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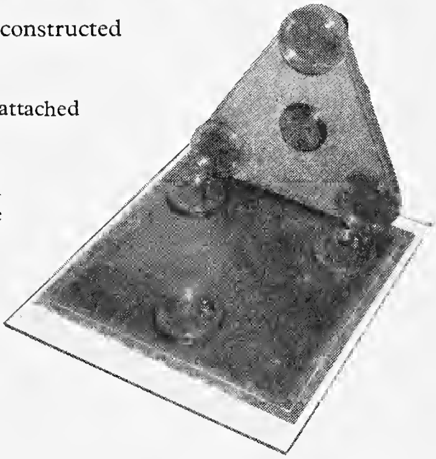

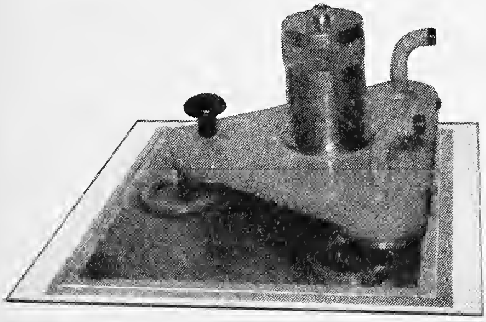

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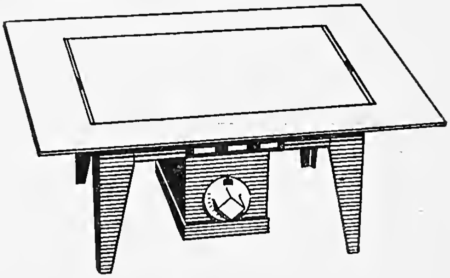

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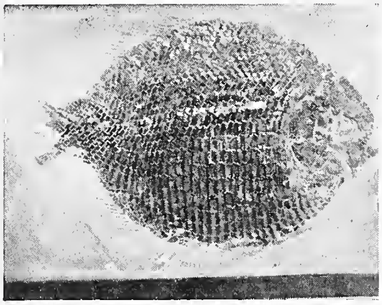

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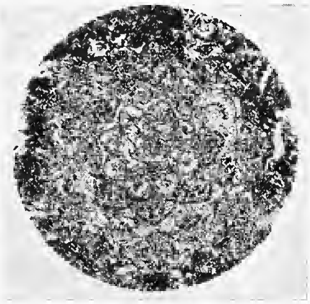

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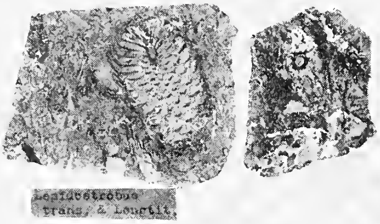

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THE CLASSIFICATION AND STRATIGRAPHICAL DISTRIBUTION OF THE GLOBIGERINACEAE

PART 1

by F. T. BANNER and W. H. BLOW

ABSTRACT. In this paper, the first of a series on the superfamily Globigerinaceae (Carpenter, emended), a new classification is given, comprising three families and eleven subfamilies. Two new subfamilies (Globorotaloidinae and Sphaeroidinellinae), two new genera (*Pseudohastigerina* and *Sphaeroidinellopsis*), two new subgenera (*Praeglobotruncana* (*Clavihedbergella*) and *Hastigerina* (*Bolliella*)), and one new species (*Hastigerina* (*Bolliella*) *adamsi*) are proposed. Particular attention is given to problems resulting from iterative evolution, and the broad aspects of the phylogeny of the superfamily are discussed.

INTRODUCTION

THE history of previous attempts satisfactorily to classify the planktonic foraminifera, grouped in this paper as members of the Globigerinaceae, has been given adequately by Bolli, Loeblich, and Tappan (1957, pp. 17–21), and little could be added to it here. The recent work of Reiss (1957, pp. 127–43; 1958, pp. 68–69) on the fundamental wall-structure of the smaller foraminifera follows from that of Smout (1954) and shows great promise of providing a firm basis for general classification; it is, however, too general in scope to enable finer subdivisions within superfamilies to be made.

Bolli, Loeblich, and Tappan's work is the most comprehensive and important recent study, and appeared while our own work was in progress. Although agreeing to some extent with the results of their studies, especially with regard to the principles of generic distinctions, we disagree with them over the fundamental basis of classification. They appear to over-emphasize the importance of the precise position of the interiomarginal aperture relative to the extent of the umbilicus, and attach little value to the presence or absence of a keel. As a result, it is often difficult for these authors to distinguish satisfactorily between superficially similar but actually unrelated genera. The generic diagnoses given by them for *Praeglobotruncana* (op. cit., p. 39) and for *Globorotalia* (op. cit., p. 41) are virtually indistinguishable, even though the genera are clearly different and have quite distinct stratigraphical ranges. Their system of classification has resulted, for example, in no clear distinctions being made between their interpretations of the families 'Orbulinidae' and 'Globorotaliidae'. In both these 'families', the coiling may be trochospiral, the chambers ovate or spherical, the primary aperture may be umbilical-extraumbilical ('spiro-umbilical' in *Hastigerinella*, 'extraumbilical' in *Pulleniatina*, both referred to the Orbulinidae), and secondary sutural apertures may be present (op. cit., pp. 31, 39). The range of both families, consequently, is given as Cretaceous to Recent, the range of the superfamily.

Sigal (1958) expressed a view almost completely opposed to that of Bolli, Loeblich, and Tappan (1957); he attached little importance at family level to the position of the

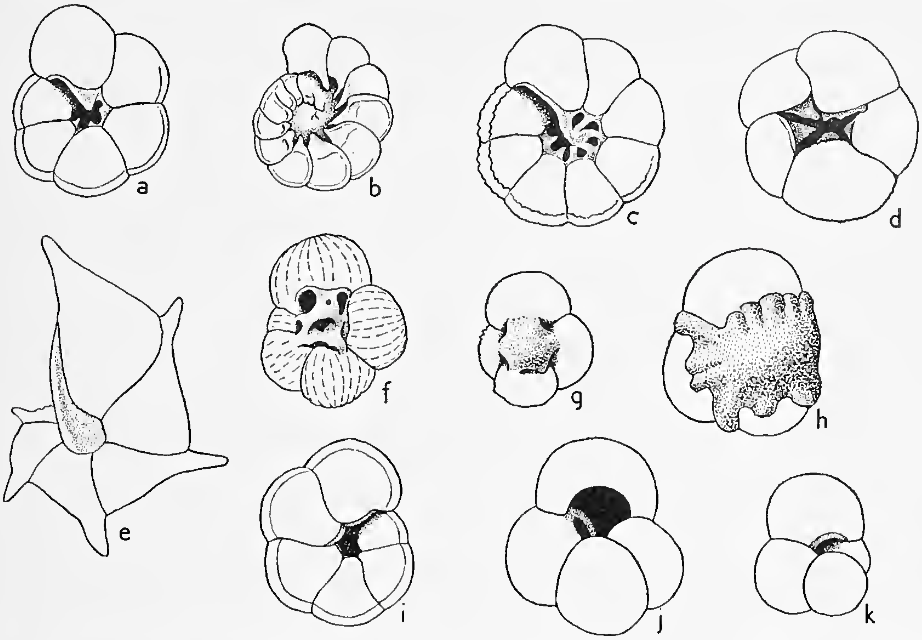
[Palaeontology, Vol. 2, Part 1, 1959, pp. 1–27, pls. 1–3.]

interiomarginal primary aperture relative to the umbilicus, but used the presence of carinae, mode of coiling and the shape of the adult chambers. These latter characters are believed by us to occur iteratively throughout the range of the superfamily, and we consider them to be of no more than generic or subgeneric importance.

We have tried to base our classification at family level on the fewest possible common morphological characters, which, in our interpretation, are of kind rather than of degree. We also consider that the least subjective means of determining the significance of any morphological character, in these very simply constructed but highly variable foraminifera, is its range in geological time. It is well known that members of the Globigerinaceae with spherical, ovate, clavate, or spinose chambers, with trochospirally or planispirally coiled adult tests, with apertures confined to the umbilicus or extending outside it or even reaching the periphery in an equatorial position, have occurred in the Cretaceous, Palaeogene, and Neogene. But it is clearly noticeable that external structural modifications of the apertures are comparatively restricted, and it is on these we have based our classification. Imperforate, distinctly asymmetrical flaps (portici) occur from the Cretaceous to Eocene (and possibly in the Oligocene—see p. 20) only; the complex imperforate umbilical coverplates (tegilla) which reached their maximum development in the younger species of *Globotruncana* are confined to the Upper Cretaceous; thin, narrow, practically symmetrical, perforate lips are often present on post-Cretaceous forms, except where they broaden to form equally symmetrical 'umbilical teeth' (e.g. *Globoquadrina*) or where they are replaced in the adult by perforate inflated bullae, which are again unknown before the Tertiary. These structures (see text-fig. 1) have been taken, therefore, to define the three families of the Globigerinaceae. Modifications of the primary apertures themselves, their shape and position, have been used to define the subfamilies; these characters can, of course, grade, and we hope that intra-family relationships will then emerge. The presence or absence of true supplementary apertures, accessory apertures, relict apertures (see Glossary), together with the development of elongate, clavate, or tubulospinose chambers and the presence or absence of imperforate peripheral keels (carinae) have been used to define the genera and subgenera. We distinguish between the true carina, which is imperforate and probably a primary structure, and which is believed to be of subgeneric value, and the pseudocarina, which is merely a peripheral thickening of the test wall, perforate uniformly with the remainder of the test, and which we consider to be of no more than specific importance.

In order to make this classification as unambiguous as possible, it has been partly set out in tabular form, the comment reduced to a minimum. It has been found necessary to erect two new genera and two new subgenera. The known ranges of the taxonomic groups are inserted in parentheses. This paper is an introduction to an exhaustive and fully illustrated study of all published species of the Globigerinaceae, which is now in preparation. In this, and in all succeeding parts, the authors' names are alphabetically arranged, and the arrangement implies no seniority of authorship whatsoever.

Throughout our work we have adhered strictly to the Rules of the International Commission on Zoological Nomenclature; failure to do so has often caused confusion in terminology, and we are strongly of the opinion that excessive invocation of exceptions is highly undesirable since they tend to make the rules themselves ineffective. We greatly regret the opinion rendered by the I.C.Z.N. (opinion 552), which rejected the prior family name Orbulinidae Schultze in favour of Globigerinidae Carpenter on the grounds of usage, since the change seems to us to be quite unnecessary, and some of the facts given in the proposal (Dusenbury 1957, *Bull. Zool. Nomencl.* **13,** part 6) can be shown to be incorrect—for example, the range of the genus *Globigerina* is not so great as that claimed by Dusenbury (op. cit., p. 194) and the apparent abundance of the genus *Globigerina* in Recent deposits is reduced when the interpretation of that genus is restricted.



TEXT-FIG. 1. Diagrams illustrating the apertural accessory structures of the Globigerinaceae. *a*, *Praeglobotruncana* (*Praeglobotruncana*) *stephani* (Gandolfi); after Reichel (1949) 1950, ×50; showing umbilical–extraumbilical primary aperture furnished with an asymmetric imperforate porticus. *b*, *Planomalina* (*Planomalina*) *cheniourensis* (Sigal); after Sigal 1952, ×37·5; showing asymmetric imperforate portici covering the primary and the relict parts of the previous apertures. *c*, *Ticinella alpha* (Reichel); after Reichel (1949) 1950, ×50 ('*Globotruncana* (*Thalmanninella*) *ticinensis* var. *alpha* Gandolfi' of Reichel, first valid transliteration of '*Globotruncana ticinensis* var. α' Gandolfi 1942); showing distal fusion of the portici, and formation of accessory apertures. *d*, *Globoquadrina altispira* (Cushman and Jarvis); after Bolli, Loeblich, and Tappan 1957, ×35; showing essentially perforate, practically symmetrical 'umbilical teeth'. *e*, *Hantkenina* (*Hantkenina*) *alabamensis* Cushman; after Brönnimann 1950, ×*c*. 50; showing the accentuated asymmetry of the porticus by its distal elongation and extension over the umbilicus. *f*, *Rugoglobigerina* (*Rugoglobigerina*) *rugosa* (Plummer); after Bolli, Loeblich, and Tappan 1957, ×*c*. 50; showing imperforate complex tegillum covering the umbilicus. *g*, *Catapsydrax dissimilis* (Cushman and Bermúdez); after Bolli, Loeblich, and Tappan 1957, ×30; showing perforate, convex bulla covering the umbilicus, and its marginal accessory apertures. *h*, *Tinophodella ambitacrena* Loeblich and Tappan; after Loeblich and Tappan 1957, ×72·5; showing the morphologically advanced form of the single, perforate, inflated bulla which covers the umbilicus. *i*, *Globorotalia* (*Globorotalia*) *menardii* (d'Orbigny); after Phleger, Parker, and Peirson 1953, ×17; showing the perforate, symmetrical lip and umbilical–extraumbilical aperture. *j*, *Globigerina bulloides* d'Orbigny; after Bolli, Loeblich, and Tappan 1957, ×57·5; showing the intraumbilical aperture, and the loss of the apertural lip in morphologically advanced forms of the Globigerininae. *k*, *Globigerina triloculinoides* Plummer; after Loeblich and Tappan 1957, ×72·5; showing the intraumbilical aperture, with the symmetrical perforate lip of the morphologically more primitive forms of the Globigerininae.

CLASSIFICATION

Order FORAMINIFERA

Superfamily GLOBIGERINACEAE Carpenter 1862, emended; nom. transl.

(Synonyms Globigerinidea Schwager 1876, Globigerinidea Morozova 1957)

Diagnosis. Coiled, multilocular Foraminifera with hyaline, perforate, calcareous walls which are radial in structure and characteristically more or less spinose or hispid superficially, although this hispidity is reduced in advanced forms and is often lost in the later chambers of adult individuals. Usually trochospirally coiled, at least in the young of the microspheric form; sometimes becoming involute and turgid; or planispiral, evolute and laterally compressed in the adult or in advanced forms; very occasionally becoming enrolled biserial, never rectilinear. Septa simple, lacking canal systems. Imperforate peripheral carinae (which may tend to become occluded internally but which never form discrete canals) may be present, but no tectoria or associated infundibulae occur. No umbilical plugs, pillars, or canal systems are present. No internal tubes, toothplates, tongues, or other structures internally modifying the apertures occur; apertural accessory structures are always external. Habitat believed to be always planktonic in normal marine environments, at least in the juvenile stage.

Family GLOBIGERINIDAE Carpenter 1862, nom. correct.

(Synonym Orbulinida Schultze 1854; suppressed by I.C.Z.N. Op. 552)

Diagnosis. Globigerinaceae which possess apertures unmodified by tegilla or portici, but which may possess narrow, perforate, symmetrical lips, or, in advanced forms, perforate bullae or umbilical teeth, or in which the primary aperture may be concealed in the adult and is replaced by multiple small apertures or large pores. Tests trochoid, adults dorsally evolute, ventrally involute, or completely involute, or evolute both ventrally and dorsally [Range: Danian to Recent].

Subfamily ORBULININAE Schultze 1854, emended, nom. transl.

(Synonym Candeininae Cushman 1927 in part)

Globigerinidae with no distinct primary aperture visible externally in the adult; adult apertures sutural and/or areal, a series of slit-like or pore-like openings, with no specialized accessory structures [Eocene; L. Miocene to Recent].

1. Apertures a series of discontinuous pores, some at least areal in position:
   (*a*) Last chamber embracing all or nearly all of earlier test:
      genus *Orbulina* d'Orbigny 1839 (L. Miocene to Recent), type species *O. universa* d'Orbigny, 1839.
      (Synonym *Candorbulina* Jedlitschka 1934, type species *C. universa* Jedlitschka 1934.)
   (*b*) Penultimate chamber embracing all or nearly all of earlier test:
      genus *Biorbulina* Blow 1956 (L. Miocene to Recent), type species *Globigerina bilobata* d'Orbigny 1846.

2. Apertures confined to sutures:
   - (*a*) Last chamber embracing much of earlier test:
     - (i) Apertures small, slit-like or pore-like, present between earlier as well as later chambers: genus *Porticulasphaera* Bolli, Loeblich, and Tappan 1957 (M. Eocene and L. Miocene), type species *Globigerina mexicana* Cushman 1925.
     - (ii) Apertures arched, in suture of last chamber only: genus *Globigerapsis* Bolli, Loeblich, and Tappan 1957 (M. to U. Eocene), type species *G. kugleri* Bolli, Loeblich, and Tappan 1957.
   - (*b*) Last chamber not embracing earlier test; chambers in relatively high trochoid spire, few in number in last whorl; apertures a series of small arched openings: genus *Candeina* d'Orbigny 1839 (L. Miocene to Recent), type species *C. nitida* d'Orbigny 1839.

Subfamily GLOBIGERININAE Carpenter 1862, emended, nom. transl.

Globigerinidae, in which the adult test is clearly trochoid, and possesses a distinct primary interiomarginal intraumbilical aperture in the adult. Wall structure simple [Danian to Recent].

1. Without supplementary apertures:
   - (*a*) Aperture intraumbilical throughout ontogeny: genus *Globigerina* d'Orbigny 1826 (Danian to Recent), type species *G. bulloides* d'Orbigny 1826.
   - (*b*) Aperture initially extraumbilical in part, but becoming solely intraumbilical in ontogeny; typically with exceptionally strong lips (umbilical teeth): genus *Globoquadrina* Finlay 1947 (Aquitanian to Pliocene), type species *Globorotalia dehiscens* Chapman, Parr, and Collins 1935.

2. With supplementary sutural dorsal apertures: genus *Globigerinoides* Cushman 1927 (Danian to Recent), type species *Globigerina rubra* d'Orbigny 1839.

Subfamily SPHAEROIDINELLINAE, new subfamily

Globigerinidae, in which the adult test is clearly trochoid, and possesses a distinct primary interiomarginal umbilical aperture throughout life. Wall structure complex, consisting, at least in part, of more than one layer of shell material; primary wall covered by a secondary cortex, superficially smooth and shiny, in which the perforations of the primary wall may be much reduced or absent. Lips thickened to become flange-like, often crenulate, but still fundamentally symmetrical [L. Miocene to Recent].

1. Without supplementary sutural apertures in the adult: genus *Sphaeroidinellopsis* gen. nov. (L. to U. Miocene), type species *S. subdehiscens* (Blow) = *Sphaeroidinella dehiscens subdehiscens* Blow 1959.

2. With supplementary sutural apertures in the adult: genus *Sphaeroidinella* Cushman 1927 (U. Miocene? to Pliocene to Recent), type species *Sphaeroidina bulloides* (d'Orbigny) var. *dehiscens* Parker and Jones 1865.

Subfamily CATAPSYDRACINAE Bolli, Loeblich, and Tappan 1957

Globigerinidae, in which the test is clearly trochoid, and possesses a primary interiomarginal intraumbilical aperture which is covered in the adult by a swollen perforate plate (bulla) or by a bulla-like extension of the last chamber, and which opens to the exterior by accessory apertures at the margins of, or within the area of, the bulla [Eocene to Recent].

1. Without supplementary apertures in the primary chambers:
   - (*a*) Umbilicus and primary aperture covered by a discrete bulla:
     - (i) Primary chamber wall and bulla similar in structure; accessory apertures few and unrestricted:
       - genus *Catapsydrax* Bolli, Loeblich, and Tappan 1957 (L. Eocene to L. Miocene), type species *Globigerina dissimilis* Cushman and Bermúdez 1937.
     - (ii) Primary wall thicker and more coarsely perforate than bulla; accessory apertures small, numerous, often restricted by lips:
       - genus *Tinophodella* Loeblich and Tappan 1957 (L. Miocene to Recent), type species *T. ambitacrena* Loeblich and Tappan 1957.
   - (*b*) No discrete bulla; umbilicus covered by perforate, bulla-like extension of last chamber wall:
     - genus *Globigerinita* Brönnimann 1952 (L. Miocene to Recent), type species *G. naparimaensis* Brönnimann 1952.

2. With supplementary sutural apertures in primary chambers, covered by bullae:
   - (*a*) With an early *Globigerinoides*-stage; supplementary apertures present in sutures of last chamber and some at least of earlier chambers:
     - genus *Globigerinoita* Brönnimann 1952 (M. Miocene), type species *G. morugaensis* Brönnimann 1952.
   - (*b*) With an early *Globigerapsis*-stage; supplementary apertures present only in the suture of the last chamber:
     - genus *Globigerinatheka* Brönnimann 1952 (M. to U. Eocene), type species *G. barri* Brönnimann 1952.

3. Supplementary apertures sutural and areal; bullae formed in at least two series, with secondary bullae covering accessory apertures in primary bullae:
   - genus *Globigerinatella* Cushman and Stainforth 1945 (L. Miocene), type species, *G. insueta* Cushman and Stainforth 1945.

Subfamily GLOBOROTALIINAE Cushman 1927 emended, nom. transl.

(Synonym, in part, Pulleniatininae Cushman 1927)

Globigerinidae, in which the test is clearly trochoid, possessing a primary aperture which is umbilical–extraumbilical and ventral in ontogeny, and in the adult [Danian to Recent].

I. Test uniformly trochospiral throughout life:
   - (1) No dorsal supplementary apertures:
     - genus *Globorotalia* Cushman 1927 (Danian to Recent), type species *Pulvinulina menardii* (d'Orbigny) var. *tumida* Brady 1877.
     - (Synonyms *Truncorotalia* Cushman and Bermúdez 1949, type species *Rotalina truncatulinoides* d'Orbigny 1839; ? *Pseudogloborotalia* Haque 1956, type species *P. ranikotensis* Haque 1956; *Planorotalites* Morozova 1957, type species *Globorotalia pseudoscitula* Glaessner 1937.)
   - (*a*) Test with an imperforate peripheral carina, at least in part:
     - Subgenus *Globorotalia* (U. Palaeocene to Recent).
   - (*b*) Test without imperforate peripheral carina:
     - (i) Chambers not radially elongate:
       - Subgenus *Turborotalia* Cushman and Bermúdez 1949 (Danian to Recent), type species *Globorotalia centralis* Cushman and Bermúdez 1937.
       - (Synonyms *Acarinina* Subbotina 1953, type species *A. acarinata* Subbotina 1953; *Globanomalina* Haque 1956, type species *G. ovalis* Haque 1956.)

(ii) Adult chambers radially elongate:
Subgenus *Hastigerinella* Cushman 1927 (L. Miocene to Recent), type species *Hastigerina digitata* Rhumbler 1911 (not *Globigerina digitata* Brady 1879) = *Hastigerinella rhumbleri* Galloway 1933.

(2) With dorsal sutural supplementary apertures:
genus *Truncorotaloides* Brönnimann and Bermúdez 1953 (L. to U. Eocene), type species *T. rohri* Brönnimann and Bermúdez 1953.

II. Test becoming streptospiral in adult:
genus *Pulleniatina* Cushman 1927 (M. Miocene? to U. Miocene to Recent), type species *Pullenia sphaeroides* d'Orbigny var. *obliquiloculata* Parker and Jones 1869.

Subfamily GLOBOROTALOIDINAE new subfamily

Globigerinidae, in which the test is clearly trochoid, possessing a primary aperture which is interiomarginal umbilical–extraumbilical during ontogeny, but which is covered in the adult by a bulla [Eocene to Miocene].

genus *Globorotaloides* Bolli 1957 (M. Eocene to M. Miocene), type species *G. variabilis* Bolli 1957.

Subfamily HASTIGERININAE Bolli, Loeblich, and Tappan 1957, emended

Globigerinidae, in which the test is initially distinctly trochospiral, but becomes nearly, but imperfectly, planispiral in the adult; juvenile interiomarginal umbilical–extraumbilical aperture becomes extraumbilical–peripheral (equatorial) in the adult [L. Miocene to Recent].

genus *Hastigerina* Thomson 1876 (L. Miocene to Recent), type species *H. murrayi* Thomson 1876 = *Nonionina pelagica* d'Orbigny 1839.
(Synonym *Globigerinella* Cushman 1927, type species *Globigerina aequilateralis* Brady 1879.)

1. Chambers not radially elongate in adult:
Subgenus *Hastigerina* (L. Miocene to Recent).

2. Chambers radially elongate in adult:
Subgenus *Bolliella* subgen. nov. (Recent), type species *Hastigerina* (*Bolliella*) *adamsi* sp. nov.

Subfamily CASSIGERINELLINAE Bolli, Loeblich, and Tappan 1957

Globigerinidae with an initial trochoid stage followed by enrolled biserial ('cassiduliniform') coiling in the adult [Oligocene to Lower Miocene].

