraphical subcommission on Carboniferous stratigraphy of the International Geological Congress (Part 28, pp. 284–90) accepted the following resolution: ‘7. The Subcommission proposes, that . . . the strata containing the earliest occurrence of *Cravenoceras leion* Bisat be taken for the present as the base of the Namurian. . . .’ This resolution ended nearly thirty years of controversy and the compulsory biostratigraphical scheme is now as follows:

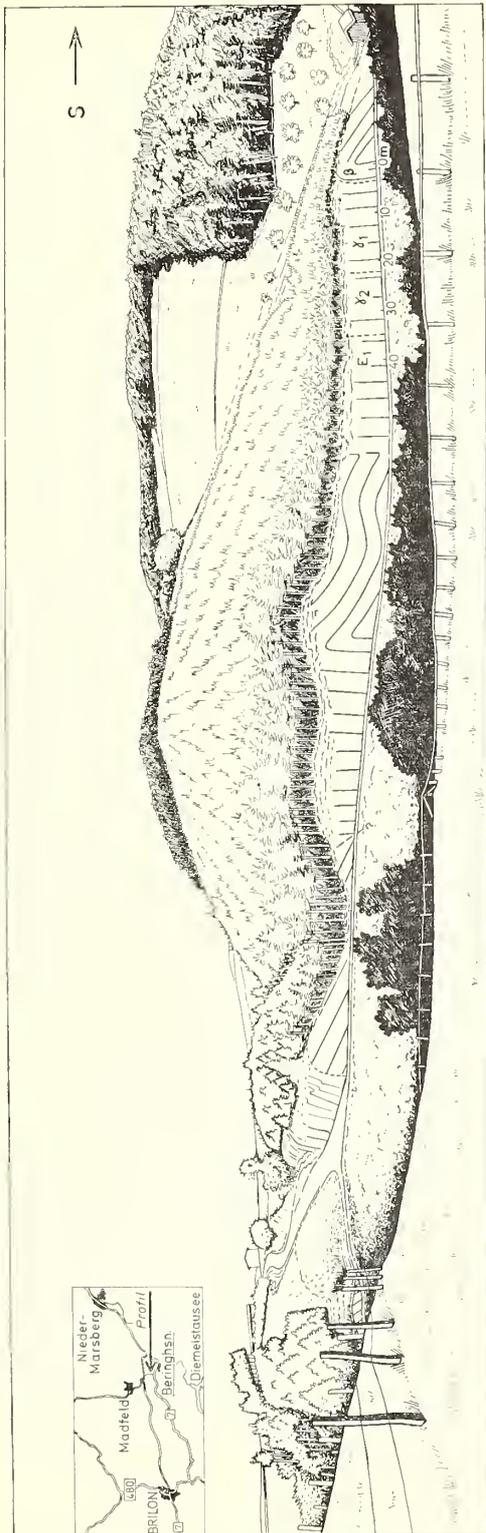
Zone of the <i>Eumorphoceras pseudobilingue</i> <i>Cravenoceras leion</i>	E_1
Zone of the <i>Goniatites schaelkensis</i>	$Go\gamma_1^2$
Zone of the <i>Goniatites graunosus</i>	

Since a section with a complete and uninterrupted succession of these strata is very rare in Germany, a description of one which allows the boundary between the Viséan and the Namurian to be placed within a range of 50 cm. seems to be justified. Furthermore, it can be expected that important parts of the exposure may be covered with refuse within a short time.

STRATIGRAPHY

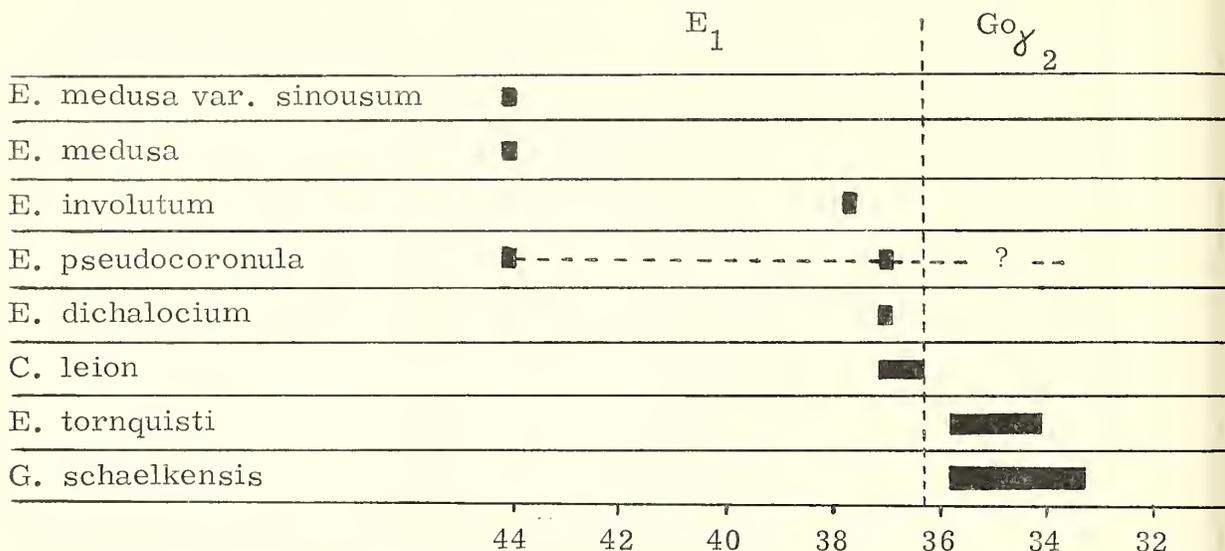
Situation of the section. Some hundred metres west of the village of Beringhausen (sheet 4518, Madfeld, 1:25 000 map of Germany) a small road turns off the ‘Bundesstrasse 7’ to the north in the direction of the village of Madfeld. About 150 m. north of the turning the road cuts across Carboniferous strata which yielded the fauna here described (point R 34 82 200, H 56 97 670, sheet 4518, Madfeld) (fig. 1).

The section begins in the core of an anticline overturned towards the north, stratigraphically belonging to the upper Go_β zone. To the north a disturbed syncline abuts the anticline. Its northern flank—dipping 45° SE.—is exposed about 250 m. further north in a refuse pit at the point R 34 82 140, H 56 97 800. It is mainly from here that the well-preserved fauna has been obtained. Lithologically the rocks are shales with a rather high calcareous component in the basal parts, sometimes even grading into true limestone. In the upper part, however, an increasing arenaceous component passes up into ‘Streifenschiefer’, that is, rocks with a more or less regular alternation of shales and thin beds of greywacke. These greywackes are the first indications of the deposit of the coarse-grained clastics of the lower ‘Flözleeres’ beginning in this area somewhat later in the Namurian (Wachendorf 1965, p. 712).



TEXT-FIG. 1. Section of the Carboniferous strata west of Beringhausen (Eastern Rhenisches Schiefergebirge).

Biostratigraphical succession. The lowermost faunal band containing *Goniatites striatus falcatis* (Roemer) has been found near the refuse pit of Beringhausen. The higher sub-zones of the Go_{β} zone could not be proved, but only little attention was paid to them since they are of less value for the outstanding problem. In regard to the Go_{β}/Go_{γ} boundary the statement of Ruprecht (1936, p. 241) and Hermann Schmidt (1942, p. 54 and pl. 1, fig. 4) was confirmed. Two alum shale beds, the so-called 'Actinopteria beds', containing abundant specimens of the lamellibranch *Pteronites lepidus* Goldfuss represent the characteristic key horizon of the lower $Go_{\gamma 1}$.



TEXT-FIG. 2. Goniatile fauna of the Viséan/Namurian boundary from exposures in the road-cutting west of Beringhausen at the distances shown (see text-fig. 1).

The name 'Actinopteria beds' originates from a former denomination of the lamellibranch *Actinopteria persulcata* McCoy and is still used in Germany as a definite stratigraphical term of long standing.

In the lower part of the $Go_{\gamma 1}$, *Neoglyphioceras subcirculare* is abundant. It is gradually replaced by *Goniatites granosus* without any sharp boundary between them. Their vertical interfingering can be well observed in other areas, too (Figge 1964, p. 776).

Unfortunately the boundary between the $Go_{\gamma 1}$ and $Go_{\gamma 2}$ subzones is not exposed. There is a gap of about 7 m. between the uppermost *Goniatites granosus* band and the lowermost *Goniatites schaelkensis* band. The index fossil of the $Go_{\gamma 2}$, *Goniatites schaelkensis*, is associated with *Eumorphoceras tornquisti* and a questionable *Eumorphoceras pseudocoronula*.

The base of the Namurian is marked by the first occurrence of *Cravenoceras leion*, its lowermost occurrence being 50 cm. above the highest *G. schaelkensis* bed. 75 cm. above the earliest *Cravenoceras leion*, *E. pseudocoronula* and *E. dichalocium* have been found; the latter being apparently restricted to this single horizon at the base of the Namurian. Its great similarity to *E. tornquisti* and its stratigraphical position indicate its evolution from *E. tornquisti*, probably as a link to *E. pseudocoronula*.

This fauna is overlain by beds containing *Peytonoceras? involutum* and further above by the *Eumorphioceras medusa* forms described by Yates in 1961. The latter were proved for the first time in Germany, obviously in the same stratigraphical position as in Ireland (Yates 1962, table 1). In spite of an intensive search not a single specimen of *E. pseudo-bilingue* could be found in the overlying arenaceous 'Streifenschiefer'.

Bisat (1950, p. 12) doubting the independence of *G. schaelkensis* supposes that it might be a form of *C. leion* or *Sudeticeras* or *Lyrogoniatites tonksi*. The species described here as *Goniatites schaelkensis*, however, differs distinctly in its form and stratigraphical position from the other species, so that its independence cannot be doubted.

SYSTEMATIC DESCRIPTIONS

All specimens are preserved as shale impressions. Many of them are tectonically distorted parallel to the B-axis. Proportional numbers given in the following resulted from measuring at an angle of 45° between the longest and the shortest axis of the fossil. In this direction any mistake originated by distortion can be neglected.

The fossils described are housed under the registration numbers mentioned in the Museum of the Department of Geology of the University of Göttingen.

Goniatites schaelkensis (Brüning)

Plate 47, figs. 5, 6

1923 *Paraglyphioceras schaelkense* Brüning, p. 29, figs. 8e, 9e.

Material. Seven specimens, partly fragmentarily preserved (nos. 573:1 to 7).

Diagnosis. Rather involute *Goniatites* with simply curved growth-lines being bent backwards completely. Spiral striation is indicated by a crenulation of the growth-lines.

Description. The conch seems to be rather broad. The ratio of the diameter to the width of the umbilicus is on an average 6:1, in the largest specimen it amounts to 7:1. The umbilical wall is steep, the umbilical edge moderately rounded.

Near the umbilicus the growth-lines are directed forward. But very soon they turn back running into a smooth, backwardly directed bow across the flanks and the venter. In several specimens a periodical thickening of the shell has been observed, mainly on the dorsal half of the flanks. There are between the thickenings about five growth-lines. At first glance only these thickenings can be seen, the very fine growth-lines are usually not so distinct.

Microscopically a crenulation of the growth-lines indicating a spiral striation can be seen. This crenulation, however, is absent in *Cravenoceras leion*. Following Brüning (1923, p. 29) *G. schaelkensis* can be easily recognized by this crenulation and its convex growth-lines.

Discussion. Bisat (1950, p. 12) suspects that different species are grouped together under the term *G. schaelkensis*, viz. a form of *Sudeticeras*, *Cravenoceras leion*, and *Lyrogoniatites tonksi*. This concept, however, does not apply to my material or that of the Museum of the Department of Geology of the University of Göttingen. *Cravenoceras*

leion has absolutely straight growth-lines without any crenulation or even spiral-striation. *G. schaelkensis*—on the contrary—has clearly curved and crenulated growth-lines. All species of *Sudeticerus* which I have seen so far show indications of spiral-striation, mainly near the umbilicus and the lingua.

Furthermore, the growth-lines of *Sudeticerus* always show a lateral—though sometimes rather small—salient. Also the stratigraphical range does not support the idea of Bisat.

Occurrence. Go₂.

Eumorphoceras (*Edmooroceras*) *torquisti* (Wolterstorff)

Plate 46, figs. 1–3

1899 *Dimorphoceras?* *torquisti* Wolterstorff, p. 34, pl. 2, figs. 12–14.

Material. Eleven specimens (nos. 573:8 to 18).

Diagnosis. *Eumorphoceras* with a rather narrow umbilicus, sickle-shaped growth-lines, and short comma-shaped deepenings near the umbilicus. Lateral furrow not divided into two.

Description. *Eumorphoceras torquisti* is characterized by its relatively narrow umbilicus, somewhat resembling *Girtyoceras* from which it probably evolved (Yates 1962, p. 367; Gordon 1964, p. 228). The ratio of the diameter to the width of the umbilicus remains rather constant during the different growth-stages and amounts to 5:1. The umbilical edge is slightly raised, the resulting rim, however, does not appear as strong as in *E. pseudocoronula*.

The growth-lines leave the umbilicus in a forward direction but turn back very soon. About in the middle of the flank they bow forward again forming a salient on the shoulder. The ventral sinus is deep.

E. torquisti has short, comma-shaped deepenings around the umbilicus, about six per half whorl (573:12). No constrictions can be observed.

While in all species of the genus *Eumorphoceras* the lateral furrow is divided into two by an intermediate ridge—the ventral furrow is often much shallower—*E. torquisti* has only a single furrow, as described by Wolterstorff (1899, p. 35, and pl. 2, figs. 11–14) in the type description. In contrast to this, the furrow in the stratigraphically younger *E. dichalocinum* is always clearly divided into two. Since these species have not yet been properly separated it can be often read that *E. torquisti* has a divided furrow.

Discussion. Elias (1956, p. 132) erected *Edmooroceras* as a subgenus of *Eumorphoceras*, describing as one of the main features a 'subangular and nodose umbilical edge'. Horn (1960) regarded these features as so important that he placed *E. torquisti* and, like Elias, *E. pseudocoronula* in this subgenus. Yates (1961), however, for certain reasons, preferred to retain these species as *Eumorphoceras sensu stricto*. It should be the object of a special investigation, including a reappraisal of the type specimens, to decide whether these features justify a subgenus. Until this has been done the subgenus *Edmooroceras* erected by Elias is valid and therefore is still used here.

Occurrence. Go₂.

Eumorphoceras (*Edmooroceras*) *dichalocium* sp. nov.

Plate 46, figs. 5–7

Derivatio nominis. Greek: δίχα = double, ἄλοξ = furrow.*Holotype.* No. 573:19.*Paratypes.* Nos. 573:20 to 22.*Diagnosis.* Very closely related to *Eumorphoceras tornquisti*, but with a division of the lateral furrow into two and slightly longer constrictions in the umbilical region.*Description.* This new species which is very similar to *E. tornquisti* has been found at the base of the Namurian associated with *Cravenoceras leion*. As in *E. tornquisti* the umbilicus is relatively small. In the holotype the ratio of the diameter to the umbilical width amounts to 5:1. The umbilical edge is raised into a rim as is characteristic of the subgenus *Edmooroceras*. Especially in the smallest specimen there is to be seen a slight beading of the rim. The growth-lines are sickle-shaped, forming a high lateral salient on the shoulder and a sinus of equal depth on the venter. Around the umbilicus there are regular constrictions running parallel to the growth-lines and dying out just before they reach the middle of the flank. Compared with the comma-shaped deepenings in *E. tornquisti* specimens of equal size they are slightly longer.

The well-pronounced lateral furrow is divided into two by a strong ridge. The ventro-lateral groove is little shallower than the dorso-lateral one.

Discussion. The close relationship of this new species with *E. tornquisti* has been pointed out repeatedly. The occurrence of a divided lateral furrow in contradistinction to the single furrow in *E. tornquisti* is a diagnostic feature and justifies the separation of both species. The other differences, such as the longer constrictions and the somewhat higher lateral salient are of more subtle nature. Therefore, *E. dichalocium* seems to grade phylogenetically between *E. tornquisti* and *E. pseudocoronula* and this is also indicated by its stratigraphical position. Since *E. dichalocium* has been previously included with *E. tornquisti*, the latter was considered to have a greater stratigraphical range (according to Horn 1960, *E. tornquisti* is associated with *Cravenoceras leion*). In the section described here *E. tornquisti*, however, does not reach the base of the Namurian whilst *E. dichalocium* lies just above the base.Moore (1946, p. 418) described a *Eumorphoceras* sp. form A which he places also between *E. tornquisti* and *E. pseudocoronula*. This form seems to be similar to *E. dichalocium*. Moore, however, did not mention any constrictions and only shallow lateral double-furrows. Nevertheless it cannot be excluded that these differences are due to the state of preservation and both species may turn out to be identical. There is no similarity between *E. dichalocium* and *Sagittoceras costatum* Ruprecht which has a much stronger sculpture.*Occurrence.* E_{1a}.

Cravenoceras leion Bisat

Plate 47, fig. 4

1930 *Cravenoceras leion* Bisat, p. 28, fig. 1.*Material.* Seven partly fragmentary specimens (nos. 573:23 to 29).*Diagnosis.* Rather broad form with numerous very fine and straight growth-lines.*Description.* Even from the shale impressions it can be concluded to be a rather broad shell. The umbilicus is moderate in size. The sculpture consists of very fine and tight growth-lines. Horn's statement (1960, p. 334) that there are about 5-7 lines per mm. in the middle of the flanks has been confirmed. In the smaller specimens there are probably even more.

The growth-lines leave the umbilicus in a slight forward direction but after a very short distance they bend into a radial direction crossing the flanks and the venter completely straight. No indication of spiral striation could be found and no crenulation of the growth-lines was observed.

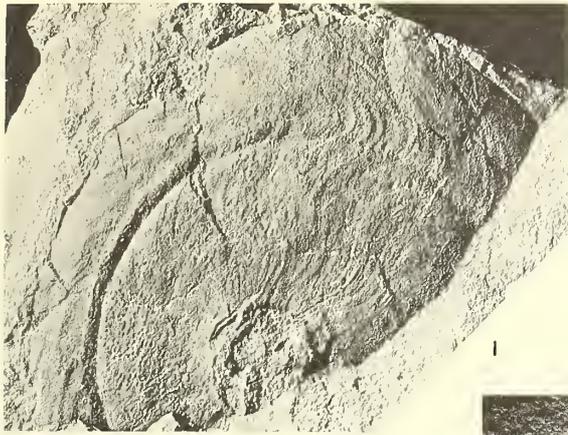
The absence of spiral sculpture, the very straight direction of the growth-lines and their delicacy are the most important features of *C. leion*.*Occurrence.* E_{1a}.*Eumorphoceras (Edmooroceras) pseudocoronula* Bisat

Plate 46, figs. 8-9

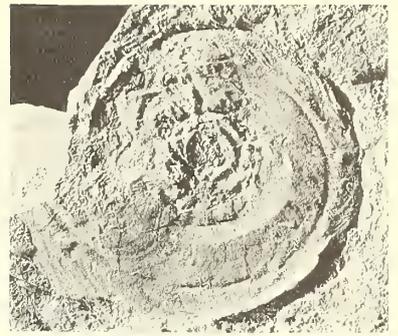
1950 *Eumorphoceras pseudocoronula* Bisat, p. 19, pl. 2, fig. 4.*Material.* Ten partly fragmentary specimens (nos. 573:30 to 39).*Diagnosis.* Because of the raised umbilical edge these belong to the subgenus *Edmooroceras*. In youth the sculpture consists of short ribs which become shorter with increasing age until they are only knots. Regular constrictions are present. They form a high lingua and run parallel to the growth-lines.*Description.* The umbilicus is widened in youth; with increasing age, however, it becomes smaller. At a diameter of 8 mm. the ratio diameter to the width of the umbilicus amounts to 2:1, at 16 mm. nearly 3:1 (specimen no. 573:32). Contemporaneously the ribs fade more and more and at a diameter of 10 mm. they can be seen only as knots on

EXPLANATION OF PLATE 46

Figs. 1-3. *Eumorphoceras (Edmooroceras) tornquisti* (Wolterstorff). Go₂. 1. No. 573:8. 2. No. 573:17. 3. No. 573:18.Fig. 4. *Peytonoceras? involutum* (Horn), E_{1a}, no. 573:40.Figs. 5-7. *Eumorphoceras (Edmooroceras) dichalocium* sp. nov. E_{1a}. 5. No. 573:19. 6. No. 573:20. 7. No. 573:21.Figs. 8-9. *Eumorphoceras (Edmooroceras) pseudocoronula* Bisat. E_{1a}. 8. No. 573:30. 9. No. 573:31.



1



2



5



3



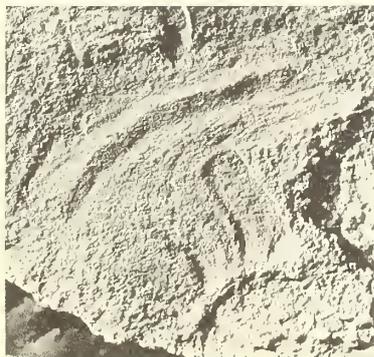
4



8



6



7



9

FIGGE, Carboniferous goniatites

the raised umbilical edge. I wrote in a former paper (Figge 1964, p. 778) that the number decreases continuously. This could not be proved with the present material since the shale impressions do not show the inner whorls. This observation, however, may hold true here, too, because the knots on the umbilical edge are much wider spaced, sometimes even disappearing in the adult specimens. A striking feature of *E. pseudocoronula* are the regular constrictions. They are bordered on each side by marked edges, the distal one being often raised. Between two constrictions there are mostly two short riblets which start on the umbilical edge and fade out on the middle of the flanks. In adult specimens these riblets are represented only by knots on the umbilical edge. The constrictions leave the umbilicus radially, but in the middle of the flank they bend forward in a smooth bow forming a high salient on the shoulder. The ventral sinus is not as deep as the salient. The depth of the constrictions decreases in the region of the salient. On the venter they are often scarcely visible.

The furrow on the shoulder is divided by a marked ridge into a dorso-lateral groove and a slightly shallower ventro-lateral one. The constrictions divide the ridge into longish knots.

Owing to the raised umbilical edge this species has to be placed in the subgenus *Edmooroceras* (Elias 1956).

Discussion. *E. pseudocoronula* is well characterized by the regularity and the form of its constrictions. Therefore it can be hardly mistaken for another species. The strongly ribbed youth-form, however, resembles *E. pseudobilingue*. There are also relations to *E. medusa* which represents a later stage of evolution of *E. pseudocoronula* (Yates 1961, p. 54).

Occurrence. E_{1a} (Lower Namurian).

Peytonoceras? involutum (Horn)

Plate 46, fig. 4

1960 *Eumorphoceras? involutum* Horn, p. 330, figs. 4–5, pl. 1, figs. 3–5.

Material. One specimen (no. 573:40).

Diagnosis. Very involute, with a clearly marked double-furrow and sickle-shaped growth-lines.

Description. Horn (1960) and Yates (1961) describe a very involute *Eumorphoceras* from the *Cravenoceras leion*-bearing beds of the lower Namurian. The umbilical edge is not clearly marked, the flanks curve gently to the umbilicus.

The prominent shoulder ridge together with the minute umbilicus is typical of *Peytonoceras? involutum*. This strong and narrow ridge divides the lateral furrow into a dorso-lateral and a ventro-lateral one of equal depth. Yates made the same observation, whilst Horn described the ventral groove as being shallower. Judging from Horn's paratypes this difference might well be caused by the state of preservation.

The sculpture consists of very faint growth-lines which are little prominent near the lingua. After leaving the umbilicus radially, they bend back before they turn forward close to the shoulder forming a high lingua. The depth of the ventral sinus is not visible. There are no constrictions.

Discussion. *P.?* *involutum* (Horn) is obviously a synonym of *E. rota* Yates, but Horn has priority. The relationship between *Peytonoceras?* *involutum* and other species, viz. *Eumorphoceras* sp. form A of Moore, *Sagittoceras costatum* Ruprecht etc. has been discussed by Horn and Yates. Both authors concluded that *P.?* *involutum* is an independent species.

Saunders introduced a new genus *Peytonoceras* which he described as follows (1966, p. 43): 'The genus *Peytonoceras* is characterized by a subdiscoidal, involute conch with a narrowly rounded venter and sharply sculptured lateral grooves or sulci. Conch sculpture, in addition to the narrow ventrolateral grooves, includes sinuous lateral ribs and extremely fine spiral lirae on the flanks.' And: 'In some respects *Peytonoceras* is morphologically similar to *Eumorphoceras*. These similarities include ventrolateral grooving and lateral ribbing, which are features shared by all species of *Eumorphoceras*. *Peytonoceras*, however, is involute beyond the third or fourth whorl, whereas *Eumorphoceras* remains evolute to the fifth whorl in most cases. The narrow, deep ventrolateral groove of *Peytonoceras* is a feature shared by few, if any, species of *Eumorphoceras*, which may have two ventrolateral grooves separated by a ventrolateral ridge. Where only one groove is present, as in *E. bisulcatum*, it is shallow and wide. The external suture serves to distinguish *Peytonoceras* from some species of *Eumorphoceras*.'

Since no sutures are preserved either in the specimen 573:40 or in Horn's material, *P.?* *involutum* can be described and identified only by its shell morphology. On this basis it has more features which are typical of *Peytonoceras* than of *Eumorphoceras* where it has been placed by Horn with certain reservations. Therefore it is placed here in *Peytonoceras*, but with reservation, too, because of the absence of sutural evidence and the fact that *P.?* *involutum* has a divided lateral furrow while the genus *Peytonoceras* has only a single one. The latter difference is not regarded as essential for distinguishing the genera, but only the species. In *Eumorphoceras*, for instance, there are both types of furrows present.

Occurrence. E_{1a} (close to the base of the Namurian).

Eumorphoceras medusa Yates

Plate 47, fig. 1

1961 *Eumorphoceras medusa* Yates, p. 54, pl. 6, figs. 1, 2.

Material. Three specimens (nos. 573:41 to 43).

Diagnosis. A *Eumorphoceras* with a relatively small umbilicus. The sculpture consists mainly of regular, sickle-shaped constrictions.

EXPLANATION OF PLATE 47

Fig. 1. *Eumorphoceras medusa* Yates. E_{1a}. No. 573:41.

Fig. 2. *Eumorphoceras medusa*, var. *sinuosum* Yates. E_{1a}. No. 573:44.

Fig. 3. *Eumorphoceras* (*Edmooroceras*) *pseudocoronula* Bisat. E_{1a}. No. 573:32.

Fig. 4. *Cravenoceras leion* Bisat. E_{1a}. No. 573:24.

Figs. 5, 6. *Goniatites schaelkensis* (Brüning). Go₂. 5. No. 573:1. 6. No. 573:2.



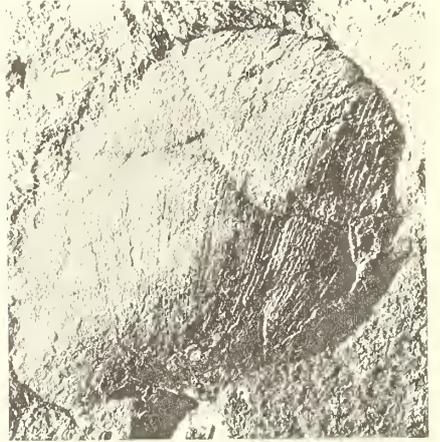
1



2



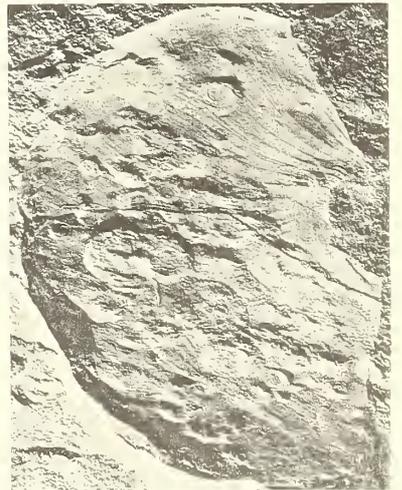
3



4



5



6

FIGGE, Carboniferous goniatites

Description. When Yates (1961) described *E. medusa* for the first time, she mentioned the close relationship between this species and *E. pseudocoronula*. This relationship is indicated by the regular constrictions and the more reduced ventral part of the lateral furrow. The main differences are as follows. The umbilicus of *E. medusa* is smaller. The ratio diameter to width of the umbilicus of the specimen 573:41 amounts to about 5:1, against 3:1 in *E. pseudocoronula* of equal size. The umbilical edge is raised, but not beaded. There are no intermediate ribs between the constrictions in *E. medusa* which are typical of *E. pseudocoronula*.

As mentioned above, the constrictions are very regular; in specimen 573:43 there are six per half whorl. After leaving the umbilicus in a forward direction they bend back in the middle of the flank, then bend forward again and form a high lingua. The depth of the ventral sinus cannot be measured exactly: it seems, however, to be smaller.

In the region of the lingua there are two furrows, divided by a broad and shallow ridge. The ventro-lateral groove is much fainter and often scarcely visible.

Occurrence. E_{1a}.

REFERENCES

- BISAT, W. S. 1930. On *Cravenoceras leion* sp. nov., the basement goniatite of the Namurian, Upper Carboniferous. *Trans. Leeds geol. Ass.* **20**, 28–32.
- 1950. The junction Faunas of the Viséan and Namurian. *Ibid.* **6**, 10–26, pl. 1, 2.
- BRÜNING, K. 1923. Beiträge zur Kenntnis des rheinisch-westfälischen Unterkarbons insbesondere der Goniatiten und Korallen in der stratigraphischen Stellung und Gliederung. 1–59.
- ELIAS, M. K. 1956. Upper Mississippian and Lower Pennsylvanian Formations of South-Central Oklahoma. *Petrol. Geol. Southern Oklahoma*, Amer. Ass. Petrol. Geol. 56–134, pl. 1–6.
- FIGGE, K. 1964. Das Karbon am Nordwestende des Harzes. *Geol. Jb.* **81**, 771–808, pl. 44–46.
- GIRTY, G. H. 1909. The Fauna of the Caney Shale of Oklahoma. *Bull. U.S. geol. Surv.* **377**, 5–106, pl. 1–13.
- GORDON, M. 1964. Carboniferous Cephalopods of Arkansas. *Prof. Pap. U.S. geol. Surv.* **460**, 1–322, pl. 1–30.
- HORN, M. 1960. Die Zone des *Eumorphoceras pseudobilingue* im Sauerland. *Fortschr. Geol. Rheinld. Westf.* **3**, 1303–42, pl. 1–5.
- HUDSON, R. G. S. 1945. The goniatite zones of the Namurian. *Geol. Mag.* **82**, 1–9.
- MCCAULEB, J. A., QUINN, J. H., and FURNISH, W. M. 1964. The Ammonoid Family Girtyoceratidae in the Southern Midcontinent. *Circular Oklahoma geol. Surv.* **67**, 1–41, pl. 1–4.
- MOORE, E. W. J. 1946. The Carboniferous goniatite genera *Girtyoceras* and *Eumorphoceras*. *Proc. Yorks. geol. Soc.* **25**, 387–445, pl. 22–37.
- PAREYN, C. 1961. Les massifs carbonifères du Sahara Sud-Oranais. I and II. *Publs Cent. Rech. sahar. Géol.* **1** (2), 9–244, pl. 1–28.
- PATTEISKY, K. 1930. Die Geologie und Fossilführung der mährisch-schlesischen Dachschiefer- und Grauwackenformation. *Naturwissenschaftlicher Verein in Troppau, CSR*, f. 1929. 1–354, pl. 1–26, 28 figs., 1 map.
- 1950. Die Goniatiten im Namur des niederrheinisch-westfälischen Karbongebietes. *Mitt. westf. Bergwerkschafskasse*, **14**, 3–65, pl. 1–14, 18 figs.
- 1961. Contributions to the Stratigraphical Colloquium. Antrag auf Klärung der Abgrenzung zwischen Unter- und Oberkarbon. *Congrès Avanc. Étud. Stratigr. carb. Heerlen 1958*, **2**, 511.
- QUINN, J. H., MCCAULEB, J. A., and WEBB, J. H. 1962. Pennsylvanian *Eumorphoceras* from Arkansas. *J. Paleont.* **36**, 112–14, pl. 21.
- RUPRECHT, L. 1936. Die Biostratigraphie des obersten Kulm im Sauerlande. *Jb. preuss. geol. Landesanst.* **57**, 238–83, pl. 9–10.
- SAUNDERS, W. B. 1966. New Goniatite Ammonoid from the late Mississippian of Arkansas. *Oklahoma Geology Notes*, **26** (2), 43–48, pl. 1.