1. Aperture interiomarginal, simple:
genus *Cassigerinella* Pokorńy 1955 (Oligocene to Lower Miocene), type species *C. boudecensis* Pokorńy 1955.
(Synonym *Globalternina* Ivanova, *in* Subbotina, Glushko, and Pishvanova 1955, type species (by monotypy) *G. globoloculata* Ivanova 1955 MS. (nom. nud.) = *Cassigerinella globolocula* Ivanova 1958.)

Family HANTKENINIDAE Cushman 1927, emended

Diagnosis. Globigerinaceae with tests which are primitively or initially trochospiral (at least in the microspheric form), advanced forms often becoming planispiral. The test is characterized by a primary aperture which is modified by an imperforate porticus, which is essentially an asymmetric, imperforate flap-like projection from the chamber wall into the umbilicus, more or less covering the primary aperture. The portici may, in primitive forms, be so strongly developed over the relict apertures in all chambers of the last whorl that they fuse to form accessory apertures (Rotaliporinae, in part); in advanced forms they may be visible on the later chambers or last chamber only. No bullae, tegilla, true lips, or umbilical teeth are present [Range: Lower Cretaceous to Palaeogene].

Subfamily ROTALIPORINAE Sigal 1958, emended, nom. transl.

Hantkeninidae which are trochospirally coiled throughout life, and which possess an umbilicus and apertures on the ventral side only. Primary aperture interiomarginal, umbilical–extraumbilical, not extending beyond the periphery on to the dorsal side. Portici strong on all chambers of the last whorl [Aptian to Maestrichtian].

1. Portici fuse distally:
   - (*a*) No supplementary apertures; relict parts of primary apertures open to exterior through accessory apertures between unfused proximal parts of portici:
     - genus *Ticinella* Reichel 1950 (Aptian? to Albian to Turonian to L. Coniacian?), type species *Anomalina roberti* Gandolfi 1942.
     - (Synonym *Helvetoglobotruncana* Reiss 1957, type species *Globotruncana helvetica* Bolli 1945.)
   - (*b*) With true supplementary ventral sutural apertures, opening to exterior beyond the portici:
     - genus *Rotalipora* Brotzen 1942 (U. Albian? to L. Turonian), type species *R. turonica* Brotzen 1942 = *Globorotalia cushmani* Morrow 1934.
     - (Synonym *Thalmanninella* Sigal 1948, type species *T. brotzeni* Sigal 1948.)

2. Portici distinct, separate or fused proximally, but not forming accessory or supplementary apertures:
   - genus *Praeglobotruncana* Bermúdez, 1952 (Aptian to Maestrichtian), type species *Globorotalia delrioensis* Plummer 1931 (non *Globigerina cretacea* var. *delrioensis* Carsey 1926 = *Praeglobotruncana* (*Hedbergella*) *delrioensis* (Carsey)) = *Globotruncana stephani* Gandolfi 1942, s.l.
   - (Synonyms *Rotundina* Subbotina 1953, type species *Globotruncana stephani* Gandolfi 1942; *Globotruncanella* Reiss 1956, type species *Globotruncana citae* Bolli 1951.)
   - (*a*) With imperforate peripheral band and carina or carinae, at least in part:
     - Subgenus *Praeglobotruncana* (U. Albian? to Cenomanian to Maestrichtian).
   - (*b*) Without imperforate peripheral band or carina:
     - (i) Chambers not radially elongate:
       - Subgenus *Hedbergella* Brönnimann and Brown 1958 (Aptian to Maestrichtian), type species *Anomalina lorneiana* (d'Orbigny) var. *trocoidea* Gandolfi 1942.
     - (ii) Chambers radially elongate in the adult:
       - Subgenus *Clavihedbergella* subgen. nov. (U. Albian to Turonian), type species *Hastigerinella subcretacea* Tappan 1943.

Subfamily PLANOMALININAE Bolli, Loeblich, and Tappan 1957 nom. transl., emended

Hantkeninidae with biumbilicate tests which become planispiral in the adult; primary aperture interiomarginal, umbilical–extraumbilical, equatorial, a low arch not elongate in the plane of coiling; adult individuals often possess paired primary apertures in the last chambers and often tend to become biserial. Portici present both ventrally and dorsally in adult [Aptian to Eocene to Oligocene?]

1. Relict parts of primary apertures open between distinct, long portici both ventrally and dorsally in all or nearly all chambers of the last whorl:
   genus *Planomalina* Loeblich and Tappan 1946 (Aptian to Maestrichtian), type species *P. apsidostroba* Loeblich and Tappan 1946.
   (*a*) With imperforate peripheral carina:
      Subgenus *Planomalina* (Aptian to Cenomanian).
   (*b*) Without imperforate peripheral carina:
      (i) Chambers not radially elongate:
         Subgenus *Globigerinelloides* Cushman and ten Dam 1948 June (Aptian to Maestrichtian), type species *G. algeriana* Cushman and ten Dam 1948.
         (Synonyms *Biglobigerinella* Lalicker 1948 September, type species *B. multispina* Lalicker 1948; *Biticinella* Sigal 1956, type species *Anomalina breggiensis* Gandolfi 1942.)
      (ii) Chambers radially elongate:
         Subgenus *Hastigerinoides* Brönnimann 1952 (Cenomanian to Santonian), type species *Hastigerinella alexanderi* Cushman 1931.
         (Synonym *Eohastigerinella* Morozova 1957, type species *Hastigerinella watersi* Cushman 1931.)

2. Relict apertures and umbilical parts of portici weak; visible on last few chambers only:
   (*a*) Chambers radially elongate:
      genus *Schackoina* Thalmann 1932 (Aptian? to Albian to Maestrichtian), type species *Siderolina cenomana* Schacko 1896 (1897).
      (i) Chambers with slender extensions (which are not true tubulospines, and have unthickened walls):
         Subgenus *Schackoina* (Cenomanian to Maestrichtian).
      (ii) Chambers with bulb-shaped extensions:
         Subgenus *Leupoldina* Bolli 1957 (Aptian? to Albian to Cenomanian?), type species *L. protuberans* Bolli 1957.
   (*b*) Chambers not radially elongate:
      genus *Pseudohastigerina* gen. nov. (Palaeocene? to L. Eocene to U. Eocene to Oligocene?), type species *Nonion micrus* Cole 1927.

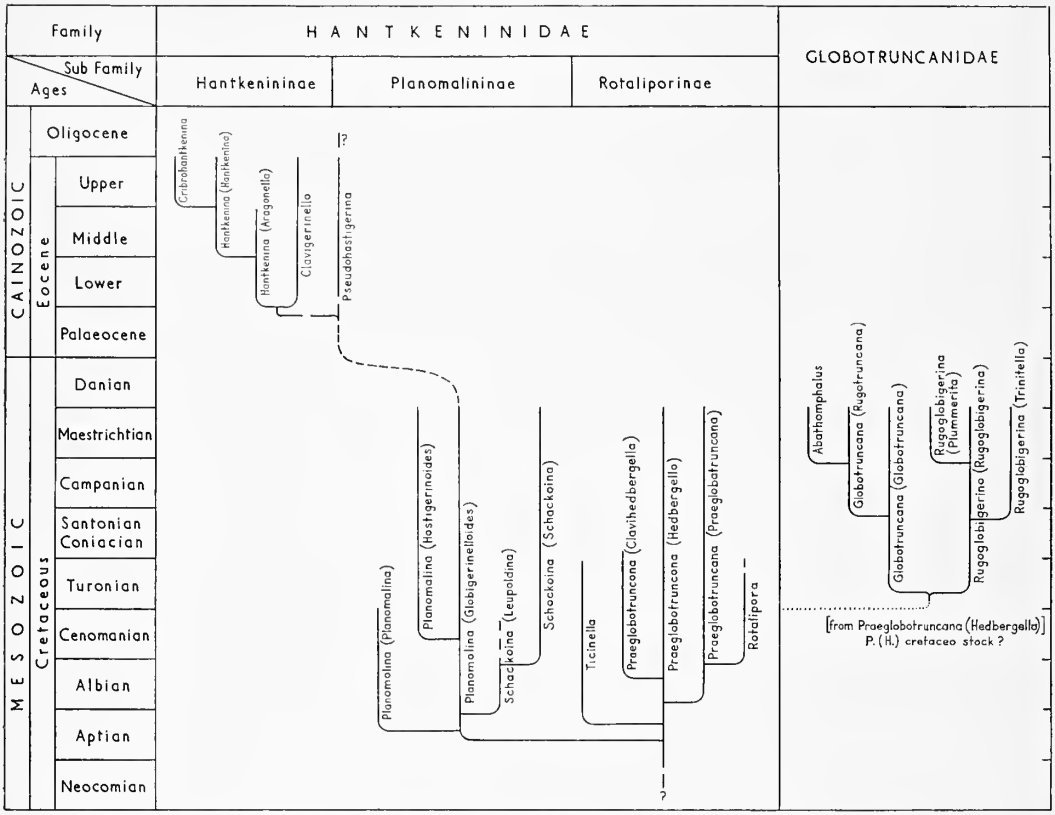
Subfamily HANTKENININAE Cushman 1927, emended

Hantkeninidae with biumbilicate, planispiral adult tests; the test possesses an interiomarginal, umbilical–extraumbilical equatorial primary aperture in the shape of a high arch, elongated in the apertural face in the plane of coiling, or a subdivided tripartite arch, also elongated in the plane of coiling, or areal and cribrate. No paired primary apertures known. Portici visible on the last chamber only, where they broaden strongly to form distinct lateral flanges in both ventral and dorsal umbilici [Eocene].

1. Chambers with thick-walled true tubulospines:
   (*a*) No supplementary areal apertures:
      genus *Hantkenina* Cushman 1925 (Eocene), type species *H. alabamensis* Cushman 1925.
      (Synonyms *Sporohantkenina* Bermúdez 1937, type species *Hantkenina brevispina* Cushman 1925; *Hantkeninella* Brönnimann 1950, type species *Hantkenina mexicana* Cushman var. *primitiva* Cushman and Jarvis 1929.)
      (i) Primary aperture tripartite, with well developed basal lobes:
         Subgenus *Hantkenina* (M. to U. Eocene).
      (ii) Primary aperture a simple arched opening, with insignificant basal lobes:
         Subgenus *Aragonella* Thalmann 1942 (L. to M. Eocene), type species *Hantkenina mexicana* Cushman var. *aragonensis* Nuttall 1930.
         (Synonym *Applinella* Thalmann 1942, type species *Hantkenina dumblei* Weinzierl and Applin 1929.)

(*b*) With supplementary apertures areal in apertural face:
genus *Cribrohantkenina* Thalmann 1942 (U. Eocene), type species *Hantkenina* (*Cribrohantkenina*) *bermudezi* Thalmann 1942 = *H. danvillensis* Howe and Wallace 1934.

2. Chambers elongate, with no true tubulospines, but rather clavate:
genus *Clavigerinella* Bolli, Loeblich, and Tappan 1957 (L. to U. Eocene), type species *C. akersi* Bolli, Loeblich, and Tappan 1957.



TEXT-FIG. 2. Suggested phylogeny of the Hantkeninidae and Globotruncanidae.

Family GLOBOTRUNCANIDAE Brotzen 1942
(Synonym Globotruncanidae Morozova 1957)

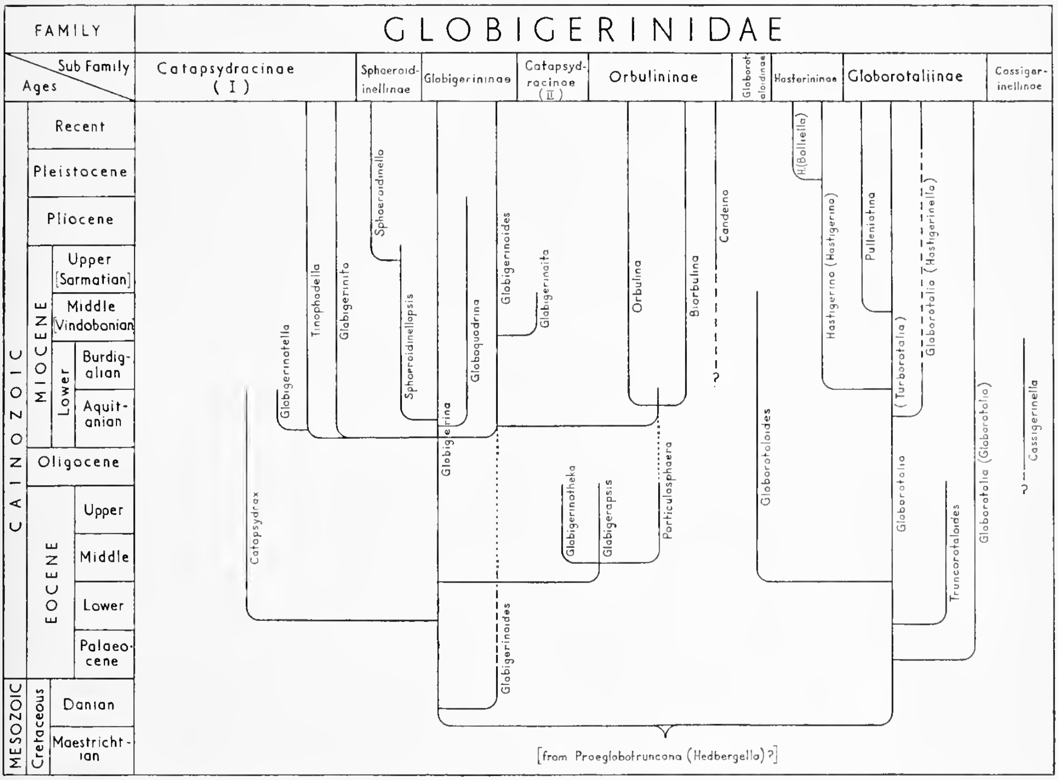
Diagnosis. Globigerinaceae with trochoid tests, dorsally evolute, ventrally more or less involute and umbilicate; primary aperture interiomarginal, intraumbilical or umbilical–extraumbilical, characteristically modified by an imperforate complex umbilical cover-plate (tegillum). Relict parts of primary apertures open into umbilicus beneath the tegillum, and thence to exterior through accessory apertures in the tegillum [Range: Turonian to Maestrichtian].

1. Primary aperture intraumbilical:
(*a*) With imperforate peripheral band, usually with carinae:
genus *Globotruncana* Cushman 1927 (Turonian to Maestrichtian), type species *Pulvinulina arca* Cushman 1926.

(Synonyms *Rosalinella* Marie 1941, type species *Rosalina linneiana* d'Orbigny 1839; *Marginotruncana* Hofker 1956, type species *Rosalina marginata* Reuss (1845) 1854; *Globotruncanita* Reiss 1957, type species *Rosalina stuarti* de Lapparent 1918.)

(i) Chambers without costellae:
Subgenus *Globotruncana* (Turonian to Maestrichtian).

(ii) Chambers with meridionally arranged costellae more or less developed:
Subgenus *Rugotruncana* Brönnimann and Brown 1955 (1956) (Santonian? to Campanian to Maestrichtian), type species *R. tilevi* Brönnimann and Brown 1955 (1956).
(?Synonym *Bucherina* Brönnimann and Brown 1955 (1956), type species *B. sandidgei* Brönnimann and Brown 1955 (1956).)



TEXT-FIG. 3. Suggested phylogeny of the Globigerinidae (simplified). The Catapsydracinae has been subdivided arbitrarily into two parts, to emphasize its polyphyletic nature.

(*b*) Without imperforate peripheral band or true carinae; costellae more or less well developed; with or without pseudocarinae:
genus *Rugoglobigerina* Brönnimann 1952 (Turonian to Maestrichtian), type species *Globigerina rugosa* Plummer 1927.
(Synonym *Kuglerina* Brönnimann and Brown 1955 (1956), type species *Rugoglobigerina rugosa rotundata* Brönnimann 1952.)

(i) Chambers uniformly inflated throughout ontogeny and without pseudocarinae:
Subgenus *Rugoglobigerina* (Turonian to Maestrichtian).

(ii) Chambers in adult dorsally flattened, and/or with pseudocarinae:
Subgenus *Trinitella* Brönnimann 1952 (Santonian? to Campanian to Maestrichtian), type species *T. scotti* Brönnimann 1952.

(iii) Chambers in adult radially elongate:

Subgenus *Plummerita* Brönnimann 1952 (Maestrichtian) (new name for *Plummerella* Brönnimann 1952, non *Plummerella* de Long 1942, Insecta.), type species *Rugoglobigerina* (*Plummerella*) *hantkeninoides hantkeninoides* Brönnimann 1952.

2. Primary aperture umbilical–extraumbilical:

genus *Abathomphalus* Bolli, Loeblich, and Tappan 1957 (Maestrichtian), type species *Globotruncana mayaroensis* Bolli 1951.

SYSTEMATIC DESCRIPTIONS

Family GLOBIGERINIDAE Carpenter 1862

Subfamily HASTIGERININAE Bolli, Loeblich, and Tappan 1957, emended

Emended diagnosis. Globigerinidae with tests which are initially trochospiral but which become nearly, but imperfectly, symmetrically planispiral in the adult. In the young, the interiomarginal aperture is umbilical–extraumbilical–peripheral; in the adult, it becomes umbilical–extraumbilical–peripheral–equatorial, and may be bordered in advanced forms by a very narrow, partly or wholly perforate, thin lip, which is equally developed throughout the length of the aperture. The adult equatorial aperture is a broad arch, never subdivided or tripartite, and lacks asymmetrical imperforate apertural flanges. Relict apertures absent, except in loosely coiled adult specimens of some species, where the last chamber or chambers are not in direct contact with the preceding whorl; in such a case, the aperture of the penultimate chamber may remain open, facing the periphery of the preceding whorl. The juvenile chambers are subglobular; this form may be retained in the adult, or they may become depressed and subreniform, or radially elongate and subcylindrical or subconical. Tubulospines are not known.

Remarks. The Hastigerininae show evidence of descent from the Globorotaliinae in their imperfect planispiral coiling and *Globorotalia*-like initial stage which possesses an umbilical–extraumbilical aperture. This family is distinct from the Hantkeninidae in lacking imperforate apertural portici and in never attaining a truly planispiral symmetrical test.

Genus HASTIGERINA Thomson 1876 emended

Type species by original designation and monotypy: *Hastigerina murrayi* Thomson 1876 = *Nonionina pelagica* d'Orbigny 1839.

Subgenus HASTIGERINA Thomson 1876 sensu stricto

Emended diagnosis. Hastigerininae in which the adult chambers are subglobular or slightly depressed, not radially elongate.

Subgenus BOLLIELLA subgen. nov.

Type species here designated: *Hastigerina* (*Bolliella*) *adamsi* sp. nov.

Diagnosis. Hastigerininae in which the adult chambers are radially elongate.

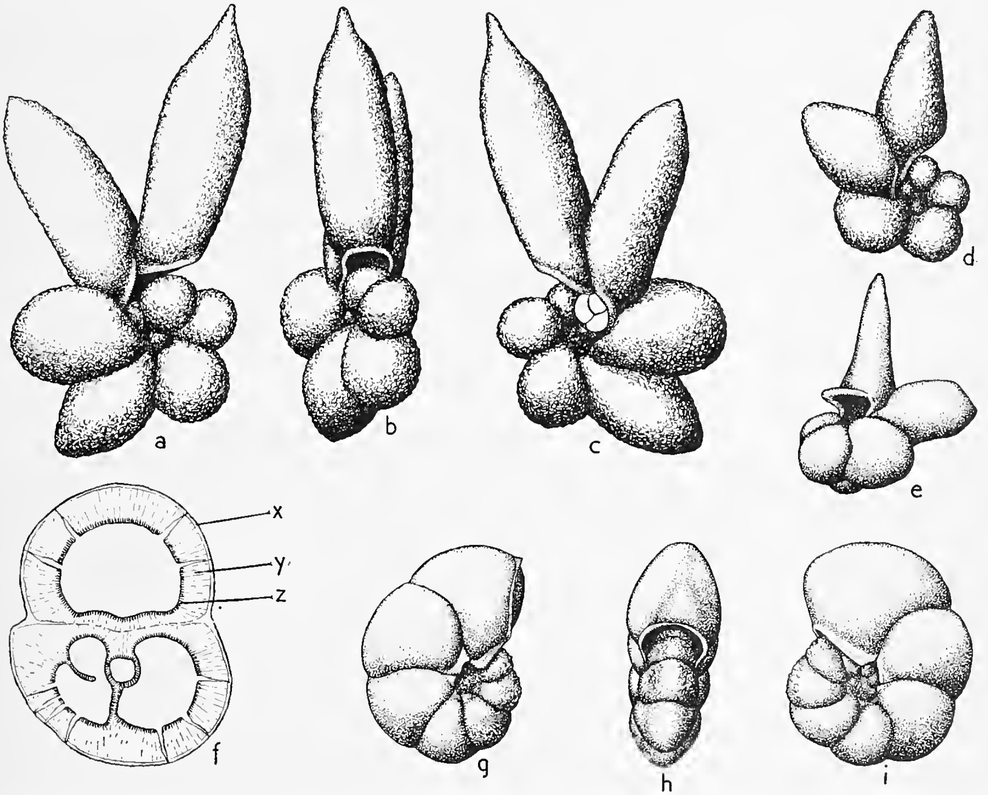
Remarks. This subgenus is named after Dr. H. M. Bolli, Caracas, Venezuela, in recognition of his work on planktonic foraminifera.

Hastigerina (*Bolliella*) *adamsi* sp. nov.

Text-figs. 4 *a–d*

Globigerina digitata Brady; Brady 1884 (part), *Challenger Exped. 1873–76 Rept., Zool.* 9 (pt. 22), pl. 82, figs. 6 [holotype], 7 [paratype] (not pl. 80).
Hastigerinella digitata (Brady); Cushman, Todd, and Post 1954, p. 369, pl. 91, figs. 9, 10.

Description. The adult test is very slightly trochoid, being almost, but not perfectly, planispiral. The globular proloculum is followed by a whorl of about six rapidly enlarging subglobular chambers in the megalospheric generation; the microspheric



TEXT-FIG. 4. *a–d*, *Hastigerina* (*Bolliella*) *adamsi* sp. nov. *a–c*, holotype, × 50, British Museum (Natural History) No. 1958.8.18.1. *a*, ventral view; *b*, edge view showing imperfect planispiral coiling; *c*, dorsal view showing extension of the aperture into a dorsal umbilicus (a juvenile foraminifer is attached to this side of the specimen, in the umbilicus). *d*, paratype, × 50, B.M. (N.H.) No. 1958.8.18.2. *e*, *Globorotalia* (*Hastigerinella*) *digitata* (Brady), lectotype, × 50, B.M. (N.H.) No. 1958.8.18.3. Ventral view refigured (this specimen was figured by Brady 1884, pl. 80, fig. 10, as *Globigerina digitata* Brady). *f*, *Sphaeroidinellopsis subdehiscens* (Blow); diagram after Blow 1959, × 100 approx., showing wall structure in this section; *x*, outer cortex, approx. 0·005 mm. thick; *y*, radial middle layer, approx. 0·05 mm. thick; *z*, inner radial layer. *g–i*, *Pseudohastigerina micra* (Cole), × 100, from the Upper Eocene of Tanganyika. *g*, showing portici and position of relict apertures in the last two or three chambers; the last chamber of this specimen has been broken off. *h*, edge view showing apparently perfect planispiral coiling. *i*, side view showing portici of last two chambers (that of the last chamber is incomplete). B.M. (N.H.) No. P. 43657.

generation is not known. The juvenile aperture extends from the ventral umbilicus to the periphery and reaches an interiomarginal equatorial position, but is clearly asymmetrical and *Hastigerina*-like. In the succeeding whorl (also of about six chambers) the chambers are more nearly planispiral and become radially elongate without lateral compression; the chambers may become four times as high as broad. The later chambers are more loosely coiled, and by the end of the second whorl the test is almost equally biumbilicate, and the aperture has an equal extension into each umbilicus. A very thin and narrow, very finely perforate, apertural lip is present on the later chambers, extending back along the umbilical border of each chamber to meet the preceding chamber. The last formed adult chamber may be in contact only with the immediately preceding chamber, and not directly attached to the penultimate whorl; when this occurs, the primary apertures of the later chambers are not wholly closed, and remain open as relict apertures, which occur first on the ventral umbilical margin, and then (often by the third whorl) on both ventral and dorsal umbilical margins. The wall of the test is thin, uniformly and finely perforate, distinctly and uniformly hispid.