- SCHMIDT, H. 1925. Die carbonischen Goniatiten Deutschlands. *Jb. preuss. geol. Landesanst.* **45**, 489–609, pl. 19–26.
- 1942. Nach Goniatiten gegliederte Profile im sauerländischen Kulm. *Decheniana*, **101**, AB, 49–63, pl. 2–4.
- WACHENDORF, H. 1965. Wesen und Herkunft der Sedimente des westfälischen Flözleeren. *Geol. Jb.* **82**, 705–54, pl. 49–52.
- WOLTERSTORFF, W. 1899. Das Unterkarbon von Magdeburg–Neustadt und seine Fauna. *Jb. Kgl. preuss. geol. Landesanst.* **19**, 3–64, pl. 2, 3.
- YATES, P. J. 1961. New Namurian goniatites of the genus *Eumorphoceras*. *Palaeontology*, **4**, 54–8, pl. 6.
- 1962. The palaeontology of the Namurian rocks of Slieve Anierim, co. Leitrim, Eire. *Ibid.* **5**, 355–443, pl. 51–62.

DR. K. FIGGE
Geologisch-Paläontologisches Institut
der Georg-August-Universität
34 Göttingen
Germany

Typescript received from author 14 June 1967

FORM AND FUNCTION OF THE STEM IN A PSEUDOPLANKTONIC CRINOID (*SEIROCRINUS*)

by A. SEILACHER, G. DROZDZEWSKI, and R. HAUDE

ABSTRACT. The position of crowns and stems in the rock indicates that *Seirocrinus subangularis* lived attached to floating logs in spite of its unusual size. The distribution of weight and flexibility along its stem is inverse to most other crinoids, but corresponds to the assumed habitat. A few general growth gradients seem to control this and other adaptive modifications of the crinoid stems.

FUNCTIONAL morphology is a most important tool in the interpretation of specialized forms that deviate ecologically from their relatives. Such deviation may be expressed by an unusual shape, as in the case of rudist pelecypods (Vogel 1960), richthofeniid brachiopods (Rudwick 1961), or *Pygope* (Vogel 1966). In other forms, an unusual mode of life is indicated by their regular occurrence in types of facies in which we would not normally expect to find them.

The case to be discussed in this paper is of the latter type. Its main object is a 4.50 × 7 m. slab which was found in the Posidonia Shales (Lias ϵ) of Reutlingen a hundred years ago and has been one of the major attractions of the Tübingen Museum since (Pl. 48, fig. 1). It contains about fifty exceptionally large specimens of *Seirocrinus subangularis* (Miller), the more common crinoid species found in the bituminous shales. F. A. Quenstedt (1868), who gave a most complete description of these fossils, referred to them as 'Schwabens Medusenhaupt'. *Seirocrinus subangularis* (long stem), as well as the rare species *Pentacrinus briareus* Miller (short stem with dense cirral fur) are regular elements of the Posidonia Shale fauna. Many beautiful specimens have been obtained by museums and private collectors from the famous Hauff workshop at Holzmaden. *Isocrinus*, though common in other members of the Lias, has never been found in these shales.

The fact that the two crinoids occur in a black shale of apparent euxinic origin becomes understandable if we think of the specimens still attached to driftwood. Even so, some uncertainty remains whether they were exclusively pseudoplanktonic or whether they could survive benthonically after the log had eventually settled to the bottom.

The pseudoplanktonic model becomes particularly critical in the Medusenhaupt specimen: about fifty calyces with an average diameter of 80 cm. and stems of more than 15 m. in length must have formed a considerable load and may have taken years to grow to this size. Could this all happen on a drifting log? After all, the layer of stagnant bottom water might have troubled only the juvenile individuals, while older ones had stems long enough to hold the calyces above the interface. Did *Seirocrinus* ever make use of this possibility? Or, viewed in another way: ought such slabs to be displayed with the crinoids standing up, as is customary, or hanging down? The burial position will give us a clue to this basic ecological question.

[Palaeontology, Vol. 11, Part 2, 1968, pp. 275-82, pl. 48.]

1. *Mode of life derived from biostratinomic evidence*

While in most Holzmaden specimens of *Seirocrinus* the calyces lie on their sides, the Medusenhaupt crowns spread their arms radially. In this position two geopetal orientations are theoretically possible: the arms either cover the stem or are overlain by it, depending on whether stem or calyx reached the floor first.

The Medusenhaupt slab—as is usual with Posidonia Shale fossils—was prepared from the lower side (Quenstedt 1868, p. 18) because the upper one would be less well preserved. Knowing this, we can readily confirm that each crown lies *underneath* its respective stem and must have touched the bottom first. Subsequent tilting of the stems did not change the original position of the arms on the mud, but it often made the arms break near their bases when the calyx tipped over together with the stem (Pl. 48, fig. 2).

Using simple laws of superposition, we can also disentangle the whole colony (text-fig. 1). It seems that the crinoid stems grew bundled over most of their length, with only the calycal parts of the stems having some individual freedom.

As the trunk sank, it must have drifted slightly to the right. This drift aligned the settling stems, while it was too weak to disarrange the radial position of the arms. At two stages, however, sinking exceeded the drift and made the stems settle in broad loops.

Conclusion. The Medusenhaupt crinoids were attached to some floating object throughout life. Their crowns hung down and were the first parts to touch the bottom when the float sank.

2. *Functional morphology of the stem*

(a) *Paradigms.* If, then, *Seirocrinus* was pseudoplanktonic, we should expect it to deviate in certain respects from regular crinoids. *Encrinus liliiformis* (Lamarck) for instance, a familiar Middle Triassic crinoid, would have suffered from lethal deficiencies when placed on a drifting log. Its calyx, instead of hanging down in the sea water, would probably have floated at the surface—if we accept Linck's (1954; 1965, p. 138) conclusion that detached *Encrinus* drifted along the bottom in an upright position. But even if it could somehow adjust its buoyancy to an inverse position it would break off in the first storm. The basal part of its stem, breakable even under bottom conditions, would be much too stiff to withstand the tension that any wave would cause between calyx and float.

Buoyancy of the *calyx* would seem to control the upright position of rooted sea-plants and animals most effectively. Still, we have no record whether attached crinoids of the present use this principle, i.e. whether calyces sink to the bottom or float up when

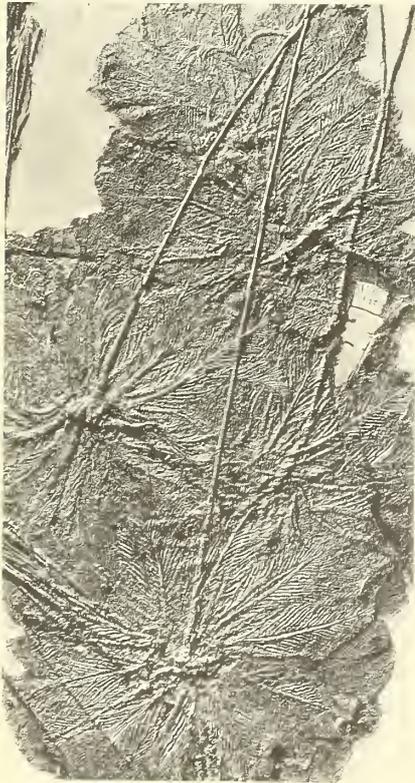
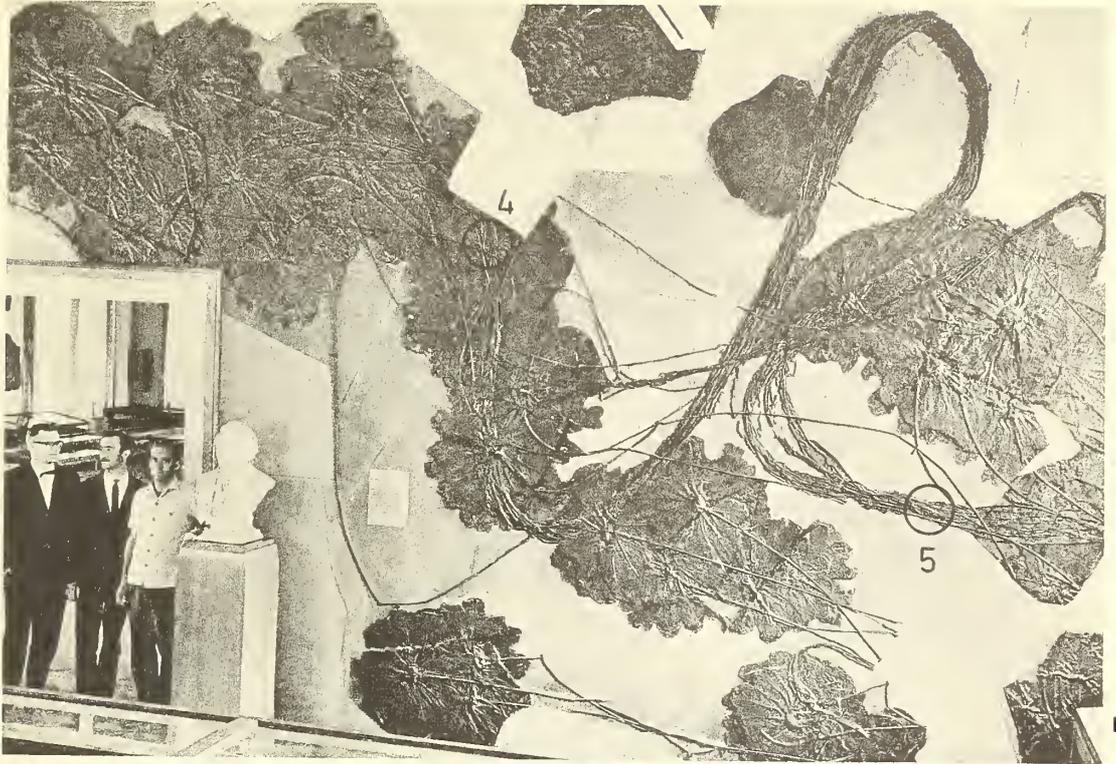
EXPLANATION OF PLATE 48

Fig. 1. Colony of *Seirocrinus subangularis* (Mill), ('Schwabens Medusenhaupt' of Quenstedt) mounted in the Geological Institute of the Tübingen University. Authors as scale.

Fig. 2. The arms, seen from below, spread radially and underlie the respective stems. This indicates that the arms touched the bottom first and the stems fell over them.

Fig. 3. Normal gradation in crinoid stems (*Encrinus liliiformis*; after Linck 1954, pl. 1): rhythmic alternation of internodal generations, still pronounced near the calyx, smoothes out towards the roots.

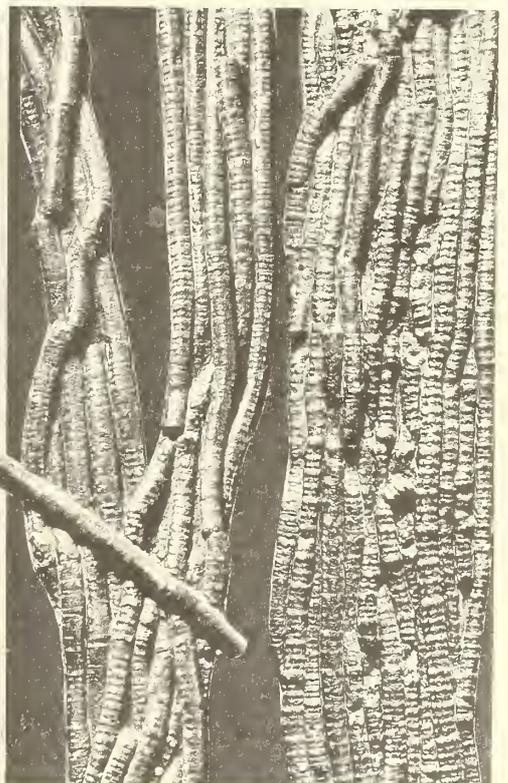
Figs. 4–5. In *Seirocrinus* stems gradation is reversed: fig. 5, although showing more pronounced alternation, is taken 9 m. further away from the calyces than fig. 4 in the same bundle.



2

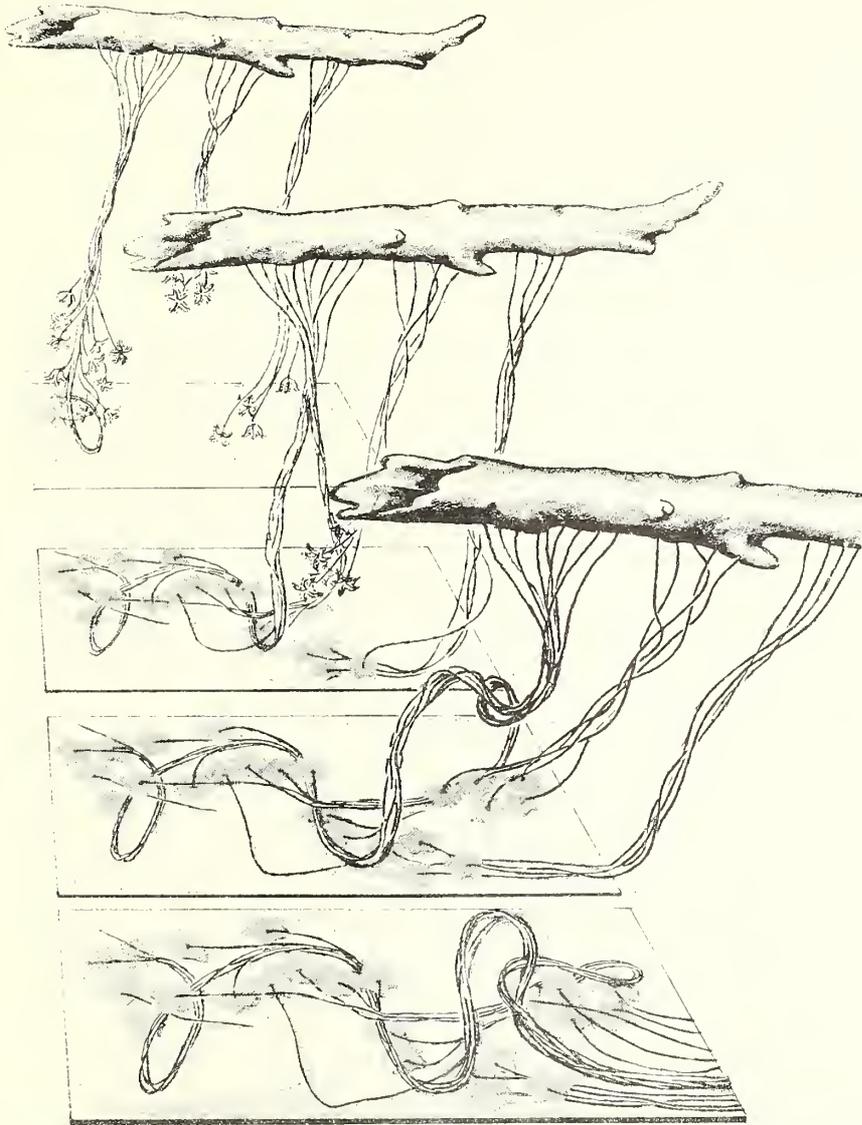


3



4

5



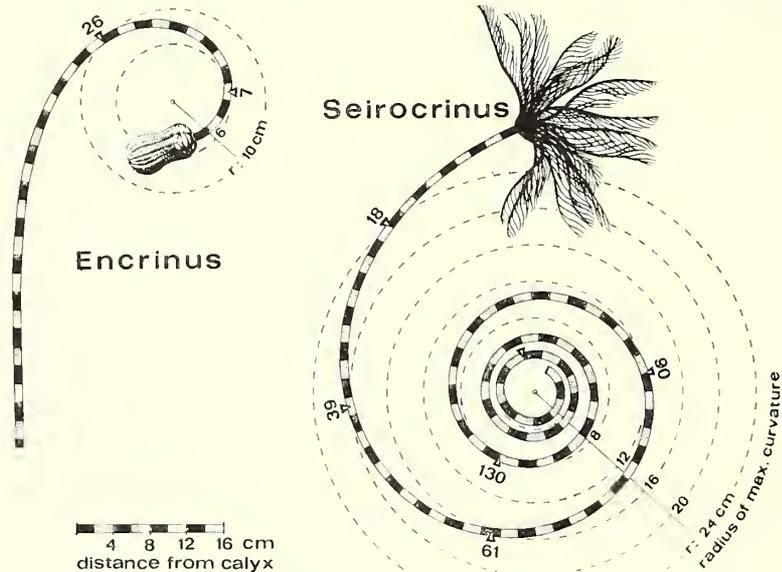
TEXT-FIG. 1. Settling of the colony as inferred from the final arrangement on the slab.
Figure drawn as a mirror image to facilitate comparison with Plate 48, fig. 1.

clipped off their stems. The question of how buoyancy may be expressed in calycal morphology is therefore premature.

The effect of an inverse attitude on *stem* morphology should be easier to recognize because of the relative simplicity of its functional framework. The paradigm of a buoyant calyx would require the stem to be heavy and stiff near the root, light and flexible near the calyx. In the pendant model, as suggested for *Seirocrinus*, weight and flexibility should grade in the opposite direction.

Both relative weight and flexibility can be studied in fossil crinoid stems. Thin columnals with wide intercolumnal spaces would have resulted in low specific weight, while high and massive columnals made the stem heavier. The degree of flexibility on the other hand is recorded by the maximum curvature of different parts of complete specimens.

(b) *The stem of Encrinus liliiformis.* There is no doubt that the immature calycal parts were lighter than the massive basal sections of the *Encrinus* stem. Flexibility, measured



TEXT-FIG. 2. uses the maximum bend observed in some fairly complete stems of *Encrinus* and *Seirocrinus* as an expression of the original flexibility distribution.

In *Encrinus* flexibility is high near the calyx and disappears towards the root which serves as a rigid column to support the calycal parts.

In *Seirocrinus* flexibility grades in the opposite direction. In terms of growth gradients, this may be due to limited accretionary growth and strong intercalation. In a functional sense it may express the stress distribution in a stem that hung from a floating log. (Measured on specimens in Tübingen Museum; Kat. Nr. 1325/1.)

from the beautiful slabs excavated by Linck (1954), decreased in the same direction (text-fig. 2).

The causes are obvious. Here, as in all crinoids, new nodals were formed as thin discs at the base of the calyx. Columnal growth was concentrated initially at the rim, leaving a saucer-shaped depression in the articulating surface. Secondary columnals (internodals) then developed in the protected space (Biese 1927, Aldinger 1928). After about four generations intercalation of new internodals ceased, but accretionary growth of individual columnals continued, flattening the articulation surfaces and rounding the slightly pentagonal outline. As a result of the process, the distinction between different generations of columnals, so obvious near the calyx, is lost towards the root (Pl. 48, fig. 3).

Both intercalation of additional columnals and accretionary growth in the axial direction increase the length of the stem, but have a different effect on its flexibility: while intercalation maintains the flexibility, accretion diminishes it.

Only the root zone may at first have retained some of its original flexibility. In this zone accretionary growth was radial rather than axial. Thereby the columnals remained fairly thin without appreciable reduction of articulations per unit length. However the original crenulation became exaggerated towards the periphery and an over-all callous cortex eventually was added to fuse the root columnals into a rigid and heavy base for the rest of the stem.

(c) *Stem differentiation in Seirocrinus.* *Seirocrinus* and other pentacrinid stems are easier to analyse. Not only do we know a larger number of fairly complete and well-preserved specimens, but the fact that nodals bear cirri while internodals do not, allows one to trace and measure nodal cycles well into older parts of the stem, where internodals have grown to the same size.

Growth and form, compared to the *Encrinus* stem, are completely different:

1. The 'young' aspect with hierarchic cycles of smaller and larger columnals is not restricted to the calycal end but extends over the whole stem. Moreover, alternation is more pronounced, and the stems become narrower away from the calyx (Pl. 48, figs. 4-5).
2. As far as internodes can be recognized, their length as well as the number of columnals per internode continues to increase geometrically towards the base (text-fig. 3). By projecting the observed growth rate, an internode of about 250 cm. and 1,023 columnals would be reached at about 20 m. from the calyx.
3. This trend does not continue indefinitely. Complete specimens (particularly the one figured by Müller 1963, fig. 511) show that axial growth, as in the *Encrinus* stem, decreased again near the root. In this part the cirri become stronger and densely crowded—in spite of the fact that we are dealing with the oldest part of the stem. There must have been a rapid decrease of internodal intercalation towards the base, to the point where internodals are lacking altogether.

In the case of *Seirocrinus*, the basal growth retardation did not increase flexibility, but had another functional effect: the concentration of nodals produced a dense tuft of cirri acting as a hold-fast to the driftwood.

As a whole, the stem of *Seirocrinus* meets the requirements set up in our paradigm: weight decreases and flexibility increases towards the root (text-fig. 2).

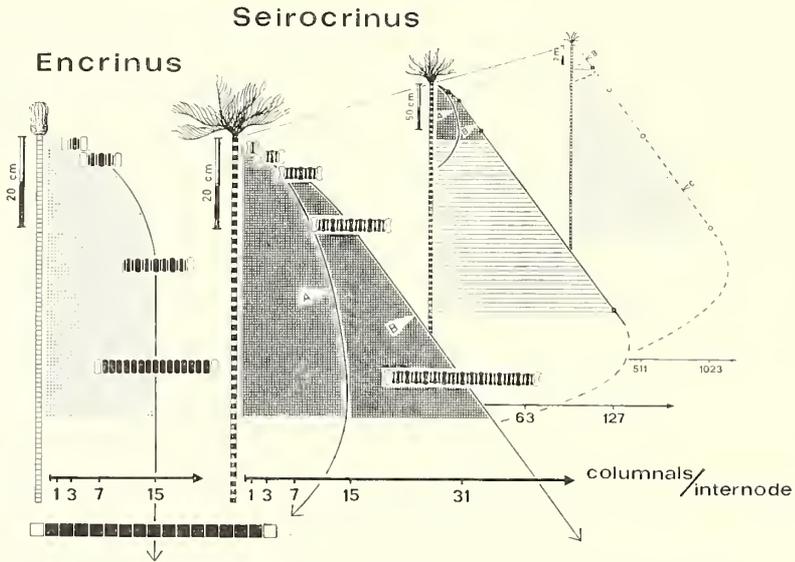
Conclusion. Weight and flexibility of the *Seirocrinus* stem grade inversely to *Encrinus*, as required by the pendant versus buoyant paradigm.

3. *Growth gradients and countergradients in the crinoid stem*

Comparing the two examples one feels that, no matter how different crinoid stems may appear, their basic morphology can be described in terms of a few common *growth gradients*:

1. Longitudinal growth by intercalation

(a) *Gradient*. Because the number of internodals increases with age, the internodes become longer with increasing distance from the calyx.



TEXT-FIG. 3. Longitudinal growth by intercalation and accretion of columnals (white = nodals; black = internodals).

Encrinurus. Initial growth by intercalation stops after a few generations of internodals. Accretionary growth continues, however, so that all generations reach the same size. (Measurements made at Lauffen Cement Factories.)

Seirocrinus. Columnals never become uniform in size and seem to reach an unlimited number of generations. Close to the root, however, the internodes are increasingly shorter and a dense tuft of cirri bursts from the crowded columnals.

The three diagrams use different scales. Curves (A, B, C) are based on following specimens:

- (A) Müller 1963, fig. 511 (Humboldt University, Berlin);
- (B) Tübingen Museum (Kat. Nr. 1325/1);
- (C) Large slab (Pl. 48, fig. 1).

Of these specimens, only (A) was complete. In the other two the deflection of the curve near the root is inferred.

(b) *Countergradient*. The rate of internodal intercalation is accelerated from the older to the younger parts of the stem, so that the number of internodals decreases again in the older parts of the stem close to the root.

The curves in text-fig. 3 result from the two gradients.

2. Longitudinal growth by accretion

(a) *Gradient*. Accretionary growth of the columnals is a function of time and increases away from the calyx.

(b) *Countergradient*. Similar to internodal intercalation, longitudinal accretion accelerates in younger parts of the stem, i.e. away from the root.

3. Radial growth

(a) *Gradients*. Primary control of nodal diameter lies in the generating area at the base of the calyx. The size of the nodals in turn determines the diameter of the initial internodals. A stem exclusively controlled by calicular growth would thicken from the base towards the calyx.

(b) *Countergradients*. Secondary modifications are brought about by accretionary growth in radial direction. As this growth is another time rate problem, it works in the opposite sense and tends to produce a trunk-like stem tapering from base to calyx.

The resultant of the two gradients is shown by the actual stems, which in most cases thicken at both ends.

4. *Callous overgrowth* may cover several columnals. It is used to add non-flexible structures such as anchors or lobes to the root.

This or a similar set of growth gradients should theoretically allow the crinoid stem to adjust to a variety of functional situations by speeding or slowing any one relative to the others. The flexibility in particular may thus be varied, or cirri concentrated, in different parts of the stem.

A species in which the root eventually acts as a trunk will thus emphasize gradients 3 (b) and 4 (*Encrinus*), while in the prehensile roots of some crinoids the same gradients are suppressed in order to retain the original state of a tapering and highly flexible tendril.

Conclusion. Similar to what we know from higher plants, a few general growth gradients seem to control a variety of adaptive modifications of the crinoid stem.

Acknowledgements. The present study grew out of a seminar on General Palaeontology at the Department of Geology, University of Tübingen. While this work was not being credited or supported in any way, the manuscript did receive helpful criticism from various colleagues. Thanks are particularly due to our Tübingen guests in 1965 and 1966: Dr. A. G. Fischer (Princeton) who willingly discussed the subject and tailored the English text, and to Dr. D. M. Raup (Rochester) who taught us how fossils can be understood in terms of theoretical morphology. Dr. H. Jaeger (Humboldt University, Berlin) provided photographs of a complete *Seirocrinus*. The Cement Factories at Lauffen am Neckar kindly allowed us to study crinoid slabs in their museum.

Addendum

Dr. Jefferies (London) has kindly brought to our attention a note by the late J. F. Jackson (*Geol. Mag.* **103**, 365–6, 1966), stating that *Pentacrinus briareus* in the Lyme Regis Lias is regularly found underneath the lignitized driftwood to which it was attached. This fact further supports our conclusions.

REFERENCES

- ALDINGER, H. 1928. *Beiträge zur Stratigraphie und Bildungsgeschichte des Trochitenkalkes im nördlichen Württemberg und Baden*. Diss. Tübingen.
- BIESE, W. 1927. Über die Encriniten des unteren Muschelkalks von Mitteldeutschland. *Abh. preuß. geol. Landesanst.* n.f., **103**, 1–119.
- LINCK, O. 1954. Die Muschelkalkscelilie *Encrinus liliiformis*. Ergebnisse einer Grabung. *Aus der Heimat*, **62**, H. 11/12. Öhringen.
- 1965. Stratigraphische, stratonomische und ökologische Betrachtungen zu *Encrinus liliiformis* Lamarck. *Jb. geol. Landesanst. Baden-Württ.* **7**, 123–48. Freiburg i. Br.
- MÜLLER, A. H. 1963. *Lehrbuch der Paläozoologie*, Bd. II Invertebraten, T. 3. Jena.

- QUENSTEDT, F. A. 1868. *Schwabens Medusenhaupt. Eine Monographie der Subangularen Pentacriniten.* Tübingen.
- RUDWICK, M. J. S. 1961. The feeding mechanism of the Permian Brachiopod *Prorichthofenia*. *Palaeontology*, 3, 450-71.
- VOGEL, K. 1960. Zu Struktur und Funktion der 'Siphonalpfeiler' der Hippuriten (Lamellibranchiata). *Paläont. Z.* 34, 275-94. Stuttgart.
- 1966. Eine funktionsmorphologische Studie an der Brachiopodengattung *Pygope* (Malm-Unterkreide). *Neues Jb. Geol. Paläont., Abh.* 125, 423-42.

ADOLF SEILACHER
GÜNTHER DROZDZEWSKI
REIMUND HAUDE
Geolog.-Paläontolog. Institut
Universität Tübingen
74 Tübingen, Germany

Typescript received 23 December 1966

SOME LARGER FORAMINIFERA FROM THE TERTIARY OF CENTRAL AMERICA

by F. E. EAMES, W. J. CLARKE, F. T. BANNER, A. H. SMOUT, and
W. H. BLOW

ABSTRACT. Some larger foraminifera are recorded from various localities in the Central American region, many of them being illustrated. Additional information concerning, and new illustrations of, topotype material of some previously known forms are given. New subgenera *Vlerkina* and *Vlerkinella* (of the genus *Heterostegina*) are proposed; four new species and one new subspecies are described and illustrated. Certain aspects of the stratigraphy of the region are discussed, and the genus *Pliolepidina* is acknowledged to range down to the Late Eocene. The Oligocene age of certain occurrences of large foraminifera is confirmed by the associated planktonic foraminifera.

RECENTLY, one of us (W. H. B.) has had the opportunity of studying good planktonic foraminiferal assemblages from the Oligocene of Ecuador, Jamaica, and Alabama and from the Early Miocene of Puerto Rico. He has found that in each of these areas larger foraminifera are closely associated with planktonic foraminiferal assemblages which can be placed accurately in the planktonic foraminiferal scheme outlined by Banner and Blow (1965). In Ecuador, Jamaica, and Alabama the larger foraminiferal species are associated with the Early Oligocene Zone P. 18 planktonic faunas, whilst in Puerto Rico the Early Miocene (Zones N. 1 in part, and N. 2) has been recognized. Zone N. 2 on Carriacou has yielded *Miogypsina* cf. *gunteri* and *M. septentrionalis* and therefore we have little hesitation in considering this Zone N. 2 Early Miocene. Zone N. 1 (= P. 20), however, may be entirely Miocene or entirely Oligocene, or more probably includes both the latest Oligocene and the earliest Miocene, but as yet no direct independent evidence of its age has been found. On the other hand, Zone P. 19 has yielded *Nummulites fichteli* in East Africa (Eames *et al.* 1962) and therefore represents much of the so-called Rupelian (Middle Oligocene) of authors. In this paper we discuss those larger foraminifera from Ecuador, Jamaica, Alabama, and Puerto Rico which have been found associated with good Oligocene or Miocene planktonic assemblages and which can be placed in the zonal scheme of Banner and Blow, as well as some Late Eocene faunas from Venezuela and Panama. Synonymies are deliberately restricted to accurately identified material. British Museum (Natural History) registration numbers of material are in the sequence P47281 to P47352. Measurements of all chambers are external dimensions.

There are many varied opinions about the precise application of age and stage divisions in the Cainozoic sequence, and we have not attempted to resolve these problems in this paper. However, in order to provide the reader with an unambiguous biostratigraphic frame of reference, we have referred the horizons of provenance of the assemblages to the sequence adopted by Eames *et al.* (1962). For example, 'early part of Early Miocene' refers to faunas of which those listed (loc. cit., pp. 12, 14) against the column 'Aquitanian' constitute a part, and 'late part of Early Miocene' refers to faunas of which those listed (loc. cit., pp. 12, 14) against the column 'Burdigalian' constitute a part.

REVIEW OF THREE PERTINENT SPECIES

Some of the material to be described had to be compared with, among other forms, *Lepidocyclina yurnagunensis*, *Eulepidina undosa*, and *L. armata*. It appeared to us that the morphological characters of these forms were not adequately known and we are indebted to Dr. R. Cifelli for providing some toptype material of the first two species and to Dr. C. W. Drooger for lending us the type material of *L. armata* for study; the additional information concerning these three species is given below.

Lepidocyclina yurnagunensis Cushman 1919

Plate 49, figs. 1-5

1919 *Lepidocyclina canellei* Lemoine and Douvillé var. *yurnagunensis* Cushman, p. 57, text-fig. 6, pl. 12, figs. 7, 8.

Type locality. Dr. Cifelli informs us that the original information was incorrectly given, and that 'Sample 7348' should have read 'Sample 7548'. The locality is 'U.S. Geol. Surv. Locality 7548: Yuraguana, near Guantanamo, prov. Oriente, Cuba; flexure in rocks on west side of Yateras R., about 2½ miles south of Yuraguana, 3 miles (more or less) north of El Jigue; altitude, short distance above stream level, perhaps 150 ft. A.T.; from folded beds near contact between conglomerate and shale with overlying limestone'.

Remarks. The thin section from which Cushman's pl. 12, figs. 7 and 8 illustration was taken has kindly been re-photographed at the Smithsonian Institution, and is re-illustrated here as Plate 49, figs. 1, 2. The illustrations clearly show the very low and broad lateral chambers with convexly arched floors as originally mentioned, and also an indication that some specimens have a few small pillars, in spite of the fact that *yurnagunensis* was originally proposed as a variety of *L. canellei*, which has no pillars. Consequently, oriented sections of toptype specimens of *yurnagunensis* were prepared and are illustrated here as Plate 49, figs. 3-5 (P47281-3); they show that there may be a few small pillars having diameters of up to about 0.07 mm.