Occurrence. The type specimens were collected by the *Challenger* Expedition from 580 fathoms off the Kai (Ewab) Islands (*Challenger* Station 191A). The specimens collected by Cushman, Todd, and Post (1954) came from the outer slopes of Bikini Atoll and from Sylvania Guyot (1954, pp. 321–2). No records of fossil occurrences of this species are known to us.

Types. The holotype and paratype (Brady's figured specimens) are deposited in the British Museum (Natural History), *Challenger* Collection; Holotype—No. 1958.8.18.1. Paratype—No. 1958.8.18.2.

Subfamily SPHAEROIDINELLINAE new subfamily

Genus SPHAEROIDINELLA Cushman 1927, emended

Type species by original designation and monotypy: *Sphaeroidinella dehiscens* (Parker and Jones) = *Sphaeroidina bulloides* (d'Orbigny) var. *dehiscens* Parker and Jones 1865.

Emended diagnosis. Test trochoid throughout life; chambers rapidly enlarging, subglobular or subreniform, inflated, often becoming increasingly embracing in the adult. Primary wall calcareous, radial, coarsely perforate; pores usually broader in diameter at their inner ends than externally, where they narrow. Primary wall more or less covered by a secondary layer or layers of calcareous material, probably radial in structure, which is thickest near the apertures and in the sutures. The secondary layers of shell material (cortex) are shiny superficially in reflected light, and tend to restrict the pores of the primary wall, either greatly reducing the external openings or in some cases completely sealing them, especially in the apertural and adjacent sutural regions. The primary aperture is interiomarginal, intraumbilical throughout life, a low arch or slit; supplementary sutural apertures are present, at least in the adult. Both the primary and the supplementary apertures are furnished with lips, which may be smooth or crenulate, and which are often secondarily thickened with imperforate shell material (which is an extension of the cortex), and may become flange-like.

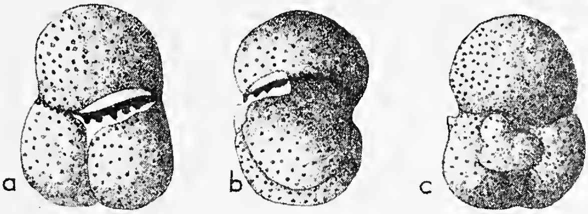
Remarks. Bolli, Loeblich, and Tappan (1957, pp. 32, 33, pl. 6, fig. 5) record and illustrate the presence of 'bullae' in some specimens of *Sphaeroidinella dehiscens*; we have seen similar structures on specimens of this species and believe them to be no more than thin-walled abortive chambers abnormally placed, more or less covering the sutures; we consider it probable that the structures seen by Bolli, Loeblich, and Tappan were the same. Similar structures have been observed by us in *Globigerinoides* where they are clearly aborted end chambers. Such abortive chambers are known in many genera of the Globigerinaceae, and are characterized by exceptionally thin walls, lack of hispidity, reduction of pore size, and erratic position. The erratic position and infrequent occurrence of abortive chambers serves to distinguish them clearly from true bullae. The cortex of *Sphaeroidinella* appears to be composed of less stable shell material than that of the primary wall, and is readily subject to loss, partial loss, or alteration during or after the process of fossilisation.

Genus SPHAEROIDINELLOPSIS gen. nov.

Text-figs. 4*f*, 5

Type species here designated: *Sphaeroidinellopsis subdehiscens* (Blow) = *Sphaeroidinella dehiscens subdehiscens* Blow 1959.

Diagnosis. Test trochoid throughout life; chambers regularly enlarging, subglobular, or subreniform, or showing a tendency to become radially elongate in the adult, or embracing. Wall structure similar to that of *Sphaeroidinella*, but in some species the cortex is less strongly developed. Primary aperture interiomarginal, intraumbilical, a low arch or slit, furnished with a smooth or crenulate lip. No supplementary apertures are present.



TEXT-FIG. 5. *Sphaeroidinellopsis subdehiscens* (Blow), holotype, ×47, after Blow 1959. *a*, ventral view; *b*, side view showing thickening of the outer cortex around the apertural margins; *c*, dorsal view.

Remarks. This genus is distinguished from *Sphaeroidinella* by its lack of supplementary sutural apertures in the adult, notwithstanding that in some species (e.g. *S. seminulina kochi* (Caudri)) the dorsal sutures are very deeply incised. '*Sphaeroidinella*' *seuni* Beckmann is of doubtful generic position, but lacks a cortex and thickened apertural lips and does not belong to the Sphaeroidinellinae. We consider that *Globigerina seminulina* Schwager 1866 (= *S. disjuncta* Finlay 1940), *Globigerina kochi* Caudri 1934 (= *S. rutschi* Cushman and Renz 1941 [part, holotype] = *G. grimsdalei* Keijzer 1945), and *S. multiloba* LeRoy 1944 belong to *Sphaeroidinellopsis*.

Subfamily GLOBOROTALIINAE Cushman 1927 emended

Emended diagnosis. Globigerinidae with tests which are trochoid throughout life, dorsally evolute, ventrally more or less involute and umbilicate; the test possesses a ventral, interiomarginal, umbilical–extraumbilical primary aperture, which may possess a thin, more or less perforate, symmetrical, narrow lip, which usually extends the full length of the aperture and is of uniform breadth. In some specialized forms dorsal (sutural) supplementary apertures may be present.

Remarks. The Globorotaliinae (emend.) differ from the Globigerininae by possessing a primary aperture which extends out of the umbilicus, but which does not become peripheral and equatorial as in the Hastigerininae. No bullae are present. The Globorotaliinae are clearly separated from the Hantkeninidae by their lack of imperforate apertural portici, and from the Globotruncanidae by their lack of umbilical tegilla.

Genus GLOBOROTALIA Cushman 1927, sensu lato, emended

Type species by original designation: *Pulvinulina menardii* (d'Orbigny) var. *tumida* Brady 1877.

Emended diagnosis. Globorotaliinae which lack dorsal, sutural, supplementary apertures.

Subgenus HASTIGERINELLA Cushman 1927, emended

Type species by original designation: *Hastigerina digitata* Rhumbler 1911 (not *Globigerina digitata* Brady 1879) = *Hastigerinella rhumbleri* Galloway 1933 (nom. nov.).

Emended diagnosis. Globorotalia in which the adult chambers become radially elongate, and which possess no carinae.

Remarks. This subgenus differs from *Globorotalia* (*Turborotalia*) in the same way as *Praeglobotruncana* (*Clavihedbergella*) differs from *Praeglobotruncana* (*Hedbergella*). It differs from *P.* (*Clavihedbergella*) in lacking the assymmetric imperforate portici of that genus, and from *Hastigerina* (*Bolliella*) in possessing neither a peripheral, equatorial aperture nor a biumbilicate test.

Globorotalia (*Hastigerinella*) *digitata* (Brady) emended

Text-fig. 4*e*

Globigerina digitata Brady (part) 1879, *Quart. J. Micr. Soc. London*, n.s., **19**, p. 286 (no figures).
Globigerina digitata Brady; Brady (part) 1884, *Challenger Exped. 1873–76 Rept., Zool.* **9** (pt. 22), pl. 80, fig. 10 (*lectotype, here designated*); pl. 80, figs. 6–9 (*not* pl. 82).
Globigerina digitata Brady; Phleger, Parker, and Peirson 1953, p. 12, pl. 1, figs. 9, 10.
Globigerina (*Globigerinella*) *digitata* Brady; Hofker 1956, p. 225, pl. 34, figs. 6–7 only.
Hastigerinella digitata (Brady); Bolli, Loeblich, and Tappan 1957, p. 32, pl. 5, fig. 3.

Description. The test is distinctly and nearly uniformly trochoid throughout life, evolute dorsally and involute ventrally, with a small umbilicus. In the megalospheric form the globular proloculum is followed by a whorl of about four rapidly enlarging, subglobular chambers, each possessing a semicircular unlipped aperture, umbilical—slightly extraumbilical in position. This whorl is followed by a second trochoid whorl of about five rapidly enlarging chambers, in which the aperture broadens until it becomes a high arch, increasingly extraumbilical in extent, later reaching, but not extending over and beyond, the periphery. In the adult, a very narrow, thin, perforate apertural lip is developed. In the last whorl the chambers become radially elongate without lateral compression, and become two to three times higher than broad. The wall is finely and uniformly perforate and very slightly roughened superficially; it is distinctly less hispid and more finely perforate than *Hastigerina* (*Bolliella*) *adamsi* sp. nov.

Remarks. When Brady first described *Globigerina digitata* (1879), no specimens were illustrated; in his subsequent figures (Brady 1884, pls. 80, 82) two species and genera were included under this name, and no type specimen was designated. Subsequent records by other authors are confused in consequence, the two forms not being distinguished. By designating a lectotype here, we are able to divide Brady's figured specimens, and to show that they exemplify the phenomenon of radial elongation of the adult chambers in the Globorotaliinae and in the Hastigerininae (*Hastigerina* (*Bolliella*) *adamsi* nov.), paralleling similar morphological developments known in the Rotaliporinae (*Praeglobotruncana* (*Clavihedbergella*)) and the Planomalininae (*Planomalina* (*Hastigerinoides*)). All these subgenera appear to be phylogenetic end-forms, leaving no descendants, and have shorter stratigraphic ranges than the genera to which they belong.

Occurrence. The lectotype (here designated) and topotypes figured by Brady (1884, pl. 80) were collected by the *Challenger* Expedition at station 338, from 1,990 fathoms in the North Atlantic. This species has been recorded from Recent seas by Phleger, Parker, and Peirson (1953), Hofker (1956), and Bolli, Loeblich, and Tappan (1957), but apparently it has never been found fossil.

Lectotype. The lectotype of *Globigerina digitata* Brady 1879, is in the British Museum (Natural History), No. 1958.8.18.3.

Family HANTKENINIDAE Cushman 1927, emended

Subfamily ROTALIPORINAE Sigal 1958, emended

Genus PRAEGLOBOTRUNCANA Bermúdez 1952, emended

Type species by original designation: *Globorotalia delrioensis* Plummer 1931.

Emended diagnosis. Test trochoid, evolute dorsally, more or less involute and umbilicate ventrally. Chambers subglobular, or reniform, or compressed, or radially elongate. Periphery rounded or truncate, or subacute, with or without imperforate peripheral bands and carinae. Primary aperture is interiomarginal, umbilical–extraumbilical, bordered by an asymmetric imperforate porticus. The portici of the last whorl do not fuse, and the relict parts of primary apertures of the last whorl open directly to the exterior through the umbilicus. Neither supplementary nor accessory apertures are present.

Subgenus PRAEGLOBOTRUNCANA Bermúdez 1952, emended

Emended diagnosis. Praeglobotruncana which possess an imperforate peripheral band and a carina or carinae. The carina may not be fully developed on the last formed chamber. Adult chambers not radially elongate.

Remarks. This subgenus differs from *Rotalipora* in lacking supplementary apertures, and from *Abathomphalus* in lacking a tegillum.

Subgenus HEDBERGELLA Brönnimann and Brown 1958, emended

Type species by original designation: *Anomalina lorneiana* (d'Orbigny) var. *trocoidea* Gandolfi 1942.

Emended diagnosis. Praeglobotruncana in which there are no imperforate peripheral bands or carinae, and in which the adult chambers are not radially elongate, but which are uniformly subglobular or subreniform.

Remarks. Praeglobotruncana (*Hedbergella*) differs from *Ticinella* in lacking the distally fused portici characteristic of that genus; it is not surely known to possess dorsal pseudocarinae, which often occur in *Ticinella.* Costellae do not occur.

It was the apparent intention of Brönnimann and Brown (1955 (1956)) to erect a genus to cover a group of simple Cretaceous 'globigerines' which were unkeeled and possessed no tegilla, and yet which were distinct from true *Globigerina* d'Orbigny. This genus was named *Hedbergina* and was based, unfortunately, upon *G. seminolensis* Harlton 1927, as type species. However, as pointed out by Bolli, Loeblich, and Tappan (1957, pp. 39, 40), the holotype of *G. seminolensis* is the only known specimen. It is badly preserved, and the umbilical apertural characters are indeterminate. No topotype material of this species can be obtained as its true provenance is unknown. Subsequently, Brönnimann and Brown (1958) proposed the genus *Hedbergella* as a 'new name' (*sic*) for the same morphological group, designating *Anomalina lorneiana* (d'Orb.) var. *trocoidea* Gandolfi 1942, as the type species. We believe that the species *Globigerina seminolensis* Harlton, and consequently the genus *Hedbergina* Brönnimann and Brown, should be regarded as *nomina dubia* and it is our intention to make application for it to be considered as such to the Secretary to the International Commission on Zoological Nomenclature.

Subgenus CLAVIHEDBERGELLA subgen. nov.

Type species here designated: *Praeglobotruncana* (*Clavihedbergella*) *subcretacea* (Tappan) = *Hastigerinella subcretacea* Tappan 1943, p. 513, pl. 83, fig. 4.

Diagnosis. Test trochoid, evolute dorsally, more or less involute ventrally and umbilicate. Early chambers subglobular, later becoming increasingly elongate in a radial direction. Wall generally hispid, uniformly perforate, lacking imperforate peripheral bands, carinae or costellae. Aperture ventral, interiomarginal, umbilical–extraumbilical, sometimes reaching periphery of the preceding whorl but not extending on to the dorsal surface or becoming equatorial. Test not biumbilicate. Apertures furnished with portici, but lacking tegilla or bullae. No supplementary or accessory apertures, but relict apertures may be present.

Remarks. This subgenus differs from *Praeglobotruncana* (*Praeglobotruncana*) in lacking an imperforate peripheral band and in possessing radially elongate chambers in the adult. It differs from *P.* (*Hedbergella*) in possessing radially elongate adult chambers, and is related to that subgenus in the same way as *Globorotalia* (*Hastigerinella*) is related to *G.* (*Turborotalia*). It differs from *G.* (*Hastigerinella*) in possessing characteristically

Hantkeninid portici, and it may be distinguished from *Planomalina* (*Hastigerinoides*) by its lack of an equatorial primary aperture and its uniumbilicate test.

Hastigerinella simplex Morrow 1934, and *Hastigerinoides simplicissima* Magné and Sigal 1954, are also considered to belong to *Praeglobotruncana* (*Clavihedbergella*).

Subfamily PLANOMALININAE Bolli, Loeblich, and Tappan 1957, emended

Genus PSEUDOHASTIGERINA gen. nov.

Text-figs. 4 *g*, *h*, *i*

Type species here designated: *Pseudohastigerina micra* (Cole) = *Nonion micrus* Cole 1927 (*Bull. Amer. Paleont.* **14** (51), p. 22, pl. 5, fig. 12).

Diagnosis. Test planispirally coiled throughout in the megalospheric form, biumbilicate. Aperture is a low, interiomarginal, equatorial, symmetrical arch, extending into the umbilici, not subdivided or elongate in the plane of coiling, furnished with an imperforate porticus. The porticus is narrowest at its mid-point (that is, in the part immediately above the periphery of the preceding whorl), and broadens slightly towards the dorsal and ventral umbilici. Very small relict apertures present at umbilical margins of last two or three chambers only, and the portici are only clearly visible on these chambers. The chambers are subglobular, or slightly depressed, and enlarge regularly; they are not radially elongate or furnished with tubulospines. The wall is uniformly perforate, with no imperforate peripheral bands or carinae, and more or less hispid; the hispidity usually becomes obsolete in the adult.

Remarks. This genus is morphologically intermediate between the Planomalininae and the Hantkenininae. It is distinguished from *Planomalina* (*Globigerinelloides*) by its strongly reduced relict apertures, and the consequent lack of visible portici except on the last few chambers. It differs from *Schackoina* (sensu lato) by its lack of radial extensions of the chambers, and by its true planispiral coiling in the megalospheric form. *Pseudohastigerina* differs from the Hantkenininae (emended) by its lack of an apertural elongation in the plane of coiling, by its less strongly developed portici (which do not form distinct lateral flanges), and by its lack of chamber elongation or tubulospines. We believe that an (as yet) unrecorded species of this genus is probably ancestral to the Hantkenininae; greater development laterally of the portici, elongation of the aperture in the plane of coiling and the appearance of tubulospines would produce the subgenus *Hantkenina* (*Aragonella*); subsequent modification of the aperture would lead to *Hantkenina* sensu stricto and to *Cribrohantkenina*. Parallel modifications of the aperture, but associated with chamber elongation rather than with the development of tubulospines, probably gave rise to *Clavigerinella*.

Pseudohastigerina micra is hispid on the earliest parts of the last whorl; this is a feature common to the Globigerinaceae, and is distinct from *Nonion*, which is also clearly distinguished by its microgranular wall structure. An ancestral form to *Pseudohastigerina* may prove to be *Protelphidium* Haynes (1956, pp. 86–87), but the aperture is not adequately enough known in this genus to enable its relationships to be ascertained; Haynes (1956, pl. 16, fig. 9) illustrates the type species, *P. hofkeri*, as having a *Nonion*-like aperture without portici. *Nonion sublaeve* ten Dam, placed by Haynes in *Protelphidium* (op. cit., p. 87), seems unrelated to *Pseudohastigerina*.

Pseudohastigerina differs from *Hastigerina* by its true planispiral coiling throughout ontogeny, and by its possession of apertural portici.

Occurrence. Nonion micrus was first recorded from the Guayabal Formation of Mexico by Cole (1927, p. 22); he considered that this was probably equivalent to the Upper Claiborne, and is probably Middle Eocene in age. This species has been recorded subsequently from the higher parts of the Lower Eocene to the top of the Upper Eocene (e.g. Hornibrook 1958, pp. 29, 34 [as '*Globigerinella*' *iota* (Finlay)]; Bolli 1957, p. 161; Subbotina 1953, p. 88; &c.). Bykova (1953, p. 86) has recorded *G. micra* (Cole) from beds in the Tadjikstan depression, which are probably of Upper Palaeocene age; her specimen was not illustrated, however, and her determination cannot be checked. *G. naguewichiensis* Myatliuk probably belongs to this genus, but its age is not well known; Myatliuk (1950, p. 281) thought it to be possibly Oligocene. No species referable to this genus have been recorded from beds of other than Palaeogene age. Specimens of '*G. aspera* (Ehrenberg)', recorded by Haynes (1956, p. 98) from the Palaeocene Thanet Beds of East Kent, may prove to belong to *Pseudohastigerina*; his specimens require further study, but they may confirm the suspected Palaeocene occurrence of this genus.

DISCUSSION

We have already pointed out in the introduction to this work those morphological characters which we consider to be of fundamental taxonomic importance. We have endeavoured to base our classification on characters which occur only singly and are not repeated. However, many of the more obvious characters of the Globigerinaceae are apparently repeated, and occur in a repetitive manner in widely divergent stocks. Unfortunately, many previous workers have only recognized these more obvious characters, so that in the results of their work, the ranges of the genera, as interpreted by them, are much extended in geological time. This work illustrates the importance of those less obvious apertural structures which in the past have been largely neglected, and which may be broadly analogous to such structures as the toothplates of the Buliminidae, &c.

Moreover, having recognized the importance of these structures associated with the apertures, we have been led to reinvestigate other characters, such as 'keels', which in the past have been considered homologous in many different genera. Our results indicate that structures such as the 'keel' are also fundamentally different in different stocks, and confirm our views, not only of the taxonomic importance of the individual apertural structures, but also as to the validity of the phylogeny our classification suggests. We believe that all the subfamilies employed here (with the single major exception of the polyphyletic but taxonomically convenient Catapsydracinae) are biologically natural groupings (text-figs. 2, 3).

The more obvious differences of test shape, used by past authors to define their genera and to illustrate their phylogenetic concepts, and which we believe to occur iteratively in distantly related or unrelated stocks, include radial elongation of adult chambers, acquisition of supplementary apertures, planispirality, umbilical cover-plates, 'keels', &c. Some aspects of these characters are discussed below.

The gross aspects of the 'keels' seen in the solid specimens of *Globotruncana*, *Globo-*

rotalia, *Ticinella*, *Rotalipora*, and *Praeglobotruncana* are, in many species, apparently similar; but in thin section and under high magnification subtle but significant differences are apparent (Pls. 2, 3). In *Ticinella roberti* (Gandolfi) and *T. helvetica* (Bolli) the 'keel' is seen to be no more than an external perforate thickening of the dorsal periphery, fully contiguous with the primary wall, and of fundamentally similar structure (Pl. 3). It appears to be secondary and superficial, and has been shown by Schijfsma (1955) to develop proterogenetically in *T. helvetica* from a 'grosse globigerine', which is referable to *Praeglobotruncana* (*Hedbergella*). Evidence from specimens seen by us from East Africa confirm Reiss's (1957) conclusions as to the eventual fusion of the portici in the later ontogeny of *T. helvetica*, but our sectioned specimens do not confirm his belief in the imperforate nature of the 'keel'. Consequently, we consider this 'keel' to be a pseudocarina, and not a true carina (Pl. 3, fig. 2*b*).

In the well-known evolutionary sequence '*Globorotalia fohsi barisanensis*'–'*G. fohsi fohsi*'–'*G. fohsi lobata*'–'*G. fohsi robusta*' (Bolli 1950; Blow 1959), we find that *barisanensis* is without any sort of 'keel' or marginal thickening, and the chamber wall is uniformly perforate throughout (Pl. 1, fig. 1); in advanced forms of '*fohsi fohsi*' there is a beginning in the last few chambers of a thickening of the peripheral margin, which is, however, still fully perforate (Pl. 1, fig. 2). In '*fohsi lobata*' the perforate peripheral thickening (which is termed here pseudocarina) is increasingly emphasized, and an imperforate, apparently exogenous layer is laid down on the thickened margins of the last one or two chambers (Pl. 1, fig. 3). It is at this stage that we consider that a true carina is developed. The imperforate layer gradually increases in strength and thickness, and proceeds palingenetically throughout the whole test to give the most advanced and final subspecies '*fohsi robusta*' (Pl. 1, fig. 4). We regard the 'keel' to be a true carina when imperforate shell material makes its appearance, and believe that this character can be used to subdivide the many species ascribed to *Globorotalia* (s.l.). We have found that in thin sections of *Globorotalia menardii tumida* the 'keel' consists of distinctly imperforate shell material, whereas in *G. centralis* the wall is uniformly perforate throughout. Accordingly the supraspecific taxa *Globorotalia* and *Turborotalia* are employed here, based on the presence or absence of a true carina. We regard these taxa as only of subgeneric status, since gradations from forms without any 'keels' to forms with pseudocarinae, and from these to other forms with true carinae, are known not only in the evolutionary series outlined above but also in other lineages, such as those discussed by Blow (1959), including that leading from *G.* (*T.*) *praescitula* to *G.* (*G.*) *menardii menardii*.

In *Globotruncana*, the imperforate peripheral band is broad, and always bears two imperforate ridges (here termed carinae); some species may appear to possess one carina only (e.g. *G. stuarti*), but this always dichotomises to produce two carinae, one running dorsally and the other ventrally, a character never seen in the Globorotaliinae. No transitions from pseudocarinae to true carinae are known in the Globotruncanidae as here emended, although pseudocarinae occur in *Rugoglobigerina* (*Trinitella*). In species of *Globotruncana* where the carinae are widely spaced, as in *G. tricarinata*, the perforations of the test wall end abruptly against the margins of the imperforate peripheral band, which extends the full breadth of the wall between the carinae, and which appears to possess a texture different from both that of the perforate parts of the *Globotruncana* wall and from the imperforate parts of the wall of *Globorotalia*. It is not unlikely that the actual nature of the imperforate carinae of *Globotruncana* is different from that of the carinae of *Globorotalia*; further work, using other techniques, is necessary and this is in progress.

The acquisition of planispiral or nearly planispiral modes of coiling is accompanied by a migration of the primary ventral interiomarginal aperture to an equatorial position. This has occurred in the Planomalininae, Hantkenininae and Hastigerininae, without radical change in the fundamental nature of the apertural accessory structures; thus, portici have not been lost in the Planomalininae or Hantkenininae, but in some cases have even been accentuated. In the Hastigerininae the lipped Globorotaliid aperture is preserved. However, some further specialized modifications of the shape of the primary aperture may occur in some genera; in *Planomalina* (*Globigerinelloides*) and in *Schackoina* (*Leupoldina*) the primary interiomarginal equatorial aperture tends to become bipartite, with enlargement laterally, giving incipient biseriality in the later chambers. The last one or two chambers may become fully biserial, and the primary aperture becomes fully divided and opens only on the lateral shoulders of the penultimate whorl (Subbotina 1953, pl. 13, figs. 8*b*, 9*b*, 11*b*; Bolli 1957, pl. 2, figs. 7*a*, 8*a*). This character is not known in other subfamilies. With the achievement of planispirality and equatorial apertures in the Hantkenininae, elongation of the aperture normal to the axis of coiling also occurs, but the lateral accentuation of the aperture is by no means diminished, at least in *Hantkenina* itself. On the other hand, there is no fundamental modification of the *Globorotalia*-like aperture in *Hastigerina*; no elongation or other modification is present, save that of an extension of the aperture over and beyond the periphery on to the dorsal surface. This seems to be associated with the fact that complete and true planispirality has not yet been attained.