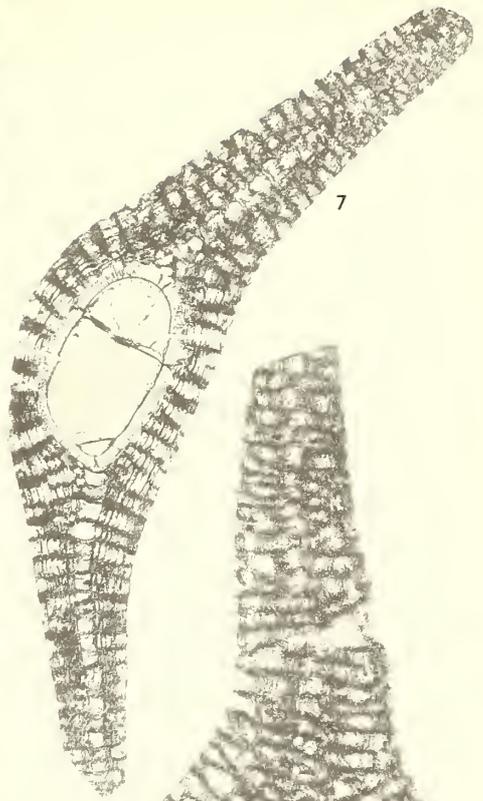
As is well known, the nucleocoenoch of this species is a little variable, and may be isolepidine or slightly pseudonephrolepidine; the example shown in Cushman's text-fig. 6a is not, however, of pliolepidine type as originally stated, and we have never seen an equatorial section, with a pliolepidine nucleocoenoch, which could be ascribed to the species *yurnagunensis*. Both Vaughan (1924, pl. 33, fig. 8) and Vaughan and Cole (1941, pl. 38, fig. 3) have published illustrations of the equatorial section of toptype specimens of *L. yurnagunensis*. The figures published by Seiglie (1965), if not strictly toptypic, are effectively very near toptypes.

EXPLANATION OF PLATE 49

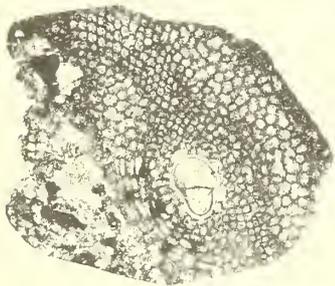
- Figs. 1, 2. *Lepidocyclina yurnagunensis* Cushman ($\times 20$). Re-illustration of original figures. U.S. Geol. Surv. Locality 7548, Cuba.
 Figs. 3-5. *Lepidocyclina yurnagunensis* Cushman ($\times 20$). Topotype. 3, axial section, P47281; 4, axial section, P47282; 5, equatorial section, P47283.
 Figs. 6, 7. *Eulepidina undosa* (Cushman) ($\times 15$). Topotype, U.S. Geol. Surv. Locality 6869, Antigua. 6, equatorial section, P47284; 7, axial section, P47285.



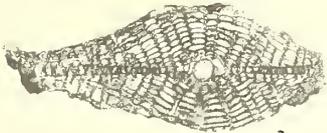
1



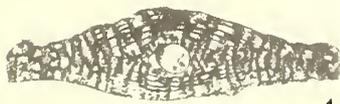
7



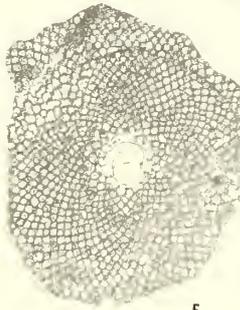
2



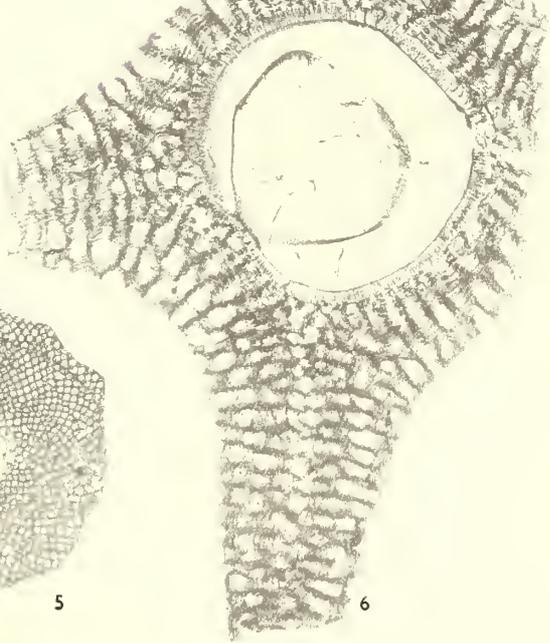
3



4



5



6

Eulepidina undosa (Cushman) 1919

Plate 49, figs. 6, 7

1919 *Lepidocyclina undosa* Cushman, p. 65, pl. 2, fig. 1a.*Type locality.* U.S. Geol. Surv. Station 6869, Long Island, Antigua.

Remarks. The original single illustration represented numerous entire specimens embedded in a lump of rock. Vaughan (1924, pl. 34, figs. 6, 7; *non* fig. 5 = *Lepidocyclina* (*s.s.*) or *Lepidocyclina* (*Nephrolepidina*)) illustrated the central portions of the equatorial sections of two megalospheric individuals from the type locality, and Vaughan and Cole (1941, pl. 41, fig. 1) illustrated an axial section of a topotype specimen. We illustrate here an equatorial (P47284) and an axial (P47285) section of topotype *E. undosa* to supplement previous descriptions.

The megalospheric nucleoconch has a protoconch of about 1.75 mm. diameter and a deutoconch of about 2.6 mm. diameter. In equatorial section it is seen that the chambers of the median chamber layer are arcuate; the section does not show any hexagonal chambers such as originally recorded, those visible being more like those in the example illustrated by Vaughan (1924) as his pl. 34, fig. 6. However, Vaughan's fig. 7 shows the presence of hexagonal median chambers at later growth stages, and such chambers may well occur in specimens referable to *E. undosa*. In axial section it is seen that, in contradiction to the original record that the species had no pillars, small pillars attaining a diameter of 0.15 mm. are present. In axial section, chambers of the equatorial layer, close to the nucleoconch, have at least 10 foramina penetrating each intercameral septum, the layer itself being up to 0.27 mm. thick there, but near the margin (eighteenth cycle of equatorial chambers) it is only 0.2 mm. thick.

No other references are included at present since it is evident that other forms have been incorrectly included in *E. undosa*. For example, specimens illustrated by Cole (1934, pl. 4, figs. 4, 5, ?10, 11, ?14, *non* fig. 13) have no centrum, no pillars, are not saddle-shaped, and have too small a megalosphere to be *E. undosa*.

Lepidocyclina armata Rutten 1928

Plate 50, figs. 1-5

1928 *Lepidocyclina* (*Isolepidina*) *rdouvillei* Lisson var. *armata* Rutten, p. 944, text-figs. 24l-m, 29a-d; pl. 2, figs. 27, 28.*Type locality.* Locality 42, west of Cerro Pinal, neighbourhood of Punta Sal, north-west Peru.

Remarks. The syntypic series described by Rutten consisted of four slides (D10591, 10597-9) from the type locality, three slides (D10600-2) from locality 69 Los Organos, and unillustrated forms from locality 44 Quebrada Seca, all being of Eocene age. The lectotype here selected is specimen no. 2 on Slide D10591; this and four other thin sections from the syntypic series are illustrated in Plate 50, figs. 1-5.

In addition to the characters recorded by Rutten, the following observations have been made. Specimen 1 on Slide D10599 shows that the true pillars attain a diameter of about 0.1 mm. at the surface: the same specimen shows that the equatorial chamber

layer attains a thickness of 0.1 mm. at a distance of 0.9 mm. from the centre. The microspheric form shows that the equatorial chambers attain a radial length of 0.055–0.06 mm. at the margin, their shape being arcuate, adjoining chambers in an annulus not touching. A specimen 0.85 mm. thick has 8 lateral chambers in a tier in the central region, the dimensions of the lumen of the eighth chamber being about 0.03 mm. high and 0.1 mm. wide. In axial section the chambers of the equatorial layer are seen to have only two apertures per chamber in the region of the centrum. Dimensions (in mm.) of three nucleocoenchs are:

		Slide 10591 specimen 1	Slide 10591 specimen 2	Slide 10601
<i>Protoconch:</i>	<i>width</i>	0.20	0.21	0.22
	<i>height</i>	0.12	0.16	0.14
<i>Deuteroconch:</i>	<i>width</i>	0.19	0.23	0.21
	<i>height</i>	0.15	0.16	0.16
<i>Sum of heights</i>		0.27	0.32	0.30

There are two primary auxiliary chambers, and about eight other auxiliary chambers, apparently symmetrically disposed in four spirals; although larger than the earlier equatorial chambers, they are not very noticeably so. The combined information given above and by Rutten convinces us that *armata* is specifically different from *L. rdouvillei* Lisson; the nucleocoenoch of *armata* is somewhat smaller, its test possesses distinct pillars, and its centrum is more clearly defined.

LATE EOCENE OF VENEZUELA

Faunas are recorded from the following three samples kindly made available for study by the Bataafse International Petroleum Maatschappij N.V.:

- (a) Beach of Laguna Unare, Estado Anzoategui; Peñas Blancas Limestone (type area).
- (b) Sample Kb5018, Cerro La Pedrera, 6 km. south of Boca de Unare, 14 km. north of Clarines, Distrito Peñalver, State of Anzoategui; Peñas Blancas Limestone (type locality).
- (c) Sample Kb5019, Cerro La Pedrera, 6 km. south of Boca de Unare, 14 km. north of Clarines, Distrito Peñalver, State of Anzoategui; Peñas Blancas Limestone (type locality).

Faunas are also recorded from the following two samples kindly made available for study by the Creole Petroleum Corp.:

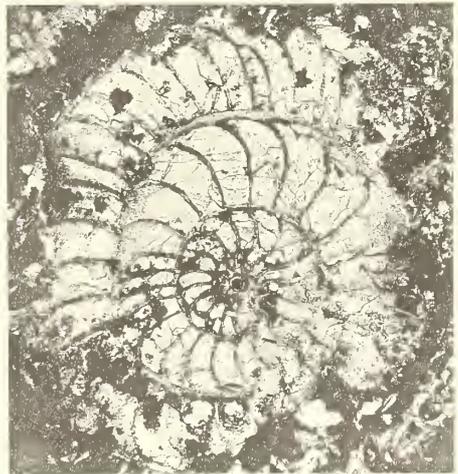
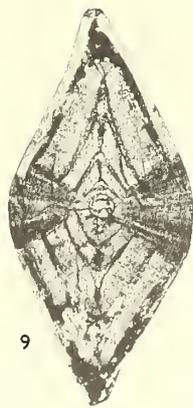
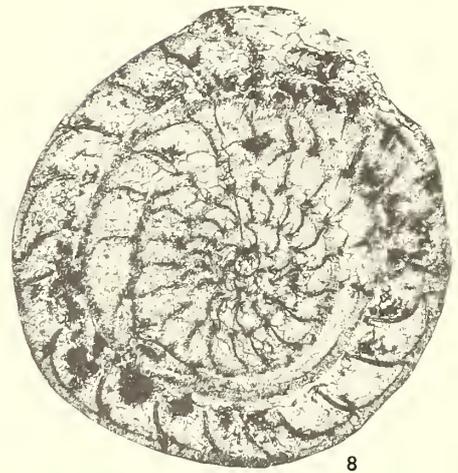
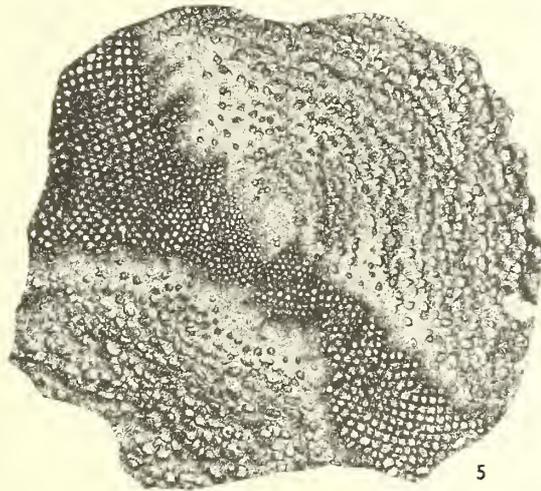
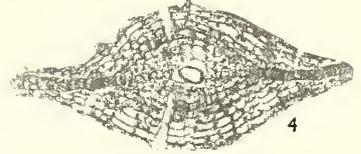
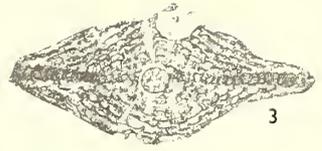
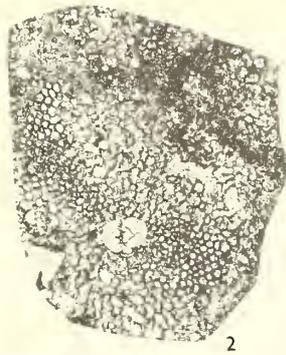
- (d) Sample 110746, Rio Chacual section, 1.85 km. upstream from Manarito; Peñas Blancas Limestone.
- (e) Sample 110786, 6 ft. from 110746; Peñas Blancas Limestone.

EXPLANATION OF PLATE 50

Figs. 1–5. *Lepidocyclina armata* Rutten ($\times 20$). Locality 42, W. of Cerro Pinal, Peru, Eocene. 1, equatorial section, lectotype; 2, equatorial section, syntype; 3, axial section, syntype; 4, axial section, syntype; 5, equatorial section of microspheric form, syntype.

Figs. 6, 7. *Palaeonummmlites kugleri* (Vaughan and Cole) ($\times 20$). Sample 110786, Rio Chacual section, Venezuela, Peñas Blancas Limestone, Late Eocene. 6, equatorial section P47288; 7, axial section, P47289.

Figs. 8, 9. *Palaeonummmlites palmarealensis* (Barker) ($\times 20$). Beach of Laguna Unare, Peñas Blancas Limestone, Late Eocene. 8, equatorial section, P47290; 9, axial section, P47291.



Asterocyclina asterisca (Guppy) 1866

1866 *Cisseis asteriscus* Guppy, p. 584, pl. 25, figs. 19a, b.

1941 *Discocyclina* (*Asterocyclina*) *asterisca* (Guppy); Vaughan and Cole, p. 60, pl. 23. (*cum bibl.*)

Material. Several thin sections in sample Kb5018.

Helicolepidina paucispira Barker and Grimsdale 1936

1936 *Helicolepidina paucispira* Barker and Grimsdale, p. 243, pl. 31, figs. 11, 12; pl. 33, figs. 4–6; pl. 36, figs. 1, 3; pl. 38, fig. 4.

1941 *Helicolepidina paucispira* Barker and Grimsdale; Vaughan and Cole, p. 76, pl. 45, fig. 2.

1962a *Helicolepidina spiralis* (Tobler); Cole, p. 145 (*pars*).

1962 *Helicolepidina paucispira* Barker and Grimsdale; Hanzawa, p. 144, pl. 6, fig. 32.

Material. One thin section in sample Kb5019.

Remarks. We agree with Hanzawa in regarding *paucispira* distinct from *spiralis*.

Helicostegina soldadensis Grimsdale in Vaughan and Cole 1941

1941 *Helicostegina soldadensis* Grimsdale, in Vaughan and Cole, pp. 77, 86, pl. 45, fig. 4; pl. 46, figs. 1–7.

Material. Many thin sections in sample Kb5018, a few thin sections in sample 110786, and several thin sections in the sample from Laguna Unare.

Lepidocyclina montgomeriensis Cole 1949

1949 *Lepidocyclina montgomeriensis* Cole, p. 270. (*cum bibl.*)

Material. Numerous thin sections from sample Kb5019.

Palaeonummulites kugleri (Vaughan and Cole) 1941

Plate 50, figs. 6, 7

1941 *Operculinoides kugleri* Vaughan and Cole, p. 42, pl. 10, figs. 3–5, 7, 8; pl. 13, figs. 1, 2.

1952 *Operculinoides kugleri* Vaughan and Cole; Cole, p. 9, pl. 3, figs. 1, 5, ?6, ?7.

Material. Several thin sections (including P47288–9) from sample 110786, many thin sections from sample Kb5018, and one thin section from sample Kb5019.

Remarks. The two illustrations of axial sections given by Cole (1952) do not seem to match well the original illustrations of axial sections given by Vaughan and Cole (1941). Although Cole (1958, p. 273) placed *kugleri* in the synonymy of *P. trinitatensis* (Nuttall), our material from Venezuela is a good match compared with the type description and illustrations of *kugleri*, but is not so inflated or so tightly coiled as *trinitatensis*, which we accordingly regard as different.

Palaeonummulites palmarealensis (Barker) 1939

Plate 50, figs. 8, 9

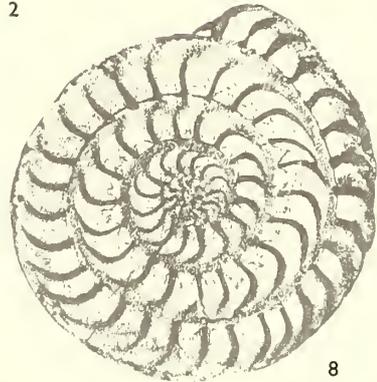
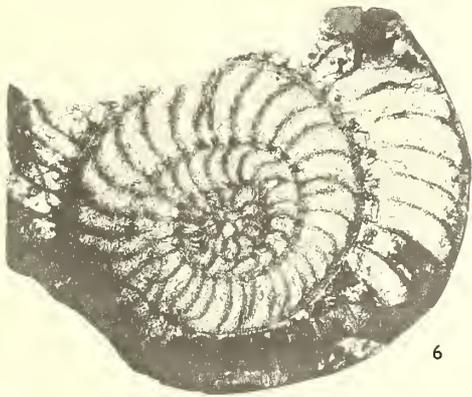
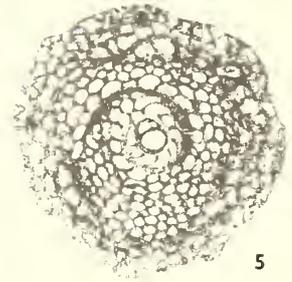
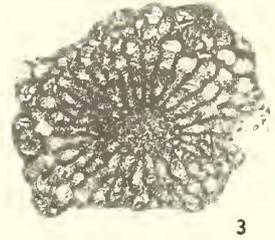
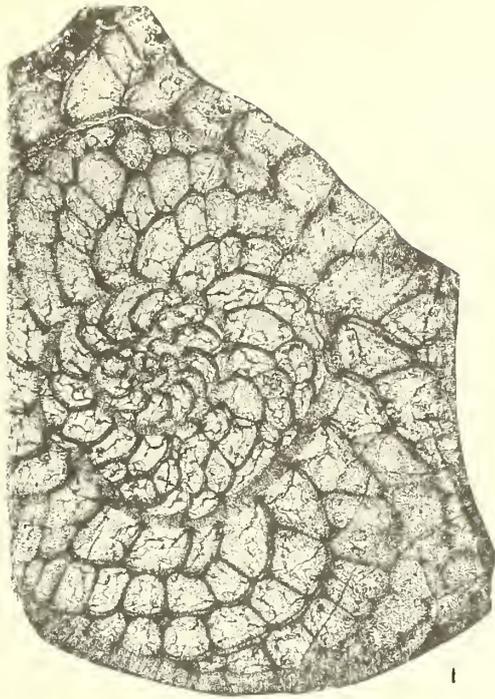
1939 *Operculioides paluarealensis* Barker, p. 314, pl. 13, fig. 8; pl. 18, fig. 1; pl. 22, figs. 7, 8.*Material.* Several thin sections (including P47290-1) from the Laguna Unare sample.*Remarks.* The original type material was recorded as having come from the 'Lower Oligocene Alazan formation', but one of us (W. H. B.) has evidence to show that it is really of Late Eocene age.*Palaeonummulites stainforthi* sp. nov.

Plate 51, figs. 6, 7

Material. Several thin sections (including P47292, the holotype, and P47293) from sample 110786, abundant thin sections in sample Kb5018, and one thin section in the Laguna Unare sample.*Description.* The axial section (of a representative specimen) indicates a diameter of 3.35 mm. and a thickness of 0.5 mm., giving a ratio of 6.7:1, so that the species is a fairly flat one. The small protoconch has a diameter of 0.13 mm. There is 1 whorl in a radius of 0.24 mm., and there are 2 in 0.4 mm., 3 in 0.73 mm., 4 in 1.4 mm., and 4½ in 1.55 mm. There are 7 septa in the first whorl, 14 in the second whorl, 24 in the third whorl, and 31 in the fourth whorl; they are quite closely spaced so that the chambers are considerably higher than long, and their tips are moderately well curved backwards distally.*Remarks.* Although similar to the Early Miocene species *P. dia* (Cole and Ponton) in its great compression and general septal shape, it is more tightly coiled and the septal ends are less strongly curved distally than in that species. Compared with the Middle Eocene *P. prenummulitifformis* (Barker), while similarly compressed, the new species lacks the granules (showing as small pillars in axial section) and the septal ends are distinctly less curved backwards distally.

EXPLANATION OF PLATE 51

- Figs. 1, 2. *Heterostegina (Vlerkiua) kugleri* subgen. et sp. nov. (×25). Beach of Laguna Unare, Peñas Blancas Limestone, Late Eocene. 1, equatorial section, P47286; 2, axial section, holotype, P47287.
- Figs. 3, 4. *Halkyardia bikiuiensis* Cole (×50). Sample 2049, type area of Playa Rica Formation, Ecuador, Early Oligocene. 3, transverse section, P47309; 4, vertical section, P47310.
- Fig. 5. *Helicolepidina paucispira* Barker and Grimsdale (×30). Ecuador, Playa Rica Sands, Early Oligocene. Equatorial section, P47311.
- Figs. 6, 7. *Palaeonummulites stainforthi* sp. nov. (×20). Sample 110786, Rio Chacual section, Venezuela, Peñas Blancas Limestone, Late Eocene. 6, equatorial section, holotype, P47292; 7, axial section, P47293.
- Figs. 8, 9. *Palaeonummulites antiguensis* (Vaughan and Cole) (×20). Sample PO. 35-1, La Rambla, Puerto Rico, Juana Diaz Formation, Early Miocene. 8, equatorial section, P47351; 9, axial section, P47352.





Pliolepidina tobleri (Douvillé) 1917 subsp. *panauensis* (Cushman) 1918

Plate 52, figs. 1–5; Plate 53, figs. 1–4; Plate 54, fig. 3

1918 *Lepidocyclina panamensis* Cushman, pp. 94, 95, pl. 39, figs. 1–6; pl. 42.1924 *Lepidocyclina* (*Pliolepidina*) *panamensis* Cushman; Vaughan, p. 819, pl. 33, fig. 1.

Material. Numerous thin sections (P47294–303) from sample 110746, and numerous thin sections from the Laguna Unare sample.

Remarks. The material illustrated here is a reasonable match for the form illustrated by Vaughan (1924, fig. 1) which is re-illustrated later in this paper. In our opinion these populations from Venezuela and Panama differ from those from Trinidad in that they are less inflated, the nucleoconch walls are thinner, and there may be as many as 7 to 12 small chambers arranged within the large nucleoconch chamber; the relationship is close, but since the different populations can be recognized, we regard *panauensis* as a subspecies of *P. tobleri* (neotypified by Eames and Clarke 1965). The general form of our megalospheric forms of *Pliolepidina* from the Vista Bella Limestone of Trinidad is strongly inflated, and they are referable to *P. tobleri* (*s.s.*). Again, some of the specimens illustrated by Sachs (1964, e.g. pl. 2, figs. 1–4, 6–9) as *Lepidocyclina* (*Eulepidina*) *undosa* are, in our opinion, *Pliolepidina tobleri* (*s.s.*); the specimens are from his Locality 3 (Cibao formation of Puerto Rico), which is within one foot of a sample yielding a rich *opina* Zone planktonic fauna and is therefore of Early Miocene age. Certain illustrated equatorial sections such as those of Cole (1960, pl. 3, fig. 1; 2 miles north of David, Panama) and Cole (1962*b*, pl. 8, fig. 8; loose block from Grenada) probably belong to the subspecies *panauensis* rather than to *P. tobleri* (*s.s.*).

Pliolepidina(?) *sp.*

Plate 54, figs. 1, 2

Material. A few specimens in matrix and one axial thin section (P47305) and one equatorial thin section (P47304) from the Laguna Unare sample; a few specimens in matrix and one axial thin section from sample 110746.

Description. These are microspheric forms. The equatorial section from the Laguna Unare sample was distinctly more than 11·0 mm. in diameter, and its accompanying axial section had a diameter of a little more than 14·0 mm. and a thickness of 2·0 mm. The axial section from sample 110746 had a diameter of more than 13·0 mm. and a thickness of 2·8 mm. In equatorial section the chambers are low-arcuate, with an occasional tendency to be slightly spatulate, attain a radial length of 0·12 mm. near the periphery, and adjacent ones of a cycle are not touching or occasionally just touching. In axial section the pillars are seen to attain a diameter of 0·11 mm., and in the equatorial chamber layer at least 14 intercameral apertures are developed in each septum near the periphery.

Remarks. In both these samples these microspheric forms appear to be the B form of *Pliolepidina tobleri panauensis*. It is noteworthy that they are considerably less inflated than the microspheric form of *Lepidocyclina trinitatis* and also *L. pustulosa* (possibly the microspheric form of *P. tobleri*), and that the pillars are also smaller.

Pseudophragmina (Proporocyclina) flintensis (Cushman) 1917

1917 *Orthophragmina flintensis* Cushman, p. 115, pl. 40, figs. 1, 2.

1941 *Pseudophragmina (Proporocyclina) flintensis* (Cushman); Vaughan and Cole, p. 61, pl. 20, figs. 8, 9.

Material. Two thin sections in sample Kb5018.

Some heterosteginid forms

Family NUMMULITIDAE

Genus HETEROSTEGINA d'Orbigny 1826

Subgenus HETEROSTEGINA

Type species. *Heterostegina depressa* d'Orbigny 1826; Recent.

Remarks. The subgenus is characterized by having the chamber lumina completely evolute, at least in the megalospheric form.

Subgenus VLERKINA subgen. nov.

Type species. *Heterostegina borneensis* van der Vlerk 1929, early part of Early Miocene ('e' stage).

Comparative diagnosis. The subgenus is characterized by having the chamber lumina partly involute, at least in the megalospheric form.

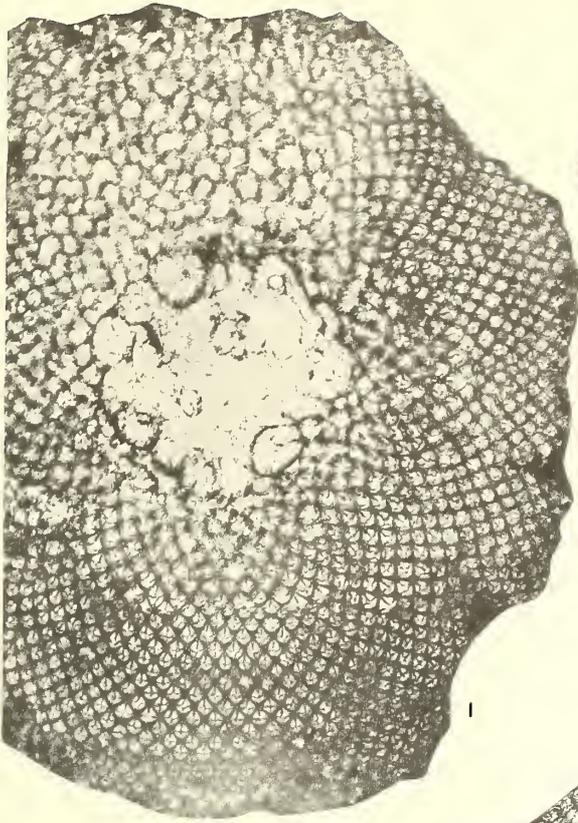
Remarks. Topotypic or near-topotypic material, donated to the British Museum (Natural History) by Professor I. M. van der Vlerk, has been sectioned by Dr. C. G. Adams, who has kindly let us study the material. The subgeneric comparative diagnosis is based on the axial section, which matches van der Vlerk's original description and illustration. *Vlerkina* differs from the genus *Grzybowskiia* Bieda 1950 in lacking the pentagonal/hexagonal chamberlets which are arranged in a favose pattern in equatorial view. The subgenus is named after Professor van der Vlerk.

'*Heterostegina borneensis*' auct. has been used extensively in the Far East to indicate the early part of the T_e 'letter stage' (Leupold and van der Vlerk 1931, van der Vlerk 1955). These forms, originally called 'spiroclypoid heterostegina' by Rutten (MS.), have proven stratigraphic value but poorly known infrageneric taxonomy. '*H. borneensis*' auct. probably comprises many species of *H. (Vlerkina)*; however, the new subgeneric taxon can now be used biostratigraphically for the various forms which have been recorded (e.g. Adams 1965, cf. Cole 1957c) as '*H. borneensis* van der Vlerk'.

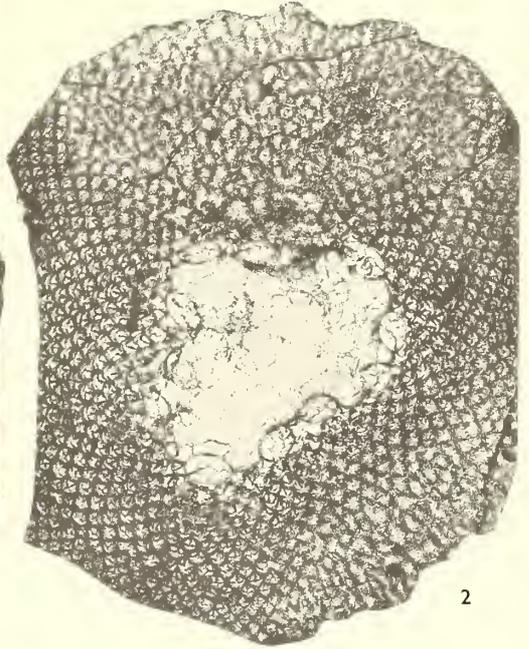
The stratigraphically youngest record of *Vlerkina* which can be related directly to planktonic foraminiferal zones is that by Coleman and McTavish (1964), who found

EXPLANATION OF PLATE 52

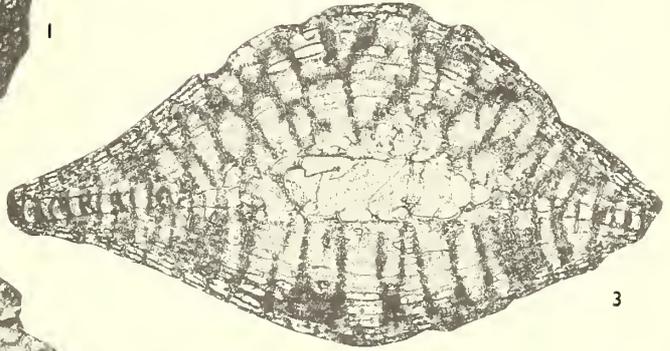
Figs. 1-5. *Pliolepidina tobleri* (Douville) subsp. *panamensis* (Cushman). Sample 110746, Rio Chacual section, Venezuela, Peñas Blancas Limestone, Late Eocene. 1, equatorial section ($\times 25$), P47294; 2, equatorial section ($\times 25$), P47295; 3, axial section ($\times 25$), P47296; 4, equatorial section ($\times 25$), P47297; 5, three axial sections ($\times 15$), P47298.



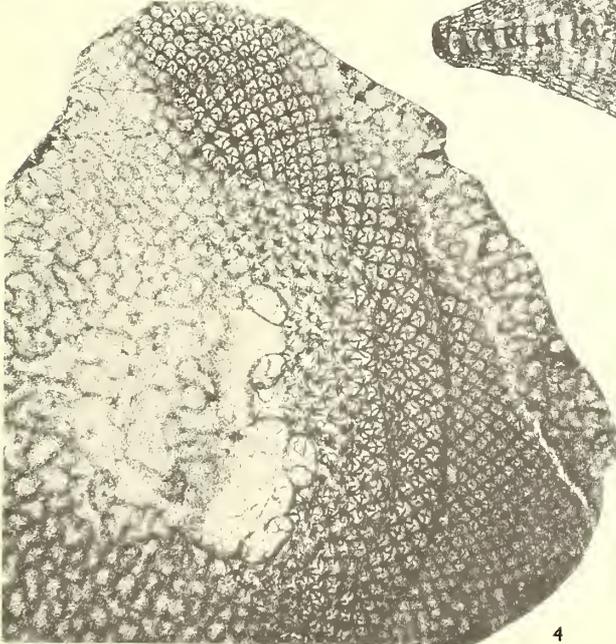
1



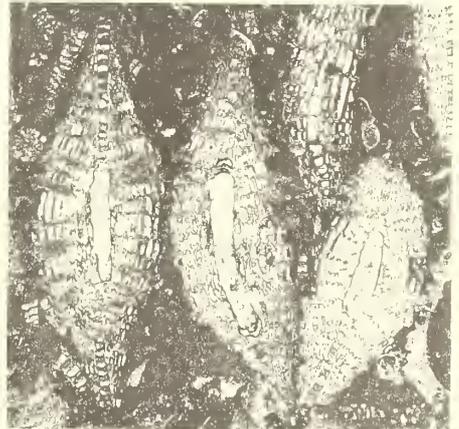
2



3



4



5

'*H. borneensis*' in direct association with *Miogypsina*, *Miogypsinoides*, *Eulepidina*, *Spiroclypeus*, *Globigerinoides quadrilobatus*, *Globoquadrina dehisceus*, *Globigerinita dissimilis*, and *G. unicava*. This assemblage is clearly referable to the T_e 'letter-stage', to the interval from latest Zone N. 4 to Zone N. 6, and to the Aquitanian stage.