A tendency towards planispirality may be recognized in morphologically advanced

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EXPLANATION OF PLATE 1

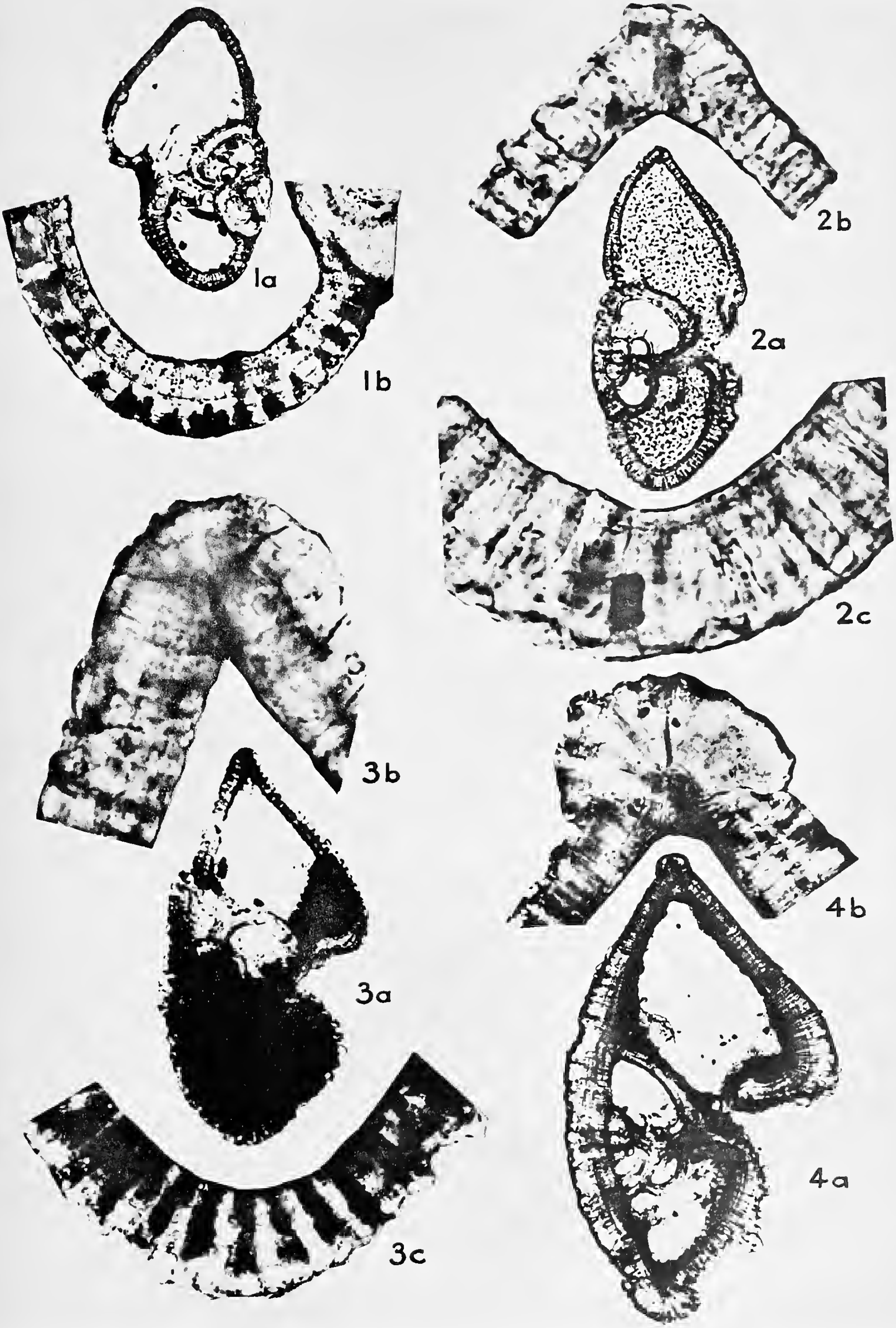
Thin sections photographed to show carina development in some Globorotaliinae.

Fig. 1. *Globorotalia* (*Turborotalia*) *fohsi barisanensis* (LeRoy), from the Lower Burdigalian, Pozón Formation, near Pozón, Eastern Falcón, Venezuela; 1*a*, axial section, ×125 approx.; 1*b*, same specimen, peripheral part of a chamber in the last whorl, showing uniformly perforate structure (the pores are partly infilled with ferruginous material), ×500 approx.

Fig. 2. *Globorotalia* (*Turborotalia*) *fohsi fohsi* Cushman and Ellisor, from the Middle Burdigalian, Pozón Formation, near Pozón, E. Falcón, Venezuela; 2*a*, axial section, ×125 approx.; 2*b*, same specimen, periphery of a late chamber, showing development of a fully perforate pseudocarina, ×1,000 approx.; 2*c*, same specimen, periphery of an earlier chamber, showing perforate structure without formation of a pseudocarina, ×1,000 approx.

Fig. 3. *Globorotalia* (*Globorotalia*) *lobata lobata* Bermúdez, from the lower part of the Upper Burdigalian, Pozón Formation, near Pozón, E. Falcón, Venezuela; 3*a*, axial section, ×125 approx.; 3*b*, same specimen, periphery of a late chamber, showing formation of a wedge of imperforate radial shell material at the extreme periphery, ×1,000 approx.; 3*c*, same specimen, periphery of an earlier chamber, showing retention of a uniformly perforate wall-structure in the early part of the test, ×500 approx. The appearance of imperforate peripheral shell material (a morphologically primitive carina) is taken as the arbitrary distinction between *Globorotalia* sensu stricto and *Globorotalia* (*Turborotalia*) in this and other evolutionary series.

Fig. 4. *Globorotalia* (*Globorotalia*) *lobata robusta* (Bolli), from the Upper Burdigalian, Pozón Formation, near Pozón, Venezuela; 4*a*, axial section, showing development of a carina throughout the last whorl, ×125 approx.; 4*b*, the peripheral carina, showing its radial structure and the inner residuum of perforate material overlain by thick imperforate layers, ×500 approx.



BANNER and BLOW, Globigerinaceae

forms of other genera, such as *Praeglobotruncana* (*Hedbergella*) and *Rugoglobigerina. P.* (*H.*) *gautierensis* (Brönnimann) and *R. macrocephala* (Brönnimann) both possess flattened or concave dorsal surfaces and very low trochospiral tests.

Radial elongation, or a tendency towards this, occurs commonly in nearly all the families and subfamilies, in both planispiral and trochoid tests, but it is most noticeable in those in which the coiling is either planispiral or very low trochospiral and which do not possess carinae. In general, three broad morphological types seem to occur independently in unrelated stocks. Broadly elongate clavate chambers occur in the Cretaceous *Praeglobotruncana* (*Clavihedbergella*), *Schackoina* (*Leupoldina*) and *Planomalina* (*Hastigerinoides*), the Eocene *Clavigerinella*, and the Neogene *Globorotalia* (*Hastigerinella*) and *Hastigerina* (*Bolliella*). Narrowly elongate, digitate chambers occur in the Cretaceous *Schackoina* (*Schackoina*), *Rugoglobigerina* (*Plummerita*), some species of *Planomalina* (*Hastigerinoides*) (e.g. *P.* (*H.*) *alexanderi* (Cushman)), in some specimens of the Palaeogene *Clavigerinella jarvisi* (Cushman) and in some individuals of Recent *Globorotalia* (*Hastigerinella*) *digitata* (Brady). True tubulospines, which differ from the chamber elongations of *Schackoina* (*Schackoina*) by their thickened walls and much reduced lumina, occur only in the Palaeogene *Hantkenina* and *Cribrohantkenina*. Tendencies towards radial elongation of the adult chambers have been observed in other genera; both *Globigerina inaequispira* Subbotina and *G. bulbosa* LeRoy show deep separation and slight elongation of the later chambers. It is probable that this character has arisen independently within individual genera as well as within individual lineages. Thus, the early stages of the Lower Miocene *Globorotalia* (*Hastigerinella*) *bermudezi* (Bolli) are those of a *Globorotalia* (*Turborotalia*) (Blow 1959); Blow (loc. cit.) has pointed out that there appears to be no direct relationship between this species and any known Recent species of *G.* (*Hastigerinella*).

Supplementary sutural apertures have been acquired in the Rotaliporinae (Hantkeninidae) and in most subfamilies of the Globigerinidae. The Cretaceous Rotaliporinae are clearly distinguished by possessing supplementary sutural apertures on the ventral side only, in contrast to the almost invariably dorsal sutural supplementary apertures of the Cainozoic Globigerinidae. No other Cretaceous group besides the Rotaliporinae is known to possess true supplementary apertures, although accessory apertures and relict apertures are common. In the Globigerinidae supplementary sutural apertures are associated with either normal trochospiral coiling and a retention of a primary aperture (e.g. *Truncorotaloides*, *Globigerinoides*) or with the development of highly involute tests (tending to become spherical) associated with reduction or loss of an external primary aperture (e.g. *Globigerapsis*, *Porticulasphaera*). In extreme spherical forms (e.g. *Globigerinatella*, *Orbulina*) areal supplementary apertures occur. Whereas *Globigerinoides triloba* (s.l.) has been shown by Bolli (1957, *Bull. U.S. Nat. Mus.* **215,** p. 110) and by Blow (1959) to develop from a form similar to that illustrated by Fornasini (1897) as *Globigerina trilocularis* d'Orbigny in the Middle Aquitanian, Blow (loc. cit.) has demonstrated that *Globigerinoides bollii* originates in the Upper Burdigalian from a different species of *Globigerina*. This indicates that the genus *Globigerinoides* itself is polyphyletic. Similarly, it is probable that *Truncorotaloides topilensis* and *T. rohri* have originated from two distinctly different species of *Globorotalia* (s.l.), at two distinctly different times within the Palaeogene.

Umbilical plate-like structures are known throughout the Mesozoic and Cainozoic,

EXPLANATION OF PLATE 2

Thin sections photographed to compare carina development in different families of the Globigerinaceae.

Fig. 1. *Globorotalia* (*Globorotalia*) *menardii menardii* (d'Orbigny), from the Burdigalian, approx. 2 miles SSW. of Kilindone, Mafia Island, Tanganyika; British Petroleum Co. Ltd., Sample No. S.P. 56/30′; 1*a*, axial section, ×125 approx.; 1*b* and 1*c*, same specimen, the periphery of early and late parts of the last whorl, showing radial perforations in the lateral parts of the test wall contrasting with the imperforate carina; 1*b*, ×500 approx.; 1*c*, ×1,000 approx.; the carina is morphologically advanced even in geologically early specimens of this species, and the crystalline radial structure of the carina is frequently obscure.

Fig. 2. *Globotruncana* (*Globotruncana*) *elevata stuartiformis* Dalbiez, from the Campanian, approx. 4 miles west of Lindi, Tanganyika; British Petroleum Co. Ltd., Sample No. FCRM. 1524; 2*a*, axial section, ×83 approx.; 2*b* and 2*c*, same specimen, the periphery of early and late parts of the last whorl, showing radial perforations in the lateral parts of the test wall ending abruptly against the imperforate carina, both ×500 approx.; in this plane of section, the carina shows no indication of its anterior dichotomy, and appears superficially similar to that of *Globorotalia* (*G.*) *menardii menardii*.

Fig. 3. *Globotruncana* (*Globotruncana*) *tricarinata coronata* (Bolli), from the Campanian, approx. 3½ miles from Lindi Bridge, Tanganyika; British Petroleum Co. Ltd., Sample No. PEK. 5570; 3*a*, axial section, ×125 approx.; 3*b*, same specimen, the periphery of a late part of the last whorl, showing the broad, imperforate peripheral band with two carinae, and the abrupt termination against it of the radial perforations of the adjacent chamber walls, ×500 approx.

Fig. 4. *Rotalipora globotruncanoides* Sigal, from the Cenomanian, approx. 5 miles south-west of Lindi, Tanganyika; British Petroleum Co. Ltd., Sample No. FCRM. 2050; 4*a*, axial section, ×83 approx.; 4*b*, same specimen, the periphery of the last whorl, showing the imperforate carina and the abrupt ending of the perforations against it, ×500 approx.

EXPLANATION OF PLATE 3

Fig. 1. *Praeglobotruncana* (*Hedbergella*) *sp.* (= the 'grosse globigerine' of Schijfsma (1955)), from the Turonian of the BP-Shell Petroleum Development Co. (Tanganyika) Ltd. test-well Lindi No. 2, near Lindi, Tanganyika; British Petroleum Co. Ltd., Sample No. Lindi No. 2, 334 ft.; 1*a*, axial section, ×125 approx.; 1*b*, same specimen, periphery of the last whorl. Showing uniformly perforate structure, but slightly flattened dorsal surface, ×500 approx.

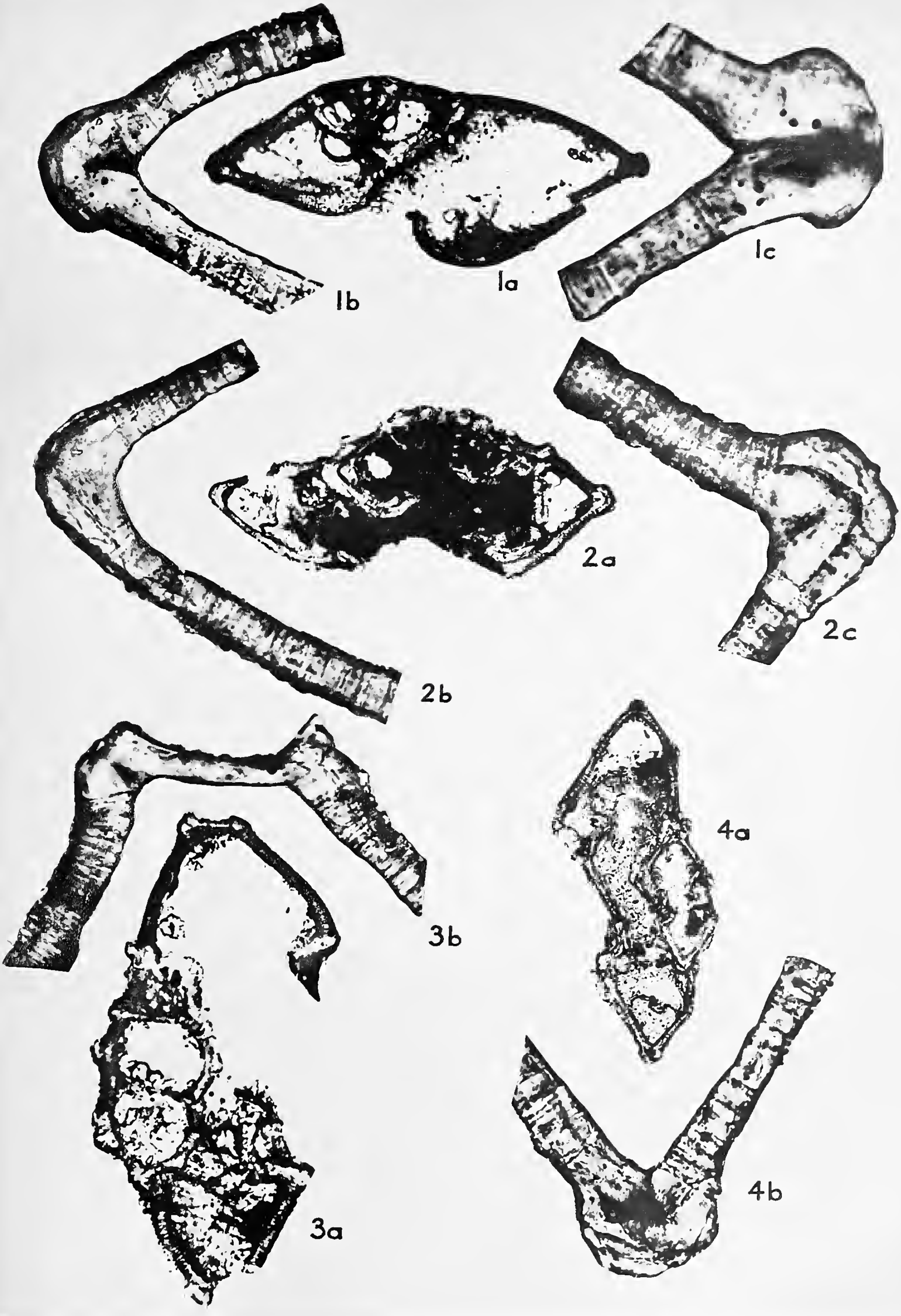
Fig. 2. *Ticinella helvetica* (Bolli), from the Turonian, approximately 8½ miles north west of Lindi, Tanganyika; British Petroleum Co. Ltd. Sample No. FCRM. 1907; 2*a*, axial section, ×110 approx.; 2*b*, same specimen, periphery of last whorl, showing perforate thickening (pseudocarina), and more strongly flattened dorsal surface, ×1,000 approx.

Fig. 3. *Ticinella roberti* (Gandolfi), from the Upper Albian or Lower Cenomanian of the BP-Shell Petroleum Development Co. (Tanganyika) Ltd. Test Well Wingayongo G.1 (90 ft.), Luhohi River, approximately 3½ miles west of Wingayongo Hill, Tanganyika; axial section, ×110 approx.

Fig. 4. *Praeglobotruncana* (*Praeglobotruncana*) cf. *stephani* (Gandolfi), from the Upper Cenomanian of the BP-Shell Petroleum Development Co. (Tanganyika) Ltd. Test Well Lindi No. 2 (829 ft.), near Lindi, Tanganyika; 4*a*, axial section, ×110 approx.; 4*b*, same specimen, periphery of the early part of the last whorl, showing imperforate peripheral band and development of a broad carina, ×500 approx.; 4*c*, same specimen, periphery of the last chamber, showing imperforate area, without development of a carina, ×1,000 approx.

Fig. 5. *Globotruncana* (*Globotruncana*) *arca* (Cushman), from the Campanian near Kilwa cross-roads, Tanganyika; British Petroleum Co. Ltd., Sample No. RS. 48; deformed specimen, the two carinae typical of this species being present on one side of the test, but being represented by a 'single' carina on the other side; 5*a*, axial section, ×125 approx.; 5*b*, same specimen, showing the normal development of the imperforate peripheral band on an otherwise abnormal chamber, ×500 approx.

Fig. 6. *Pseudohastigerina micra* (Cole), from the Upper Eocene, approximately 2½ miles south-west of Mhanya, Lindi District, Tanganyika; British Petroleum Co. Ltd., Sample No. FCRM. 1923; 6*a*, equatorial section, ×125 approx.; 6*b*, same specimen, showing monolamellar and imperforate nature of the septa, ×500 approx.



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1a


1b


2a


2b

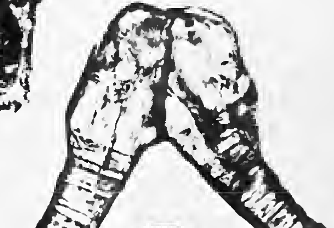

3


4a

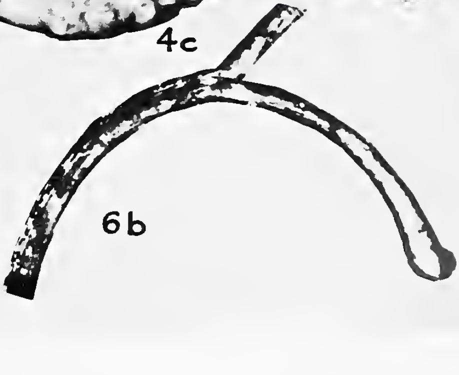

4b


4c


5a


5b


6a


6b

BANNER and BLOW, Globigerinaceae

but are of completely different type and origin in the two eras. In the Cretaceous such plate-like structures within the umbilici appear to have been formed in at least two ways. The origins of the tegilla in the Globotruncanidae are not known, but from their detailed morphology and their arrangement relative to the chambers ('protruded umbilical cover-plate' of Brönnimann and Brown 1955 (1956), p. 509 et seq.) they are clearly different from the plates formed in *Ticinella* from fused elongate portici ('depressed umbilical cover-plate' of Brönnimann and Brown, loc. cit.). In the case of the fundamentally distinct bullae, characteristic of the Globorotaloidinae and Catapsydracinae, it is probable that this structure has arisen independently in different genera, possibly in different ways. Blow (1959) believes that the bulla of *Tinophodella ambitacrena* (i.e. *Globigerinita naparimaensis* of Blow 1959, not of Brönnimann 1951, emended by Loeblich and Tappan 1957) has arisen from the well-marked lip of *Globigerina juvenilis* Bolli, indicating no close genetic relationship with other bulla-bearing forms. It has already been noted in this paper that *Globigerinatheka* possesses a *Globigerapsis* juvenile stage, and it is probable that *Globigerinatheka* is descended from *Globigerapsis*. Similarly, *Globigerinoita* has a juvenile *Globigerinoides* stage, and is probably descended directly from that genus. Even within the genus *Catapsydrax*, it is highly probable that polyphyleticism will become apparent when the interrelationships of its species become better known. The subfamily Catapsydracinae is therefore a polyphyletic group of specialized end-forms, which possesses unity only in the uniformity of its specialized characters, but which possesses definite stratigraphic value. No bullae are indisputably known in the Mesozoic.

From the above discussion, it is clear that great care must be exercised in determining the relative taxonomic importance of the morphological characters present in the Globigerinaceae. It is felt that the use of non-iterative characters in the higher taxa, and the discriminating use of iterative characters in the lower taxa, has produced a classification which (with the exception of the Catapsydracinae) closely approaches a natural order, and which is both stratigraphically and biologically significant.

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GLOSSARY

As some new terms have been introduced in this paper, and others modified or restricted in their usage, a short list of definitions is given below.

Apertures, accessory: apertures which do not open directly from the lumina of the primary chambers, but which open from beneath structures accessory to the primary aperture or the primary chambers

Apertures, equatorial: apertures which are symmetrical to the plane of coiling, extending from the ventral to the dorsal side of the test (most perfectly and symmetrically developed in planispiral, biumbilicate tests).

Apertures, extraumbilical: apertures which, although ventral in position, extend, in part at least, outside the umbilicus.

Apertures, intraumbilical: apertures which open into the umbilicus of the test and which do not extend outside it.

Aperture, primary: the single, principal aperture opening to the exterior from the lumen of the last-formed primary chamber, constant in position within the subfamily; typically the largest external aperture.

Apertures, relict: those parts of the primary apertures of chambers, other than the last-formed, which remain open to the exterior when successive chambers are added (the parts which no longer open to the exterior often becoming the septal apertures, communicating between successive chambers).

Apertures, supplementary: apertures opening to the exterior directly from the lumen of a primary chamber, which are additional to the primary aperture (often sutural in position, but may be areal in the apertural face).

Apertures, umbilical: apertures which open, in part at least, into the umbilicus of the test.

Bulla: a perforate, inflated, plate-like structure which covers the umbilicus (and sometimes the supplementary apertures) in the Catapsydracinae and Globorotaloidinae; accessory apertures are present at the margins of the bulla, or areally within it.

Carina: an imperforate, ridge-like thickening of the chamber wall, present on the periphery of the test, lying in the plane of coiling.

Costellae: ridge-like thickenings present on the dorsal and/or ventral chambers walls, typically running in a meridional direction, to converge at a 'pole' situated at the mid-point of the chamber periphery (maximum development in *Rugoglobigerina* s.s.), but sometimes running in directions normal or oblique to the periphery (e.g. *Globotruncana* (*Rugotruncana*) spp.).

Dorsal: the more evolute side of a trochospirally coiled test, usually, but not always, lacking an umbilicus.

Lip: a fairly narrow structure which appears to be a reflexed continuation of the actual chamber wall, projecting above and along an interiomarginal aperture or surrounding an areal aperture; typically symmetrically developed about the aperture (i.e. of uniform breadth throughout its length, or of maximum breadth at its mid-point).

Porticus: an imperforate, narrow or broad structure projecting from, and apparently additional to, the chamber wall, above and along an interiomarginal aperture; typically asymmetrically developed about the aperture (i.e. broadening towards one end of the aperture (typically the posterior end), where it often becomes flap-like or flange-like); portici may remain separate, or may fuse.

Pseudocarina: a perforate, ridge-like thickening of the peripheral part of the chamber wall, lying approximately in the plane of coiling.

Tegillum: a complex, often irregular structure of imperforate plates which covers the umbilicus; it may cover apertural portici (which are revealed when the tegillum is broken off), and is often pierced by accessory apertures; the later-formed plates may extend the full breadth of the umbilicus, and fuse on to the walls of chambers oppositely placed.

Umbilical teeth: lips which are exceptionally broad in their mid parts, so that they project as subtriangular, perforate flaps into the umbilicus.

Ventral: the more involute side of a trochospirally coiled test, typically possessing an umbilicus.

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A REVISION OF THE JURASSIC STROMATOPOROIDS *ACTINOSTROMINA*, *ASTROSTYLOPSIS*, AND *TRUPETOSTROMARIA* GERMOVŠEK

by R. G. S. HUDSON

Abstract. Seven species of stromatoporoids described by Germovšek in 1954 from the Tithonian of Jugoslavia are redescribed and allocated to his genera *Actinostromina* and *Astrostylopsis* and placed in the family Actinostromariidae and the superfamily Actinostromariicae *nov.* The genus *Trupetostromaria* Germovšek is considered to be a junior synonym of *Astrostylopsis*. Structural changes illustrated are the development of tubular coenotubes and cellular sclerenchyme, the reduction of the transverse lamellae, and the replacement of normal astrosystems by individual axial astrotubes with the omission, or considerable reduction, of transverse astrotubes, coenosteal structure thus becoming generally tubular.

INTRODUCTION

In 1954 G. Germovšek described various hydrozoans from the Upper Jurassic of Jugoslavia and in doing so founded ten new species of Stromatoporoidea, species not easy to evaluate since some of the technical terms used are of uncertain connotation and many of the illustrations inadequate. Some of the species are allocated to Palaeozoic genera, others to new genera, two of which are grouped to form a new family. It is evident that the species so founded are of importance in any systematic study of the Mesozoic Stromatoporoidea and certain of them have therefore been restudied and are redescribed in this paper. The material described by Germovšek is now in the collections of the Institute of Geology of the Slovene Academy of Science and Arts at Ljubljana and, by the kindness and courtesy of Dr. I. Rakovec, the holotypes and figured thin sections of *Actinostroma grossum grossum*, *A. g. robustissimum*, *Actinostromaria tubulata*, *Actinostromina oppidana*, *Astrostylopsis slovenica*, *A. grabenensis*, and *Trupetostromaria circoporea*, all species founded by Germovšek, have been lent to the author for study. The work resulting in this paper was carried out in the Geological Department of the Iraq Petroleum Company and the author here records his thanks to the Directors and Chief Geologist of that company for those facilities.

All specimens described and figured in this paper are from the Upper Jurassic (Tithonian) of Graben, near Novo mestro, Slovenia, Yugoslavia. The thin sections have been remounted and thus do not exactly correspond to those photographed by Germovšek. Structural dimensions stated in this paper give neither the average nor the range. They are the general dimensions, rather arbitrarily chosen. Measurements across coenotubes, &c., are from one calcification band to the other.

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SKELETAL MORPHOLOGY

Skeletal tissue. Though the microstructure of the various skeletal elements is not as yet understood, it has been recognized that there are at least two fundamental methods of tissue (sclerenchyme) growth of both pillars and lamellae. In one, the crystal fibres which make up most of the sclerenchyme are grouped in fascicles arising from individual centres of calcification, which usually show as clear minute spheres, or from linear centres of calcification showing as vertical clear cylindrical rods. A single succession of such centres would result in a continuing series of fibre fascicles and would form a simple trabecula. Such single series are not known: all recorded sclerenchymal microstructure shows that the crystal fibres arise from groups of solitary or linear centres; all trabeculae are thus compound and individual fascicles can rarely be recognized. These centres are enveloped in fine dark granular tissue or may themselves be darker than the surrounding tissue. Continuing upward repetition, they form in a pillar a dark-coloured calcification strand, and in a lamella a midplane calcification band. Such fibrous secretion is therefore puntal with all fibres directed generally upwards (*clinogonal*). When centres are loosely grouped, the fibres may vary slightly in direction.

In the other (*orthogonal*) method of skeletal secretion, the crystal fibres also originate from a calcification strand, or band, of dark mottled granular calcite in which individual centres cannot be definitely recognized. These fibres are at right angles to the calcification strand (or band) and do not form fascicles. Such fibre secretion is therefore planar or linear and not puntal. In both methods of fibre secretion, the calcification bands may vary greatly in thickness (in some forms they may almost complete the trabeculae, the fibrous envelope being thin).

Much of the distinction envisaged by Germovšek for his various species and genera was based on differences in microstructure of the sclerenchyme. The microstructure of *Actinostroma grossum* and its subspecies was stated to be radially (orthogonal) fibrous; that of *Actinostromaria tubulata* to be between radial and clinogonal fibrous as considered by him to be characteristic of *Epistromatopora*; that of *Actinostromina oppidana* to be finely granular and homogeneous; that of *Astrostylopsis slovenica* to be crystal-fibrous; that of *A. grabenensis* to be granular with no true crystal-fibres; that of *Trupetostromaria circoporea* to be crystal-fibrous in all directions. The author, contrary to Germovšek, considers that they are *all* definitely orthogonal, the main difference between them being in the width of the calcification band and the fineness of the crystal-fibres. The skeletal microstructure of each of the species is figured on Pl. 6.

Coenospaces and coenotubes. The pattern of the reticulum is often a matter of specific importance in the Mesozoic Stromatoporoidea. It is often best expressed not in terms of the shape and direction of its skeletal elements but rather in the form and direction of the spaces between them. To facilitate description a space between pillars or vertical lamellae, or between transverse lamellae, is here called respectively a *vertical* or *transverse coenospace*. When the vertical lamellae are all linked together and form, in transverse section, a net of polygonal or circular mesh, the spaces may be termed *coenotubes*. These often have no great vertical extent.

Fenestrate vertical lamellae. The linking of adjacent vertical pillars by connecting lamellae is effected, both in the Milleporellicae and the Actinostromariicae, by vertical repetition of transverse trabeculae. The process is not continuous for at regular intervals the trabeculae are not constructed so that any connecting lamella consists of a vertical alternation of vertically joined transverse trabeculae and small gaps, or, possibly, an alternation of single transverse trabeculae and gaps. Connecting lamellae are therefore fenestrate.

Cellular sclerenchyme. Trabecular growth in the vertical lamellae, though generally retaining its vertical and transverse directions, may become irregular and incomplete with the result that the lamellae, instead of being regularly fenestrate, become cellular, the cellules being generally small, rounded, completely enclosed, and completely filled with fibrous tissue. Such lamellae may widen considerably and become, within the reticulum, individual structures of cellular sclerenchyme. In general they retain their vertically lamellate character and act as walls dividing astrosystems, or enclosing astrotubes. Such sclerenchyme is well developed in most of Germovšek's species. It is not unusual in other genera of the Actinostromariicae.

Tubular reticulum. The species founded by Germovšek all have, within the reticulum, solitary vertical tubes wider than the normal coenotube. Some of these, as in species of *Astrostylopsis* (Pl. 5, figs. 6, 7, 8), are associated with radial transverse tubes and are evidently axial astrotubes (Pl. 4, fig. 1). Even where not so associated, as in species of *Actinostromina*, the occasional presence of grouped axial offsets identifies such tubes as astrotubes (Pl. 4, fig. 7). In addition to such as these, there are often, in *Astrostylopsis* but not in *Actinostromina*, numerous others not so identifiable and with no relationships among themselves or with the reticulum to suggest that they are astrotubes (Pl. 5, figs. 1–3). Such tubes, it is true, might be autotubes (as in *Milleporidium* Steinmann and *Promillepora* Dehorne) or they might be lateral astrotubes (as in *Actostroma* Hudson): they have not, however, the clear-cut origin, individuality, and distribution of the former, or the pattern of distribution of the latter. In some cases they make up a large part of the reticulum; in other cases they are only sporadically scattered through it. The walls which enclose them are as fenestrate as other vertical lamellae and the microstructure is the same. They are, in effect, normal coenotubes which have developed vertically and become consistently tubular.

Laminae. When tabulae are vertically continuous within a considerable part of the reticulum they form an unbroken transverse platform which, in the study of Mesozoic stromatoporoids, is called a *lamina*. This is formed of tabulate tissue only, is not fibrous, and is formed subsequent to the pillars and vertical lamellae which thus pass through it. It should not be confused with the transverse lamellae which consist of either orthogonal or clinogonal fibrous trabeculae. It is not the laminae of the Palaeozoic stromatoporoids.

Astrosystem. The term astrorhizae was first used for the unwalled, branching, radiating grooves or gutters on the coenosteal surface of a stromatoporoid. It is now often used not only as a general term covering both these structures and those associated with them, whether on the surface of the coenosteum or within it, but also as a term for structures homologous with the astrorhizae and their associates even when the former are not present. Since the term has not only a specific meaning but also a functional one, it is not suitable for such general use. The term *astrosystem* is here used for such a group of associated structures or for single structures homologous with them. Particular structures within the astrosystem are linked to it by use of the prefix *astro-* resulting in such terms as *astrotube*, *astrotabulae*, and *astrocorridor*.

Transverse astrotubes and offsets. The astrosystems of the Actinostromariidae consist of axial astrotubes with a number of transverse astrotubes radiating at vertical intervals and at right angles from them. These transverse tubes occur between adjacent transverse lamellae and since they are thus in general conformity with the rectangular pattern of the reticulum they are hardly distinguishable in vertical section from the transverse coenospaces except on polished surfaces (Pfender 1937, pl. 1, fig. 3). As far as is known such transverse tubes never ramify in the reticulum otherwise than horizontally or approximately so, nor do they develop vertically and become astrocorridors. In some of the species described these transverse tubes are so short that they are merely offsets from the vertical tubes.

SYSTEMATIC PALAEONTOLOGY

The superfamily Milleporellicae Hudson 1959 is characterized by clinogonal fibrous tissue. Forms belonging to the Actinostromariidae Hudson 1955 and the Siphostromidae Steiner 1932 have orthogonal or heterogonal fibrous tissue and are part of a group which has a well-defined identity in the Mesozoic Stromatoporoidea. It is here given systematic rank as a superfamily, the Actinostromariicae.

Though Germovšek rightly emphasized the marked variation in his six species mentioned earlier, it was not necessary to allocate them to five genera or to place them in different families. It is here shown that in all his species the microstructure of the skeletal tissue is orthogonal fibrous and the vertical pattern of the reticulum is, basically, regularly rectangular. They should therefore be all included in the Actinostromariidae.

[The family Trupetostromidae was founded by Germovšek (1954, p. 368) to include *Trupetostroma* Parks and his own two genera *Astrostylopsis* and *Trupetostromaria*. Its nominate genus *Trupetostroma* Parks 1936 is a Devonian genus of which the type species *T. warreni* Parks 1936 has only superficial resemblance to Germovšek's genera. The value and validity of this family can therefore be left to students of Palaeozoic stromatoporoids: it does not concern us.]

Generic allocation of Germovšek's species is difficult since the material on which they were founded is sparse and must not be completely sectioned. His species differ, in general, from described forms in the Actinostromariidae by the occurrence of cellular sclerenchyme, by the marked development of tubular reticulum, and by astrosystems of axial astrotubes usually with no, or limited, transverse tubes. These features are an expression towards structural verticality of the coenosteum, a trend which also occurs in the Milleporellicae and in other groups in the Actinostromariicae. In the former, vertical pillars or lamellae tend to be the sole structural element of the reticulum (as in *Milleporella* Deninger or *Stromatoporellina* Kühn): in both superfamilies there is a tendency for complex astrosystems with their important lateral elements to be replaced by isolated vertical astrotubes (as in *Actostroma* Hudson) and for the reticulum to include autotubes (as in *Milleporidium* Steinmann and *Promillepora* Dehorne). Germovšek's species can be linked with species of *Actinostromaria* in a morphological series (not at present a phylogenetic one) illustrating such a structural change. There is thus justification for their inclusion in the Actinostromariidae.

Actinostroma Nicholson 1886, to which Germovšek allocated his species *grossum*, is a Silurian to Devonian genus with the holotype of its type species from the Middle Devonian of Gerolstein, Germany. The genus is characterized by non-fibrous skeletal tissue. Germovšek's species cannot therefore belong to it.

Actinostromaria Haug 1909, to which Germovšek's species *tubulata* was allocated, is defined below. A characteristic feature of *tubulata* is a marked tubular reticulum, a character which excludes it from *Actinostromaria*.

The three genera founded and named by Germovšek are *Actinostromina*, *Astrostylopsis*, and *Trupetostromaria*. The last two names, in my opinion, are synonyms, naming the same genus. For the following reasons, I here chose *Astrostylopsis* as the valid name for that genus and declare *Trupetostromaria* a junior subjective synonym of it. This latter genus was founded by Germovšek for the species *circoporea*, one of its diagnostic characters being the occurrence of vertically aligned cellular sclerenchyme, considered by Germovšek to form structures comparable to the 'porous pillars' of *Trupetostroma*. The comparison with *Trupetostroma* is superficial and since the name *Trupetostromaria* might be held to imply a relationship or similarity which does not exist, it is not preferred as the name of the genus in question.

When founding the genus *Actinostromina*, Germovšek considered the sole diagnostic feature to be a homogeneous granular microstructure which he stated was the only structural component of the trabeculae in the type species, *Actinostromina oppidana*. It is true that in the holotype, the greater part of any trabecula consists of an evenly mottled dark-coloured fine calcite. There is, however, in places, very fine crystal fibrous tissue orthogonally radial to it (Pl. 6, fig. 8). The dark-coloured calcite is, therefore, the calcification band and *Actinostromina* does not basically differ in trabecular structure from *Astrostylopsis* or from other genera of the Actinostromariicae. The species of the genus have, however, a coenosteal structure which differs from that of those genera and maintains *Actinostromina* as a functional genus.

Generic diagnostic morphology

Actinostromina. The reticulum of *A. oppidana* does not differ significantly from that of *Actinostromaria*. The abundant well-developed vertical tubes are considered to be astrotubes and therefore *Actinostromina*, like *Actinostromaria*, is characterized by astrosystems. Its astrotubes have, however, no associated transverse tubes, as are common in *Actinostromaria*, but only offsets which tend to be vertically developed. This distinction is of phylogenetic importance and *Actinostromina* Germovšek is therefore retained as an active genus. Germovšek recognized that *Actinostromina oppidana* and *Actinostroma grossum* were, structurally, basically similar and, but for the difference in microstructure, now shown to be non-existent, would be cogeneric, a conclusion with which the author agrees.

Actinostroma grossum grossum and *Actinostroma grossum robustissimum* were considered by Germovšek to be subspecifically distinct on the grounds that the reticulum mesh of the latter was slightly wider and its coenosteum was ellipsoid whereas that of *A. grossum grossum* was subsphaerical. These differences are so slight, if they do exist, that they are within the range of individual variation: the subspecies are therefore considered synonomous.

Astrostylopsis. The two species, *A. slovenica* and *A. grabenensis*, for which this genus was founded are characterized by a partly tubular reticulum with some cellular sclerenchyme. The vertical tubes are considered to be coenotubes, and the reticulum to be transitory to an entirely tubular reticulum such as that of *Siphostroma* Steiner. This structure does not occur in any known genus of Actinostromariidae and *Astrostylopsis* Germovšek is therefore considered to be an active genus.

References were made to Germovšek's genus *Astrostylopsis* by Hudson (1957, 1958). In the first of these papers the genus was considered to be a synonym of *Stromatorhiza* Bakalow 1906, a conclusion now known to be ill founded since its skeletal issue is orthogonal fibrous whereas that of *Stromatorhiza* is generally granular. In the 1958 paper *Astrostylopsis* and *Trupetostromaria* were compared with *Actostroma* Hudson 1958 and considered to be generically distinct.

Actinostromaria darroensis was described from the Upper Jurassic of southern Ethiopia by Zuffardi-Comerci (1932, p. 74, pl. 2, fig. 7) and by Wells (1943, p. 49, pl. 8, figs. 6–8) from eastern Ethiopia. The species has a tubular polygonal reticulum with scattered axial astrotubes with small irregularly developed transverse tubes. The species should be placed in the genus *Astrostylopsis*.

Trupetostromaria. This genus was founded for the species *circoporea* which differs from the species of *Astrostylopsis* only by the much wider mesh of its more tubular reticulum and by the much more abundant cellular sclerenchyme, that is, it has the characteristic features of *Astrostylopsis* better developed. There are no structures in *Trupetostromaria* not present in *Astrostylopsis*: the two genera are therefore synonymous.

Superfamily ACTINOSTROMARIICAE nov.

Stromatoporoidea with radial or bilateral orthogonal or heterogonal fibrous trabeculae.

Family ACTINOSTROMARIIDAE Hudson 1955

Actinostromariicae with reticulum of vertical pillars and/or pillar-lamellae, and transverse bars or widely meshed transverse lamellae. Vertical reticulum variously rectangular; transverse reticulum labyrinthic or tubular. Cellular sclerenchyme variously developed or absent. Astrosystems of axial astrotubes with or without variously developed and variously radial transverse astrotubes or offsets. Trabeculae orthogonal fibrous.

Genus ACTINOSTROMARIA Haug 1909

Type species (by monotypy) *Actinostromaria stellata* Haug 1909.

Diagnosis. Actinostromariidae with vertical reticulum regularly but discontinuously rectangular with vertical pillars better developed and slightly coarser than the transverse bars. Transverse reticulum puntal or with angular labyrinthic or polygonal mesh. Axial astrotube(s) about same width as coenospaces, with, at regular vertical intervals, well-developed branching transverse astrotubes.

Genus ACTINOSTROMINA Germovšek 1954

Type species (by monotypy) *Actinostromina oppidana* Germovšek 1954.

Diagnosis. Actinostromariidae with reticulum of discontinuous vertical pillars and connecting lamellae, and a very open transverse lamellar net, both about equally developed; sparse cellular sclerenchyme. Vertically the reticulum is irregularly and discontinuously rectangular; transversely it is a loose irregular mesh of open (rarely closed) labyrinthic coenospaces. Astrosystems of well-developed, sparsely tabulate; walled, solitary astrotubes with or without offsets or, more rarely, indefinite irregular transverse tubes, both vertically disposed. No coenotabulae.

EXPLANATION OF PLATES 4 AND 5

All figures are of thin sections of the holotypes of various species of Germovšek. The dark line in all figures is the calcification band in the mid-plane of the trabeculae: the light grey on either side of it is the fibrous tissue, the clear white being where this has been removed during preparation of the section. The fibrous tissue often completely fills the coenospace or coenotube. Some of the coenotubes and astrotubes, filled with dark mud, have been cleared in the photos.

PLATE 4

Figs. 1, 2, 8. *Astrostylopsis circoporea* (Germ.). 1, Trans. sect. P14*d*, ×8. Note radial transverse tubes separated by cellular sclerenchyme. 2, Vert. sect. P14*b*, ×8. Grouped tubes are probably through astrosystem though not through axial astrotubes. 8, Vert. sect. P14*a*, ×6·7, as Germovšek, pl. 8, fig. 1*a*.

Fig. 3. *Actinostromina oppidana* Germ. Trans. sect. P5*b*, ×8. No vertical section available.

Fig. 4. *Actinostromina grossa* (Germ.). Vert. sect. P1*a*, ×6·7, as Germovšek, pl. 1, fig. 1*a*. Right side crushed. Note astrosystem and cellular sclerenchyme lower left.

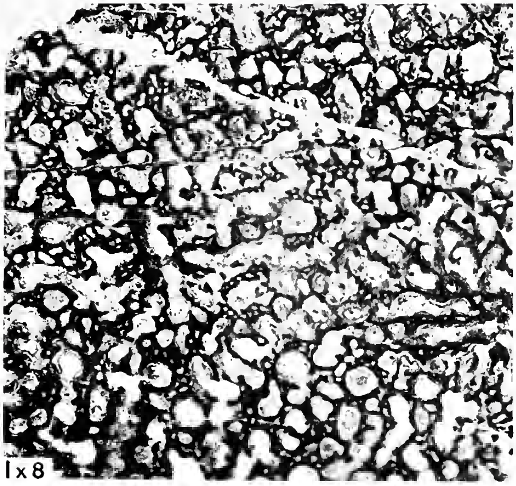
Figs. 5, 6, 7. *Actinostromina grossa* (Germ.), from holotype of *Actinostroma grossum robustissimum* Germ. 5, Trans. sect. P2*a*, ×12. Reticulum mesh partly destroyed. 6, Trans. sect. P2*b*, ×8. Note widely cellular sclerenchyme. 7, Vert. sect. P2*b* (same section as fig. 6), ×8. Section through astrosystems.

PLATE 5

Figs. 1–3. *Astrostylopsis tubulata* (Germ.). 1, Vert. sect. P3*b*, ×6. Note fenestrate vertical lamellae, axial and transverse astrotubes on upper left, vertical tubes on upper right probably through astrosystem though not through axis. 2, Trans. sect. P3*d*, ×8. Note coarse cellular sclerenchyme. 3, Vert. sect. P3*a*, ×6·7, same sect. as Germovšek, pl. 1, fig. 2. Note coenotubes separated by cellular sclerenchyme.

Figs. 4–6. *Astrostylopsis slovenica* Germ. 4, Trans. sect. P12*c*, ×8. Note cellular sclerenchyme bounding transverse astrotubes. 5, Vert. sect. P12*e*, ×8. Note narrow transverse tubes radial to axial astrotube. 6, Trans. sect. P12*d*, ×8. Note irregular transverse astrotubes.

Figs. 7, 8. *Astrostylopsis grabenensis* Germ. 7, Trans. sect. P13*b*, ×8. Note coarse cellular sclerenchyme in astrosystems. 8, Vert. sect. P13*a*, ×6·7, as Germovšek, pl. 7, fig. 2. Lower part crushed. Note fenestrate lamellae in upper part.