Subgenus *VLERKINELLA* subgen. nov.

Type species. Heterostegina (Vlerkinella) kugleri sp. nov.; Late Eocene.

Comparative diagnosis. Axial section of the megalospheric form completely involute, the alar prolongations of the chambers extending to the centre; equatorial section of the megalospheric form as in *Heterostegina* (*s.s.*).

Remarks. Compared with *Vlerkina*, the alar prolongations of the chamber lumina in axial section extend to the centre, the test being completely involute. *Vlerkinella* also differs from the genus *Grzybowskiia* Bieda 1950 in lacking the pentagonal/hexagonal chamberlets which are arranged in a favose pattern in equatorial view. The subgenus is named after Professor van der Vlerk.

Heterostegina (Vlerkinella) kugleri subgen. et sp. nov.

Plate 51, figs. 1, 2

Material. One axial section (the holotype, P47287) and one equatorial section (P47286) in the sample from Laguna Unare.

Specific description. The axial section is of a specimen with a diameter of 4.14 mm. and a thickness of 0.93 mm., the species being complanate with a gently convex median portion, and completely involute. The megalosphere is subcircular, with a diameter of about 0.12 mm. There is 1 whorl in a radius of 0.21 mm., there are 2 in a radius of 0.51 mm., and 3 in a radius of 1.43 mm. There are 5 septa in the first whorl, 12 in the second whorl, and 15 in the third whorl. The first 9 chambers are undivided, and in the later stages 4-6 chamberlets are developed from each primary chamber; proximal chamberlets are subpentagonal, the others subhexagonal.

Remarks. We can find no record of any closely similar species in the literature. The species is named after Dr. H. G. Kugler.

LATE EOCENE OF PANAMA

Lepidocyclina rdouvillei Lisson 1921

Plate 55, fig. 4

1921 *Lepidocyclina (Isolepidina) rdouvillei* Lisson, p. 53, pl. 3, figs. 1-3; pl. 4, fig. 1; pl. 5, figs. 1-3.

Material. Four equatorial sections (of which one, P47306, is illustrated here) from U.S. Geol. Surv. Locality 6586e, given as near mouth of Tonosi River, Panama.

Pliolepidina tobleri (Douvillé) 1917 subsp. *panamensis* (Cushman) 1918

Plate 55, figs. 1-3

Synonymy. See p. 289.*Material.* Two equatorial sections (P47307-8 here illustrated) from U.S. Geol. Surv. Locality 6586e, given as near mouth of Tonosi River, Panama. By kind permission of the Smithsonian Institution, Vaughan's (1924, pl. 33, fig. 1) illustration of an equatorial section from the same locality is reproduced (Pl. 55, fig. 1).

EARLY OLIGOCENE OF ECUADOR

During the Caribbean Geological Congress held in Trinidad in 1965, Dr. Stainforth drew attention to his earlier (1948, p. 134) record of *Lepidocyclina yurnagunensis*, *L. undosa*, and *L. (Pliolepidina) tobleri* from beds regarded as of Early Oligocene age in Ecuador, although the presence of the latter species was regarded by him as puzzling since it had been considered an established Late Eocene index form.

The material described here has two origins. First, sample 2049, collected by Mr. Benton Stone and donated to the American Museum of Natural History, and subsequently presented, by exchange, to Dr. W. H. Blow, from the type area of the Playa Rica Formation in Ecuador. Second, three *Lepidocyclina*-bearing samples (nos. 17332, 17441, and 17429) forming part of a series of samples collected along the type section (17332 an offset sample) of Cushman and Stainforth's Unit 18 (Playa Rica Sands), all of which were kindly loaned to us by Drs. F. Zúñiga y Rivero and A. D. Euribe of the International Petroleum Co. Ltd. in Peru. The faunas are described below.

Halkyardia bikiniensis Cole 1954

Plate 51, figs. 3, 4

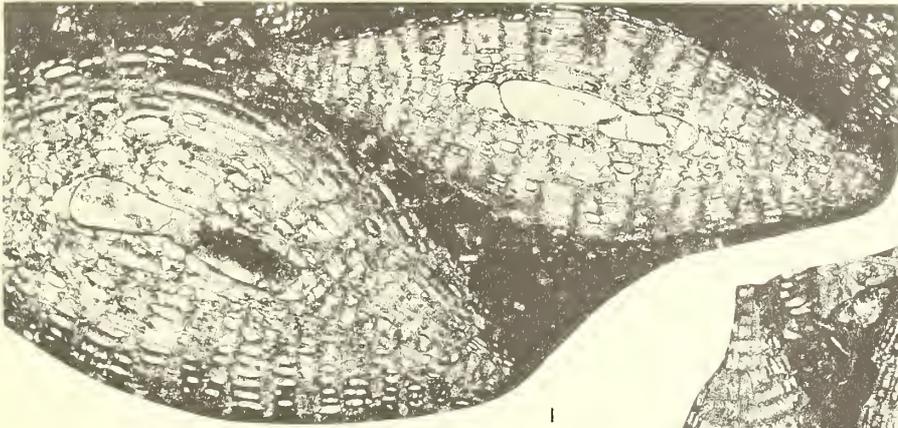
1954 *Halkyardia bikiniensis* Cole, p. 584, pl. 210, figs. 1-5.1957b *Halkyardia bikiniensis* Cole; Cole, p. 336, pl. 102, figs. 10, 11.*Material.* One specimen, and two thin sections (P47309-10) from the Early Oligocene sample 2049 of the Playa Rica Formation.*Remarks.* The species was previously recorded from the probable Oligocene of Bikini and the Late Eocene of Saipan.*Helicolepidina paucispira* Barker and Grimsdale 1936

Plate 51, fig. 5

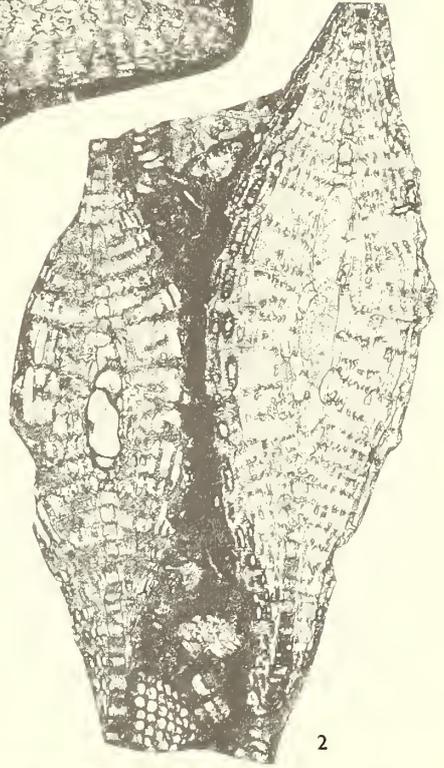
1936 *Helicolepidina paucispira* Barker and Grimsdale, p. 243, pl. 31, figs. 11, 12; pl. 33, figs. 4-6; pl. 36, figs. 1, 3; pl. 38, fig. 4.*Material.* Five hand specimens and one thin section (P47311) from the Early Oligocene sample 17441.*Remarks.* Neither the genus nor the species has been recorded from above the Late Eocene before. Sample 17441 contains a planktonic fauna representative of an Early

EXPLANATION OF PLATE 53

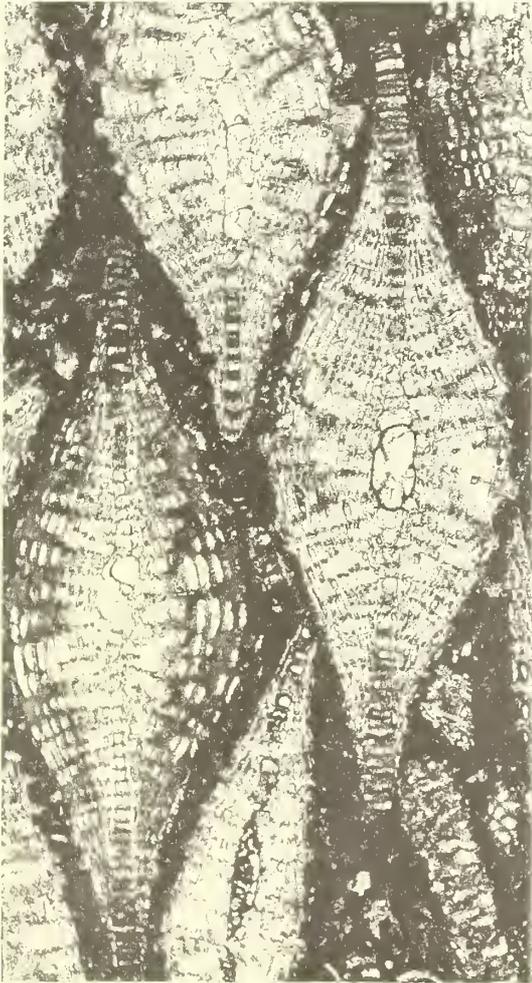
Figs. 1-4. *Pliolepidina tobleri* (Douvillé) subsp. *panamensis* (Cushman) ($\times 25$). Sample 110746, Rio Chacual section, Venezuela, Peñas Blancas Limestone, Late Eocene. 1, two axial sections, P47299; 2, two axial sections, P47300; 3, three axial sections, P47301; 4, equatorial section, P47302.



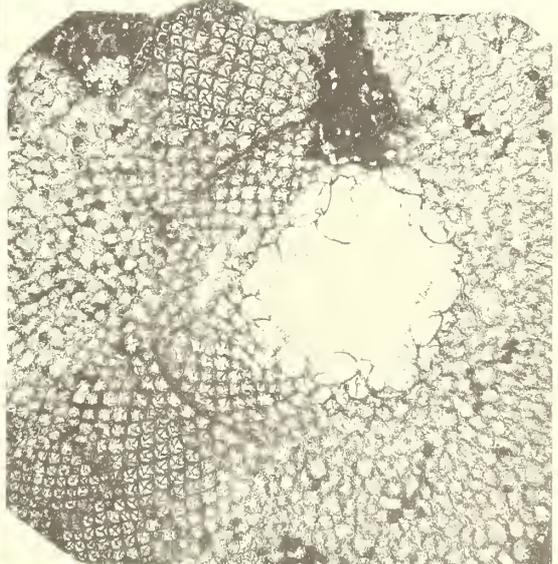
1



2



3



4

Oligocene age (Zone P. 18, *teste* W. H. B.), but, before extending the range of the genus and species up into the Early Oligocene, it would be advisable to await further knowledge of the stratigraphy of underlying horizons in the area, since the specimens might be reworked. In the initial stage of the equatorial section here illustrated there are 9 undivided chambers as against 5 in the type material, but we know of no reason at present why this should be regarded as even of subspecific value.

Lepidocyclus yurnagunensis Cushman 1919 subsp. *morganopsis* Vaughan 1933a

Plate 55, figs. 5-9; Plates 56, figs. 1, 2

1919 *Lepidocyclus morganii* Lemoine and R. Douvillé; Cushman, p. 59, text-fig. 7; pl. 11, figs. 1-3.

1933a *Lepidocyclus yurnagunensis* Cushman var. *morganopsis* Vaughan, p. 354.

1948 *Lepidocyclus yurnagunensis* Cushman; Stainforth, p. 134.

Material. Numerous hand specimens (1 registered P47312) and 7 (6 registered P47313-8) thin sections from sample 2049; 6 hand specimens and 1 thin section from sample 17441; 11 hand specimens and 1 thin section from sample 17429; numerous specimens and 3 thin sections from sample 17322. All four samples associated with planktonic faunas of Early Oligocene age.

Description of Ecuadorean material. The hand specimens have an inflated median centrum surrounded by a thin flange. An axial section (P47315) has a diameter of 3.3 mm. and a thickness of 1.0 mm.; another axial section has a diameter of 2.5 mm. and a thickness of 0.9 mm. An equatorial section has a diameter of 4.0 mm. The hand specimens have up to 16 pillars in the region of the centrum, such pillars attaining a diameter of 0.15 mm. to 0.2 mm., and not reaching the equatorial chamber layer. The lateral chambers attain approximately the same dimensions. The nucleoconch is isolepidine, dimensions (in mm.) of four examples being:

	(a)	(b)	(c)	(d)
<i>Protoconch:</i> width	0.25	0.27	0.23	0.19
height	0.15	0.14	0.14	0.10
<i>Deuteroconch:</i> width	0.23	0.28	0.23	0.19
height	0.16	0.18	0.16	0.12
<i>Sum of heights</i>	0.31	0.32	0.30	0.22

There are two primary auxiliary chambers which are usually a little larger than other chambers of the equatorial chamber layer, but no adauxiliary chambers; there are two or three smaller inter-auxiliary chambers in series in each of the four quadrants of the embryont; the periebryonic chambering is completed by one protoconchal and one deuteroconchal symmetrical auxiliary chamber. The normal equatorial chambers are ogival, but become spatulate later and attain a radial length of about 0.11 mm. near the periphery; they present a fairly definite engine-turned appearance in general view; some are separate, some just contiguous. In axial section the equatorial chamber layer attains a thickness of 0.15 mm. near the margin. In the outer 0.3 mm. of the central region there are 6 lateral chambers in a tier. Although the lumina of these lateral chambers attain a height of 0.03 mm. and a width of 0.11 mm. in the central region near the bigger pillars, normal lumina have a height of 0.03 mm. and a width of 0.08 mm.

Remarks. This form shows some similarity to *L. armata* (Rutten) which differs, however, in having smaller pillars which reach the equatorial chamber layer, and in having ogival equatorial chambers which do not present any marked engine-turned appearance. Although *L. yurnagunensis* (s.s.) is somewhat similar, the nucleoconch is usually more elongate, true pillars are smaller or absent, and the lateral chambers as seen in axial section are normally relatively wider and less high; these characters readily distinguish *L. yurnagunensis* (s.s.) from the subspecies *morganopsis* with which we identify the Ecuadorean material described above. It is evident that there has been some confusion in the identification of these two forms, but, although the subspecies *morganopsis* was originally described from beds we believe to be of Early Miocene age and is now shown to range down into the Early Oligocene, we have no acquaintance with, or knowledge of any reference to, *yurnagunensis* (s.s.) occurring below the Early Miocene.

Lepidocyclina (*Nephrolepidina*) *wilsoni* sp. nov.

Plate 56, figs. 3-5

1948 *Lepidocyclina undosa* Cushman; Stainforth, p. 134.

Material. Nine hand specimens, and three thin sections (P47319-21, of which P47321 is the holotype) from the Early Oligocene sample 2049 from the type area of the Playa Rica formation. Eighteen specimens and three thin sections from the Early Oligocene sample 17322.

Description. Flatly lenticular, the holotype having a diameter of 4.85 mm. One topotype specimen has a diameter of 6.6 mm. and a thickness of 1.9 mm., giving a ratio of 3.5:1; a second topotype specimen has a diameter of 4.8 mm. and a thickness of 0.8 mm., giving a ratio of 6:1. The holotype shows that the megalospheric nucleoconch is nephrolepidine and has the following dimensions:

Protoconch: width 0.45 mm., height 0.29 mm.

Deuteroconch: width 0.55 mm., height 0.28-0.36 mm.

Sum of heights (along median line): 0.55 mm.

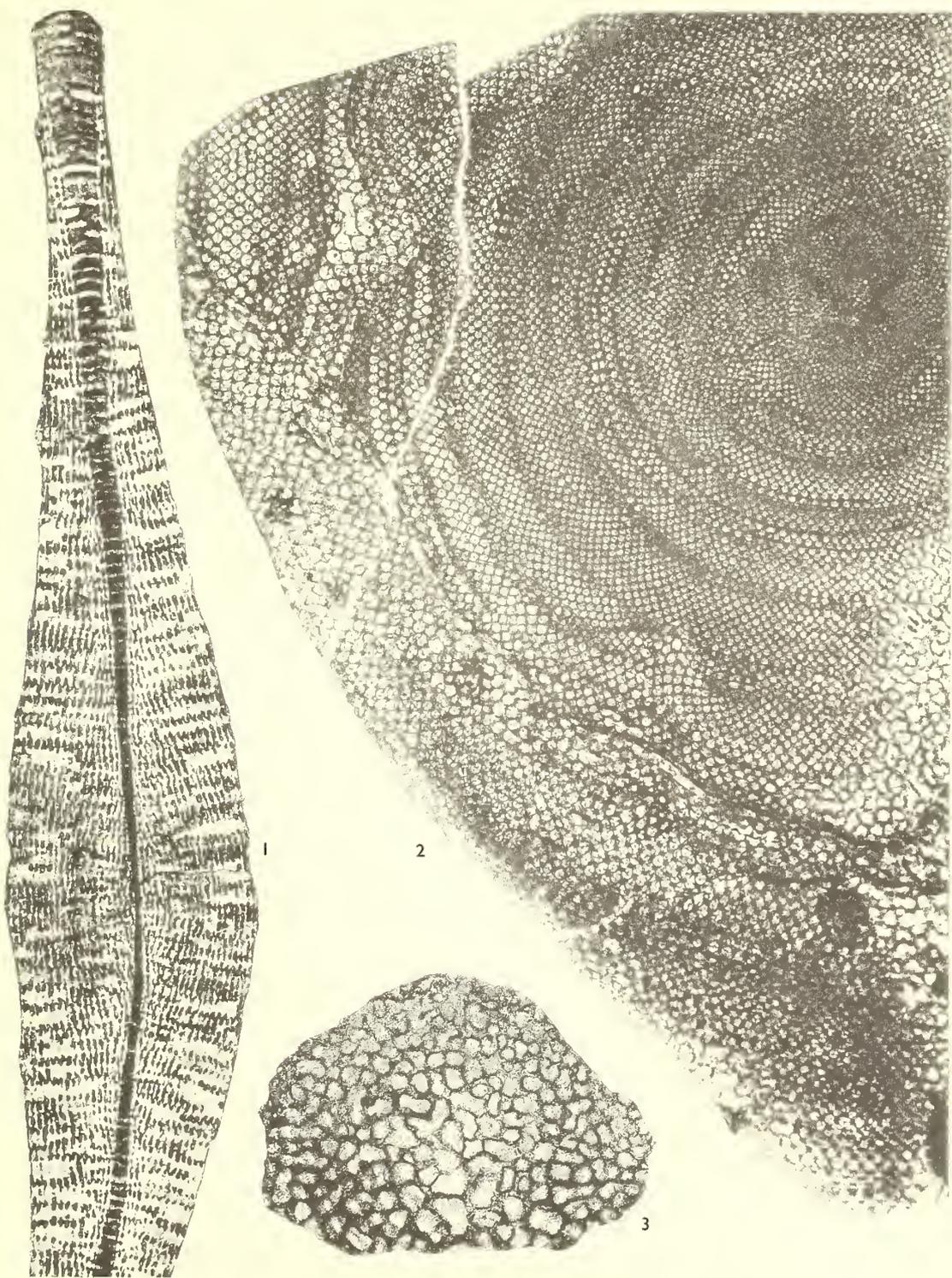
The auxiliary chambers are not well seen, but, although a few may be rather long, they are not conspicuously larger than the subsequent chambers of the equatorial layer. The equatorial chambers are low ogival, conjoint, not separate, with a radial length of about 0.1 mm. near the outer margin of the holotype. Tangential and axial sections confirm the appearance of the hand specimens in that there is no sign of pillars. In axial section there are 7 lateral chambers in a tier in the central region of the test; they are wide and low, their lumina being about 0.09 mm. wide and 0.02 mm. high.

Remarks. This species is named after Mr. C. C. Wilson who has contributed much to the stratigraphy of the Central American region. The most closely similar species seems

EXPLANATION OF PLATE 54

Figs. 1, 2. *Pliolepidina*(?) sp. ($\times 15$). Sample 110746, Rio Chacual section, Venezuela, Peñas Blancas Limestone, Late Eocene. 1, axial section of microspheric specimen, P47305; 2, equatorial section of microspheric specimen, P47304.

Fig. 3. *Pliolepidina tobleri* (Douville) subsp. *panamensis* (Cushman) ($\times 25$). Sample 110746, Rio Chacual section, Venezuela, Peñas Blancas Limestone, Late Eocene. Tangential section, P47303.



to be *L. (N.) sanfernandensis* Vaughan and Cole, which, however, is papillate and has small pillars, and which has a nucleoconch about twice as large as *L. (N.) wilsoni*; the illustrations of *L. (N.) sanfernandensis* also indicate the presence of a median boss on many of the specimens.

Dr. Hofker has kindly let us see some notes and illustrations of a form from the same or an equivalent horizon in Ecuador. His form evidently belongs, at least in part, to *L. (N.) wilsoni*; although the nucleoconchs of some of his specimens are rather more trybliolepidine in form, they are not eulepidine, and, like our specimens, they also differ from *E. undosa* in the complete absence of pillars and in the nucleoconch being less than half as large.

EARLY OLIGOCENE OF JAMAICA

Lepidocyclina yurnagunensis Cushman 1919 subsp. *morganopsis* Vaughan 1933a

Plate 56, fig. 6, 7

Synonymy. See p. 293.

Material. Two rock slides (P47322–3) from sample 621 (presented by Mr. E. Robinson), uppermost part of the Bonny Gate Formation in St. Mary's Parish, Jamaica, of Early Oligocene age.

Remarks. This material is indistinguishable from the specimens of the same subspecies from the Early Oligocene of Ecuador (see p. 293). The Jamaican sample also contains a good planktonic fauna of Early Oligocene age (Zone P.18, *teste* W. H. B.).

EARLY OLIGOCENE OF ALABAMA

Lepidocyclina mantelli (Morton) 1833

Plate 56, figs. 8–11; Plate 57, figs. 1–5

1833 *Nummulites mantelli* Morton, p. 291, pl. 5, fig. 9.

1928 *Lepidocyclina (Lepidocyclina) mantelli* (Morton); Vaughan, pl. 23, fig. 2.

1965 *Lepidocyclina mantelli* (Morton); Ellis and Messina (*pars*), e.g. figs. 67, 68.

Material. Several specimens from the Red Bluff (Early Oligocene) samples UWS110 and 111 (P47324–5 from UWS111); several specimens from samples UWS124, 125, 126, 127, 132, 133, many specimens from UWS134, 135, several specimens from UWS 136, 137, 138, and many specimens from UWS139, 140, and 141, all from the so-called Marianna Limestone (Early Oligocene) of Little Stave Creek (P47326–31, from sample UWS140).

Remarks. We illustrate (Pl. 57, fig. 4) for comparison an equatorial view of toptype *L. mantelli* from the Professor Morris Collection in the British Museum (Natural History). Material from samples UWS 109–41 was provided by Dr. Brooks Ellis and Miss Messina.

EARLY MIOCENE OF PANAMA

Miogypsina cushmani Vaughan 1924

1924 *Miogypsina cushmani* Vaughan, pp. 802, 813, pl. 43, figs. 1, 2 (*non* figs. 3–8).

Material. Many specimens from the Culebra Formation at sample stations 6010 and 6012a. 6010 is 600–700 ft. south of Miraflores Locks and also contains a rich planktonic fauna of Zone N. 7/N. 8 (high in the early part of the Early Miocene) age; 6012a is from south of Empire Bridge, Gaillard Cut, and is probably of much the same age. From what we have seen in the portions of these samples lent to us by Dr. Cifelli, we can confirm Cole's (1952, p. 17) statement that *Pliolepidina tobleri* does not occur in them as had been suggested earlier by Cushman (1918 (1919)).

EARLY MIOCENE (EARLY PART) OF PUERTO RICO

Dr. K. N. Sachs Jr. kindly donated a sample (PO35-1) to Dr. W. H. Blow for study. The sample comes from near the middle of the Juana Diaz Formation, from an excavation for a new house, NE.-trending segment of Calle G, La Rambla, Ponce quadrangle SW., Puerto Rico. The location is only 1 m. below other samples which, according to Blow, yield good planktonic foraminiferal faunas determinative of the *opima* Zone (of Bolli 1957, see also Pessagno 1963); this is virtually equivalent to Zone N. 2 of Banner and Blow (1965) which they consider to be very early in the Early Miocene.

Eulepidina favosa (Cushman) 1919

Plate 57, fig. 6

1919 *Lepidocyclus favosa* Cushman, p. 66, pl. 3, figs. 1b, 2; pl. 15, fig. 4.

1941 *Lepidocyclus (Eulepidina) favosa* Cushman; Vaughan and Cole, p. 75, pl. 40, figs. 1-4 (cum bibl.).

1952 *Lepidocyclus (Eulepidina) favosa* Cushman; Cole, p. 30, pl. 22, figs. 1-5 (cum bibl.).

Material. Two hand specimens and one thin section (P47332).

Remarks. These specimens are fully representative of the species, which has not yet been found below the early part of the Early Miocene (see Eames *et al.* 1962).

Eulepidina undosa (Cushman) 1919 subsp. *laramblaensis* subsp. nov.

Plate 57, figs. 7, 8

1962 *Lepidocyclus (Eulepidina) undosa* Cushman; Sachs and Gordon, p. 15 (*pars*), pl. 1, fig. 9.

Material. Four hand specimens, one equatorial section (the holotype, P47333), and one axial section (P47334).

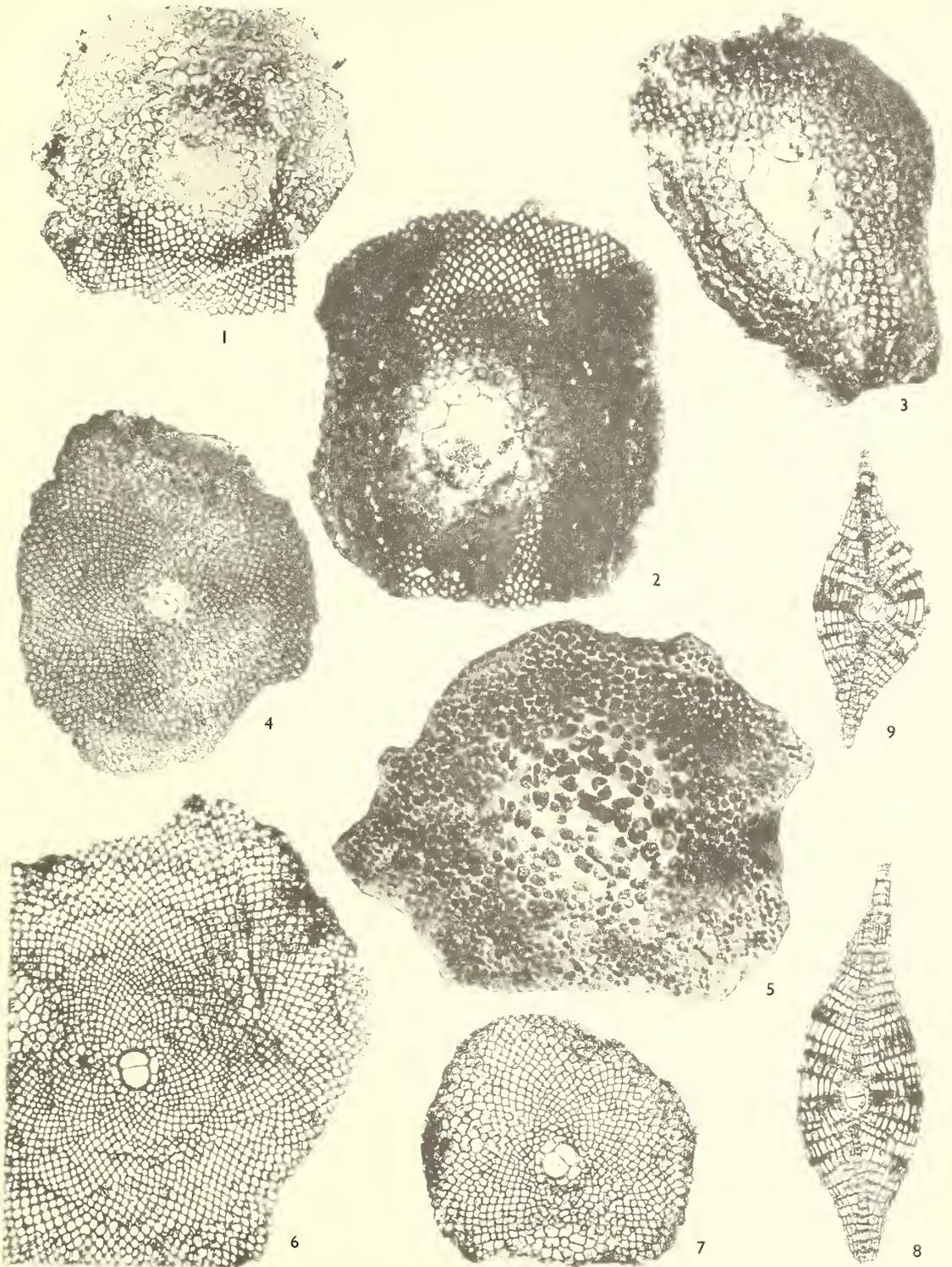
Description. The specimens are gently saddle-shaped, and have a small, distinct centrum; one specimen has a diameter of 7.2 mm. and a thickness of 1.2 mm. The holotype has a diameter of 3.7 mm. The centrum occupies about one-quarter to one-half of the diameter; it has a regular scatter of pillars attaining a diameter of up to 0.13 mm. and they are from 0.15 mm. to 0.2 mm. apart (centre to centre), gradually decreasing in size on the flange, and have 4-7 lateral chambers around them. The megalosphere is eulepidine,

EXPLANATION OF PLATE 55

Figs. 1-3. *Pliolepidina tobleri* (Douville) subsp. *panamensis* (Cushman) ($\times 25$). U.S. Geol. Surv. Locality 6586e, near mouth of Tonosi River, Panama, Late Eocene. 1, reproduction of Vaughan's (1924, pl. 33, fig. 1) illustration of an equatorial section; 2, equatorial section, P47307; 3, equatorial section, P47308.

Fig. 4. *Lepidocyclus rdouvillei* Lisson ($\times 25$). U.S. Geol. Surv. Locality 6586e, near mouth of Tonosi River, Panama, Late Eocene. Equatorial section, P47306.

Figs. 5-9. *Lepidocyclus yurnaguensis* Cushman subsp. *morganopsis* Vaughan ($\times 20$). Sample 2049, Ecuador, type area of Playa Rica Formation, Early Oligocene. 5, hand specimen, P47312; 6, equatorial section, P47313; 7, equatorial section, P47314; 8, axial section, P47315; 9, axial section, P47316.



the protoconch being rounded (with one side a little flattened) and measuring (holotype) 1.05×0.85 mm., the deutoconch being rounded and with a diameter of 1.55 mm. The chambers of the equatorial layer are oval to subhexagonal and do not vary much in size with growth although somewhat variable individually; their radial length varies from about 0.06 mm. to 0.1 mm. The equatorial chamber layer has a thickness of about 0.15 mm. both near the margin and near the middle; on the outer part of the flange the equatorial chambers do not seem to develop more than 6 intercameral apertures.

Remarks. This subspecies evidently includes some forms included by some authors in *E. undosa* (*s.s.*). However, in the subspecies *laramblaensis* the megalosphere is distinctly smaller, and the equatorial chamber layer is less massive, has thinner walls, and is not so thick, and the chambers themselves have fewer intercameral apertures.

Lepidocyclus (*Lepidocyclus*) *canellei* Lemoine and R. Douvillé 1904

Plate 59, fig. 7

1904 *Lepidocyclus caneliei* Lemoine and R. Douvillé, pp. 20, 22, pl. 1, fig. 1; pl. 3, fig. 5.

1941 *Lepidocyclus* (*Lepidocyclus*) *canellei* Lemoine and R. Douvillé; Vaughan and Cole, p. 70, pl. 35, figs. 6, 7; pl. 41, figs. 4, 5 (*cum bibl.*).

1962 *Lepidocyclus* (*Lepidocyclus*) *canellei* Lemoine and R. Douvillé; Sachs and Gordon, p. 14, pl. 3, fig. 3 (*cum bibl.*).

Material. One hand specimen, one polished specimen, and one thin section (P47335).

Remarks. The characters of these specimens are typical of the species, which has not yet, apparently, been recorded from below the Miocene (see Eames *et al.* 1962).

Lepidocyclus (*Lepidocyclus*) *cf. crassica* Vaughan and Cole 1933

Plate 58, figs. 1-3

1962 *Lepidocyclus* (*Lepidocyclus*) *giraudi* R. Douvillé; Sachs and Gordon (*pars*), p. 14 (*pars*), pl. 1, figs. 8, 11; pl. 2, fig. 9; pl. 3, figs. 2, 9 (*non* pl. 1, fig. 6 = *L. (L.) sachsi* sp. nov.; *nec* pl. 3, fig. 4 = ?)

Material. Two hand specimens, and three thin sections (P47336-8).

Description. Test lenticular, not clearly differentiated into centrum and flange. An axial section has a diameter of 2.75 mm. and a thickness of 1.15 mm., and cuts 3 large pillars. A hand specimen shows about 13-14 pillars in the middle half of the surface and attaining a diameter of 0.15 mm. on it, although as much as 0.3 mm. in the axial section. The nucleococonch is isolepidine and has the following dimensions:

<i>Protoconch:</i>	<i>height</i> 0.12 mm.
	<i>width</i> 0.18 mm.
<i>Deutoconch:</i>	<i>height</i> 0.13 mm.
	<i>width</i> 0.18 mm.
<i>Sum of heights:</i>	0.25 mm.

There are two fairly distinct primary auxiliary chambers but no adauxiliary chambers. The chambers of the equatorial layer are very squat ogival and noticeably annular in their arrangement; they attain a radial length of 0.07 mm. near the margin. In axial section the equatorial chamber layer is 0.08 mm. thick near the middle and 0.16 mm. thick near the margin, where as many as 4 apertures are developed. The floors of the lateral chambers are relatively quite thick, and the lateral chambers themselves are not very wide.

A larger individual, 6.7 mm. in diameter, proved on sectioning to be microspheric, the chambers of the equatorial layer being of the same general shape and same general size as in the megalospheric individuals, attaining a radial length of 0.15 mm. near the margin.

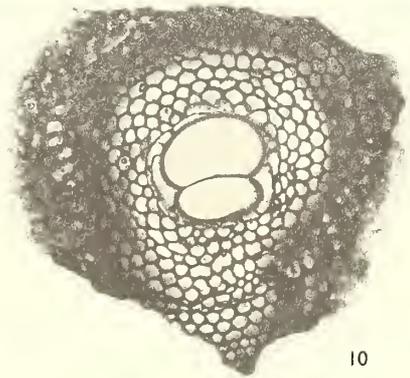
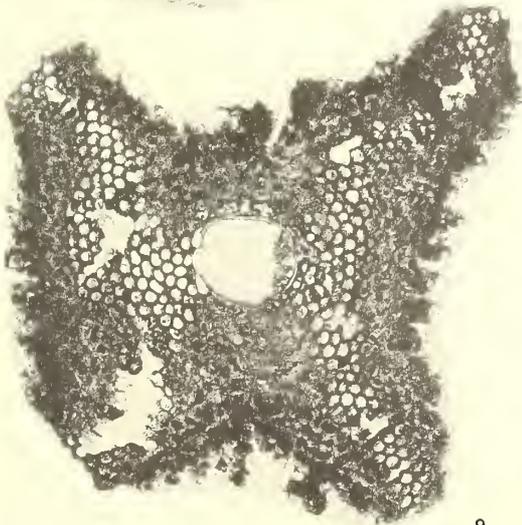
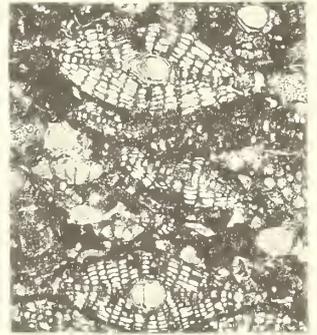
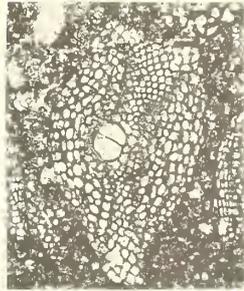
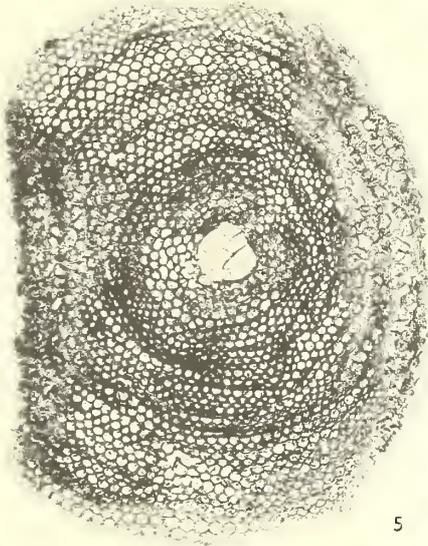
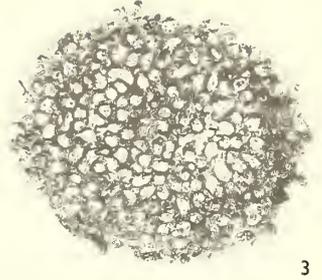
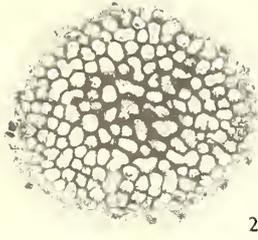
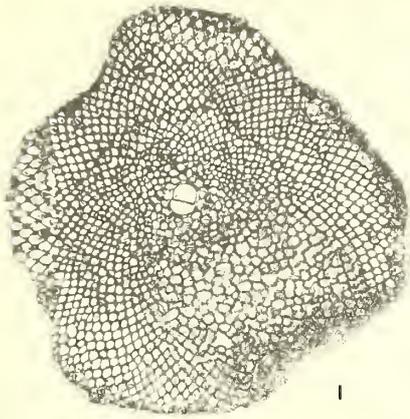
Remarks. This material matches very well those specimens illustrated by Sachs and Gordon (1962) on their pl. 1, figs. 8, 11, pl. 2, fig. 9, and pl. 3, figs. 2, 9 as *L. (L.) giraudi*. These combined collections, however, completely lack the 'long, radial pustules' and flattened centrum of that species. Compared to the specimens from the Morne Diablo Quarry (Trinidad) that Cole (1957a) illustrated as *L. (L.) giraudi* the nucleocoenchs of these combined collections are only about one-third the size; on their morphological characters the specimens illustrated by Cole in 1957 are neither *L. (L.) giraudi* nor the species here recorded. Although Cole (1957a) placed both *L. (L.) parvula* and *L. (L.) parvula crassicosta* in the synonymy of *L. (L.) giraudi*, we would, on their morphological

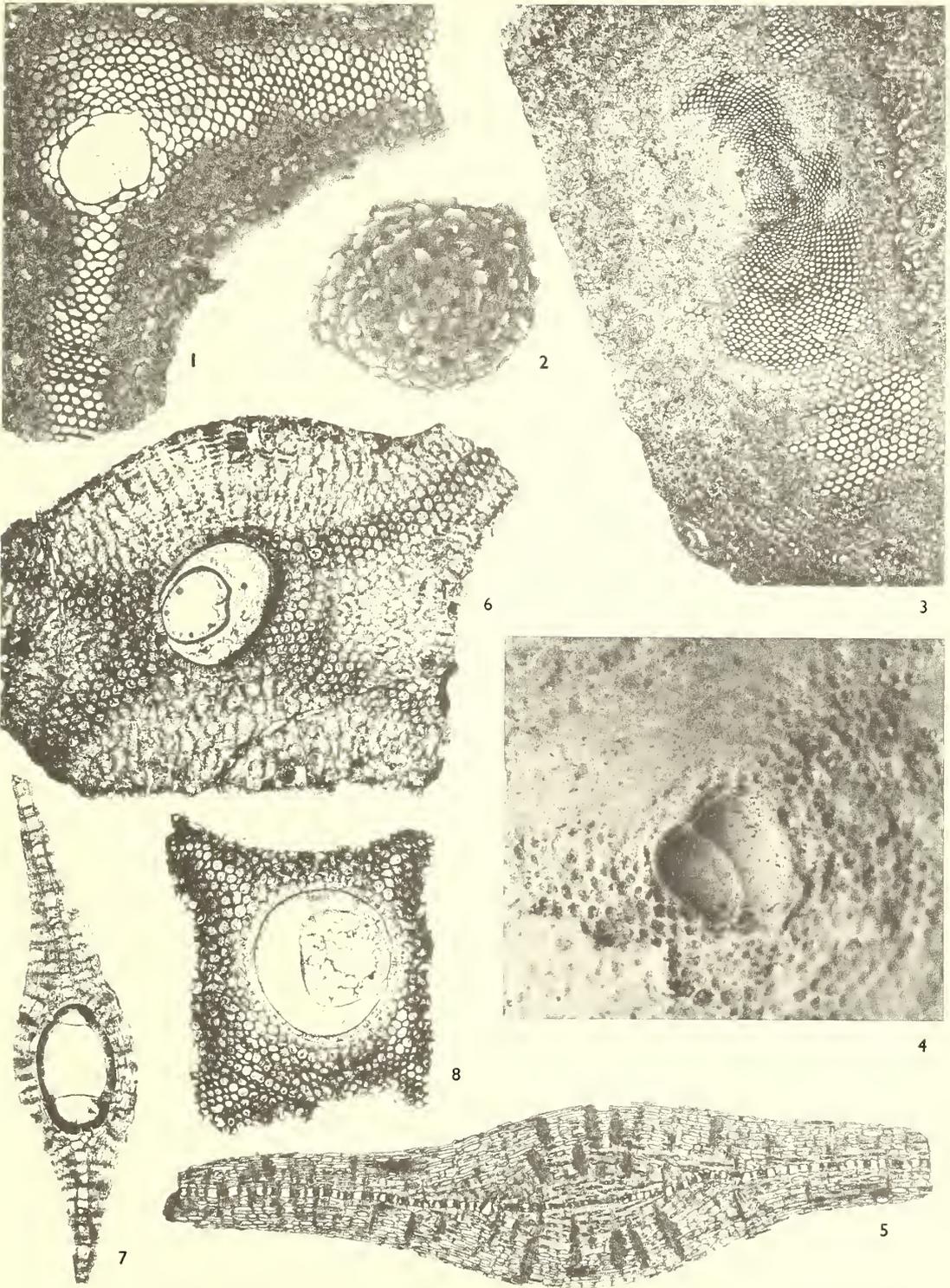
EXPLANATION OF PLATE 56

- Figs. 1, 2. *Lepidocyclina yurnagunensis* Cushman subsp. *morganopsis* Vaughan ($\times 20$). Sample 2049, Ecuador type area of Playa Rica Formation, Early Oligocene. 1, equatorial section, P47317; 2, tangential section, P47318.
- Figs. 3-5. *Lepidocyclina (Nephrolepidina) wilsoni* sp. nov. ($\times 15$). Sample 2049, Ecuador, type area of the Playa Rica Formation, Early Oligocene. 3, tangential section, P47319; 4, axial section, P47320; 5, equatorial section, holotype, P47321.
- Figs. 6, 7. *Lepidocyclina yurnagunensis* Cushman subsp. *morganopsis* Vaughan ($\times 20$). Sample 621, St. Mary's Parish, Jamaica, uppermost part of Bonny Gate Formation, Early Oligocene. 6, equatorial section, P47322; 7, axial section, P47323.
- Figs. 8, 9. *Lepidocyclina mantelli* (Morton) ($\times 15$). Sample UWS111, Little Stave Creek, Alabama; Red Bluff, Early Oligocene. 8, axial section, P47324; 9, equatorial section, P47325.
- Figs. 10, 11. *Lepidocyclina mantelli* (Morton) ($\times 15$). Sample UWS140, Little Stave Creek, Alabama, so-called Marianna Limestone, Early Oligocene. 10, equatorial section, P47326; 11, axial section, P47327.

EXPLANATION OF PLATE 57

- Figs. 1-3, 5. *Lepidocyclina mantelli* (Morton) ($\times 15$). Sample UWS140, Little Stave Creek, Alabama, so-called Marianna Limestone, Early Oligocene. 1, equatorial section, P47328; 2, tangential section, P47329; 3, equatorial section of a microspheric specimen, P47330; 5, axial section of a microspheric specimen, P47331.
- Fig. 4. *Lepidocyclina mantelli* (Morton) ($\times 20$). View of equatorially split megalospheric topotype specimen from the Professor Morris collection in the British Museum (Natural History).
- Fig. 6. *Eulepidina favosa* (Cushman) ($\times 15$). Sample PO.35-1, La Rambla, Puerto Rico, Juana Diaz Formation, Early Miocene. Equatorial section, P47332.
- Figs. 7, 8. *Eulepidina undosa* (Cushman) subsp. *laramblaensis* subsp. nov. ($\times 15$). Sample PO.35-1, La Rambla, Puerto Rico, Juana Diaz Formation, Early Miocene. 7, axial section, P47334; 8, equatorial section, holotype, P47333.





characters, regard them as specifically distinct from *L. (L.) giraudi*, and, moreover, regard themselves as different species. The megalospheric forms here recorded from Puerto Rico seem to match best the microspheric forms described as *L. (L.) parvula* Cushman var. *crassicosta* Vaughan and Cole 1933a, and are here provisionally referred to that form. It should be recalled that *crassicosta* greatly resembles *L. partita* Douvillé 1925 from the Mediterranean area, which, however, although only known by the microspheric form, has been referred to the subgenus *Nephrolepidina*.

Lepidocyclina gigas Cushman 1919

1919 *Lepidocyclina gigas* Cushman, p. 64, pl. 1, figs. 3-5; pl. 5, fig. 4.

1941 *Lepidocyclina gigas* Cushman; Vaughan and Cole, p. 76 (*cmi bibl.*).

Material. One hand specimen and one thin section.

Remarks. The Puerto Rican material conforms well to the known characters of the species. Vaughan and Cole (1941, p. 76) and Sachs and Gordon (1962, pp. 15, 16), amongst others, have suggested that *L. gigas* is the microspheric form of *L. undosa*; Sachs and Gordon (*loc. cit.*), however, place *gigas* in the synonymy of *undosa* although the name *gigas* has page priority. The type material of the two species does not come from the same locality, although both localities are on Antigua. Since *gigas* is not saddle-shaped and *undosa* is strongly saddle-shaped, the two forms are here retained separately. The suggestion by Cole and Applin (1961) that *L. (Eulepidina) favosa* should also be included in synonymy cannot, in our opinion, be maintained, because the two forms are morphologically quite different. As far as we know, the species has not yet been recorded from below the Early Miocene (see Eames *et al.* 1962).

Lepidocyclina (Lepidocyclina) sachsi sp. nov.

Plate 58, figs. 4-6

1962 *Lepidocyclina (Lepidocyclina) giraudi* R. Douvillé; Sachs and Gordon, p. 14 (*pars*), pl. 1 fig. 6. (*non* pl. 1, figs. 8, 11; pl. 2, fig. 9; pl. 3, figs. 2, 4, 9. *Max. pars* = *L. (L.) cf. crassicosta* (Vaughan and Cole).)

Material. Two hand specimens and three thin sections (P47339-41), of which the equatorial section (P47339) is the holotype.

Description. The megalospheric hand specimen has a diameter of about 1.65 mm. and a thickness of about 0.75 mm., and the axial section has a diameter of 1.75 mm. and a thickness of 1.1 mm. There is a prominent centrum passing with slightly concave curvature into a small flange; the centrum itself is almost completely formed of one large pillar. The nucleoconch is isolepidine, the dimensions of that of the holotype being:

Protoconch: height 0.11 mm.

width 0.16 mm.

Deuteroconch: height 0.08 mm.

width 0.16 mm.

Sum of heights: 0.19 mm.

The nucleocoenoch in a second equatorial section is slightly smaller, the sum of the heights being 0.15 mm. There are two relatively small primary auxiliary chambers, but no adauxiliary chambers can be distinguished. The chambers of the equatorial chamber layer are ogival-rhombic, without a very strong appearance of engine-turning, attain a radial length of about 0.06 mm. near the margin, and are noticeably smaller than the lateral chambers. In axial section the equatorial chamber layer attains a thickness of 0.08 mm. near the margin, and the chamber walls do not seem to develop more than 2 apertures; apart from the 2 huge central pillars there are no others, and the floors of the lateral chambers are fairly thin and the chamber lumina not very wide.

A larger specimen with a diameter of 3.2 mm. and a thickness of 1.6 mm., very similar in appearance but with a relatively somewhat smaller median pillar, proved on polishing to be a microspheric individual with the chambers of the equatorial layer of the same shape and same general size as in the megalospheric forms described above.

Remarks. The external appearance and internal characters are quite different from those of *L. (L.) giraudi* (e.g. the complete lack of 'long radial pustules'); of the forms illustrated by Sachs and Gordon (1962) as *L. (L.) giraudi*, the axial section (loc. cit., pl. 1, fig. 6) differs from the others and is referable to *L. (L.) sachsi*, which is named after the senior author.

Lepidocyclina (Nephrolepidina) bikiniensis Cole 1954

Plate 58, figs. 7-9

1954 *Lepidocyclina (Nephrolepidina) bikiniensis* Cole, p. 586, pl. 214, figs. 1-8.

1954 *Lepidocyclina (Nephrolepidina) bikiniensis* Cole var. *unipilaris* Cole, p. 587, pl. 214, figs. 11-14, 18.

1962 *Lepidocyclina (Eulepidina) yurnagunensis* Cushman; Sachs and Gordon, p. 16 (*pars*), pl. 1, fig. 1. (*non* pl. 2, figs. 1, 3-6, 8 = *L. (N.) bikiniensis* Cole subsp. *pumilipapilla* Cole; *nec* pl. 2, fig. 7; pl. 3, fig. 8 = *L. (L.) yurnagunensis* Cushman.)

Material. Six hand specimens and three thin sections (P47342-4).

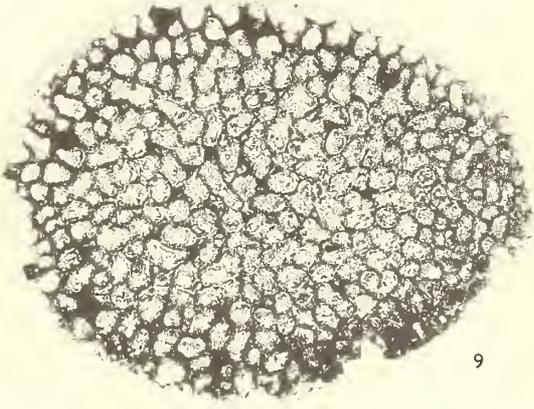
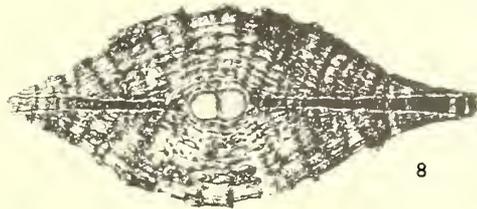
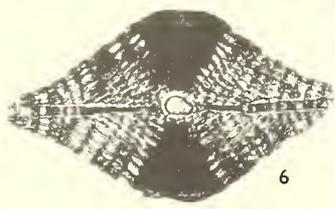
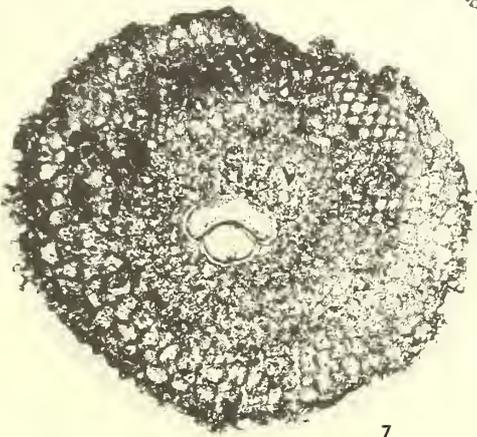
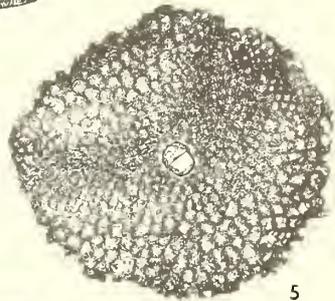
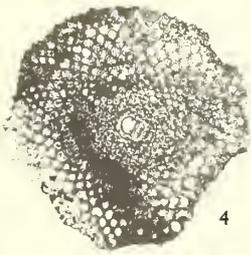
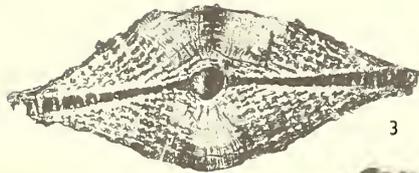
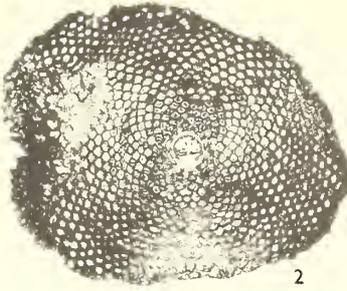
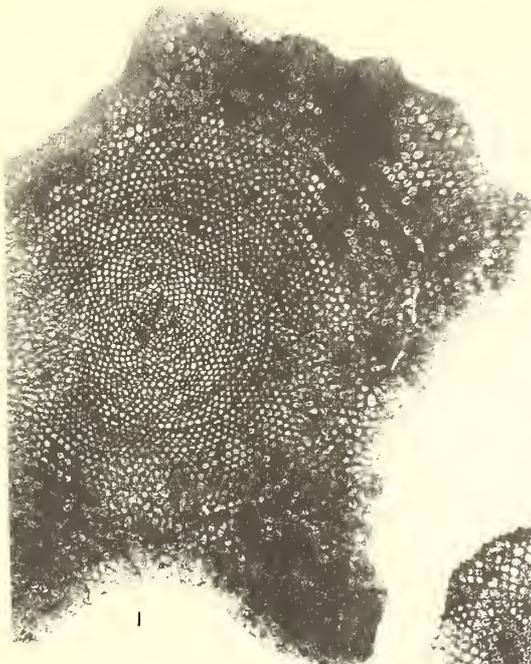
Remarks. This material forms an excellent match with *L. (N.) bikiniensis* from the upper part of the 'e' stage (early part of Early Miocene) of Bikini. The 'variety' *unipilaris* being merely an extreme variant, we would place it in synonymy. One of the specimens (an axial section) illustrated by Sachs and Gordon (1962) as *L. (Eulepidina) yurnagunensis* is neither a *Eulepidina* nor, on the characters of the lateral chambers, does it belong to the species *yurnagunensis*; it matches well the 'variety' *unipilaris* of *L. (Nephrolepidina) bikiniensis*.

EXPLANATION OF PLATE 58

Figs. 1-3. *Lepidocyclina cf. crassicosta* Vaughan and Cole. Sample PO.35-1, La Rambla, Puerto Rico, Juana Diaz Formation, Early Miocene. 1, equatorial section of a microspheric specimen, $\times 15$, P47336; 2, equatorial section, $\times 20$, P47337; 3, axial section, $\times 20$, P47338.

Figs. 4-6. *Lepidocyclina sachsi* sp. nov. ($\times 25$). Sample PO.35-1, La Rambla, Puerto Rico, Juana Diaz Formation, Early Miocene. 4, equatorial section, holotype, P47339; 5, equatorial section, P47341; 6, axial section, P47340.

Figs. 7-9. *Lepidocyclina (Nephrolepidina) bikiniensis* Cole ($\times 25$). Sample PO.35-1, La Rambla, Puerto Rico, Juana Diaz Formation, Early Miocene. 7, equatorial section, P47342; 8, axial section, P47343; 9, tangential section, P47344.



Lepidocyclina (Nephrolepidina) bikiniensis Cole 1954 subsp. *pumilipapilla* Cole 1954

Plate 59, figs. 1-6

1954 *Lepidocyclina (Nephrolepidina) pumilipapilla* Cole, p. 592, pl. 214, figs. 15-17, 19; pl. 215, figs. 1-8.1962 *Lepidocyclina (Eulepidina) yurnagunensis* Cushman; Sachs and Gordon, p. 16 (*pars*), pl. 2, figs. 1, 3-6, 8. (*non* pl. 1, fig. 1 = *L. (N.) bikiniensis* Cole; *nec* pl. 2, fig. 7; pl. 3, fig. 8 = *L. yurnagunensis* Cushman.)

Material. One microspheric hand specimen, 1 microspheric equatorial section (P47345), and 1 microspheric axial section (P47346); 35 megalospheric hand specimens and 5 megalospheric thin sections (4 registered as P47347-50).

Remarks. This material matches well that recorded by Cole as *L. (N.) pumilipapilla* which, on account of its very close relationship, we would regard merely as a subspecies of *L. (N.) bikiniensis*. Cole's original material came from the upper part of the 'e' stage (early part of Early Miocene) of Bikini.

Palaeonummulites antiguensis (Vaughan and Cole) 1936

Plate 51, figs. 8, 9

1936 *Operculinoides antiguensis* Vaughan and Cole, p. 492, pl. 38, figs. 7-10.1941 *Operculinoides antiguensis* Vaughan and Cole; Vaughan and Cole, p. 53 (*cum bibl.*).1962 *Camerina dia* (Cole and Ponton); Sachs and Gordon, p. 13, pl. 1, figs. 2-4, 7; pl. 2, fig. 2; pl. 3, figs. 6, 7.

Material. Numerous hand specimens and 3 thin sections (including P47351-2).

Remarks. Although Cole (1958) placed *antiguensis* in the synonymy of *dia*, the consistently more tightly coiled spire and distinctly more inflated external appearance fully merit it to be specifically different. The form illustrated by Sachs and Gordon (1962) as *dia* agrees in all respects with *antiguensis*. The species has not yet, in our opinion, been recorded from below the Miocene (see Eames *et al.* 1962).

STRATIGRAPHICAL PALAEOONTOLOGY

The larger foraminifera recorded in this paper have been studied in order that their evidence may be coordinated with that of the planktonic foraminifera in the successions in the same region; the evidence of the latter is to be published shortly in detail in a book by Blow and Banner.

In Venezuela the Peñas Blancas Limestone samples have yielded *Asterocyclina asterisca*, *Helicolepidina paucispira*, *Helicostegina soldadensis*, *Heterostegina (Vlerkinella) kugleri*, *Lepidocyclina montgomeriensis*, *Palaeonummulites kugleri*, *P. palmarealensis*, *P. stainforthi*, *Pliolepidina tobleri panamensis* and its probable microspheric form associated with the worm *Tubulostium*. These forms occur in natural association, and there can be no doubt as to their Late Eocene age.

In Eames *et al.* (1962) there were recorded six localities (in Costa Rica, p. 35; in Venezuela, p. 39; on Soldado Island, p. 42; on Carriacou, p. 43; in Jamaica, p. 46; and

in Cuba, p. 47) which were regarded as being of early part of Early Miocene age on the presence of *Pliolepidina tobleri*, associated Eocene foraminifera being suggested to be derived. It is now recognized that these faunas are of Late Eocene age, and that only pre-Late Eocene foraminifera are derived. On the other hand, the study of samples from the Early Oligocene Playa Rica Formation of Ecuador (reputed to contain *Pliolepidina tobleri*) has failed to yield any trace of the species or the genus. In Panama, Eames *et al.* (1962, p. 36) recorded *P. tobleri* with an early part of Early Miocene foraminiferal fauna from the Bohio Formation, but the *P. tobleri* does not come from the same sample as the Early Miocene foraminifera. Again, the records of *Pliolepidina tobleri* from the Culebra Formation and Emperador Limestone of Panama have been indicated by Cole (1952, p. 17) to be incorrect, and our own studies of portions of the Culebra Formation samples have also failed to find any trace of the species or the genus.

The study of duplicate material from Ecuador has also shown that neither *Eulepidina undosa* nor *Lepidocyclina yurnagunensis* (*s.s.*) occurs in them. The form previously believed to be *undosa* is a new species of *Lepidocyclina* (*Nephrolepidina*), so that the genus *Eulepidina* is still unknown below the Middle Oligocene. The form recorded as *L. yurnagunensis* belongs to the subspecies *morganopsis*, so that this subspecies is now to be regarded as ranging from Early Oligocene to Early Miocene; we are not aware of any substantiated record of *L. yurnagunensis* (*s.s.*) from below the Early Miocene. The early Oligocene Ecuadorean faunas have also been found to contain *Halkyardia bikiniensis* and (in one sample near the base) *Helicolepidina paucispira*; until further knowledge is obtained of the stratigraphy of the underlying horizons in the area we feel that it would be unwise unequivocally to extend the range of the genus *Helicolepidina* up into the Early Oligocene because the relatively few specimens found might be derived.

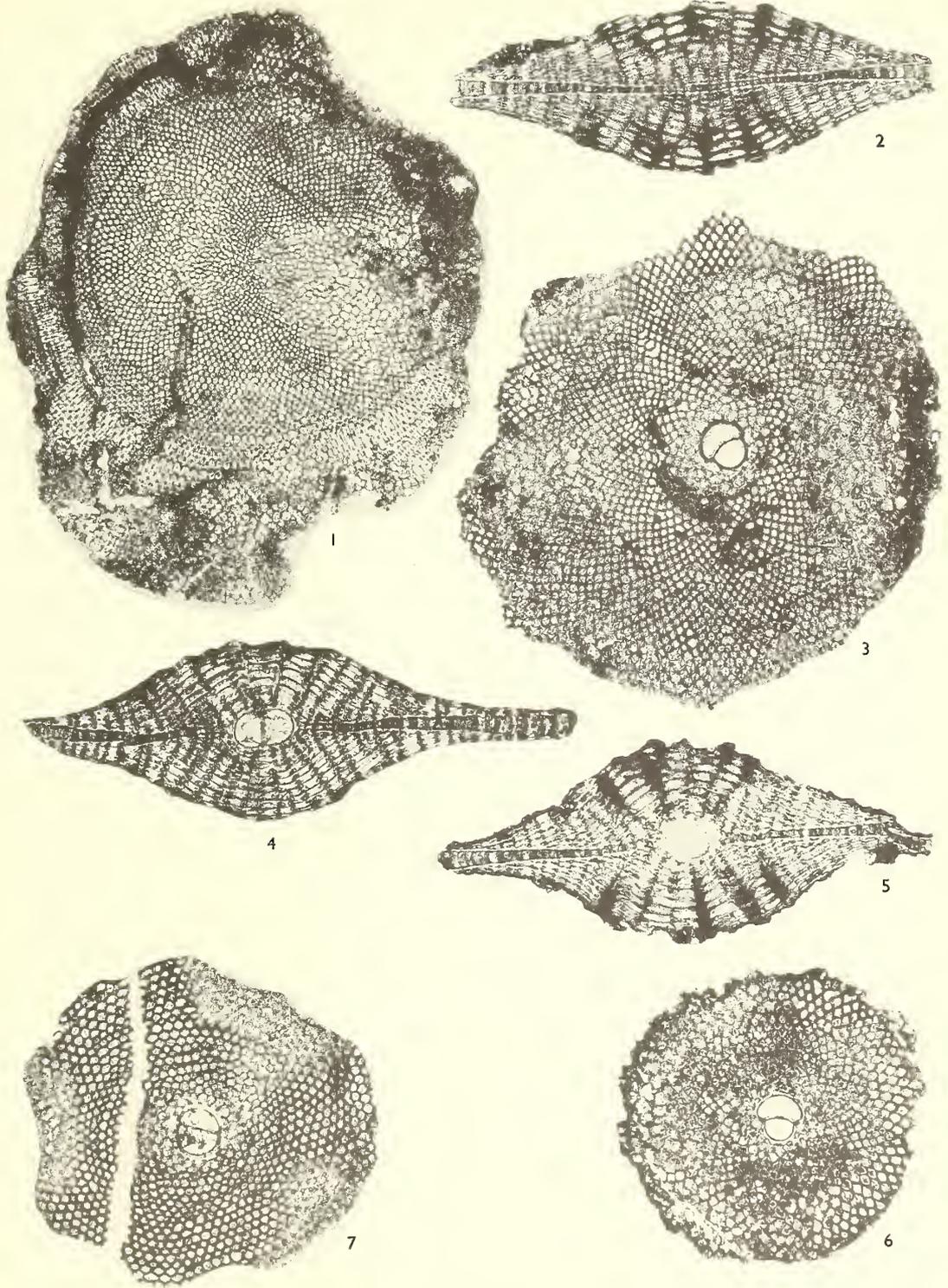
In Jamaica, *Lepidocyclina yurnagunensis* subsp. *morganopsis*, as in Ecuador, occurs in association with good planktonic faunas of Early Oligocene age, in the uppermost part of the Bonny Gate Formation.