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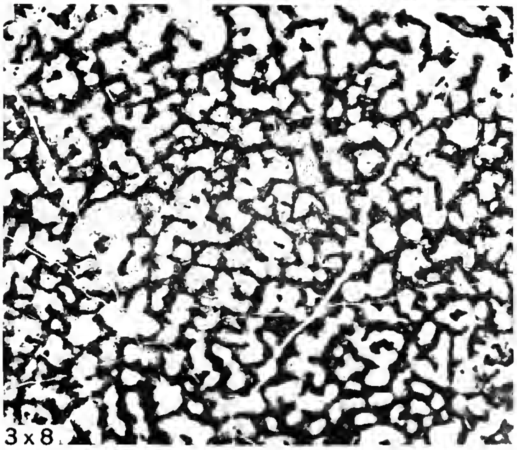
2×8



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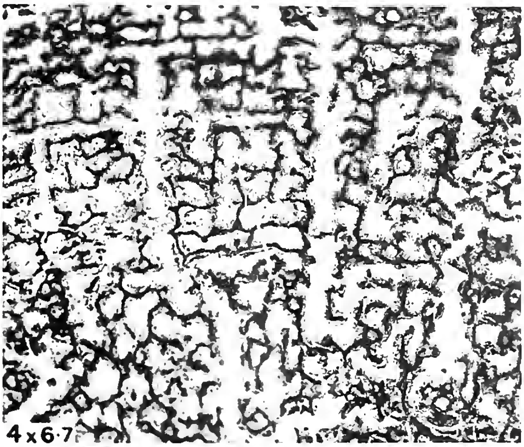
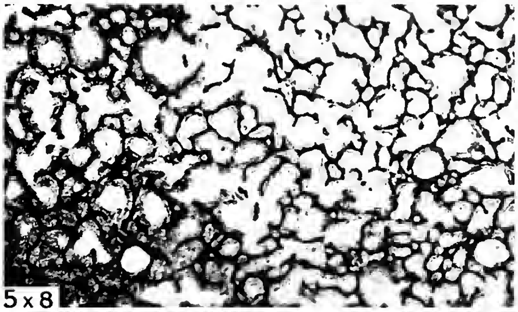


4×6·7



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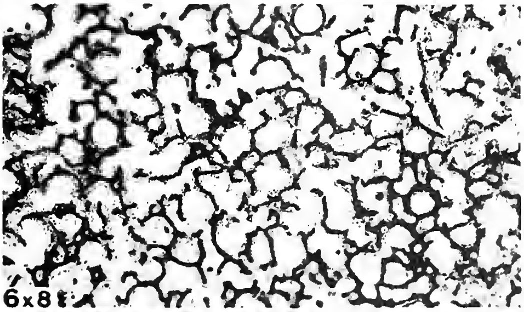
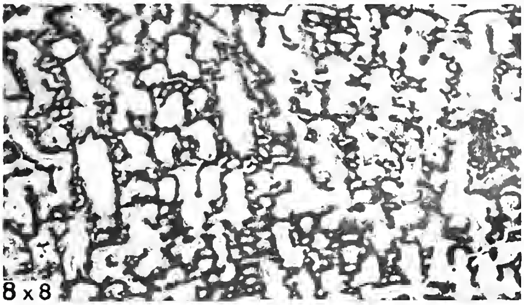


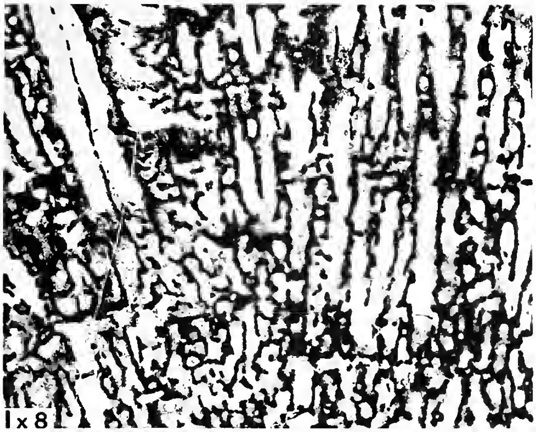
6×8

7×8



8×8

HUDSON, Jurassic stromatoporoids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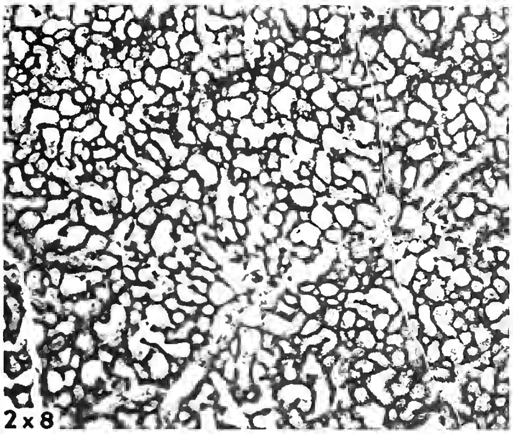
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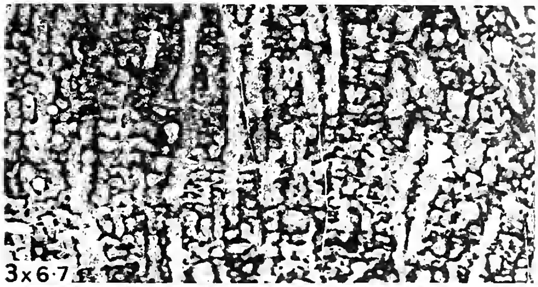
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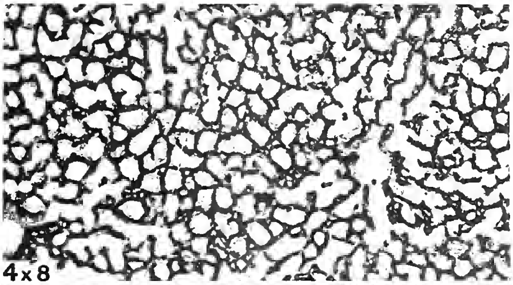
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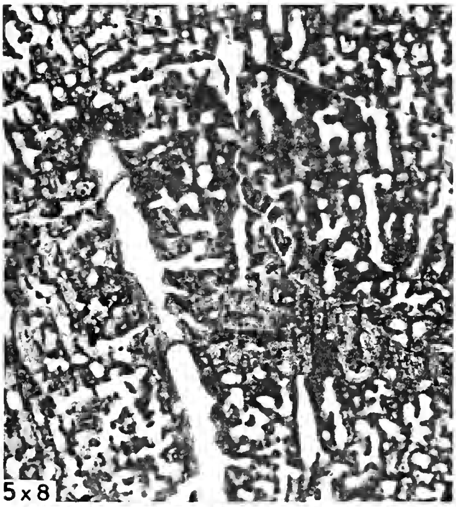
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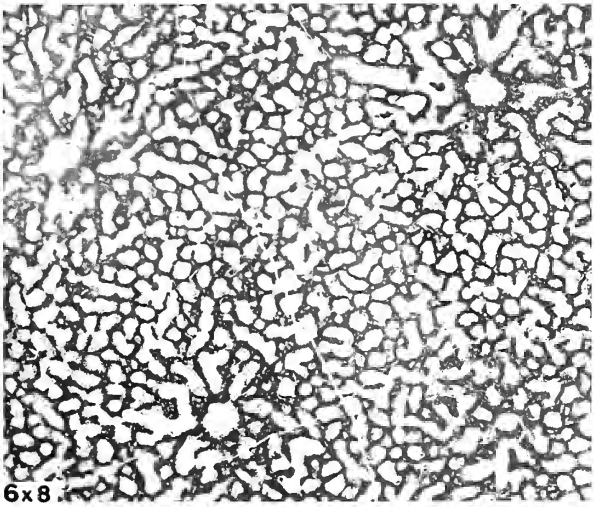
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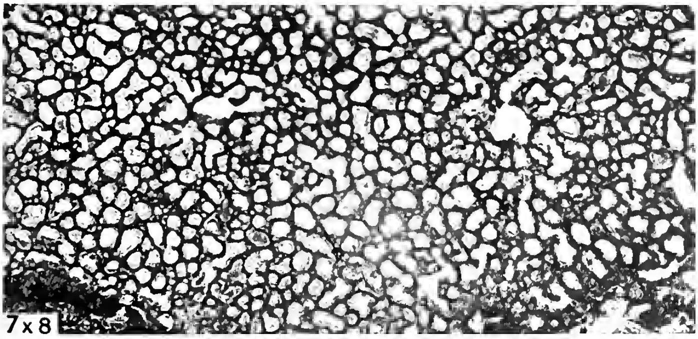
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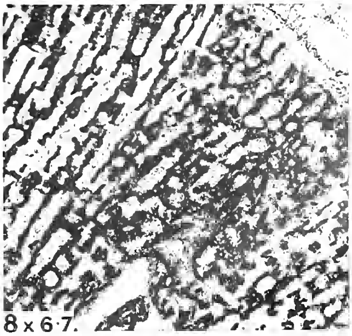

8 x 6·7

HUDSON, Jurassic stromatoporoids

Actinostromina oppidana Germovšek

Plate 4, fig. 3; Plate 6, fig. 8

Actinostromina oppidana Germovšek 1954, pp. 351–77, pl. 2, fig. 3; pl. 5, fig. 1.

Material. P5 (holotype and only recorded specimen), two pieces (Germovšek, pl. 5, fig. 1) and thin sections P5*a* (Germovšek, pl. 2, fig. 3; this paper Pl. 6, fig. 8); P5*b* (this paper Pl. 4, fig. 3) and P5*c*.

Diagnosis. Coenosteum cylindrical with axial and peripheral reticulum. Transverse reticulum of short, irregularly meandriform coenospaces and some coenotubes (*c.* 0·4 mm. across). Radial reticulum of regular, evenly spaced, transverse lamellae (*c.* 0·33 mm. apart), and less regular, rarely cellular, vertical pillar-lamellae (*c.* 0·4 mm. apart), forming together an irregular orthogonal mesh. Occasional solitary axial astrotubes (*c.* 0·7–0·8 mm. across) with irregular transverse offsets.

Actinostromina grossa (Germovšek)

Plate 4, figs. 4–7; Plate 6, figs. 9, 10

Actinostroma grossum Germovšek 1954, pp. 346 and 375, pl. 1, figs. 1*a–c*.
Actinostroma grossum grossum Germovšek 1954, p. 350.
Actinostroma grossum robustissimum Germovšek 1954, pp. 348 and 376, pl. 2, fig. 1.

Material. P1 and P2 (only recorded specimens). P1 (holotype), one piece and thin sections P1*a* (Germovšek, pl. 1, figs. 1*a*, *b*; this paper Pl. 4, fig. 4) and P1*b* (Germovšek, pl. 1, fig. 1*c*; this paper Pl. 6, fig. 9). P2 (holotype of *Actinostroma grossum robustissimum*), one piece (Germovšek, pl. 1, fig. 1) and thin sections P2*a* (this paper Pl. 4, fig. 5; Pl. 6, fig. 10) and P2*b* (this paper Pl. 4, figs. 6, 7).

Diagnosis. Coenosteum nodular and latilamellate. Reticulum of pillar-lamellae and widely meshed transverse lamellae, both *c.* 0·2–0·25 mm. across. Transverse reticulum a variably wide mesh of labyrinthic coenospaces and irregular coenotubes, both up to *c.* 0·5 mm. across, with, not common, interspersed patches of coarse cellular sclerenchyme (cellules 0·2–0·3 mm. across). Radial reticulum irregularly rectangular; vertical lamellae dominant in open latilamellae, transverse lamellae and extensive transverse coenospaces in compact latilamellae. Numerous walled astrotubes (generally 0·5–0·3 mm. across) with irregular offsets or indefinite irregular transverse tubes, both vertically disposed.

Genus ASTROSTYLOPSIS Germovšek 1954

Type species (by original designation) *Astrostylopsis slovenica* Germovšek 1954.

Diagnosis. Actinostromariidae with reticulum variously vertically tubular and subordinately rectangular, and with variously developed cellular sclerenchyme, interspersed or partly enclosing coenotubes or astrotubes. Astrosystems, abundant, of one or more tabulate axial astrotubes with offsets or irregularly radial transverse tubes.

Astrostylopsis slovenica Germovšek

Plate 5, figs. 4–6; Plate 6, figs. 1–3

Astrostylopsis slovenica Germovšek 1954, pp. 361 and 380, pl. 6, fig. 1, pl. 7, figs. 1*a–c*.

Material. P12 (holotype and only recorded specimen), three pieces (Germovšek, pl. 6, fig. 1) and thin sections P12*a* (Germovšek, pl. 7, fig. 1*a*), P12*b* (this paper Pl. 6, figs. 2, 3), P12*c* (Germovšek, pl. 7, figs. 1*b*, 1*c*; this paper Pl. 5, fig. 4; Pl. 6, fig. 1), P12*d* (this paper Pl. 5, fig. 6) and P12*e* (this paper Pl. 5, fig. 5).

Diagnosis. Astrostylopsis with nodular coenosteum. Transverse reticulum of vertical lamellae (*c.* 0·05 mm. across) forming rounded coenotubes and short vermiform coenospaces (both *c.* 0·3–0·4 mm. across); vertical reticulum partly tubular, partly rectangular (trans. lamellae *c.* 0·2–0·3 mm. apart). Axial astrotubes, common, tabulate (*c.* 0·6 mm. across); irregularly radial, branched and not well-developed transverse tubes (*c.* 0·2–0·3 mm. across), little more than coenospaces and vertically irregularly spaced. Cellular tissue, mainly within astrosystems, of closely spaced irregular vertical and transverse trabeculae (cellules *c.* 0·05–0·1 mm. across).

Astrostylopsis grabenensis Germovšek

Plate 5, figs. 7, 8; Plate 6, fig. 4

Astrostylopsis grabenensis Germovšek 1954, pp. 364 and 381, pl. 7, fig. 2.

Material. P13 (holotype and only recorded specimen), two pieces and thin sections P13*a* (Germovšek, pl. 7, fig. 2; this paper Pl. 5, fig. 8; Pl. 6, fig. 4) and P13*b* (this paper Pl. 5, fig. 7).

Diagnosis. Astrostylopsis with nodular coenosteum and reticulum, mainly tubular. Transverse reticulum of rounded coenotubes and few coenospaces (both *c.* 0·4 mm. across); vertical reticulum mainly of fenestrate vertical lamellae (*c.* 0·1 mm. across). Solitary, sparsely tabulate astrotubes (*c.* 0·5–0·6 mm. across) common; radial offsets and rare transverse tabulae interspersed with common, widely cellular sclerenchyme of rectangular interlacing trabeculae (cellules generally 0·1 mm. across).

EXPLANATION OF PLATE 6

Transverse and vertical thin sections, all × 100, of parts of the reticulum of the holotypes of the various species, showing the orthogonal fibrous microstructure of the trabeculae which form the vertical pillars and fenestrate vertical lamellae, the transverse lamellae, and the cellular sclerenchyme. The dark-coloured tissue is the calcification band. On either side of it and perpendicular to its surface, is the crystal-fibrous tissue. In most cases this completely fills the coenospace between the trabeculae; otherwise the gap is filled with coarse crystalline calcite. In a few cases there is mud filling the centre of the coenospace; this has been cleared from the photo.

Figs. 1–3. *Astrostylopsis slovenica* Germ. 1, Trans. sect. P12*c*, from same sect. as Germovšek, pl. 7, fig. 1*c*. 2, Vert. sect., P12*b*. 3, Trans. sect. P12*b*, showing cellular sclerenchyme.

Fig. 4. *Astrostylopsis grabenensis* Germ. Vert. sect. P13*a*.

Figs. 5, 6. *Astrostylopsis circoporea* (Germ.). 5, Vert. sect. P14*a*, from same sect. as Germovšek, pl. 8, fig. 1*b*. 6, Vert. sect. P14*b*, showing cellular sclerenchyme.

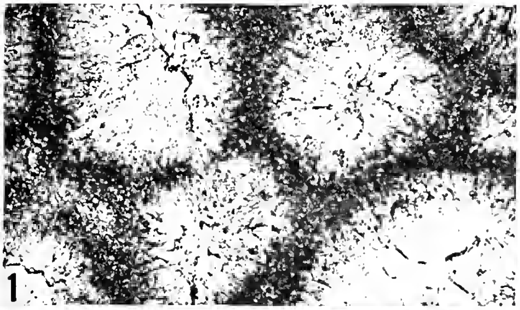
Fig. 7. *Astrostylopsis tubulata* (Germ.). Vert. sect. P3*a*.

Fig. 8. *Actinostromina oppidana* Germ. Vert. sect. P5*a*, from same sect. as Germovšek, pl. 2, fig. 3.

Fig. 9. *Actinostromina grossa* (Germ.). Trans. sect. P1*b*.

Fig. 10. *Actinostromina grossa* (Germ.). Holotype of *Actinostroma grossum robustissimum* Germ. Trans. sect. P2*a*.

PLATE 6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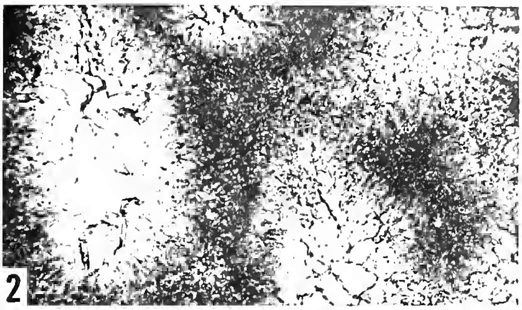
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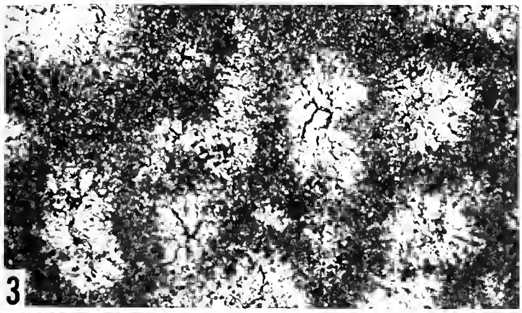
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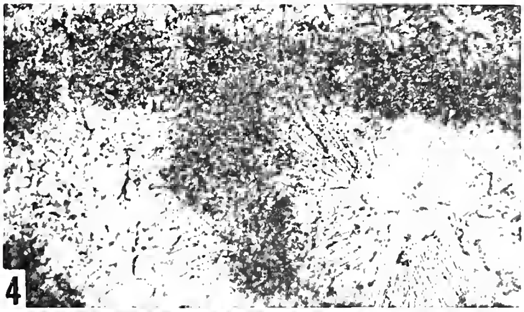
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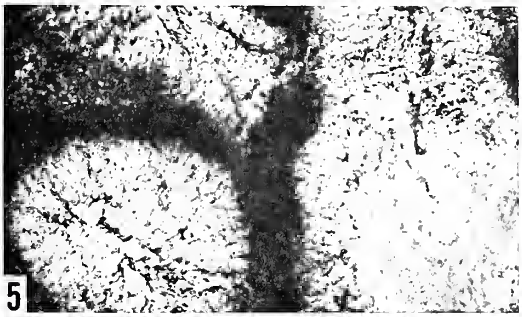
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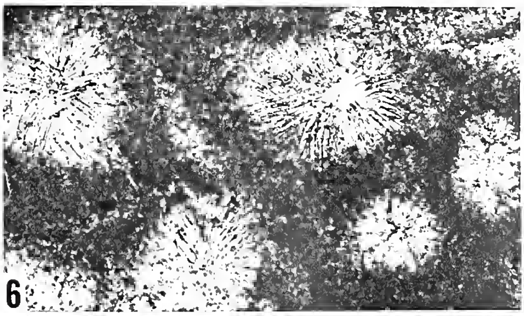
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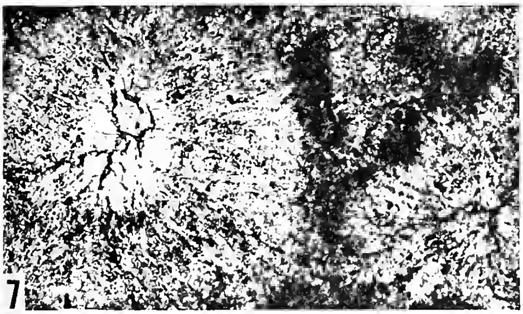
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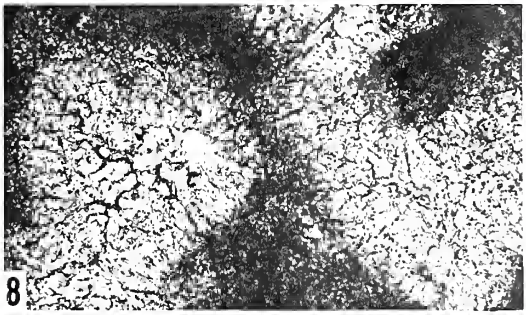
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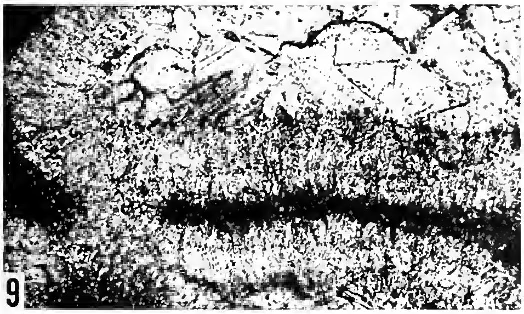
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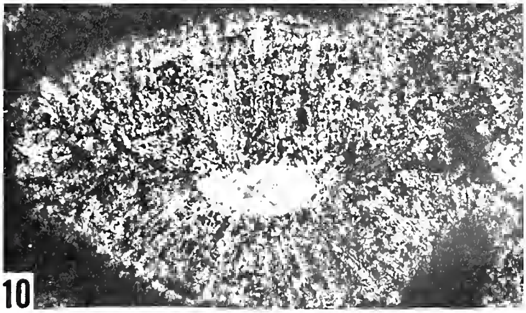
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HUDSON, Jurassic stromatoporoids

Astrostylopsis circoporea (Germovšek)

Plate 4, figs. 1, 2, 8; Plate 6, figs. 5, 6

Trupetostromaria circoporea Germovšek 1954, pp. 365 and 381, pl. 4, fig. 2; pl. 5, fig. 2; pl. 8, figs. 1*a*, *b*.

Material. P14 (holotype and only recorded specimen); three pieces (Germovšek, pl. 4, fig. 2; pl. 5, fig. 2) and thin sections P14*a* (Germovšek, pl. 8, figs. 1*a*, *b*; this paper Pl. 4, fig. 8; Pl. 6, fig. 5), P14*b* (this paper Pl. 4, fig. 2; Pl. 6, fig. 6), P14*c* and P14*d* (this paper Pl. 4, fig. 1).

Diagnosis. Astrostylopsis with coenosteum subhemispherical (type 7·5 by 6 cm.) and latilamellate. Transverse reticulum of variably sized rounded coenotubes (*c.* 0·25–0·4 mm. across) and short irregular vermiform coenospaces with, between them, irregularly lamellate areas of cellular sclerenchyme; radial reticulum of well-developed and fairly continuous coenotubes and cellular sclerenchyme, and narrower, discontinuous, parallel, interlamellae transverse coenospaces. Cellular sclerenchyme with irregularly vertical and horizontal closely spaced trabeculae, forming cells generally 0·05–0·06 mm. across. Solitary axial astrotubes (*c.* 0·5–0·6 mm. across) common, sparsely tabulate, and with, at intervals, short, narrower, irregularly radial, transverse tubes or offsets. Calcification band generally 0·05–0·06 mm. across.

Astrostylopsis tubulata (Germovšek)

Plate 5, figs. 1–3; Plate 6, fig. 7

Actinostomaria tubulata Germovšek 1954, pp. 350, 376, pl. 1, fig. 2.

Material. P3 and P4 (only recorded specimens). P3 (holotype), three pieces and thin sections P3*a* (Germovšek, pl. 1, fig. 2; this paper Pl. 5, fig. 3; Pl. 6, fig. 7), P3*b* (this paper Pl. 5, fig. 1), P3*c* and P3*d* (this paper Pl. 5, fig. 2). P4 (paratype), one piece.

Diagnosis. Astrostylopsis with reticulum of fenestrate pillar-lamellae, subordinate transverse lamellae, and cellular sclerenchyme. Transverse reticulum an irregular mesh of labyrinthic or short vermiculate coenospaces (*c.* 0·25 mm. across), abundant well-defined coenotubes (*c.* 0·3 mm. across) and interspersed patches of cellular sclerenchyme (cellules *c.* 0·15 mm. across); vertical section of coenotubes, sparsely tabulate and closely or widely separated by evenly spaced rectangular reticulum or cellular sclerenchyme of widely interlacing irregularly vertical and transverse trabeculae. Astrosystems with axial cluster of about seven or eight vertical astrotubes (each *c.* 0·4 mm. across) and a few wide irregularly radial transverse tubes (*c.* 0·4 mm. across) ramifying radially, at first obliquely then horizontally, into a reticulum with cellular sclerenchyme and coenotubes.

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STRETOSAURUS GEN. NOV., A GIANT PLIOSAUR FROM THE KIMERIDGE CLAY

by L. B. TARLO

ABSTRACT. A giant Pliosaur is described. This is the second Pliosaur from the Kimeridge Clay in which limb girdles are known associated with the axial skeleton, but it is the only giant one of any age (with the exception of *Kronosaurus* from the Lower Cretaceous) in which the post-cranial skeleton is adequately known. The pectoral girdle of this animal is so unusual that a new generic name is considered necessary for its reception; the name *Stretosaurus* gen. nov. is proposed. However, the characters of the anterior cervical vertebrae enable it to be placed in the species *S. macromerus* (Phillips). Finally, it is shown that two quite distinct giant Pliosaurs, *S. macromerus* (Phillips) and *Pliosaurus brachydeirus* Owen, must have inhabited Kimeridgian seas.

INTRODUCTION

IN 1952 a giant Pliosaur was discovered at the village of Stretham, near Ely, during excavation of Kimeridge Clay by the Great Ouse River Board, and largely due to the voluntary efforts of their employees, in particular Mr. W. W. Wolfe and Mr. B. Woolf of Stretham, this huge skeleton was preserved for the Sedgwick Museum, Cambridge. The photographs taken at the time of the discovery give a good indication of the size of the animal (see Pl. 7). The material collected by the Sedgwick Museum in 1952 is now catalogued under J. 35990 *a–z*, *aa–zz*, *A–Q*, and consists of sixty-nine bones (see Appendix 1).

The discovery of the Stretham skeleton is of considerable importance since not only is it one of the two Kimeridgian Pliosaurs in which limb girdles are known associated with the axial skeleton, but in particular it has an unusual scapula which is unlike that of any other Plesiosaurian. Besides this, it is the only giant Pliosaur of any age in which the post-cranial skeleton is adequately known (with the exception of *Kronosaurus* from the Lower Cretaceous, Romer and Lewis 1959).

The characters of the anterior cervical vertebrae show that the Stretham specimen belongs to the species *P. macromerus* Phillips, but as indicated previously (Tarlo 1959) there are two clearly defined groups of Kimeridgian Pliosaurs, one group containing *P. brachydeirus* Owen, and the other represented by *P. macromerus* Phillips. As *P. brachydeirus* is the type species the group to which it belongs must retain the name *Pliosaurus*, thus making a new generic name necessary for *P. macromerus*. The name *Stretosaurus* gen. nov. is chosen as it seems fitting that the village of Stretham where this giant skeleton was discovered should be commemorated.