In Alabama, *Lepidocyclina mantelli* occurs in association with rich planktonic foraminiferal faunas (identified by W. H. B.) of Early Oligocene age in beds which have been referred to as Red Bluff and Marianna Limestone. However, there seems to be little in common with the fauna of the type Marianna Limestone in Florida, and, indeed, there does not seem to be agreement as to the stratigraphical succession in Little Stave Creek, Alabama. Whereas the UWS samples collected in Little Stave Creek by Stanley Wissler were indicated to have come from a succession including Red Bluff, Mint Springs, and Marianna Limestone, Dr. Stearns MacNeil has informed us (*verb.*) that there is no Mint Springs in the succession since he considers it to be cut out. Again,

EXPLANATION OF PLATE 59

Figs. 1-6. *Lepidocyclina* (*Nephrolepidina*) *bikiniensis* Cole subsp. *pumilipapilla* Cole. Sample PO.35-1, La Rambla, Puerto Rico, Juana Diaz Formation, Early Miocene. 1, equatorial section of a microspheric specimen, $\times 15$, P47345; 2, axial section of a microspheric specimen, $\times 25$, P47346; 3, equatorial section, $\times 25$, P47349; 4, axial section, $\times 25$, P47347; 5, axial section, $\times 25$, P47348; 6, equatorial section, $\times 25$, P47350.

Fig. 7. *Lepidocyclina cauellei* Lemoine and R. Douvillé ($\times 20$). Sample PO.35-1, La Rambla, Puerto Rico, Juana Diaz Formation, Early Miocene. Equatorial section, P47335.



although Wissler records *Pecten* cf. *poulsoni* from low in the Mint Springs equivalent and *Pecten poulsoni* (*s.s.*) from the upper part of the Mint Springs equivalent and from throughout the Marianna Limestone, and although Dr. Stearns MacNeil has identified a specimen from sample UWS138 (sent to him on loan) as the flat valve of *Pecten poulsoni*, we consider that these forms need a thorough revision. We have abundant pectinid material from throughout this succession, and not only is there no trace whatsoever of a strongly inflated *Pecten* right valve, but the extremely dominant form present throughout the succession consists of one species of *Chlamys* (*Aequipecten*), there being over 30 portions of valves with ctenolia/byssal sinuses in our collections, such morphological characters being completely absent in the genus *Pecten*.

In Puerto Rico, a sample from within 1 m. of another containing a rich Zone N. 2 (early part of Early Miocene) planktonic foraminiferal fauna, both in the Juana Diaz Formation, contained *Eulepidina favosa*, *E. undosa* subsp. *laramblaensis*, *Lepidocyclina canellei*, *L. cf. crassicosta*, *L. gigas*, *L. sachsi*, *L. (Nephrolepidina) bikiniensis*, *L. (N.) bikiniensis* subsp. *pumilipapilla*, and *Palaeonummulites antiguensis*. On its own evidence this assemblage of larger foraminifera would be dated as early part of Early Miocene, and the associated planktonic foraminifera confirm this. From the point of view of the palaeogeography of the region it is most interesting to find that the Pacific 'e'-stage form *Lepidocyclina (Nephrolepidina) bikiniensis (s.l.)* occurs also in the early part of the Early Miocene in the Caribbean region.

Finally, some of the specimens illustrated by Sachs (1964, e.g. pl. 2, figs. 1-4, 6-9) from Locality 3 on Puerto Rico (from the Cibao Formation, which overlies the Juana Diaz Formation) as *Lepidocyclina (Eulepidina) undosa* are, in our opinion, *Pliolepidina tobleri (s.s.)*; however, some of the specimens from the same Locality (e.g. his pl. 1, fig. 4) are typical *Eulepidina*. We have found no evidence whatsoever that pliolepidine and eulepidine embryonites intergrade morphologically, and are in full agreement with Hanzawa (1962) that *Eulepidina* and *Pliolepidina* are generically distinct. For example, in some of the Peñas Blancas Limestone samples in particular, *P. tobleri* subsp. *panamensis* is extremely abundant, is very uniform in its total morphology, and there is no other form whatsoever present in the samples, of which it could be a freakish variant. Consequently, the species *Pliolepidina tobleri* is to be accepted as ranging from Late Eocene to Early Miocene; we are not aware of any true Oligocene record of the species in the Central American region, this doubtless being due to the markedly regressive nature of the Oligocene period over so much of the area.

Acknowledgements. We are indebted to the British Petroleum Company Limited for permission to publish this paper. For unstinting co-operation in the provision of material and stratigraphic data we gratefully thank: Dr. R. Lagaaij, Chief Palaeontologist of the Bataafse International Petroleum Maatschappij N.V.; Drs. R. Cifelli and K. N. Sachs Jr. of the Smithsonian Institution; Dr. R. M. Stainforth of the Creole Petroleum Corp., Caracas, Venezuela; Drs. A. D. Euribe and F. Zúñiga y Rivero of the International Petroleum Co. Ltd., Talara, Peru; Dr. C. W. Drooger of the Geologisch Institut, Utrecht; Dr. Brooks Ellis and Miss A. Messina of the American Museum of Natural History, New York; Dr. C. G. Adams of the British Museum (Natural History) and Mr. E. Robinson of the University of the West Indies, Jamaica. Except where otherwise acknowledged all the photomicrographs were prepared by Mr. E. M. Finch.

REFERENCES

- ADAMS, C. G. 1965. The foraminifera and stratigraphy of the Menilau Limestone, Sarawak, and its importance in Tertiary correlation. *Q. Jl geol. Soc. Lond.* **121**, 283–338, pl. 21–30.
- BANNER, F. T. and BLOW, W. H. 1965. Progress in planktonic foraminiferal biostratigraphy of the Neogene. *Nature, Lond.* **208**, no. 5016, 1164–6.
- BARKER, R. W. 1939. Species of the foraminiferal family Camerinidae in the Tertiary and Cretaceous of Mexico. *Proc. U.S. natn Mus.* **86**, no. 3052, 305–30, pl. 11–22.
- and GRIMSDALE, T. F. 1936. A contribution to the phylogeny of the orbitoidal Foraminifera with descriptions of new forms from the Eocene of Mexico. *J. Paleont.* **10**, 231–47, pl. 30–38.
- BOLLI, H. M. 1957. Planktonic Foraminifera from the Oligocene–Miocene Cipero and Lengua formations of Trinidad, B.W.I. *Bull. U.S. natn Mus.* **215**, 97–125, pl. 22–29.
- COLE, W. S. 1934. Oligocene orbitoids from near Duncan Church, Washington County, Florida. *J. Paleont.* **8**, 21–28, pl. 3–4.
- 1949. Upper Eocene larger Foraminifera from the Panama Canal Zone. *Ibid.* **23**, 267–75, pl. 52–55.
- 1952. Eocene and Oligocene Larger Foraminifera from the Panama Canal Zone and vicinity. *Prof. Pap. U.S. geol. Surv.* **244**, 1–41, pl. 1–28.
- 1954. Larger Foraminifera and smaller diagnostic Foraminifera from Bikini drill holes. *Ibid.* **260–O**, 569–608, pl. 204–22.
- 1957a. Variation in American Oligocene species of *Lepidocyclina*. *Bull. Am. Paleont.* **38**, no. 166, 31–51, pl. 1–6.
- 1957b. Larger Foraminifera of Saipan Island. *Prof. Pap. U.S. geol. Surv.* **280–I**, 321–60, pl. 94–118.
- 1957c. Larger Foraminifera from Eniwetok Atoll drill holes. *Ibid.* **260–V**, 743–84, pl. 231–49.
- 1958. Names of and variation in certain American larger Foraminifera, particularly the Camerinids—No. 2. *Bull. Am. Paleont.* **38**, no. 173, 261–84, pl. 32–34.
- 1960. Variability in embryonic chambers of *Lepidocyclina*. *Micropaleontology*, **6**, 133–44, pl. 1–4.
- 1961. Some nomenclatural and stratigraphic problems involving larger Foraminifera. *Contr. Cushman Fdn foramin. Res.* **12**, 136–47, pl. 8–17.
- 1962a. Periembrionic chambers in *Helicolepidina*. *Ibid.* **13**, 145–51, pl. 23–27.
- 1962b. Embryonic chambers and the subgenera of *Lepidocyclina*. *Bull. Am. Paleont.* **44**, no. 200, 29–60, pl. 4–8.
- and APPLIN, E. R. 1961. Stratigraphic and geographic distribution of larger Foraminifera occurring in a well in Coffee County, Georgia. *Contr. Cushman Fdn foramin. Res.* **12**, 127–35, pl. 6–7.
- COLEMAN, P. J. and MCTAVISH, R. A. 1964. Association of larger and planktonic foraminifera in single samples from the Middle Miocene sediments, Guadalcanal, Solomon Islands, south-west Pacific. *J. Proc. R. Soc. West Aust.* **47**, 13–24.
- CUSHMAN, J. A. 1917. Orbitoid Foraminifera of the genus *Orthophragmina* from Georgia and Florida. *Prof. Pap. U.S. geol. Surv.* **108–G**, 115–24, pl. 40–44.
- 1918 (1919). The larger fossil Foraminifera of the Panama Canal Zone. *Bull. U.S. natn Mus.* **103**, 89–102, pl. 34, 35.
- 1919. Fossil Foraminifera from the West Indies. *Publs. Carnegie Instn.* **291**, 21–71, pl. 1–15.
- and STAINFORTH, R. M. 1951. Tertiary Foraminifera of Coastal Ecuador: Part I, Eocene. *J. Paleont.* **25**, 129–64, pl. 25–28.
- EAMES, F. E. *et al.* 1962. *Fundamentals of mid-Tertiary Stratigraphical Correlation*, 1–163, pl. i–xvii. Cambridge University Press.
- and CLARKE, W. J. 1965. Douvillé's *Lepidocyclina pustulosa*, *L. trinitatis* and *L. (Pliolepidina) toberli*; a reconsideration. *Revue Micropaléont.* **8**, 3–10, pl. 1–3.
- ELLIS, BROOKS F. and MESSINA, ANGELINA R. 1940. *Catalogue of Foraminifera*. (Amer. Mus. Nat. Hist.) (supplements post-1940).
- — 1965. *Catalogue of Index Foraminifera*. Special Publ. **1**; Lepidocyclinids and Miogypsinids.
- GUPPY, R. J. L. 1866. On the relations of the Tertiary formations of the West Indies. *Q. Jl geol. Soc. Lond.* **22**, 570–90, pl. 26.
- HANZAWA, S. 1962. Upper Cretaceous and Tertiary three-layered larger foraminifera and their allied forms. *Micropaleontology*, **8**, 129–86, pl. 1–8.

- HEDBERG, H. D. and PYRE, A. 1944. Stratigraphy of Northeastern Anzoategui, Venezuela. *Bull. Am. Ass. Petrol. Geol.* **28**, 1–28.
- LEMOINE, P. and DOUVILLÉ, R. 1904. Sur le genre *Lepidocyclina* Gümbel. *Mémoires Soc. géol. Fr. Paléont.* **12**, no. 32, 5–41, pl. 1–3.
- LEUPOLD, W. and VLERK, I. M. VAN DER. 1931. Feestbundel uitgegeven ter eere van Prof. Dr. K. Martin 1851–1931. Deel I. De Palaeontologie en stratigraphie van nederlandsch oost-indië. 20. The Tertiary. *Leid. geol. Meded.* **5**, 611–48.
- LISSON, C. I. 1921. Contribución al estudio de algunos foraminiferos terciarios provenientes de la región del norte del Peru. *Archivos Asoc. peru. Prog. Cienc.* **1**, 52–55, pl. 3–5.
- MORTON, S. G. 1833. Supplement to the 'Synopsis of the organic remains of the ferruginous sand formation of the United States' contained in vols. xvii and xviii of this journal. *Am. J. Sci. Arts*, **23**, 288–94, pl. 5, 8–9.
- PESSAGNO, E. A. Jr. 1963. Planktonic Foraminifera from the Juana Diaz formation, Puerto Rico. *Micropaleontology*, **9**, 53–60, pl. 1–3.
- RUTTEN, L. 1928. On Tertiary rocks and foraminifera from north-western Peru. *Proc. K. ned. Akad. Wet.*, **B**, **31**, no. 9–10, 931–46, pl. 1, 2.
- SACHS, K. N. Jr. 1964. Multilocular embryos in *Lepidocyclina* (*Eulepidina*) *undosa* Cushman from Puerto Rico. *Micropaleontology*, **10**, 323–9, pl. 1, 2.
- and GORDON, W. A. 1962. Stratigraphic distribution of Middle Tertiary Larger Foraminifera from southern Puerto Rico. *Bull. Am. Paleont.* **44**, no. 199, 1–24, pl. 1–3 (*cum bibl.*).
- SEIGLIE, G. A. 1965. Notas sobre tres *Lepidocyclinas* de Cuba. *Boll. Ist. Oceanog., Univ. Oriente*, **4** (1), 191–213, pl. 1–5.
- STAINFORTH, R. M. 1948. Applied micropaleontology in coastal Ecuador. *J. Paleont.* **22**, 113–51, pl. 24–26.
- VAUGHAN, T. W. 1924. American and European Tertiary larger Foraminifera. *Bull. geol. Soc. Am.* **35**, 785–822, pl. 30–36.
- 1928. Notes on the types of *Lepidocyclina mantelli* (Morton) Gümbel and on topotypes of *Nannulites floridanus* Conrad. *Proc. Acad. nat. Sci. Philad.* **79** (1927), 299–303, pl. 23.
- 1933a. Report on species of corals and larger foraminifera collected in Cuba by O. E. Meinzer. *J. Wash. Acad. Sci.* **23**, 352–5.
- 1933b. Studies of American species of Foraminifera of the genus *Lepidocyclina*. *Smithson. misc. Collns.* **89**, no. 10, 1–53, pl. 1–32.
- and COLE, W. S. 1936. New Tertiary Foraminifera of the genera *Operculina* and *Operculinoides* from North America and the West Indies. *Proc. U.S. Natn Mus.* **83**, no. 2996, 487–96, pl. 35–38.
- 1941. Preliminary report on the Cretaceous and Tertiary Larger Foraminifera of Trinidad, British West Indies. *Spec. Pap. geol. Soc. Am.* **30**, 1–137, pl. 1–46.
- VLERK, I. M. VANDER. 1955. Correlation of the Tertiary of the Far East and Europe. *Micropaleontology*, **1**, 72–75.

F. E. EAMES W. J. CLARKE
 A. H. SMOUT W. H. BLOW
 British Petroleum Company Ltd.
 BP Research Centre
 Chertsey Road
 Sunbury-on-Thames, Middlesex
 F. T. BANNER
 Department of Geology
 University College
 Singleton Park, Swansea

VISBYELLA—A NEW GENUS OF RESSERELLID BRACHIOPOD

by V. G. WALMSLEY, A. J. BOUCOT, C. W. HARPER, and
N. M. SAVAGE

ABSTRACT. A new genus of resserellid brachiopod, *Visbyella*, is erected based on *Orthis visbyensis* Lindström 1861 as type species. *Visbyella* is distinguished from both *Resserella* and *Fascicostella* by its hypereline dorsal interarea, its extroverted (dorsally facing) trilobed cardinal process, the presence of an apical plate, and by its tendency to have the median ridge in the brachial valve elevated anteriorly. *Fascicostella* is distinguished from both *Visbyella* and *Resserella* by its distinctly fasciculate ribbing.

Dalmaniella visbyensis var. *nana* McLearn 1924 and *Parmorthis visbyensis* var. *pygmaea* Whittard and Barker 1950 are both considered to be distinct species and are assigned to *Visbyella* together with a new species *V. cumnockensis*, which is here described from New South Wales.

The known distribution of *Visbyella* is in beds of Silurian (Upper Llandovery and Wenlock) age from Gotland, Britain, Nova Scotia, southern New Brunswick, and New South Wales. Both *Resserella* and *Visbyella* make their first appearance in the Upper Llandovery. The more complex morphology of *Visbyella* seems to us to be more easily derived from *Resserella* than vice versa.

RESULTS of a study of some twenty species of resserellid brachiopods by Walmsley, in collaboration with Boucot, including two species from the Arisaig area of Nova Scotia which have recently been restudied by Harper (1964, C.I.T. Ph.D. thesis *The Brachiopods of the Arisaig Series (Silurian–Lower Devonian) of Nova Scotia*), are being prepared for joint publication.

In this joint work, it was proposed to erect a new sub-family to include all these species, assigned to *Resserella* [*Parmorthis*], *Fascicostella* and a new genus *Visbyella*, based on '*Orthis*' *visbyensis* Lindström. To *Visbyella* were assigned *Dalmaniella visbyensis* var. *nana* McLearn, which Harper's study has confirmed as indeed closely related to *O. visbyensis*, though now considered to be a separate species, and *Parmorthis visbyensis* var. *pygmaea* Whittard and Barker, also considered to be a distinct species.

Meanwhile, Savage independently recognized a new species of septate dalmanellid in material from New South Wales, which he proposed to describe and assign to a new genus based on this species. His species is close to *Visbyella nana* and is here assigned to the new genus *Visbyella* and described as a new species *V. cumnockensis*.

The fortunate circumstances of a recent visit to Australia by Boucot, brought to light the coincidence of interest and resulted in the collaboration of the present authors in here erecting the genus *Visbyella* and presenting descriptions of *V. visbyensis*, *V. nana*, and the new species *V. cumnockensis*.

SYSTEMATIC DESCRIPTIONS

Superfamily ENTELETACEA Waagen 1884

[*nom. transl.* Alichova, 1960, p. 193 (*ex Entelitinae* Waagen 1884, p. 548)]

Family DALMANELLIDAE Schuchert 1913

Genus VISBYELLA gen. nov.

Type species. *Orthis visbyensis* Lindström 1861, p. 366, pl. xii, fig. 8.

[*Palaeontology*, Vol. 11, Part 2, 1968, pp. 306–16, pls. 60–62.]

Diagnosis. Plano-convex to slightly concavo-convex or very unequally biconvex, dalmanellids commonly having a strongly incurved pedicle-valve beak. Apical plate present. Cardinal process trilobed and extroverted (dorsally facing). Interarea of brachial valve hypercline. Median ridge in brachial valve elevated into an anterior septum in some species.

Comparison. *Visbyella* is closest to *Resserella* and has a similar plano-convex profile and the distinctive asymmetrical pattern of costellae bifurcation in the medial region of the brachial valve (see Walmsley 1965, pp. 456–7), as well as similar brachiophores and muscle fields.

It is distinguished from *Resserella* by its hypercline interarea in the brachial valve, its extroverted (dorsally facing) trilobed cardinal process, the presence of an apical plate, and by its tendency to develop a raised median septum at the anterior end of the median ridge in the brachial valve. From *Fascicostella* it is also readily distinguished by its much finer and non-fasciculate ribbing.

Species assigned to Visbyella.

Orthis visbyensis Lindström 1861, p. 366, pl. xii, fig. 8.

Dalmanella wisbyensis var. *nana* McLearn 1924, p. 55, pl. 3, figs. 10–17.

Parnorthis visbyensis (Lindström) var. *pygmaea* Whittard and Barker 1950, p. 575, pl. viii, figs. 9–15.

Visbyella cummockensis sp. nov.

Distribution and derivation of Visbyella. Species of *Visbyella* occur in Silurian beds of late Llandoveryan age in Gotland (C₆), Britain (C₃ to C₆), Nova Scotia (middle member of the Ross Brook Formation which is considered to be C₁–C₃), southern New Brunswick (Long Reach Formation, C₆ to early Wenlockian), and in beds of late Wenlockian age (*Monograptus testis* zone) in New South Wales.

The earliest known occurrence of *Visbyella* is thus C₃ but could be as early as C₁. The oldest species assignable to *Resserella* is from beds of C₁–C₂ age. It is thus not yet clear whether *Visbyella* is derived from *Resserella* but its more complex morphology suggests that this is more likely than that *Resserella* was derived from *Visbyella*. Alternatively, they may both have been derived from an unknown ancestor of earlier Llandoveryan age.

Visbyella visbyensis (Lindström)

Plate 60, figs. 1–9

1861 *Orthis visbyensis* Lindström, p. 366, pl. 12, fig. 8.

1932 *Parnorthis visbyensis* (Lindström); Schuchert and Cooper, p. 129, pl. 21, figs. 1, 6, 8, 11, 12, and 15.

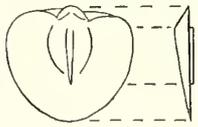
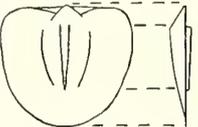
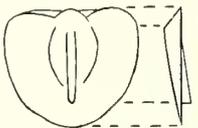
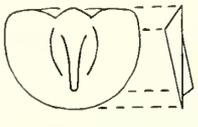
Diagnosis. Relatively large, finely costellate *Visbyella* with beak of pedicle valve distinctly overhanging the brachial valve. Median ridge in brachial valve not raised or septate at anterior extremity. Pedicle valve bears a narrow median depression.

Comparison. Comparison with other species of *Visbyella* follows their diagnoses. See also text-fig. 1, which summarizes the diagnostic characters of these species.

Description. Plano-convex to slightly concavo-convex, with sub-circular to elongately shield-shaped outline. Length slightly greater than width, and twice the thickness. Hinge line straight, equal to about two-thirds greatest width, which is at almost two-thirds

length. Cardinal angles only slightly rounded, lateral margins gently curved, sub-parallel, and anterior margin strongly rounded. Anterior third of the shell has a semicircular outline.

Pedicle valve projects one-quarter total length posterior to hinge line, with a very incurved beak, which overhangs the brachial valve. Anterior commissure crenulate, and rectimarginate. Lateral commissures straight. Costellae fine, rounded, increasing by bifurcation.

	BRACHIAL VALVE MEDIAN RIDGE Tap View Side View	BRACHIOPHORES	COSTELLAE	SIZE	SULCUS	OUTLINE	PEDICLE VALVE BEAK	
V. VISBYENSIS		Thin moderately divergent	Fine	Large	Weak	Subcircular to-elongate Shield shaped	Strongly incurved	narrow median depression in pedicle valve
V. PYGMAEA		Thin moderately divergent	Coarse	Small	Strong	Sub triangular	Fairly strongly incurved	
V. NANA		Thick very divergent	Medium coarse	Large	Strong	Sub triangular	Not strongly incurved	
V. CUMNOCKENSIS		Thick moderately divergent	Coarse	Very small	Weak	Semi circular	Not strongly incurved	

TEXT-FIG. 1. Comparison of species of *Visbyella*.

Exterior of pedicle valve. Strongly convex, with curvature decreasing slightly towards anterior margin and increasing over the strongly incurved beak. A faint, narrow median depression, increasing in depth and width anteriorly, marks the mid-line in some shells. The interarea is apsacline anteriorly, but curves strongly so that the posterior portion curves antero-dorsally beyond the commissural plane. Lateral margins of interarea very sharp. Delthyrium triangular, the margins diverging at 65°, usually open, but rarely having a small apical plate, and blocked by the large complex myophore of the cardinal process. Costellae fine, 4 per mm. at 5 mm. length, about 80 per 9 mm. wide shell.

Exterior of brachial valve. Plane, with shallow median sulcus, widening anteriorly and becoming flat or even slightly raised in the median area. In larger shells the effect of this slight sulcus is masked by a general flattening of the valve, which may even become slightly concave.

Interarea half as long as that of the pedicle valve, plane, hypercline. Notothyrium widely triangular, margins diverging more than 90°, open, filled completely by the large protruding myophore of the cardinal process, which also partially occupies the opposing

delthyrium. Branching pattern of costellae in median area of valve asymmetrical with successive branches directed alternately to left and right of preceding rib.

Interior of pedicle valve. The weakly impressed muscle field extends between a third and a half of the valve length, ending only slightly anterior to the teeth. In larger specimens, a low narrow rounded median ridge extends across the concave floor of the delthyrial cavity to just beyond mid-length. Relatively wide, shallow diductor impressions flank the median ridge. Slightly divergent thick dental lamellae extend from the margins of the delthyrium to meet the walls of the delthyrial cavity at about half their height. They bound deep lateral cavities which extend beneath the interarea and support moderately large triangular teeth. The teeth have a characteristic cross-section resembling an inverted V. They bear relatively wide, laterally inclined accessory sockets posteriorly, and are wider than long. They project further anteriorly than the short dental lamellae. Crural fossettes are indistinct.

Interior of brachial valve. The well-impressed adductor muscle field which is a third as wide and two-thirds as long as the valve, is slightly elevated on a low platform, and bounded by raised margins, which emphasize its sub-elliptical shape. A rounded median ridge, a sixth as broad as the muscle field, becomes slightly narrower as it passes between the anterior pair of impressions.

The anterior impressions are separated from the posterior pair by oblique ridges directed antero-laterally from the median ridge. The anterior impressions are smaller than the posterior pair. The brachiophores are thin plates, slightly divergent but well separated from each other by the wide median ridge. They project normal to the commissural plane, and have very steep anterior edges. The lateral faces of the brachiophores curve smoothly into the floor of the sockets which are also directed normal to the commissural plane and extend beneath the hypercline interarea. The crenulated sockets are supported on socket pads which merge into the bases of the brachiophores. The cardinal process consists of an indistinct shaft lying along the upraised median ridge between the brachiophores, and a distinctive trilobed myophore.

The median ridge and shaft become wide and flattened as they merge into the myophore which is so aligned that the typical crenulated posterior face of most resserellids is here turned through 90°. The heavily crenulated face is thus almost in the commissural plane, and is visible from the exterior of the brachial valve, projecting clear from the notothyrium.

Crenulations of the shell margin are short, strong, rounded, and separated by narrow, deep interspaces.

Type specimens. This species was described by Lindström 1861, pp. 366–7 and figured pl. xii, fig. 8. No holotype was designated. Specimens numbered Br. 102307–11 of the Swedish Museum of Natural History, Stockholm, are syntypes. According to Lindström's label they were collected from 'Gotland Wisby a'. According to Hede 1956, p. 411, Lindström distinguished three subdivisions of his 'Wisbygruppen'. In ascending order these were designated a, b, and c. These deposits are now referred to respectively as Lower Visby Marl, Upper Visby Marl, and the Hogklint group. It would appear, therefore, that the syntypes were obtained from the Lower Visby Marl which is considered (Hede 1956, p. 214) to be of late Llandoverian age and is of C₆ age as indicated by the presence of *Costistricklandia lirata*. The overlying Upper Visby Marl contains late Llandoverian graptolites.

One of the syntypes, specimen no. Br. 102310, a whole shell, which most closely matches Lindström's fig. 8, is here designated the lectotype. Specimens Br. 102307, Br. 102308, Br. 102309, and Br. 102311 are designated paratypes.

Distribution. *V. visbyensis* occurs in the Lower and Upper Visby Marls of Gotland. Lindström, 1861, pp. 367 and 381, showed this species occurring in groups a and b of his 'Wisby-gruppen'.

According to Regnell and Hede 1960, pp. 51–52, these formations are both of late Llandoveryan age and are now known to be C₆.

V. cf. visbyensis is recorded from the Long Reach Formation (C₆ to early Wenlockian) of southern New Brunswick, Canada, G.S.C. Loc. 55061 (Boucot, Johnson, Harper, and Walmsley 1966, pp. 14–15).

Visbyella pygmaea (Whittard and Barker)

Plate 61, figs. 1–5

1950 *Parmorthis visbyensis* var. *pygmaea* Whittard and Barker, p. 575, pl. 8, figs. 9–15.

Diagnosis. Small, sulcate, relatively coarsely costellate *Visbyella* with sub-triangular brachial valve in which the adductor muscle field is raised on a distinct platform and the median ridge is not elevated anteriorly. Interarea of pedicle valve, long, incurved, overhanging hinge line.

Comparison. *V. pygmaea* is closest to *V. visbyensis*, neither of which develops an anteriorly raised median septum in the brachial valve. From *V. visbyensis*, *V. pygmaea* is distinguished by its small size, its fewer and coarser ribs, the more triangular outline of the brachial valve, and by the less incurved beak of the pedicle valve.

Type specimens. In the Geological Survey Museum London. Holotype: GSM 82546 whole shell. Paratypes: GSM 82547 pedicle valve; GSM 82548 internal mould of pedicle valve; GSM 82549 brachial valve; GSM 82550 internal mould of brachial valve.

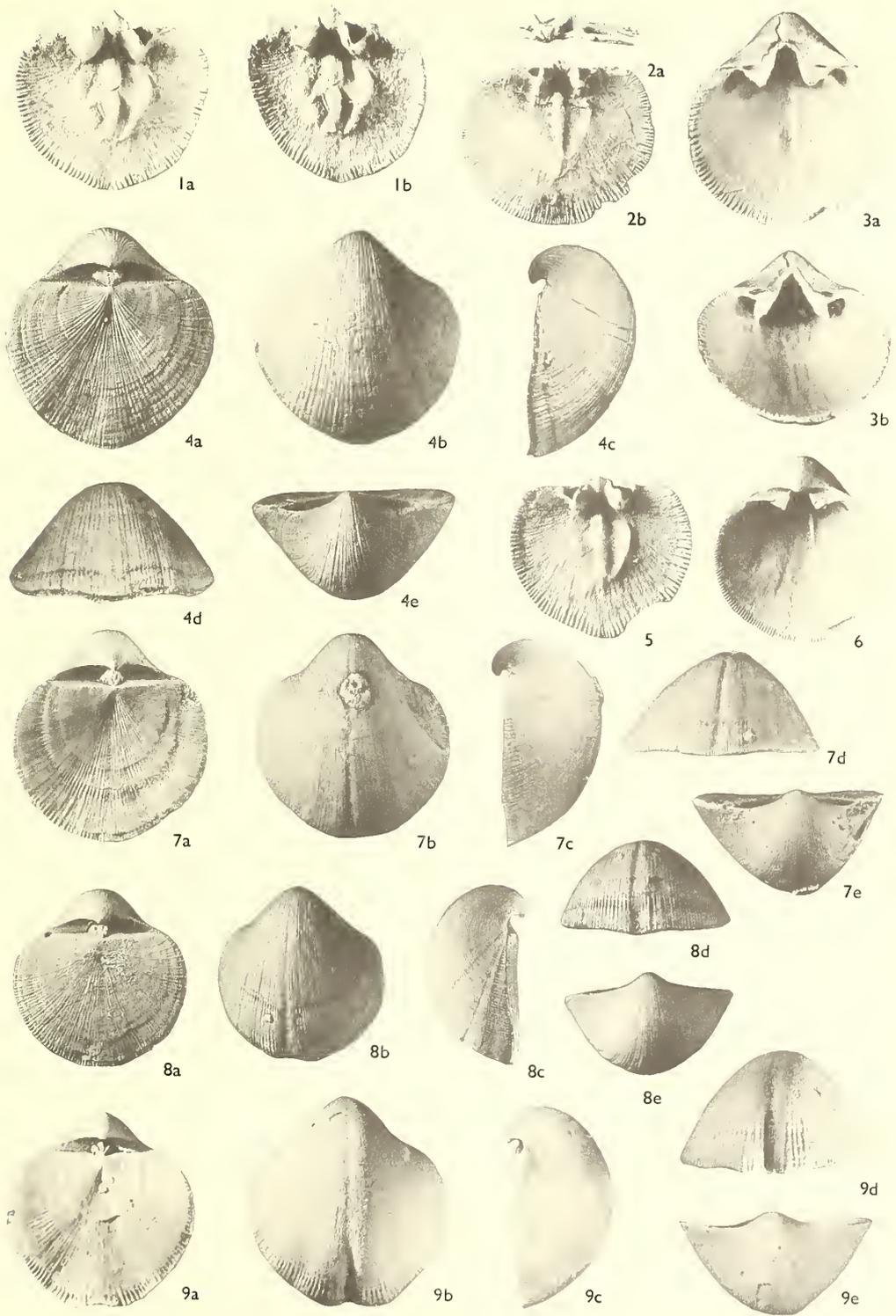
Distribution. In addition to the type material from the Purple Shales (Late Llandoveryan) of Shropshire, *V. pygmaea* is known from beds of Late Llandoveryan age ranging from C₃–C₆, from the following localities in Britain:

Llandovery district, Carmarthenshire

C₃ beds in roadside exposure on the Llandovery to Myddfai road, 300 yd. north of Cefn-cerig, Llandovery district, Carmarthenshire, grid reference SN 7752/3257, U.S.N.M. locality 10257.

EXPLANATION OF PLATE 60

Figs. 1–9. *Visbyella visbyensis* (Lindström). 1a, Interior of brachial valve, specimen no. USNM 157830 (×3). 1b, Slightly oblique view of same specimen to show brachiophore. 2a–b, Posterior and interior of brachial valve, specimen no. USNM 157831 (×3). 3a–b, Interior and anterior view of pedicle valve, specimen no. USNM 157832 (×3). 4a–e, Dorsal, ventral, lateral, anterior, and posterior views of whole shell, specimen no. USNM 157833 (×3). 5, Interior of brachial valve, specimen no. USNM 157834 (×3). 6, Interior of pedicle valve, specimen no. USNM 157835 (×1½). 7a–e, Dorsal, ventral, lateral, anterior, and posterior views of whole shell, specimen no. USNM 157836 (×2). 8a–e, Dorsal, ventral, lateral, anterior, and posterior views of whole shell, specimen no. USNM 157837 (×2). 9a–e, Dorsal, ventral, lateral, anterior, and posterior views of lectotype, Swedish Museum Natural History, Stockholm, specimen no. Br. 102310. Lower Visby Marl, Gotland (×2). 1a–b, 2a–b, and 6, Lower Visby Marl, shore exposure between 1.0 and 1.8 km. NNE. of the NW. corner of the city wall of Visby, Gotland. Collected by Dr. Hede. 3a–b, 4a–e, 5, 7a–e, and 8a–e, Upper Visby Marl, shore exposure at Gnisvårds flge., Tofta parish, Klintehamn Sheet, Gotland. Collected by Dr. Boucot, Loc. No. 56G47. USNM numbers refer to United States National Museum, Washington.



C₄ beds in disused quarry immediately west of the Myddfai to Gorllwyn-fawr road and west-northwest of Gorllwyn-fach, Myddfai, Llandovery district, Carmarthenshire, grid reference SN 7590/2966, U.S.N.M. locality 10256.

C₅ beds in the roadside exposure on the Llandovery to Myddfai road, 200 ft. west of Cefn-cerig, Llandovery district, Carmarthenshire, grid reference SN 7745/3231, U.S.N.M. locality 10259.

Shropshire

C₅ beds (with *Eocoelia curtisi*), stream section in Boathouse Coppice, 200 ft. upstream from a railway bridge, Buildwas Park, Shropshire, grid reference SJ 6206/0390, U.S.N.M. locality 10248.

Woolhope Inlier

C₆ beds in the Lower Haugh Wood Beds about 30–40 ft. below Woolhope Limestone, in trackside exposure in Kidley Coppice, 450 yd. north, 27° east of Iron House, Mordiford, Herefordshire, grid reference SO 5804/3730, U.S.N.M. locality 10230.

May Hill Inlier

C₆ beds in May Hill Inlier, Hay Farm Brook section, 465 yd. west of Hay Farm, north-east side of May Hill in Yartleton Beds, grid reference SO 6927/2263, U.S.N.M. locality 10226.

Tortworth Inlier

C₆ beds, exposure created by the straightening of route A38, 170 ft. north of the old A38 bridge over the Little Avon River, Woodford, Gloucestershire, grid reference ST 6789/9754, U.S.N.M. locality 10215.

Galway Co., Ireland

In Finny School Beds, Crumlin Valley, 550 yd. north-east of Crumlin West, at waterfall in middle of field, Galway Co., Ireland, U.S.N.M. locality 10872.

Visbyella nana (McLearn)

Plate 62, figs. 1–8

1924 *Dalmanella conservatrix* McLearn, pl. 2, fig. 26.

1924 *Dalmanella wisbyensis* var. *nana* McLearn, p. 55, pl. 3, figs. 10–17.

Diagnosis. Distinctly sulcate *Visbyella* with triangular shield-shaped outline, and medium coarse costellae. Beak of pedicle valve does not overhang brachial valve and the median ridge of the brachial valve is uniform in width but raised anteriorly.

Comparison. *V. nana* differs from *V. visbyensis* in its distinctly sulcate brachial valve, which may be very slightly convex. The narrow median depression along the arch of the pedicle valve and correspondingly slightly raised median area in the sulcus of the brachial valve which are commonly present in *V. visbyensis* are both absent from *V. nana*, which is also distinguished by its coarser ribbing and considerably less incurved beak of the pedicle valve. Internally, *V. nana* is distinguished from *V. visbyensis* by its median ridge in the brachial valve which, as it extends anterior to the muscle field, is elevated into a median septum. In the pedicle valve the median ridge is more pronounced than in *V. visbyensis*.

Description. Plano-convex to gently concavo-convex or very unequally biconvex; dorsally sulcate; outline semi-elliptical to shield-shaped with sharply obtuse cardinal

angles. Lateral and anterior commissures curved and crenulate, anterior commissure sulcate. Hinge line straight, slightly less than the greatest width which is slightly posterior to mid-length. Width varies from three-quarters of length to equal to length; thickness about half the length.

Exterior of pedicle valve. Strongly convex; surface of valve strongly arched along plane of symmetry and slopes off abruptly lateral to it. Beak strongly curved, dorsally directed at apex, and projects one-fifth the total length posterior to the hinge line. Interarea strongly curved concave, apsacline, a quarter as high as long. Delthyrium triangular enclosing about 60°, apical one-third closed by an apical plate which is gently convex outwards and has an anterior margin which is strongly concave towards the hinge line. Delthyrium partly occupied by posterior end of cardinal process.

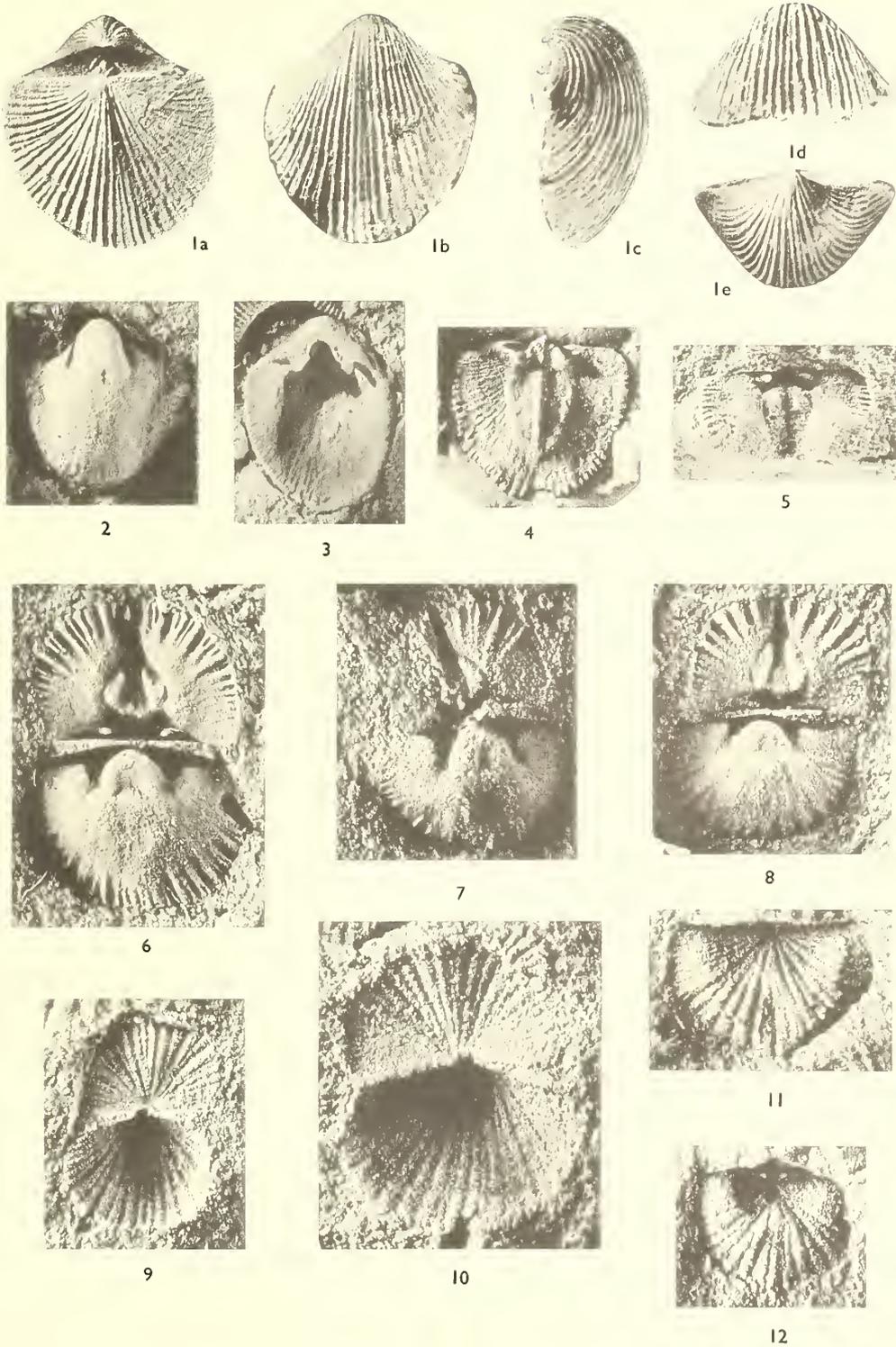
Exterior of brachial valve. Valve flat or only slightly convex in posterior portion and may be flat or gently concave along periphery. Wide, deep median sulcus widens from umbo to anterior margin where it is half as wide as the greatest width. Interarea flat, erect to hypercline, half as high as pedicle valve interarea; notothyrium triangular enclosing about 110°, occupied by the posterior end of the cardinal process. Branching pattern of costellae in median area of valve asymmetrical with successive branches directed alternately to left and right of preceding rib, resulting in many specimens in a smooth triangular median area.

Interior of pedicle valve. Delthyrial cavity deep; muscle field cordate in outline, extends a third to half the length of the valve and is three-fifths to four-fifths as wide as long. Diductor scars triangular in outline with rounded anterior margins, separated by a raised median area of uniform width which is rounded in cross-section and about a quarter as wide as the muscle field. Narrow rounded depressions of uniform width may be present on each side of the raised median area medial to the diductor scars. The raised median area in some cases extends anterior to the muscle field and tapers in height

EXPLANATION OF PLATE 61

Figs. 1–5. *Visbyella pygmaea* (Whittard and Barker). 1a–e, Purple Shales $\frac{1}{3}$ mile NE. of Brook House, Hughley, Shropshire. Dorsal, ventral, lateral, anterior, and posterior views of specimen no. GSM 82546 (holotype) ($\times 5$). 2. Purple Shales, Onny River section, Shropshire. Internal mould of pedicle valve. Specimen no. GSM 82548 (paratype) ($\times 5$). 3. Purple Shales, Harley Brook, 200 yd. NNE. of Domas, Shropshire. Interior of pedicle valve. Specimen no. GSM 82547 (paratype) ($\times 4$). 4. Purple Shales, Onny River section, Shropshire. Interior of brachial valve. Specimen no. GSM 82549 (paratype) ($\times 5$). 5. Purple Shales, Onny River section, Shropshire. Internal mould of brachial valve. Specimen no. GSM 82550 (paratype) ($\times 5$).

Figs. 6–12. *Visbyella cumnockensis* sp. nov. Manildra Formation, *Monograptus testis* horizon, 800 yd. N. of Baldry road, $1\frac{1}{2}$ miles W. of Cumnock, N.S.W., Australia. 6. Internal mould of both valves in contact. Specimen no. SU 19511 (holotype) ($\times 8$). 7. Internal mould of both valves in contact. Specimen no. SU 19512 (paratype) ($\times 8$). 8. Internal mould of both valves in contact. Specimen no. SU 19513 (paratype) ($\times 8$). 9. External mould of both valves in contact. Specimen no. SU 19514 (paratype) ($\times 8$). 10. External mould of both valves in contact. Specimen no. SU 19516 (paratype) ($\times 8$). 11. External mould of brachial valve. Specimen no. SU 19517 (paratype) ($\times 8$). 12. External mould of brachial valve. Specimen no. SU 19518 (paratype) ($\times 8$).



anteriorly. A minute linear medial ridge may be present in the posterior end of the delthyrial cavity. Teeth large, blunt, triangular in outline, crenulated on their inner surface bearing deep crural fossettes on their medial face. Dental plates flat, diverge ventro-laterally from the teeth to the floor of the valve, and extend anteriorly about a quarter the length of the valve. Anterior crenulations rounded, separated by deep rounded interspaces of about equal width.

Interior of brachial valve. Muscle field extends two-thirds the length of the valve, is three-fifths as wide as long, and is bounded by low ridges which extend parallel to the mid-line from the bases of the brachiophores to about half the length of the muscle field and then extend antero-medially so as to intersect the mid-line at about a 45° angle. Prominent median ridge extends seven-eighths the length of the valve and is a fifth as wide as the muscle field. It increases abruptly in height at the anterior end of the muscle field and then decreases in height anteriorly. The muscle field is divided into an anterior pair and a posterior pair of oval adductor impressions of about equal size by low transverse ridges which diverge antero-laterally from the median ridge. The sockets are short, crenulated, triangular in outline, and floored by socket pads with a strongly convex inner surface. Brachiophores blunt, rounded at their distal end, diverge at about a 90–120° angle to each other at their bases and are strongly curved postero-laterally. Cardinal process expands posteriorly, and has a postero-dorsally directed, markedly trilobed distal face. The median lobe of the distal face may be further divided into three small lobes. Crenulations of the anterior shell margin are rounded, may bifurcate, and are separated by deep rounded interspaces of about the same width as the crenulations.

Type specimens. Peabody Museum of Yale University. Holotype: No. 424, an articulated specimen. Paratypes: Nos. 424a, internal mould of brachial valve; 424b, internal mould of pedicle valve; and 424c, articulated specimen.

Distribution. *V. nana* occurs in the middle member of the Ross Brook Formation of late Llandovery (C₁–C₅) age and in the upper member of the Ross Brook Formation of late Llandovery (C₆)–early Wenlock age in Antigonish and Pictou Counties, Nova Scotia, at U.S. National Museum localities 10120, 10124, 10127, 10833, 10856, 11224, 11225, 11227, 11229, 11230, 11231, 11234, 11235, 11236, and 11237. It occurs in the Kerrowgare Formation in beds of late Llandovery age at U.S. National Museum locality 11228 in Pictou County, Nova Scotia.

Visbyella cummockensis sp. nov.

Plate 61, figs. 6–12

Diagnosis. Relatively small, weakly sulcate, and coarsely costellate *Visbyella* with semi-circular outline. Median ridge in brachial valve broad and low posteriorly, becoming narrower and higher to form an anterior median septum.

Comparison. *V. cummockensis* is closer to *V. nana* than to *V. visbyensis*, especially in having an anterior median septum in the brachial valve, having coarser costellae, and in not having a strongly incurved beak on the pedicle valve. However, *V. nana* has a

strongly sulcate brachial valve, a triangular outline, and an elongate delthyrial cavity; whereas *V. cummuckensis* has a weakly sulcate brachial valve, a semicircular outline, and a short delthyrial cavity.

Description. Plano-convex to very unequally biconvex with semicircular to subcircular outline. Length about two-thirds width. Hinge line straight, almost equal to greatest width which is only slightly anterior to hinge line. Cardinal angles obtuse, lateral and anterior margins evenly rounded.

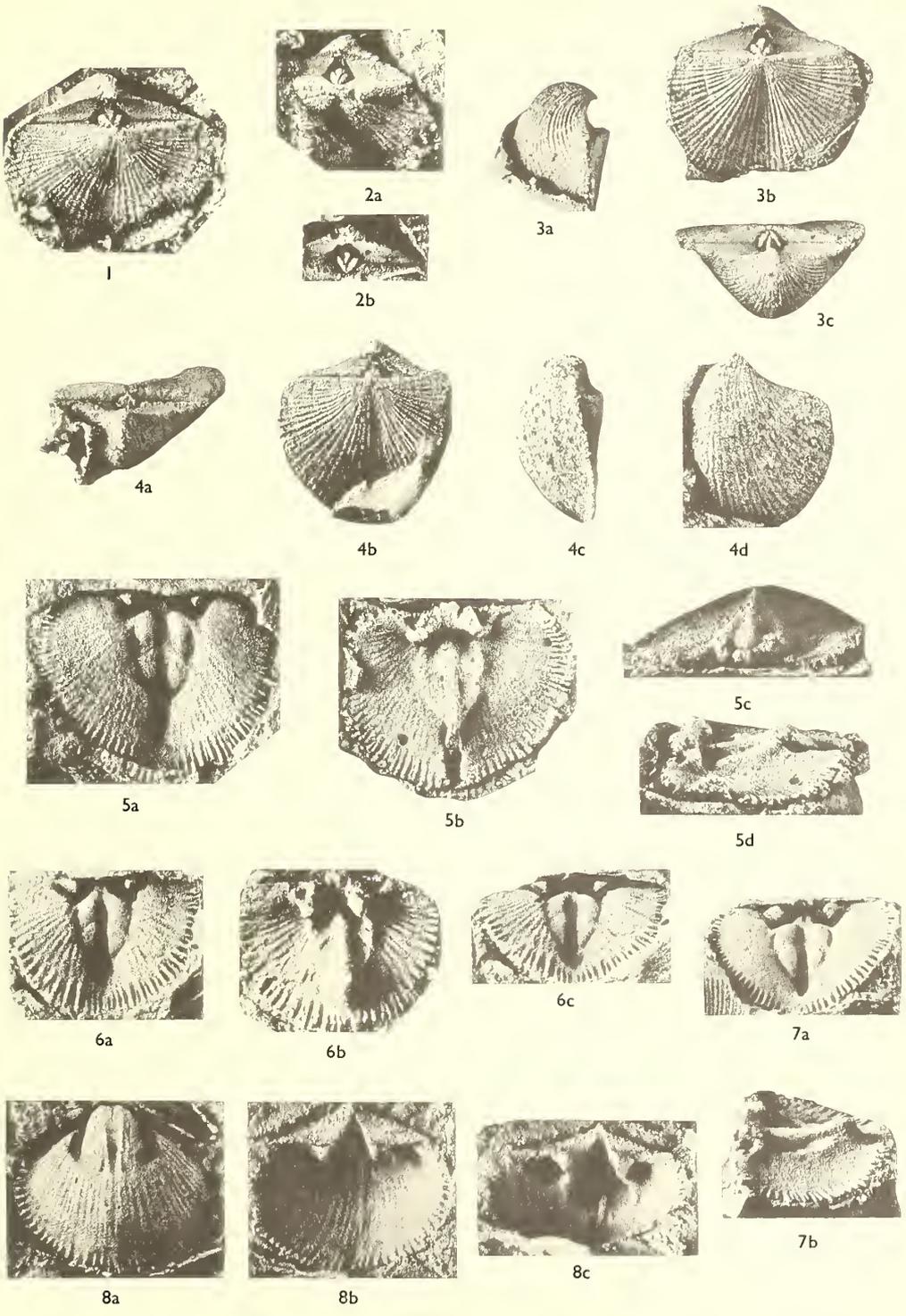
Exterior of pedicle valve. Strongly convex with greatest curvature at the umbo. Beak small, sub-erect. Interarea long, gently concave, apsacline with an apical angle of about 120°. Delthyrium includes an angle of about 60°, width equal to a quarter the length of the hinge line. Apical plate present.

Exterior of brachial valve. Planar to weakly convex with a faint broad sulcus increasing in width towards the anterior margin. Interarea planar and anacline to hypercline, apical angle of about 145°. Notothyrium includes an angle of about 90° and is filled by the cardinal process. Costellae rounded, separated by wide interspaces, 5 per mm. at the anterior margin of a shell 2 mm. long.

Interior of pedicle valve. The muscle field extends one-quarter to one-third of the valve length, diductor impressions elongate and weakly impressed, separated by a short, slightly raised median area. Stout dental lamellae diverge anteriorly at about 100° and also diverge slightly ventrally. Anterior edges of the lamellae recede and broaden to meet the valve floor at one-fifth valve length. Teeth strong, short, wide, triangular, large crural fossettes directed antero-medially.

EXPLANATION OF PLATE 62

- Figs. 1-4. *Visbyella nana* (McLearn). Upper member Ross Brook Formation, Pictou Co., Nova Scotia. USNM Loc. No. 11229. 1, Dorsal view of latex impression of external mould of articulated shell. Specimen no. GSC 19170 (×4). 2a-b, Dorsal views of latex impression of external mould of articulated shell. Specimen no. GSC 19592 (×4). 3a-c, Lateral, dorsal, and posterior views of latex impression of external mould of articulated shell. Specimen no. GSC 19168 (×4). 4a-d, Posterior, dorsal, lateral, and ventral views of latex impression of external mould of articulated shell. Specimen no. GSC 19169 (×4).
- Figs. 5a-d. *Visbyella nana* (McLearn). Middle member Ross Brook Formation, Arisaig area, Nova Scotia. USNM Loc. No. 10124. 5a, internal mould brachial valve, specimen no. GSC 19172 (×4). 5b-d, internal, posterior, and lateral views of latex impression of same specimen (×4).
- Figs. 6a-c. *Visbyella nana* (McLearn). Upper member Ross Brook Formation, Pictou Co., Nova Scotia. USNM Loc. No. 11234. 6a and 6c, views of internal mould of brachial valve, specimen no. GSC 19171 (×4). 6b, latex impression of same specimen (×4).
- Figs. 7a-b. *Visbyella nana* (McLearn). Middle member Ross Brook Formation, Arisaig area, Nova Scotia. USNM Loc. No. 10124. 7a, internal mould of brachial valve, specimen no. GSC 19174 (×4). 7b, lateral view of latex impression of same specimen (×4).
- Figs. 8a-c. *Visbyella nana* (McLearn). Upper member Ross Brook Formation, Pictou Co., Nova Scotia. USNM Loc. No. 11229. 8a, internal mould of pedicle valve, specimen no. GSC 19173. 8b-c, interior and anterior views of latex impression of same specimen (×4).



Interior of brachial valve. Prominent elongate adductor impressions become progressively elevated anteriorly, forming an inclined flank on each side of a median septum. The median septum is broad and low between the brachiophores, becoming narrower and higher as it extends to three-quarters valve length, where it decreases abruptly in height. The small round posterior adductor impressions are separated from the longer anterior pair by indistinct transverse ridges. Brachiophores stout, elliptical in cross-section, distal extremities curved slightly posteriorly. The brachiophores flank deep, evenly rounded sockets aligned parallel to the hinge line, and are fused at their posterior extremities to a very broad trilobed cardinal process which completely fills the notothyrium and projects from it. The valve margins are strongly crenulated anteriorly and antero-laterally. These crenulations may extend for a quarter of the valve length.

Type specimen. Sydney University, New South Wales. Holotype: SU 19511, internal mould with opened valves in contact. Paratypes: SU 19512, internal mould with opened valves in contact; SU 19513, internal mould with opened valves in contact; SU 19514, external mould with opened valves in contact; SU 19515, external mould with opened valves in contact; SU 19516, external mould with opened valves in contact; SU 19517, external mould of brachial valve; SU 19518, external mould of brachial valve.

Distribution. The species is described from twenty specimens finely preserved as internal and external moulds in hard shale of the *Monograptus testis* horizon within the Manildra Formation. Locality, 800 yd. north of Baldry road, 1½ miles west of Cumnock, New South Wales, Australia.

This occurrence of Wenlock Limestone age, in New South Wales, is the only one yet recorded.

Acknowledgements. It is a pleasure to record thanks to Dr. J. E. Hede for supplying specimens of *V. visbyensis* from the Lower Visby Marl, to Dr. V. Jaanusson for help in selecting and for loaning type material from the Swedish Museum of Natural History, Stockholm, and to Dr. A. Martinsson for kindly providing a translation of Lindström's original Swedish description of *Orthis visbyensis*. We are indebted to Dr. W. S. McKerrow for arranging the loan from Oxford University Museum of specimens of *V. pygmaea* from a collection made by Dr. A. Ziegler, who provided additional locality information. Also to Mr. D. White of the Geological Survey Museum, London, for the loan of the types of *V. pygmaea*. The Nova Scotia material was collected by J. Griffin and A. Ziegler under Boucot's direction in 1959. A John Simon Guggenheim Foundation Fellowship enabled Boucot to collect *V. visbyensis* from Gotland in 1956. The work carried out by Walmsley, Boucot, and Harper in Pasadena was supported by a grant from the National Science Foundation. A D.S.I.R. research grant enabled Walmsley to study the Gotland localities and to visit the Swedish Museum of Natural History, Stockholm, in 1965. These grants are gratefully acknowledged.

REFERENCES

- BOUCOT, A. J., JOHNSON, J. G., HARPER, C. W., and WALMSLEY, V. G. 1966. Silurian Brachiopods and Gastropods of Southern New Brunswick. *Bull. Can. geol. Surv.* **140**, pp. 1–44, pl. 1–18.
- HEDE, J. E. 1956. in *Lexique Stratigraphique Internationale Europe*, Fasc. 2c, Sweden. Paris.
- LINDSTRÖM, G. 1861. Bidrag till Kännedomen om Gotlands Brachiopoder. *Förh. Öfvers Vetenskapsakad.* **17** (60), 337–82.
- MCLEARN, F. H. 1924. Palaeontology of the Silurian rocks of Arisaig, Nova Scotia. *Mem. Can. geol. Survey*, **137**, pp. 1–179, pl. 1–30.
- REGNELL, G. and HEDE, J. E. 1960. The Lower Palaeozoic of Scania—The Silurian of Gotland. *Guide to Excursions A22 and C17. Int. Geol. Congr. 21st Sess., Norden.*
- SCHUCHERT, C. and COOPER, G. A. 1932. Brachiopod genera of the suborders Orthoidea and Pentamerioidea; *Mem. Peabody Mus. Yale*, **4** (1), 1–270, pl. A and 1–29.

- WALMSLEY, V. G. 1965. *Isorthis* and *Salopina* (Brachiopoda) in the Ludlovian of the Welsh Borderland. *Palaeontology*, 8, 454-77, pl. 61-65.
- WHITTARD, W. F. and BARKER, GLENYS H. 1950. The Upper Valentian Brachiopod Fauna of Shropshire—Pt. 1. Inarticulata: Articulata, Protremata, Orthoidea. *Ann. and Mag. nat. Hist.* (12), 3, pp. 553-90, pl. v-viii.

V. G. WALMSLEY
University College
Swansea

A. J. BOUCOT
California Institute of Technology
Pasadena

C. W. HARPER
University of Oklahoma
Norman, Oklahoma

N. M. SAVAGE
Sydney University
Sydney, N.S.W.

Typescript received 13 January 1967

A NEW TYPE OF DELTHYRIAL COVER IN THE DEVONIAN BRACHIOPOD *MUCROSPIRIFER*

by R. COWEN

ABSTRACT. A new type of delthyrial cover, *stegidial plates*, is described from very well-preserved specimens of *Mucrospirifer mucronatus* (Conrad) from the Traverse Group (Middle Devonian) of Michigan. Stegidial plates are unlike other delthyrial covers, such as deltidial plates and pseudodeltidia, because they are not integral parts of either valve: they are truly independent plates. As such, they can be compared only with the stegidium of some Upper Devonian spiriferides. The stegidium is re-interpreted in the light of its probable homology with stegidial plates: stegidial structures as a whole are regarded as unique within the phylum.

THE genus *Mucrospirifer* Grabau has a wide stratigraphical, geographical, and morphological range in Middle Devonian shelly faunas. This study is based on specimens in the Sedgwick Museum, Cambridge, from the Traverse Group of Michigan, collected and presented by Professor Alwyn Williams. Several authors have studied the Michigan spiriferide faunas; but Tillman (1964) has shown in a semi-quantitative study that too many 'species' have been distinguished among variable populations. On the basis of his work, all the specimens in the sample studied belong to the type species, *M. mucronatus* (Conrad).

Little attention has been paid to delthyrial structures in previous studies. Thus Stumm (1956) did not mention them at all, and Tillman (1964) regarded the deltidium as normal.

There is no normal deltidium, in the sense of a pair of so-called 'plates' continuous with the interarea both in position and mode of growth. Instead there are laminar *stegidial plates*, occupying approximately the same position and probably fulfilling the same function. But these plates are most unusual in structure and mode of growth, being entirely separate from either valve. The closest known equivalent is the stegidium described by Cooper (1954) in *Sphenospira* and *Syringospira*, two Upper Devonian spiriferides. Although the stegidial plates of *Mucrospirifer* show several distinct differences from the stegidium of Cooper, the structures appear to be homologous. Williams (1956, p. 257) mentioned that a stegidium-like structure had been found in *Mucrospirifer*, but this has not yet been described.

The stegidium and stegidial plates are very prone to removal and damage during fossilization, partly because they are not fused to the rest of the shell, and partly because of their laminar shell structure. The Michigan specimens are from a particularly favourable lithology: the shale is very fine and soft, and can be washed off the specimens without any danger of destroying the delicate delthyrial structures. Specimens of *M. mucronatus* from other lithologies in the Traverse Group rarely show any sign of stegidial plates, and it is likely that this is the general case. Even in the shales of the Traverse Group, comparatively few complete delthyrial covers have been found, and breakage and displacement of plates is common.

Terminology. A fairly complex terminology is used to describe the calcareous plate or plates covering the delthyrium or notothyrium of brachiopods (Williams and Rowell

[Palaeontology, Vol. 11, Part 2, 1968, pp. 317-327, pls. 63, 64.]

1965, pp. H85–H93). There are cases, however, where it is desirable to refer to these plates as a group, or where it is not possible to determine which interpretative name applies to any given plate. I shall use *delthyrial cover* in these circumstances as a non-interpretative descriptive term.

It is often difficult to describe the direction of growth of structures in the posterior part of the brachiopod shell. Directions are defined with reference to the commissure (*ventral* and *dorsal*) and to the position of the umbos in the plane of symmetry (*anterior*, *posterior*, and *lateral*). But these directions may be confusing when used for the posterior structures. For instance, in orthide brachiopods, an orthocline ventral interarea grows anteriorly, a catacline ventral interarea grows dorsally, and a procline ventral interarea grows posteriorly. To avoid this, I shall describe growth directions in the hinge region with respect to the umbo for any valve, as *apical* or *distal*. Thus a deltidial plate would always grow distally with respect to the ventral umbo.

GENERAL CONSIDERATIONS

Two pairs of laminar plates make up the delthyrial cover. The laminae of each plate overlap like tiles on a roof so that the smallest, central lamina is external; successive laminae underlie this as in a stepped pyramid so that the largest ('basal') lamina forms the internal side of the plate (Pl. 63, fig. 1). Because each plate is made of overlapping laminae, a broken edge has much the same appearance as an original edge which has been slightly damaged, just as a section through a pack of cards looks like the edge of the original pack. In some cases it has proved difficult to interpret fragments of plates, and I have always used the simplest hypothesis, which is to postulate as few plates as are compatible with the evidence.

As in all structures formed by accretion, growth-lines allow the shape at successive growth-stages to be determined. The stegidial plates have been studied as continuously developing parts of the organism, and this has aided their functional interpretation. It is clear from the specimens that there can be only one interpretation of the sequence of growth of the plates. The ontogenetic development from very small plates shows that the first-formed laminae were underlain by subsequently formed, larger laminae (Pl. 64, compare figs. 4, 14); that is, in every plate the youngest lamina was the largest, and was formed underneath previous ones. This interpretation has been used in the descriptions given below.

The pairs of laminar plates will be referred to as *ventral stegidial plates* and *dorsal stegidial plates*. Implications of affinity with the stegidium will be justified later.

EXPLANATION OF PLATE 63

Mucrospirifer mucronatus (Conrad), Traverse Group, Middle Devonian, Alpena County, Michigan.

All specimens whitened with ammonium chloride.

Figs. 1–5. A series of views of the delthyrium of the best-preserved specimen, SM H9251, from the Ferron Point Shale, abandoned shale pit, Alpena Portland Cement Co.; $\times 20$. This shows the detailed structure of the stegidial plates, with growth-laminae clearly visible. The dorsal plates have been displaced slightly, by slipping distally off the cardinal process into the delthyrial gap (fig. 5).

Figs. 6a, b. Stereo pair, right and left, to show the three-dimensional relationships of the broken stegidial structure of Plate 64, fig. 9.

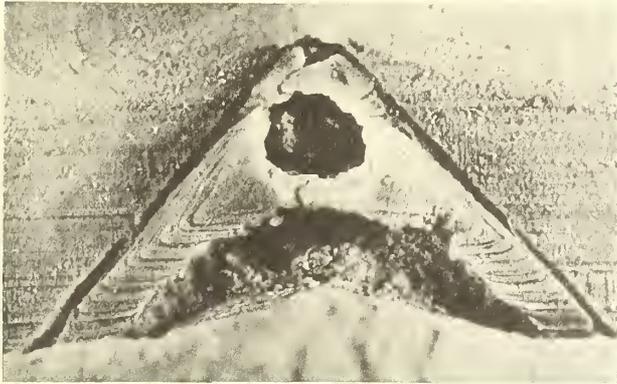
Figs. 7a, b. Stereo pair, right and left, to show the relationship of the delthyrial cover to the shell as a whole: the pedicle foramen is still relatively large. Same specimen as figs. 1–5.