All giant Pliosaur remains were previously assigned to *P. macromerus* on the basis of size alone, but it can now be demonstrated that these remains fall into the two groups previously established (Tarlo 1959). Obviously size alone is no criterion for the identification of Kimeridgian Pliosaurs. It is now possible for one group of giant remains to be assigned to *Stretosaurus macromerus* and the other to *Pliosaurus brachydeirus*.

[Palaeontology, Vol. 2, Part 1, 1959, pp. 39–55, pls. 7–9.]

SYSTEMATIC PALAEONTOLOGY

Family PLIOSAURIDAE Seeley 1874

Genus STRETOSAURUS gen. nov.

Type species *Pleiosaurus macromerus* Phillips.

Diagnosis. Teeth trithedral in cross-section, outer surface smooth and flat; mandible with short symphysis bearing five to six large caniniform teeth, total of about twenty-five teeth in each ramus; cervical vertebrae short, length less than half width or height, ventral keel absent, cervical ribs double headed; caudal vertebrae without chevron bone facets; scapula triradiate with dorsal process produced anteriorly; coracoid long with postero-lateral expansion; ischium elongated; propodials long, compressed dorso-ventrally, slightly expanded distally; epipodials short.

Stretosaurus macromerus (Phillips)

Pliosaurus grandis Owen 1849–84, pp. 152–3, pl. 18.
Pliosaurus grandis Owen 1869, pp. 3–5, pl. 1, 2.
Pliosaurus brachydeirus Owen; Seeley 1869, p. 104.
Pleiosaurus macromerus Phillips 1871, pp. 354–8, fig. 148 only.
Pliosaurus macromerus Phillips; Lydekker 1889, pp. 131–9, fig. 41 only.
Pliosaurus macromerus Phillips; Tarlo 1958*b*, pp. 193–9, figs. 1–4, pl. 36–37.

Diagnosis. As for genus.

Syntypes. Kimeridge Clay; University Museum, Oxford. J. 10437, anterior cervical centrum, Swindon, Wiltshire; J. 10438, anterior cervical centrum, Shotover Hill, Oxfordshire; J. 10439, anterior cervical centrum, Swindon; J. 10441, anterior cervical centrum, Shotover railway cutting; J. 10444, posterior cervical centrum, Sandford, Oxfordshire; J. 10445, dorsal centrum, Swindon; J. 10460, caudal centrum, St. Giles', Oxford; J. 12498, femur, Swindon. The anterior cervical centrum (J. 10441) figured Phillips 1871, fig. 148, is here chosen as the lectotype.

Description of Lectotype

Phillips (1871, p. 354) included under *P. macromerus* a large femur from Swindon and a number of vertebrae. This material was not associated and came from several different localities. Much of it is indeterminable, although three of the cervical vertebrae and the one caudal vertebra listed by him can be assigned to *P. brachydeirus* Owen (see Appendix 2 below). The first specimen figured by Phillips (fig. 148) is chosen as the lectotype (Pl. 8, figs. 1, 1*a*, 1*b*) since of those listed it is the only one exhibiting sufficient characters for it to be of use in specific diagnosis.

The length of the lectotype centrum is less than half its width (or height). Its measurements are: length 56 mm., width 138 mm., height 135 mm. This marked shortening of the cervical vertebrae is a distinguishing feature of all Pliosaurs and was noted by Conybeare as long ago as 1824.

The lateral surface of the centrum bears two rib facets which are oval in outline, their long axes being directed antero-posteriorly. In this specimen the superior facet is smaller than the inferior, the measurements of the facets (in mm.) being—superior facet: length 45, height 34; inferior facet: length 45, height 38. The lateral surface between the base of the neural arch and the superior rib facet is quite smooth, with no suggestion of a ridge.

The anterior articular surface is concave with a poorly developed mamilla at the centre; the outline of the centrum is circular with a well-marked peripheral groove, a feature noted by Phillips. The posterior articular surface is also concave and somewhat circular in outline, with its margin bevelled along the ventral edge and also between the base of the neural arch and the region of the rib facets.

The anterior and posterior margins of the ventral surface of the centrum are somewhat roughened; there is no evidence of a ventral keel, but there is a depression on each side of the ventral surface near the lower margins of the inferior rib facets, and the surface is slightly convex between the facets.

Description of Associated Skeleton from Stretham

The Stretham specimen is one of the most important Pliosaur skeletons to have come out of the Kimeridge Clay. Of the cranial skeleton only teeth and a few jaw fragments are known, but most of the post-cranial skeleton can be described.

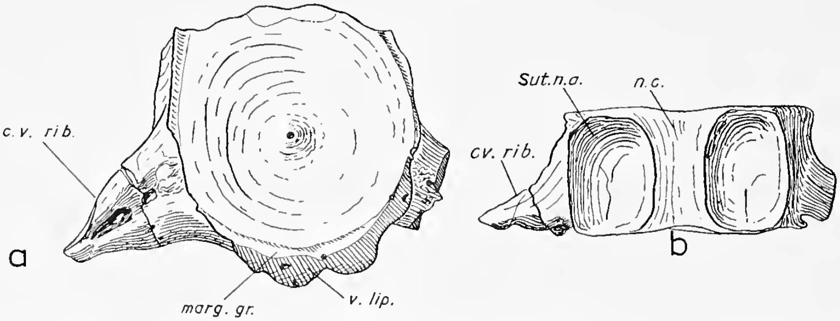
Teeth. The teeth are similar to those of *P. brachydeirus* Owen in that they are trihedral in cross-section; the enamel of the flat outer surface is smooth but the remainder of the crown is characterized by longitudinal ridges (see Pl. 9, figs. 3, 3*a*, 3*b*). This type of tooth is common to all Pliosaurs of Kimeridgian age and thus cannot be used to distinguish the different species of that age from one another (Tarlo 1958*a*).

VERTEBRAL COLUMN. Nineteen vertebrae are known from the Stretham Pliosaur. From a diagnostic point of view the most important are the anterior cervical vertebrae in which two sets of characters can be recognized: those which remain constant throughout the neck and may therefore be of diagnostic value, and those which change progressively down the neck and thus enable the relative position of the vertebrae to be established. Also of interest are the caudal vertebrae which do not bear chevron bone facets on their ventral surfaces as is the case in other reptiles.

Anterior cervical vertebrae. From the anterior part of the neck four vertebral centra are known. Their measurements are given (in mm.) in the table below:

	Length	*Width*	*Height*
J. 35990*xx* (text-fig. 1, Pl. 8, figs. 3, 3*a*) .	64	132	136
J. 35990*yy* (Pl. 8, fig. 5) . . .	64	136	132
J. 35990*A* (text-fig. 2*a*)	65	134	134
J. 35990*zz* (text-fig. 2*b*, Pl. 8, figs. 2, 2*a*) .	67	144	138

As can be seen, the length of each vertebra is less than half its width (or height). There are always double rib facets on the lateral surface of the centrum, and this feature together with the shortening of the centrum is characteristic of all Pliosaurs. There are several other characters which the four vertebrae have in common. The ventral surface is flat with no suggestion of the development of a ventral keel; the lateral surface of the centrum between the superior rib facet and the neural arch is smooth with no indication of a ridge, and in the centre of each articular surface a small mamilla is found punctured by a nutritive foramen. The constancy of these characters means that they can be used to compare this specimen with others.



TEXT-FIG. 1. *Stretosaurus macromerus* (Phillips), anterior cervical centrum. Sedgk. Mus. J. 35990*xx*. ×¼. *a*, Anterior view. *b*, Dorsal view. *cv. rib*, cervical rib; *marg. gr.*, marginal groove; *n.c.*, floor of neural canal; *Sut. n.a.*, suture of neural arch; *v. lip*, ventral lip.

The relative position of the cervical vertebrae in the neck can be ascertained in two ways: (i) by the progressive increase in the length of the vertebrae towards the back of the neck, where the rib articulation moves up from the centrum on to the neural arch, and the ribs become single headed, and (ii) by the progressive changes in the proportions of the rib facets down the neck. The latter changes are indicated by the measurements given below (in mm.).

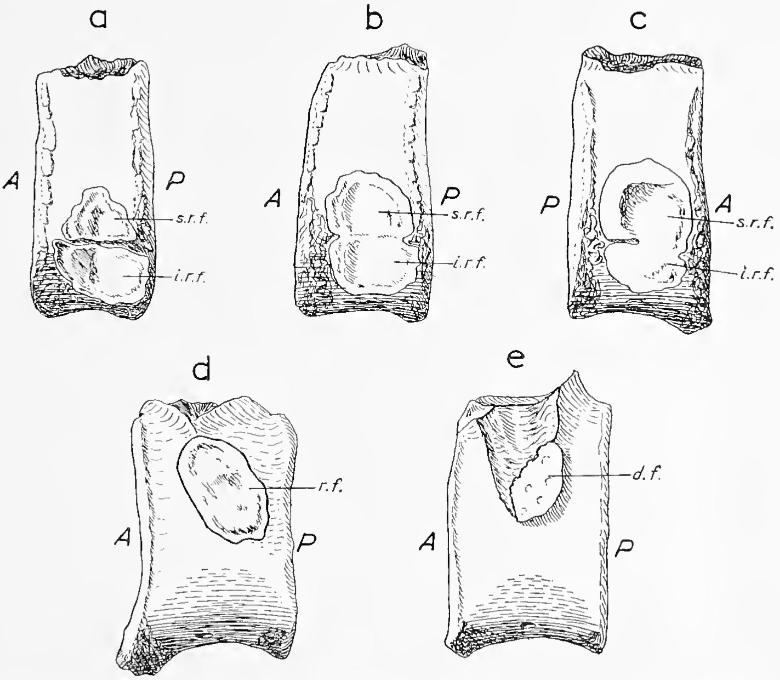
	Superior facet		*Inferior facet*	
	Length	*Height*	*Length*	*Height*
J. 35990*xx*	27	25	33	26
J. 35990*yy*	36	24	48	39
J. 35990*A*	40	34	51	36
J. 35990*zz*	47	37	49	33

The superior rib facet also changes its shape down the neck. At first it is triangular in outline, but by the time the fourth of the known centra is reached it has become oval, again confirming the order in which the vertebrae are arranged.

Once the centra are placed in order it is possible to recognize a further series of minor changes progressing down the neck. These will be given in detail, as they are relevant to the specific identification of the Stretham Pliosaur.

On the ventral margin of the anterior articular surface, a projection is developed, termed the ventral lip. This is most pronounced in the first of the four known centra, becoming reduced in the later vertebrae, so that in the last one, the only indication of it is a small roughened area on the anterior part of the ventral margin of the centrum.

There is also a well-marked marginal groove on the anterior articular surface. In the first three centra this is developed only in the ventral part, but in the fourth it runs round the periphery from the base of one neural arch to the other, and is termed a peripheral groove. The posterior articular surface of the first three vertebrae has bevelled margins; these are present on each side from the base of the neural arch to the superior rib facet, and also ventrally between the inferior rib facets. This ventral bevelling tends to produce a slight ventral lip on the posterior margin directed forwards, but both this and the bevelling disappear in the last of the four centra.



TEXT-FIG. 2. *Stretosaurus macromerus*, vertebral centra in lateral view showing progressive changes in proportions of rib facets; $\times \frac{1}{4}$. *a*, Left side, anterior cervical centrum J. 35990*A*. *b*, Left side, anterior cervical centrum J. 35990*zz*. *c*, Right side, posterior cervical centrum J. 35990*R*. *d*, Left side, posterior cervical centrum J. 35990*C*. *e*, Left side, pectoral centrum J. 35990*E*. *A*, anterior; *P*, posterior; *d.f.*, demi-facet; *i.r.f.*, inferior rib facet; *r.f.*, rib facet; *s.r.f.*, superior rib facet.

As shown from the detailed description of the lectotype centrum, it has all the constant characters outlined above. Like the fourth known vertebra of the Stretham animal it has a peripheral groove but no ventral lip and its superior rib facets are oval, and like the third the margin of its posterior articular surface is bevelled in three places and the superior rib facet is slightly smaller than the inferior facet. It thus would fit exactly into a similar series of cervical vertebrae. Agreement over such a large range of characters means that the Stretham skeleton can be placed without any hesitation into the same species as the lectotype centrum.

Posterior cervical vertebrae. Three centra are known from the posterior part of the neck. All three centra have a characteristic large rounded boss in the centre of their articular surfaces, and compared with the anterior cervical vertebrae the first two specimens show a marked reduction of the inferior rib facets, as can be seen from the following measurements (in mm.).

	Superior facet		*Inferior facet*	
	Width	*Height*	*Width*	*Height*
J. 35990*R* . .	50	43	45	29
J. 35990*D* . .	59	56	40	24

The length of the three vertebrae is proportionately greater than that of the anterior cervicals, being half or just over half the width (or height) as indicated below (in mm.).

. .	*Length*	*Width*	*Height*
J. 35990*R* (text-fig. 2*c*, Pl. 8, fig. 4) .	75	150	150
J. 35990*D*	81	155	153
J. 35990*C* (text-fig. 2*d*) . . .	84	168	145

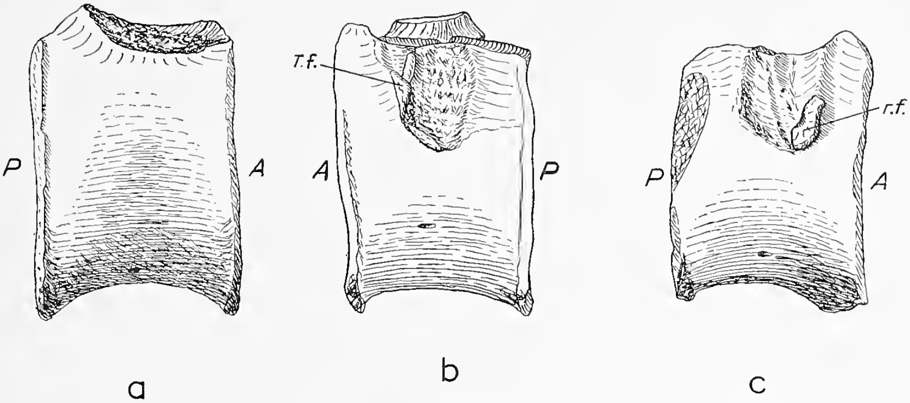
The third cervical vertebra is from the most posterior part of the neck and by the time it is reached the inferior rib facet has completely disappeared and only a single facet remains, which is borne on a pedicle situated on the upper half of the lateral surface of the centrum. A sharp ridge is developed between the dorsal edge of this pedicle and the base of the neural arch, the suture line of which extends laterally towards the rib facet.

Pectoral vertebrae. In the Stretham skeleton only one pectoral vertebra is known (J. 35990*E*, text-fig. 2*e*), measuring: length 91 mm., width 170 mm., height 150 mm. This centrum is very similar to that of the third posterior cervical vertebra just considered. The single rib facet is borne on a pedicle, but the suture line of the neural arch in this specimen extends laterally along the pedicle to reach the articular surface of the facet, the lower half only of which is present on the centrum. The upper half of the rib facet must have been borne on the neural arch, and thus this vertebra represents a stage where the rib articulates equally with the centrum and the neural arch.

Dorsal vertebrae. So far, seven dorsal centra belonging to the Stretham animal have been found. Their measurements (in mm.) are:

	Length	*Width*	*Height*
J. 35990*S* . . .	100	142	149
J. 35990*T* . . .	107	156	157
J. 35990*U* . . .	104	158	162
J. 35990*K* (text-fig. 3*a*) .	112	150	178
J. 35990*J* . . .	117	150	179
J. 35990*V* . . .	121	143	187
J. 35990*W* . . .	114	171	184

The isolated neural arch of a dorsal vertebra is also known (J. 35990*ww*). Unfortunately the dorsal vertebrae of Pliosaurs exhibit no diagnostic characters, and they can thus only be identified when found in association with other parts of the skeleton. Previously all large-sized dorsal vertebrae were considered to belong to *P. macromerus*, but with the knowledge of the existence of two different giant Pliosaurs in Kimeridgian times, the identification of isolated dorsal vertebrae becomes impossible.



TEXT-FIG. 3. *Stretosaurus macromerus*, vertebral centra in lateral view. *a*, Right side, dorsal centrum J. 35990*K*. *b*, Left side, caudal centrum J. 35990*F*. *c*, Right side, caudal centrum J. 35990*G*. × ⅛. *A*, anterior; *P*, posterior; *r.f.*, rib facet.

Caudal vertebrae. Four caudal centra are known from the Stretham skeleton, and unlike those of other Pliosaurs they do not have chevron bone facets on their ventral surfaces. Normally only the two sacral vertebrae are without chevron bone facets; their absence in the caudal vertebrae is most unusual and it is difficult to find an explanation of this fact.

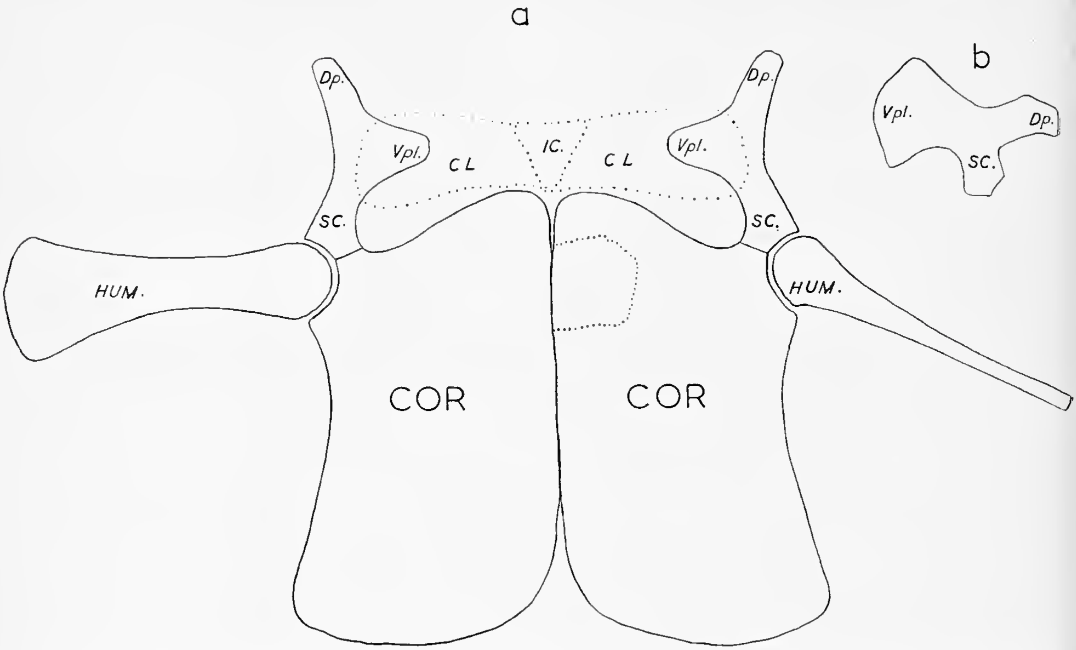
The measurements in mm. of the caudal vertebrae are as follows:

	Length	*Width*	*Height*
J. 35990*H*	106	149	146
J. 35990*I*	102	135	143
J. 35990*G* (text-fig. 3*c*) .	99	145	150
J. 35990*F* (text-fig. 3*b*) .	106	144	146

The caudal ribs are single headed, but the rib facets in these specimens have been somewhat crushed.

In the University Museum, Oxford, there is a series of caudal vertebrae from Cumnor, Berkshire, labelled *P. macromerus* in Phillips's handwriting; these belong to a giant Pliosaur, and as none of them have chevron bone facets developed on their posterior or anterior ventral margins I would include them in *S. macromerus*. However, the caudal vertebra from St. Giles', Oxford, which Phillips figured (1871, p. 356, fig. 151) cannot be included in *S. macromerus* as it bears four well-marked chevron bone facets, but it can be included in *Pliosaurus brachydeirus* Owen which has similar caudal vertebrae.

PECTORAL GIRDLE AND FORELIMB. The scapula is unusual since its dorsal process is produced anteriorly instead of laterally, and the ventral plate is not expanded towards the mid-line. The anterior part of the girdle thus appears extremely weak, but as the symphysial portion of the coracoids is greatly thickened and any appreciable movement of the forelimbs demands a strong pectoral girdle, it appears necessary to postulate the presence of a clavicular arch.



TEXT-FIG. 4. *a*, *Stretosaurus macromerus*. Reconstruction of pectoral girdle and humeri, $\times\frac{1}{20}$. Dorsal view, symphysial portion of right coracoid (J. 35990*X*) indicated, right humerus in posterior view. *b*, Scapula of *Pliosaurus brachydeirus* (B.M. (N.H.) R. 287) for comparison, dorsal view, $\times\frac{1}{20}$. *CL*, Clavicle; *COR*, Coracoid; *Dp.*, Dorsal process of scapula; *HUM.*, Humerus; *IC.*, Interclavicle; *SC.*, Scapula; *Vpl.*, Ventral plate of scapula. Dotted lines indicate possible position of clavicular arch.

Scapula. The scapula has been the subject of an earlier paper (Tarlo 1958*b*). Briefly it can be described as a triradiate bone in which the whole surface is in one plane, no part being set off at an angle. The glenoid ramus is thickened and elongated, the ventral plate is not greatly expanded, and the dorsal process is produced anteriorly and does not project laterally. By the anterior production of the dorsal process of the scapula, the preglenoid length of the whole pectoral girdle is greatly increased.

A pectoral girdle containing the type of scapula described above is so different from that of any previously known Pliosaur that it clearly warrants at least generic distinction from *Pliosaurus*.

Coracoid. Unfortunately the coracoids among other bones, were broken up and pieces were removed from the site despite the efforts of the employees of the River Board to keep the skeleton intact. The actual outline of the coracoids will thus never be known with any certainty, but an attempt at reconstruction based on the photographs of the skeleton *in situ* is given in text-fig. 4.

The symphysial portion of the right coracoid is preserved. The symphysial surface itself is roughly semicircular in outline with a diameter of 225 mm. and a radius of 110 mm. Towards the glenoid cavity the bone thins out a little so that 200 mm. from the symphysis it is only 75 mm. thick. Apart from this thickened area between the glenoid cavity and the symphysis the coracoid is a very thin sheet of bone, being in parts no more than 5–10 mm. thick.

As Watson (1924) pointed out, the muscles moving the forelimbs of a Pliosaur tend to force the heads of the humeri into the glenoid cavities, thus adding to the compression of the coracoids between the cavities. Consequently, to resist this force a marked thickening of the coracoids in this region is required. The symphysial portion of these bones is generally quite thick in Upper Jurassic Pliosaurs, but the transverse section of the Stretham symphysis, with its semicircular outline, shows a proportionately greater degree of thickening. In such a large animal as the Stretham Pliosaur the compression between the glenoid cavities must have been considerable, thus explaining the need for such a strong symphysial region.

Forelimb. The complete humerus is visible in the photograph of the skeleton *in situ* (Pl. 7, fig. 2) and although it too was broken into pieces, most of these have now been collected. The head of the bone is remarkably large compared with its narrow shaft. In this it differs from the femur which, as is shown in the following table, has more normal proportions.

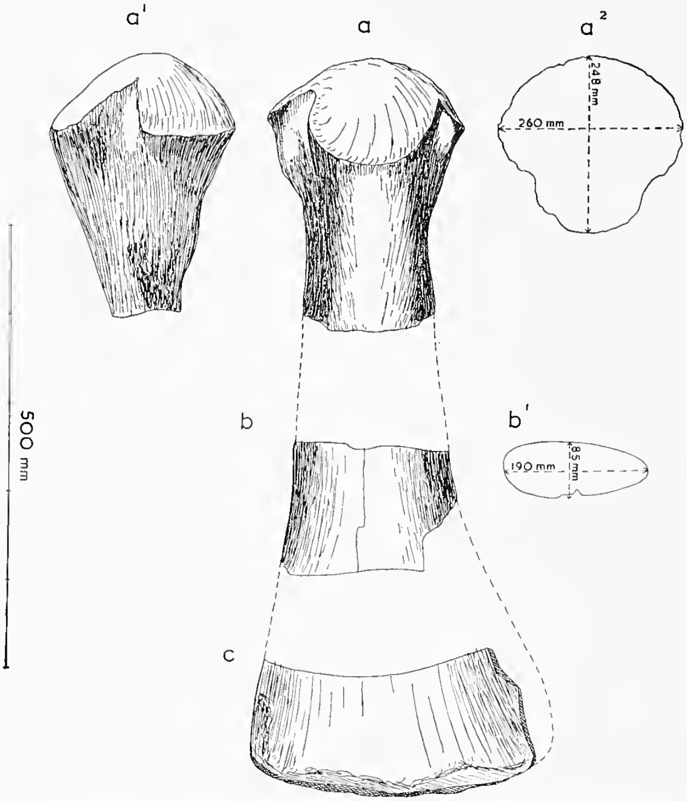
	Humerus (text-fig. 5)		*Femur (Pl. 9, fig. 1)*	
	Width mm.	*Height (thickness) mm.*	*Width mm.*	*Height (thickness) mm.*
Head	260	248	260	190
One-third-way down shaft . .	188	124	185	166
Half-way down shaft . . .	190	85	191	128
Distal end	308+	70	360	110
Total length	840 mm.		960 mm.	