1



2



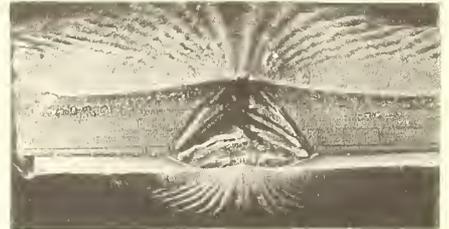
3



4



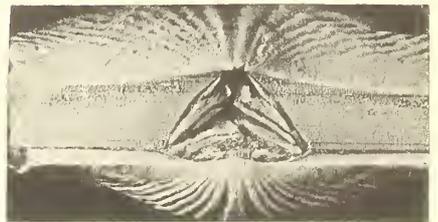
5



6a



7a



6b



7b

VENTRAL PLATES

The ventral plates are the larger pair in *Mucrospirifer*, because its ventral interarea is higher than the dorsal. The plates are clearly shown in Tillman's paper (1964, pl. 153, figs. 1-3), where they are interpreted as deltidial plates. But it is evident that the growth-lines on the plates are concentric, and can be traced completely round the edges of the plates (Pl. 63, figs. 1-4). Therefore the ventral plates cannot have been integral parts of the interarea but must have been secreted independently. They must have lain 'free' in the delthyrium, with growth by accretion proceeding on all edges. They could have been held in place only by the mantle secreting them, which must have lain in the delthyrium in a position almost exactly similar to that of the mantle secreting a normal deltidium.

Young specimens, and the growth-lines on older specimens, show that the ventral plates were first formed antero-laterally in the delthyrium (Pl. 64, figs. 4, 14) with their edges defined by the circumference of the pedicle, by the edge of the interarea, and by the functional requirement which causes the distal edge of many delthyrial covers to be curved. (In this case, the curvature is probably a response to the path of the diductors across the delthyrium to the cardinal process, but this interpretation does not affect the main argument.)

In subsequent growth the same factors continued to define the limits of the ventral plates. The growth-lines on the lateral edges are therefore straight and parallel, facing the interarea (Pl. 63, figs. 1-4). The median edge always formed an arc of the circumference of the pedicle, and the distal edge formed an arc comparable with that of a normal deltidial structure.

As the two plates grew, they came into contact in the median line. This implies that the pedicle was not growing at the same rate as the interarea. The plates joined medially, on the distal side of the pedicle, so that they then defined the pedicle foramen. The plates are conjunct, not fused; like conjunct deltidial plates in atrypides and rhynchonellides, their line of conjunction is irregular, and there is some overlapping (Pl. 63, figs. 1, 3, 4). After this stage the plates developed as one structural unit.

Laterally, the plates are often set at a high angle to the interarea, and this trend may be continued as far as the pedicle to form a pedicle tube projecting outwards from the delthyrium, very similar to that of *Cyrtia* or *Vellamo* (Pl. 64, figs. 6, 7).

There is some difficulty in interpreting the structures in the apex of the delthyrium. There seems to be no initial deposition on the apical side of the pedicle. In later ontogeny the ventral plates extended completely round the pedicle, so that it was enclosed by a calcite ring. This must have taken place very quickly, as the apical part has only one, or even no growth laminae on it, sometimes giving the impression of a single apical plate (Pl. 64, fig. 8). In very well-preserved specimens, however, this 'plate' can be seen to consist of two outgrowths, one from each side, with a line of conjunction even more irregular and asymmetrical than that distal to the pedicle (Pl. 63, fig. 3).

At this stage the pedicle had been surrounded, and had ceased to grow in absolute size; formerly its decline in growth had been relative to the rest of the interarea. From this stage the pedicle foramen shrank, and shell substance was added to the edges of the ventral plates facing the foramen (Pl. 64, fig. 13). This process is exactly analogous to the sealing off of the foramen in genera like *Cyrtia* and *Warrenella*. During the later stages of the process the remnant of the pedicle sometimes became asymmetrical (Pl. 64,

figs. 3, 6, 7): this also happened in *Cyrtia*. The laminae clearly overlap (Pl. 64, figs. 6, 7) in a way which provides further unambiguous evidence that younger laminae are formed underneath pre-existing ones.

In one specimen there is apparently a pair of apical plates separate from, and on the apical side of the ventral plates (Pl. 63, figs. 1–3). Apparent growth-laminae at the distal edge of these ‘apical plates’ appear to show growth in a distal direction. However, I interpret these edges as broken edges, and the apical structure as a part of the ventral plates, now broken away from the rest. This is the simplest hypothesis to adopt: the specimen is the only one in the sample which shows the ‘structure’; other comparable specimens show obvious mechanical breakage (e.g. Pl. 64, fig. 8).

DORSAL PLATES

These are a pair of plates in the base of the delthyrium. They are transversely elongated, together forming a diamond-shaped outline (Pl. 63, figs. 4, 5; Pl. 64, figs. 2, 5; text-fig. 2B). They are medially conjunct above the cardinal process, the line of conjunction being asymmetrical with some overlapping, as in the ventral plates (Pl. 64, figs. 2, 5). The growth-laminae show that accretion proceeded on all edges except the median edge (Pl. 63, figs. 1, 4, 5); this implies that the plates were formed as a median pair, and did not grow inwards from the lateral corners of the delthyrium as the ventral plates did. This is probably because the ventral plates were initially separated by a relatively strong pedicle; no such limitation restricted the development of the dorsal plates. In every other respect the dorsal plates are homologous with the ventral plates, and in particular

EXPLANATION OF PLATE 64

All specimens whitened with ammonium chloride.

Figs. 1–9, 11, 13–14. *Mucrospirifer mucronatus* (Conrad), Traverse Group, Michigan. Specimens 1, 2, 5–7, 9, 14 are from the Upper Bell Shale, Rockport Quarry; specimens 3, 4, 8, 11, 13 are from the Ferron Point Shale, same locality as on Plate 63. Magnification $\times 8$ unless specifically stated.

Fig. 1. Large specimen, to show development of alae. SM H9247, $\times 2$.

Figs. 2, 5. Dorsal and apical views of a specimen to show a residual gap in the centre of the delthyrium, and the dorsal plates held in place over the cardinal process. SM H9249.

Figs. 3, 13. Dorsal views of specimens with pedicle foramina almost closed; that in fig. 3 rather asymmetrical. SM H9255 and H9257 respectively.

Figs. 4, 14. Dorsal views of very young specimens with ventral stegidial plates set in the distal-lateral corner of the delthyrium. SM H9254 and H9258 respectively.

Figs. 6, 7. Dorsal and oblique dorsal views of a specimen with an extremely asymmetrical pedicle foramen in later stages of development. SM H9250.

Fig. 8. Dorsal view of a specimen with stegidial plates largely broken away, leaving an ‘apical plate’. SM H9253.

Fig. 9. Dorsal view of specimen with high ventral interarea (*M. prolificus* Stewart) in which large dorsal stegidial plates have been crushed and broken into the delthyrium. This is an extreme example of the difficulty of interpreting fragments of stegidial plates. SM H9248.

Fig. 11. Oblique dorsal view of specimen showing the ‘apical plate’ with broken edges simulating growth laminae. SM H9251, $\times 12$.

Figs. 10, 12. *Austrospirifer variabilis* Glenister, Gnendna Fm. (Frasnian), $3\frac{1}{4}$ miles S. of Gnendna Well, Carnarvon Basin, W. Australia. Dorsal view of two specimens, BMNH BB16249–50, $\times 2$, to show the remarkable resemblance to *M. mucronatus* (Conrad), and the imperfectly preserved delthyrial cover which strongly resembles stegidial plates.



1



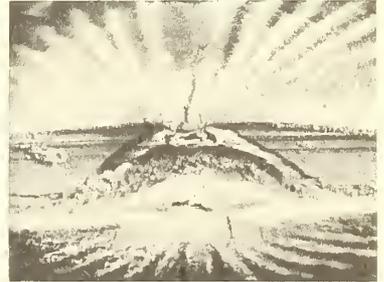
2



3



4



5



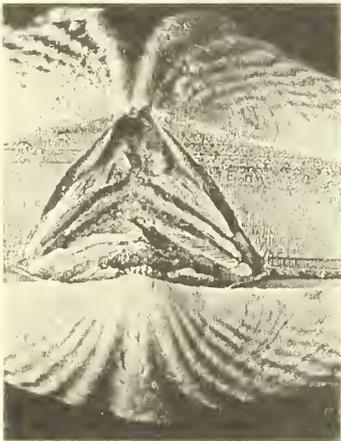
6



7



8



9



11



12



13



10



14

they must have been secreted independently from the interarea. The principles, and details, of their interpretation are the same as those for the ventral plates.

The dorsal plates are hardly supported by the sides of the interarea, and are very easily displaced. Sometimes they have been held in position by the cardinal process (Pl. 64, figs. 2, 5), but more often have been crushed down into the delthyrium, with some breakage (Pl. 63, figs. 4, 5). This may create the impression of multiple plates, especially in specimens with a high ventral interarea and correspondingly large delthyrium (Pl. 64, fig. 9), but in no case is it necessary to postulate more than one pair of original dorsal plates.

The lateral edges of the dorsal plates fit the edges of the dorsal interarea, and their distal edges form a curve which extends over the base of the delthyrium (Pl. 63, figs. 4, 5). When all the plates were in their original position, the delthyrium must have been largely closed to the exterior, except for the pedicle foramen (Pl. 63, fig. 4).

Certain exceptions to this are specimens like that shown on Plate 64, figs. 2, 5, in which there must have been an appreciable remaining delthyrial gap. It seems certain that a breakage of the delthyrial cover, as suggested by Tillman (1964, pl. 153, fig. 2, caption) did not take place; there is no sign of a median curved calcite arch over the centre of the delthyrium in any specimen, even the best preserved.

RANGE OF VARIATION

There is a wide range of morphological variation in the development of the stegidial plates, but none which implies any basic structural modification. Most of the variation can be ascribed to variation in the absolute size and relative rate of growth and decline of the pedicle (Pl. 64, compare figs. 2, 11) and in the height of the interarea (Pl. 64, compare figs. 9, 13). These contrasted forms are the former *M. alpenensis* (Grabau) and *M. prolificus* (Stewart), which form two end-members of a series showing continuous variation; they were distinguished mainly on the height of the interarea.

STEGIDIAL AND DELTIDIAL PLATES

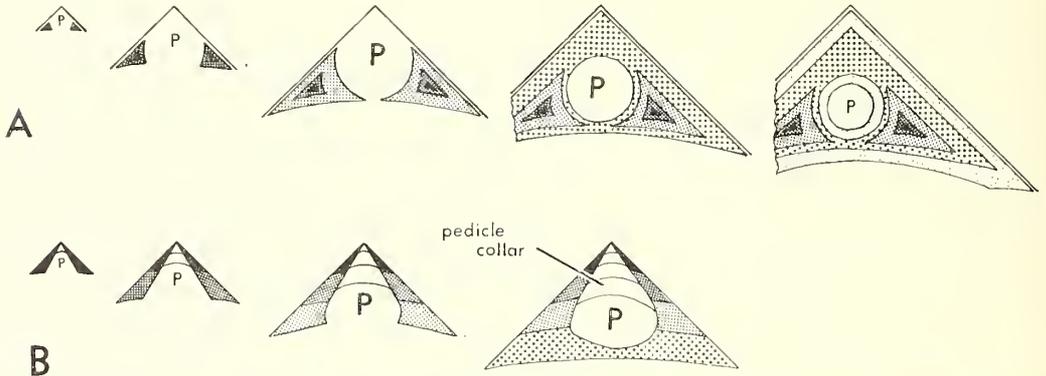
Polished sections of *Mucrospirifer* show primary and secondary layer shell present on both ventral and dorsal valves. But primary layer has not been observed on stegidial plates. If this absence is not a preservational failure, one must assume that stegidial plates were originally composed of secondary layer only. If so, their structure would be radically different from that of deltidial plates, which are homologous with the rest of the shell, and are covered by primary layer.

Text-fig. 1 shows the development of ventral stegidial plates and deltidial plates. As deltidial plates are continuations of the interarea, their growing edges face distally; deltidial plates proper are never secreted by mantle in contact with pedicle epithelium. The pedicle collar, on the other hand, *is* secreted in contact with pedicle epithelium, and is therefore not a homologous continuation of the deltidial plates. It is the only part of the delthyrial structure in this example which has a growing edge on the apical side of the pedicle.

The ventral stegidial plates were not limited by being integral parts of the ventral interarea; their growing edges were uninterrupted and peripheral. They could, and did,

include a part on the apical side of the pedicle homologous with the rest of the delthyrial cover. This can never occur in brachiopods with normal deltidia; even in amphithyrid brachiopods (e.g. *Megerlia*), the growing edge of the deltidium proper is not found on the apical side of the pedicle in a position corresponding to the apical part of the stegidial plates; instead, this position is occupied by the growing edge of the pedicle collar.

The ventral stegidial plates lay 'free' in the delthyrium, and accreted on all edges. But this occurred within a triangular gap in the shell, and a continuously expanding



TEXT-FIG. 1A, B. Diagrams to show the development of stegidial plates and deltidial plates respectively. P indicates the relative size of the pedicle at various growth stages. In spite of the very different mode of growth of the two contrasted structures, their over-all shape, size, and disposition remains much the same. A is based on *Mucrospirifer micronatus* (Conrad); B is generalized, based on study of several genera, such as *Hemithiris*, *Cyrtia*, and *Warrenella*. Note the pedicle collar on the apical side of the foramen; this bears strong growth-lines.

plate could not have been accommodated indefinitely in such a gap. It must necessarily have moved distally away from the apex (or umbo); so that any growing stegidial plate was mobile with respect to the interarea during ontogeny.

Consequently, if the pedicle was surrounded by stegidial plates, it must have moved distally down the delthyrium relative to the interarea. This would have left a gap on the apical side of the pedicle; presumably the apical part of the ventral plates served to close this gap, after an early ontogenetic stage in which an apical part was neither required nor secreted (text-fig. 1A).

These arguments can be extended to include dorsal stegidial plates, as contrasted with chilidial plates; the morphology and development of the dorsal plates are simpler because the pedicle does not affect the structures in the notothyrium.

There was a fundamental difference, therefore, between the delthyrial growing edges of epithelia forming stegidial plates and those forming deltidial plates. The distribution of epithelial surfaces in the delthyrial region can be reconstructed with some accuracy, because the stegidial plates must have lain on the mantle surface which secreted them. Therefore one can infer that the epithelium was distributed much as it is in 'normal' brachiopods with deltidia. But the epithelium differed in the type of shell secreted and in the arrangement of the growing edges.

FUNCTIONAL INTERPRETATION

Probably the primary function of the stegidial plates was protection of the delthyrium. Analogy could be drawn with the opercula of molluscan groups like some cephalopods and gastropods: growth of a calcareous plate takes place peripherally and proceeds in such a way that the plate fills an apertural gap in the rest of the shell at all stages of development. In shape, size, and developmental history the stegidial plates closely mimic the deltidium and chilidium, or pseudodeltidium and chilidium, of other brachiopods. Their mode of secretion removed some of the inherent limitations imposed upon the normal deltidium: for instance, the ventral plates surround the pedicle foramen completely, apically and distally, whilst deltidial plates cannot do this.

The stegidial plates and deltidium are interesting demonstrations of the performance of the same inferred function in two different ways; this is not because of any known difference in the physical requirements of the environment, but because of a difference in the soft-part anatomy which changed the intrinsic possibilities of shell development. In this way an important change in the inner organization of an animal is reflected in the hard-part morphology, even though the external environment of the animal may have been unchanged.

The development of the structures of the delthyrium and those of the hinge-line is closely correlated. It is apparent from the growth-lines of the shell that young individuals of *Mucrospirifer* were not alate like the adults (Pl. 63, fig. 7; Pl. 64, figs. 1, 5, 8, 11); at a certain growth-stage the hinge-line suddenly elongated by increased accretion at the cardinal angles, forming alae (Pl. 64, fig. 1). The growth-stage at which this occurred was variable; as described above, the stage at which the pedicle foramen was surrounded by the ventral stegidial plates also varied.

These two significant changes in shell morphology happened at about the same time. Usually the pedicle was surrounded by the ventral plates shortly after the first appreciable alae were formed. This can be reconstructed from the growth-lines on shell and stegidial plates. Thus in one specimen (Pl. 64, figs. 2, 5) the pedicle foramen is quite small, and situated close to the ventral umbo. But it was not surrounded by the ventral plates until fairly late in shell development.

Whatever the main function of the alae may have been, they must to some extent have helped to stabilize the shell on the substratum. It is interesting that the development of a secondary stabilizing structure, the alae, should coincide so well with the decline of the primary stabilizing structure, the pedicle.

THE STEGIDIUM

Cooper (1954) introduced the term *stegidium* for a plate covering part of the delthyrium in *Syringospira* (from the Upper Devonian of New Mexico) and *Sphenospira* (from the Upper Devonian of Ohio). These spiriferide brachiopods have a transverse apical delthyrial plate set in a high delthyrium, the plate occupying about two-thirds of the delthyrial opening. The remainder is closed by the stegidium, which is a plate made up of overlapping laminae with concentric growth-lines, set inside the delthyrium, and closely fitting the sides of the dental plates and the anterior edge of the transverse plate. The anterior edge is concave forwards, perhaps to accommodate the diductors.

Like the plates in *Mucrospirifer*, the stegidium has laminar structure and concentric growth-lines; the larger, basal laminae lie underneath the smaller, exterior laminae. Cooper considered that the stegidium grew inwards from the edges of the delthyrium, closing off the delthyrial gap by encroachment on a diminishing pedicle foramen, the last stage in this process being the formation of a central plug as the pedicle atrophied completely. This interpretation implies that the stegidium did not necessarily lie 'free' in the delthyrium, for if growth was directed inwards, the periphery of the plate could have been fixed to the edges of the delthyrium.

One difficulty in accepting this interpretation lies in the mode of overlapping of the laminae. At the edges of the brachiopod shell, and round the edges of a 'normal' pedicle foramen undergoing diminution (as in *Cyrtia*, *Warrenella*, and *Hemitliris*, for example), new growth layers are secreted to lie *underneath* preceding layers. By analogy with these examples, on Cooper's interpretation of the mode of growth of the stegidium, the overlapping on the stegidium might be expected to be in the opposite direction, with inner laminae underlying outer ones.

Dr. M. J. S. Rudwick, who has examined Cooper's material in the U.S. National Museum, suggested to me that Cooper's interpretation should be reversed, and that the direction of growth of the stegidium was outwards. The largest lamina of the stegidium would then be the last-formed. This suggestion was based on the following reasoning. If the stegidium grew by inward accretion, then one might expect the inner laminae to have deviated during growth from the shape of the original outer circumference; in other words, to have irregularities like those shown in Williams's diagram of the stegidium in the *Treatise* (1965, fig. 91). Furthermore, if the stegidium acted to define a pedicle foramen in the process of decline and atrophy, as Cooper suggested, then the successive stages of decline of the foramen should be preserved in the growth laminae, as they are in the stegidial plates surrounding the foramen of *Mucrospirifer* (text-fig. 1A).

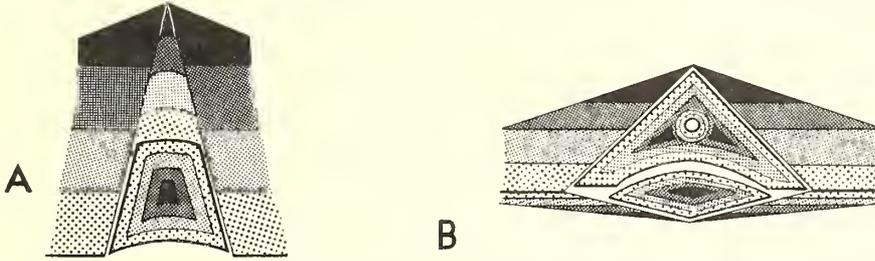
But in fact, as the growth-lines on Cooper's specimens show (see his plates), the lateral sides of the stegidium at every growth-stage were straight and parallel to the sides of the delthyrial gap, with the angle between the lateral sides remaining constant. It is particularly striking that in one specimen (Cooper 1954, pl. 37, fig. 12) an asymmetrical stegidium is lying within an asymmetrical delthyrial gap, and the growth-lines on the specimen show that the stegidium at earlier growth-stages was similarly asymmetrical; yet the growth-lines on the plate are still parallel to one another. There is therefore a rigid conservation of shape during the formation of a stegidium; this evidence strongly suggests that the stegidium was so modified in growth as to fit the delthyrial gap exactly at all times, and this implies that the mode of growth was the reverse of that suggested by Cooper. Rudwick's interpretation is shown diagrammatically in text-fig. 2A.

On Rudwick's suggestion, the growing edge of the stegidium was peripheral, and the plate could have altered in shape and grown in size continuously to fit the delthyrial gap as the latter increased. On all Cooper's figured specimens the stegidia fill the delthyrial gap exactly, even though the specimens are of various sizes; this follows naturally from Rudwick's suggestion, but is difficult to explain on Cooper's hypothesis.

Cooper's hypothesis inevitably implies that the stegidium did not begin to form until the last stage of growth, since only then would the 'first-formed', largest lamina fit the delthyrial gap. The stegidium could not be adapted to any new situation, such as further

growth of the delthyrium, because the growing edge was retreating towards the centre of the delthyrium where it would have secreted the 'pedicle plug'. In summary, on Cooper's hypothesis the stegidium performed its supposed function only at one particular growth-stage; it was not present before that stage, and became inevitably ineffective after it.

All the evidence from the comparable structures in *Mucrospirifer* shows that in this genus there is only one tenable interpretation of the mode of growth of stegidial plates;



TEXT-FIG. 2A, B. Diagrams to show the final morphology of stegidium and stegidial plates respectively, with interpretation of the sequence of ontogenetic development. A is based on *Sphenospira* and *Syringospira*, discussed by Cooper (1954); B is based on *Mucrospirifer mucronatus*. The shading on the interareas indicates the inferred growth-stages corresponding to stages in growth of the stegidium and stegidial plates, and shows the degree of relative migration of the stegidial structures down the delthyrium during growth. In 2A, the transverse delthyrial plate is overlapped by the stegidium.

this would confirm Rudwick's suggestion for the stegidium. Reinterpretation of the stegidium, based on the reasoning above, and on analogy (or homology) with *Mucrospirifer*, is now possible.

First of all, the laminar structure and concentric growth-lines of the stegidium, interpreted according to the reasoning above, show that the stegidium, like the stegidial plates of *Mucrospirifer*, must have lain 'free' in the delthyrium. This is so unusual in the brachiopods that the two structures are obviously closely allied, which justifies the term 'stegidial plates' for the delthyrial cover of *Mucrospirifer*.

The stegidium is not an integral part of the interarea, but was mobile with respect to the delthyrium. It must have migrated from the apex towards the base of the delthyrium during growth, and if it enclosed the pedicle, the latter would have been transported with it. Cooper said that the formation of the stegidium was consequent on, and contemporaneous with, the atrophy of the pedicle, 'an act of the adult animal' (1954, p. 328). This was the only possible interpretation on his hypothesis, but must now be revised.

The change in interpretation alters the *sequence* of events in the delthyrium, but the result is the same. The pedicle must have been in the centre of the stegidium if it was present at all.

This is the 'plug' of Cooper's interpretation, and there is no trace of a foramen in this region, except possibly his plate 37, fig. 14, nor is there any trace of the stegidium ever having been more than a single unit. By analogy with the development leading to the decline of the pedicle in *Mucrospirifer*, it is clear that the pedicle of *Syringospira* and

Sphenospira, if developed at all, must have atrophied extremely early in ontogeny. This inference reinforces the deduction made by Cooper about the mode of life of the two brachiopods. His suggestion that the very high wide interarea was a stable platform on a muddy or fine sandy bottom seems even more likely if the pedicle was never properly functional; and it is consistent with my observations on the alae of *Mucrospirifer*.

STEGIDIUM AND STEGIDIAL PLATES

The stegidium of *Syringospira* is obviously closely related to the stegidial plates of *Mucrospirifer* in origin, mode of formation, and structure. But there are distinct differences (see text-fig. 2):

(a) the structure of *Mucrospirifer* is multiple; in *Syringospira* it is a single (ventral) plate;

(b) the stegidium of *Syringospira* is sunk into the delthyrium, but in *Mucrospirifer* the stegidial plates occupy roughly the same positions as a normal deltidium;

(c) there is no dorsal equivalent of the (ventral) stegidium of *Syringospira*.

The first difference can be ascribed to the different development of the pedicle in the two genera. The early atrophy of the pedicle in *Syringospira* would leave an 'empty' delthyrium which could be filled by a single plate. In *Mucrospirifer* the pedicle was much stronger and longer-lasting, and the stegidial plates had to be moulded around it. An interesting analogy is *Acrospirifer*: here, early atrophy of the pedicle led to the formation, apparently, of a single structure in the delthyrium. This was in fact mistaken by de Koninck (1846) for a pseudodeltidium, although it is a true deltidium. The deltidium of *Warrenella* or *Vellamo*, on the other hand, is closely analogous to the stegidial plates of *Mucrospirifer*. The Australian Devonian spiriferide *Austrospirifer* (Pl. 64, figs. 10, 12) has a delthyrial cover closely similar to the stegidial plates of *Mucrospirifer*, and in addition, the external morphology of the two genera is strikingly close. I think it most likely that the delthyrial cover of *Austrospirifer* is a stegidium, although material I have examined is not well enough preserved to display the mode of growth of the cover.

The second difference between stegidium and stegidial plates is a reflection of the distribution of mantle epithelium in the delthyrium. In *Mucrospirifer* it must have formed a convex curve projecting above the interarea, but in *Syringospira* it was deeply sunk into the delthyrial cavity. I shall discuss elsewhere the significance of this difference.

The third difference is probably one of preservation. I hope to describe elsewhere occurrences of both ventral and dorsal components of stegidia in cyrtospiriferid brachiopods closely allied to *Syringospira* and *Sphenospira*. I predict, therefore, that a dorsal component of the stegidium exists in these two genera, but has not yet been observed. Williams and Rowell (1965, fig. 91) figure an 'antygidium' in *Syringospira* which may in fact be the dorsal component of the stegidium.

CONCLUSION

The differences between stegidium and stegidial plates cannot be regarded as great in view of the fact that both structures were secreted in the same manner, otherwise

unknown among the brachiopods. Some internal structures may be secreted independent of either valve: calcareous spicules are secreted by the internal mantle of some terebratulides, *Platidia* for example. But the only external structures laid down independent of either valve are stegidial plates and stegidia. They are true plates in the sense that deltidial 'plates', socket 'plates', dental 'plates', and so on, are not. They are a morphological alternative, and a functional equivalent, for deltidium and deltidial plates. It is likely that stegidial structures will be found very sporadically in time and space, because they are fragile and easily detached from the shell, and although they represent important modifications in the soft-part anatomy responsible for their secretion, they will probably be difficult to use in routine classification. However, they are likely to be significant at higher taxonomic levels.

Acknowledgements. I am grateful to Professor O. M. B. Bulman for the use of research facilities at the Sedgwick Museum, Cambridge; Dr. M. J. S. Rudwick, for supervising the work and guidance at all stages of preparation; Mr. A. G. Brighton for extended access to the collections of the Sedgwick Museum; and Dr. C. H. C. Brunton for access to specimens in the British Museum (Natural History). The research was supported successively by a DSIR Studentship and by a NERC grant which was awarded to Dr. M. J. S. Rudwick.

REFERENCES

- COOPER, G. A. 1954. Unusual Devonian brachiopods. *J. Paleont.* **28**, 325-32.
- DE KONINCK, L. 1846. Notice sur deux espèces de Brachiopodes du terrain paléozoïque de la Chine. *Bull. Acad. r. Belg. Cl. Sci.* **13**, 415-25.
- STUMM, E. C. 1956. A revision of A. W. Grabau's species of *Mucrospirifer* from the Middle Traverse Group of Michigan. *Contr. Mus. Paleont. Univ. Mich.* **13**, 81-94.
- TILLMAN, J. R. 1964. Variation in species of *Mucrospirifer* from Middle Devonian rocks of Michigan, Ontario and Ohio. *J. Paleont.* **38**, 952-64.
- WILLIAMS, A. 1956. The calcareous shell of the Brachiopoda, and its significance to their classification. *Biol. Rev.* **31**, 243-87.
- and ROWELL, A. J. 1965. Morphology. In MOORE, R. C. (ed.), *Treatise on Invertebrate Paleontology*, Part II, Brachiopoda, H57-H138. Univ. Kansas Press and Geol. Soc. Am.

R. COWEN

Department of Geology
University of California
Davis, California 95616

Typescript received 30 January 1967

THE PALAEOONTOLOGICAL ASSOCIATION

COUNCIL 1967-8

President

Professor T. S. WESTOLL, The University, Newcastle upon Tyne

Vice-Presidents

Dr. W. S. MCKERROW, University Museum, Oxford
Professor F. H. T. RHODES, University College, Swansea
Professor C. H. HOLLAND, Trinity College, Dublin, Ireland

Treasurer

Dr. C. DOWNIE, Department of Geology, The University, Mappin Street, Sheffield, 1

Membership Treasurer

Dr. A. J. LLOYD, Department of Geology, University College, Gower Street, London, W.C.1

Secretary

Dr. J. M. HANCOCK, Department of Geology, King's College, London

Editors

Mr. N. F. HUGHES, Sedgwick Museum, Cambridge
Dr. GWYN THOMAS, Department of Geology, Imperial College, London, S.W.7
Dr. I. STRACHAN, Department of Geology, The University, Birmingham, 15
Professor M. R. HOUSE, The University, Kingston upon Hull, Yorkshire
Dr. R. GOLDRING, Department of Geology, The University, Reading

Other members of Council

Mr. M. A. CALVER, Geological Survey Office, Leeds
Dr. C. B. COX, King's College, London
Mr. D. CURRY, Eastbury Grange, Northwood, Middlesex
Dr. GRACE DUNLOP, Bedford College, London
Mr. G. F. ELLIOTT, 60 Fitzjohn Avenue, Barnet, Herts.
Dr. T. D. FORD, The University, Leicester
Dr. A. HALLAM, University Museum, Oxford
Dr. R. P. S. JEFFERIES, British Museum (Natural History), London
Dr. G. A. L. JOHNSON, The University, Durham City
Dr. W. D. I. ROLFE, Hunterian Museum, Glasgow
Dr. A. H. SMOUT, British Petroleum Company, Sunbury-on-Thames
Dr. L. B. H. TARLO, The University, Reading
Professor H. B. WHITTINGTON, Sedgwick Museum, Cambridge

Overseas Representatives

Australia: Professor DOROTHY HILL, Department of Geology, University of Queensland, Brisbane
Canada: Dr. D. J. McLAREN, Institute of Sedimentary and Petroleum Geology, 3303-33rd Street NW., Calgary, Alberta.
India: Professor M. R. SAHNI, 98 The Mall, Lucknow (U.P.), India
New Zealand: Dr. C. A. FLEMING, New Zealand Geological Survey, P.O. Box 368, Lower Hutt
West Indies and Central America: Mr. JOHN B. SAUNDERS, Geological Laboratory, Texaco Trinidad, Inc., Pointe-à-Pierre, Trinidad, West Indies
Western U.S.A.: Professor J. WYATT DURHAM, Department of Palaeontology, University of California, Berkeley 4, Calif.
Eastern U.S.A.: Professor J. W. WELLS, Department of Geology, Cornell University, Ithaca, New York

PALAEONTOLOGY

VOLUME 11 · PART 2

CONTENTS

The microstructure and mineralogy of the shell of a Jurassic mytilid (<i>Bivalvia</i>). By J. D. HUDSON	163
Lower and early Middle Cambrian trilobites from the Pioche Shale, east-central Nevada, U.S.A. By W. H. FRITZ	183
Studies on Triassic fossil plants from Argentina. III. The trunk of <i>Rhexoxylon</i> . By D. W. BRETT	236
Fish otoliths from the Bathonian of southern England. By F. C. STINTON and H. S. TORRENS	246
The first non-marine Lower Cretaceous ostracods from Ghana, West Africa. By K. KRÖMMELBEIN	259
A goniatite fauna from the Viséan/Namurian boundary. By K. FIGGE	264
Form and function of the stem in a pseudoplanktonic crinoid (<i>Seirocrinus</i>). By A. SEILACHER, G. DROZDZEWSKI, and R. HAUDE	275
Some larger foraminifera from the Tertiary of Central America. By F. E. EAMES, W. J. CLARKE, F. T. BANNER, A. H. SMOUT, and W. H. BLOW	283
<i>Visbyella</i> —a new genus of resserellid brachiopod. By V. G. WALMSLEY, A. J. BOUCOT, C. W. HARPER, and N. M. SAVAGE	306
A new type of delthyrial cover in the Devonian brachiopod <i>Mucrospirifer</i> . By R. COWEN	317





SMITHSONIAN INSTITUTION LIBRARIES



3 9088 01375 6630