The head of the humerus is more massive than that of the femur although the humerus is as a whole a smaller bone with a very slender shaft. The articular surface of its head is divided into two facets—a small dorsal facet and a large ventral one. The shaft which is expanded distally is greatly compressed dorso-ventrally.

The only other part of the forelimb that is known is the radius which is short. According to Welles (1943) short epipodials are characteristic of the Cretaceous Polycotylids and can be used to separate them from the Jurassic Pliosaurids. However, the change from long to short epipodials took place within Jurassic times, all epipodials of Oxfordian age being long and all those of Kimeridgian age, short. The length of the epipodials can therefore no longer be used as a family distinction.

Clavicular arch. An examination of the way in which the forelimb could function with the type of pectoral girdle described above, raises certain problems. In the giant *Kronosaurus* the ventral plates of the scapulae are greatly expanded and even if they did not actually meet in the mid-line there would be little difficulty in effecting some connexion which would bind them firmly together. In *Stretosaurus*, on the other hand, the ventral plates are not expanded and they could in no circumstances have met in the mid-line.

Any forward or vertical movement of the forelimb would have tended to pull the scapulae away from the mid-line, and it is therefore necessary to postulate some way in which this could have been prevented.



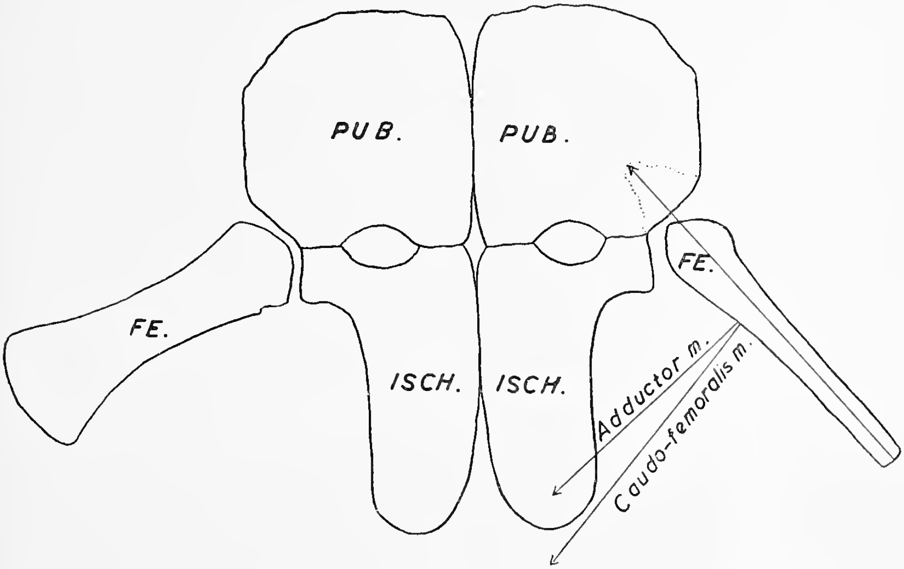
TEXT-FIG. 5. *Stretosaurus macromerus*, left humerus. a–a^2, Head J. 35990*Y*; *a*, dorsal view; a^1, lateral view; a^2, transverse section. b–b^1, Mid-part of shaft J. 35990*Z*; *b*, dorsal view; b^1, transverse section; *c*, Distal end J. 35990*AA*, dorsal view. $\times \frac{1}{9}$.

There is no evidence of cartilage having been present on the medial edge of the ventral plates of the scapulae, thus it would appear that no cartilaginous union of the two bones existed. What seems likely is that a clavicular arch was present to unite the two scapulae, and I shall now review the evidence for this conjecture.

In *Sthenarosaurus dawkinsi* Watson from the Upper Lias there is a triangular interclavicle in the mid-line, which is firmly attached by suture to the clavicles on either side of it. In section each clavicle somewhat resembles a boomerang, one arm of which points dorsally and covers most of the dorsal surface of the ventral plate of the scapula on which it lies. In this way, a clavicular arch binds the two scapulae together, rendering the anterior part of the pectoral girdle sufficiently firm to withstand the stresses imposed by movement of the forelimb.

In the other Plesiosaurians in which a clavicular arch is known, the clavicle also lies on the dorsal surface of the ventral plate of the scapula, and the roughening on the dorsal surface of the ventral plate of the Stretham scapula tends to suggest that such a clavicular arch may have been present.

No complete clavicular arch has as yet been found in either Oxfordian or Kimeridgian Pliosaurs, but in *Peloneustes philarchus* (Seeley) R. 2442 in the British Museum (Nat. Hist.) a small triangular interclavicle is known associated with two scapulae. The lateral borders of this interclavicle are crenulated and bevelled, indicating a bone-to-bone junction. The associated scapulae bear evidence of cartilage on their medial edges, and thus it appears most unlikely that they articulated directly with the interclavicle. Indeed the outlines of the interclavicle and the ventral plates of the scapulae are such that no satisfactory junction can be envisaged between them. The scapulae do not extend sufficiently towards the mid-line for the interclavicle to have lain on top of their ventral plates and so to have been the sole element binding them together. It is evident that a further bony element, a clavicle, must have been present on either side to complete the girdle, which in fact is what Andrews (1913) suggested.



TEXT-FIG. 6. *Stretosaurus macromerus*, reconstruction of pelvic girdle and femora, × $\frac{1}{24}$ approx. Dorsal view, acetabular portion of right pubis (J. 35990*DD–EE*) indicated; right femur in posterior view. *FE.*, Femur; *ISCH.*, Ischium; *PUB.*, Pubis. See text for explanation of swimming movement.

It seems reasonable to assume, therefore, that a clavicular arch somewhat similar to that found in *Sthenarosaurus* was present not only in *Peloneustes* but also in the other Upper Jurassic Pliosaurs. Both the roughening of the dorsal surface of the ventral plate of the Stretham scapula in a position where a clavicle would be attached, and the fact that, as Watson pointed out, the anterior part of the girdle must be firmly and rigidly united in the mid-line to overcome the great stress developed in this region, strongly suggest that a similar arch was present in *Stretosaurus*.

PELVIC GIRDLE AND HIND LIMBS. Apart from the acetabular portion of the pubis the pelvic girdle is known only from photographs taken of the skeleton *in situ*. The elongated ischium and the strengthened anterior part of the acetabulum provide good evidence for presuming that the main propulsive stroke was a backward adduction of the hind limbs.

Pubis. An indication of the relative size of the pubis is given in the photograph (Pl. 7, fig. 2) and as can be seen, this bone is broken into numerous fragments. I have attempted a diagrammatic reconstruction of it in text-fig. 6, but this can only give a very rough approximation of the outline of the actual bone. The acetabular portion, however, has been preserved and the shape of this fragment is indicated in the text-figure. The bone is a thin sheet but is thickened in the region of the acetabulum, the articular surface measuring 310 by 97 mm.

The force created by the backward movement of the femur is resolved into one at right angles to the bone, and a thrust along the axis of the bone which forces the head of the femur into the anterior part of the acetabulum. The strengthening of this region of the pubis is clearly due to the necessity to resist this thrust.

Ischium. The ischium is known only from photographs (Pl. 7, fig. 1, 1*b*). Unfortunately no fragment of this bone has been saved, but its relative size and outline can be ascertained (text-fig. 6).

As in other Upper Jurassic Pliosaurs, the ischium is greatly elongated posteriorly, giving the adductor muscles an increased area of attachment and a more posterior situation. This greatly increases their power, and as together with the caudo-femoralis

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EXPLANATION OF PLATE 7

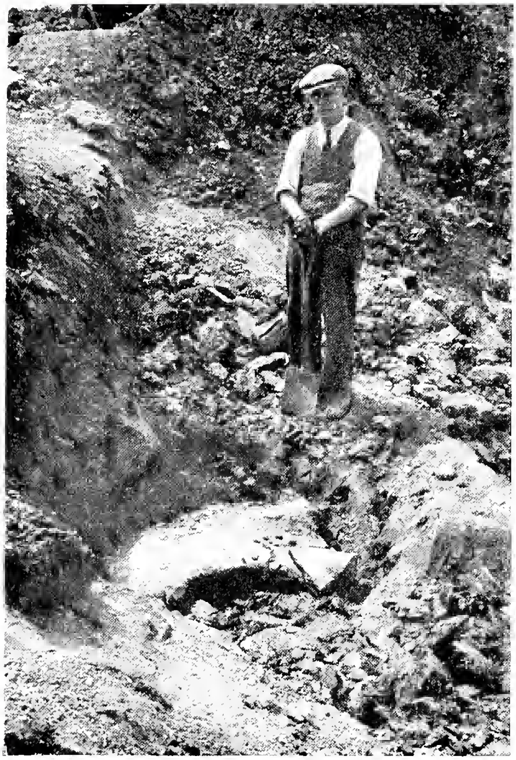
Figs. 1–2. *Stretosaurus macromerus* (Phillips), parts of Stretham Pliosaur *in situ*. 1, 1*a*, Left ischium, photographed by Mr. W. Martin Lane of Ely, scale in fig. 1 given by Mr. W. W. Wolfe. 2, Vertical view of post-cranial skeleton photographed by Mr. W. B. Harland, scale given by spades. *Cor.*, coracoid; *Fe.*, femur; *Hum.*, humerus; *Sc.*, scapula; *Pub.*, pubis.

EXPLANATION OF PLATE 8

Figs. 1–5. *S. macromerus*, Kimeridge Clay. 1, 1*a*, 1*b*. J. 10441, Univ. Mus., Oxford, anterior cervical centrum, lectotype, Shotover railway, Oxfordshire. 1, Anterior view; 1*a*, ventral view; 1*b*, posterior view (apparent shadow in figs. 1, 1*b*, due to discoloration). 2–5, J. 35990, Sedgk. Mus., Cambridge, cervical centra, Stretham, near Ely, Cambridgeshire. 2, 2*a*, Anterior cervical centrum, J. 35990*zz*; 2, anterior view; 2*a*, posterior view. 3, 3*a*, Anterior cervical centrum, J. 35990*xx*; 3, posterior view (lighting from bottom right); 3*a*, ventral view. 4, Posterior cervical centrum, J. 35990*R*, anterior view. 5, Anterior cervical centrum, J. 35990*yy*, anterior view. Photographs by Mr. W. Brackenbury.

EXPLANATION OF PLATE 9

Figs. 1–4. *S. macromerus*, Kimeridge Clay. 1–3, J. 35990, Sedgk. Mus., Cambridge, from Stretham, near Ely. 1, left hind limb, J. 35990*a–z*, *aa–dd*, dorsal view, photographed by Mr. A. Barlow. 2, fragment of mandible showing unerupted successional tooth, J. 35990*P*, internal view. 3, 3*a*, 3*b*, tooth, J. 35990*O*; 3, internal view; 3*a*, lateral view; 3*b*, external view. Figs. 2–3 photographed by Mr. W. Brackenbury. 4. J. 10454, Univ. Mus., Oxford, from Cumnor, Berkshire, symphysis of mandible in dorsal view, photographed by Mr. A. Veenstra.



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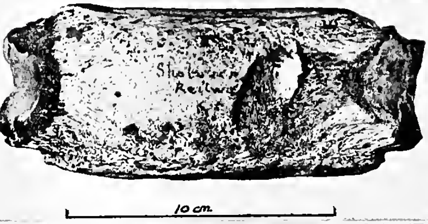
1*a*

2

TARLO, *Stretosaurus macromerus* (Phillips), *in situ*

1



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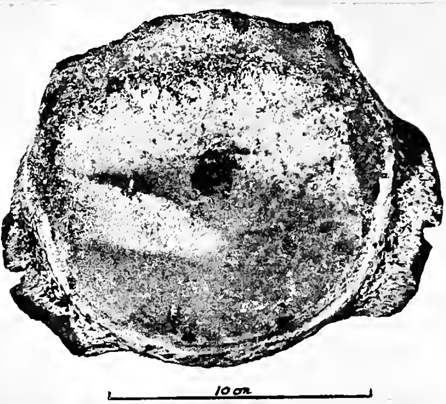

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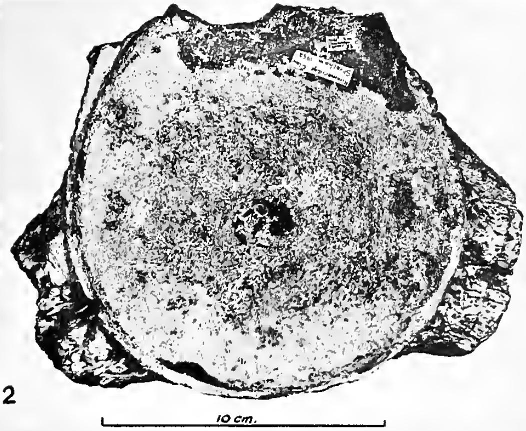

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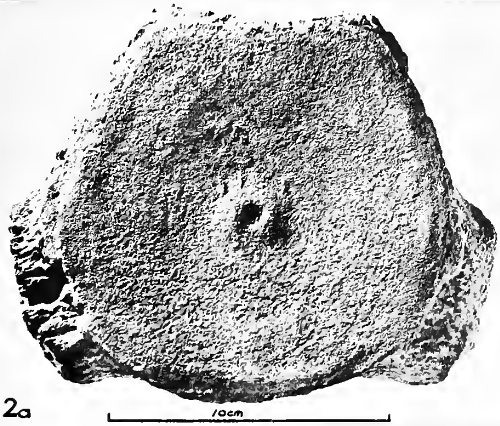
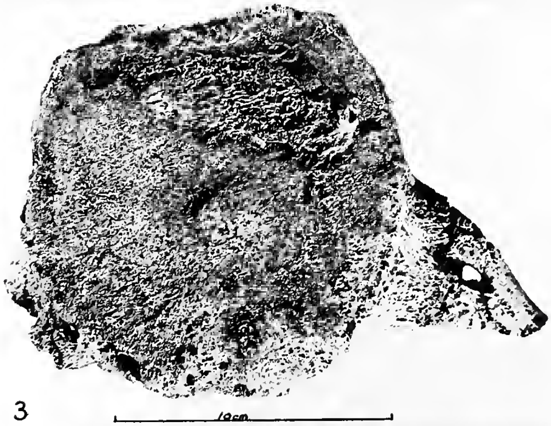
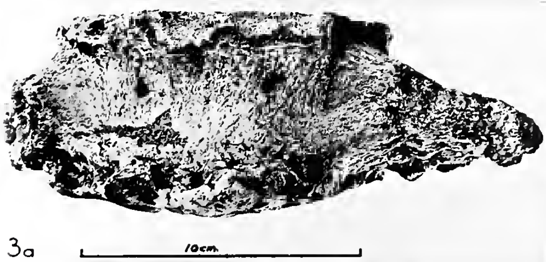


2a

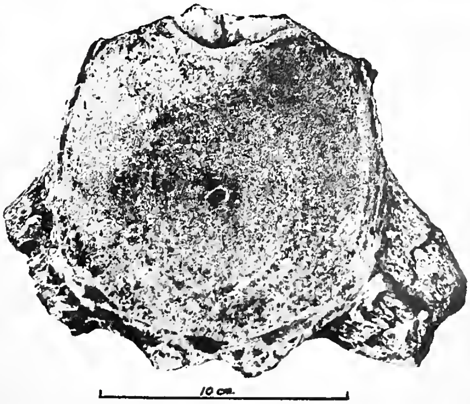


3



3a

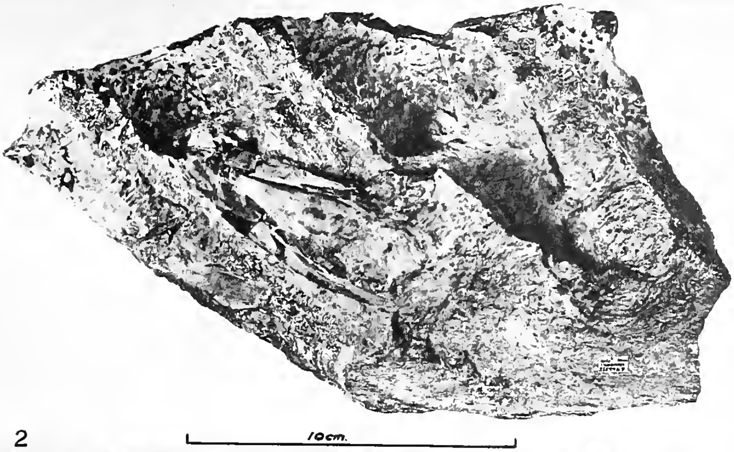
4



5

TARLO, *Stretosaurus*

1

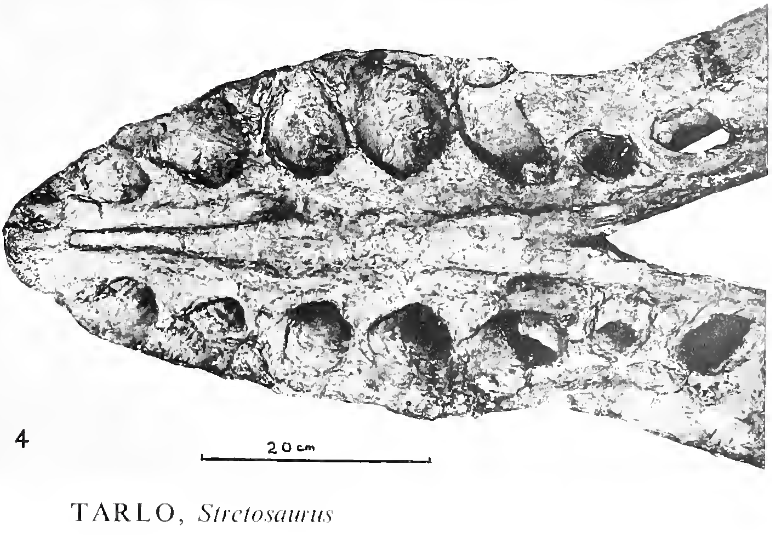


2

3

3a

3b



4

TARLO, *Stretosaurus*

muscles they draw the hind limbs backwards and in towards the body, a very strong propulsive force is produced which drives the animal forward.

Hind Limb. The articulated left hind limb is about 2,000 mm. in length and the femur alone measures 960 mm. Further measurements of the femur are given on p. 47 above where its proportions are contrasted with those of the humerus. The articular surface of the head of the femur is divided into two sub-equal facets—one dorsal and one ventral facet, the dorsal being slightly smaller than the ventral. The shaft and expanded distal end are dorso-ventrally compressed and as the origin of the adductor muscles is in the centre of the proximal half of the ventral surface, these muscles will pull the limb backwards into the body so that the maximum surface is presented to the water. The epipodials are both short, and the tarsals and metatarsals are all well preserved, their shapes being clearly indicated in Pl. 9, fig. 1. The intermedium is of some interest as it shows a pathological condition.

Swimming movement. The hind limbs are larger than the forelimbs and the femora are more stoutly constructed than the humeri. As Romer (1956) remarked, this suggests that the main propulsive force was from the hind limbs. The strengthening of the anterior part of the acetabulum, the elongation of the ischium, and the area of origin of the adductor muscles on the femur all indicate that the propulsive force was from the backward adduction of the hind limb.

This stroke would seem to have been initiated from a position in which the limb was directed postero-laterally with the plane of the limb held vertically (see text-fig. 6). In this position the insertions of the adductor and caudo-femoralis muscles on the femur would be almost at right angles to the shaft, and thus their mechanical efficiency would be at its maximum. Besides this, the force into the acetabulum would be directed to the thickened part of the pubis.

Description of mandible from Cumnor

In the centre aisle of the University Museum, Oxford, there is on exhibition a giant mandible (J. 10454) belonging to a Pliosaur from the Kimeridge Clay of Cumnor, Berkshire. It was first noted by Prestwich (1888, p. 227) and seems to have been acquired by the Museum some time between 1880 and 1888. In 1933 Mr. H. J. Hambidge completed the long and arduous task of renovating and reconstructing this specimen which he had first known in 1907. Professor W. J. Sollas had intended to describe the mandible in 1936, but unfortunately he died the same year. Since that time, this remarkable mandible has remained unidentified and undescribed and no recognition has been given to the skilful work of Mr. Hambidge. The following is an attempt to remedy this.

The length of the mandible as exhibited is 2,875 mm. Recently, however, the posterior part of the left ramus has come to light and it clearly shows that, with the angular and surangular bones restored, the total length would have been more than 3,000 mm. Without doubt it belongs to the largest Pliosaur ever recorded, somewhat exceeding the size of the Cretaceous *Kronosaurus* (White 1935; Romer and Lewis 1959).

The specimen is somewhat incomplete since the splenial bones are missing. In the region of the coronoids the rami are very deep and thin, but this is probably a post mortem effect due to lateral crushing. On the left side twenty-five alveoli are present in the dentary, while in the right ramus only twenty are preserved, the additional alveoli having been reconstructed. The small size of the 24th alveolus suggests that there were few teeth beyond it.

The symphysis is short, containing only six teeth on each side, its length being 470 mm. and its maximum width (at the 5th socket) 280 mm. The teeth in the expanded symphysial region were large and caniniform although the first pair were comparatively small. There is a sudden change in size from the 6th to the 7th sockets and thereafter the alveoli gradually diminish in size as is indicated by the following measurements:

Right dentary	*alveolus*	*diam.* (*mm.*)
(Pl. 9, fig. 4) .	1st	33
	5th	75
	7th	35
Left dentary .	24th	25

The expansion of the symphysial region is due to the presence of very large anterior teeth, for example the width of the right ramus at the 5th alveolus is 145 mm. whereas farther back (at the 10th socket) the ramus is only 75 mm. wide.

In the number of teeth and the short symphysis with its six alveoli, this specimen resembles that of the mandible B.M. (N.H.) 39362 described by Owen (1869), and as I have already shown (1959) in the discussion of *Pliosaurus brachyspondylus*, it seems reasonable to assign this type of mandible from the Kimeridge Clay to *Stretosaurus macromerus*. In the Oxfordian, the same type of mandible is also found in *P. ferox* and as previously mentioned (Tarlo 1958*a*) it seems probable that *S. macromerus* represents a continuation of the *ferox* lineage into Kimeridgian times, but with a highly specialized pectoral girdle.

DISCUSSION

Three Pliosaur skeletons of any importance are known from the Kimeridge Clay. These are the holotype of *Pliosaurus brachydeirus* Owen and the associated skeletons of *P. brachyspondylus* (Owen) and *Stretosaurus macromerus* (Phillips).

Teeth, propodials, and epipodials are known, but these have no distinguishing features. All the teeth are trihedral in cross-section; all the epipodials are short, and such differences as are present in the propodials may well be due to the relative age (and consequently size) of the individual (see Tarlo 1958*a*).

In *P. brachydeirus* the vertebral column and mandible are associated; in *S. macromerus* the scapula is known in association with the vertebral column, but *P. brachyspondylus* has both mandible and scapula associated with the axial skeleton (Tarlo 1959).

Whereas mandibles and scapulae can be used to distinguish the genera, the anterior cervical vertebrae arc the only skeletal elements which are of use when comparing species. These can readily be distinguished on the characters of the ventral surface of the centra, for in *P. brachydeirus* a ventral keel is present, while in *S. macromerus* such a keel is absent. (N.B. the anterior cervical vertebrae of *P. brachyspondylus* are also without a keel, but these are easily distinguished since they possess a characteristic rugosity on the anterior and posterior margins of their ventral surface.)

All the anterior cervical vertebrae of giant size that are known from the Kimeridge Clay fall into two groups on the character of the keel. This suggests that two giant

Pliosaur species must have inhabited the Kimeridgian seas. However, it would be unwise to base such a conclusion on the evidence of cervical vertebrae alone.

Fortunately, further evidence is available from the caudal region, as here the two species can again be recognized on the character of the ventral surface of the centra. In *P. brachydeirus* chevron bone facets are present, while in *S. macromerus* these are absent. Again, there are isolated giant-sized caudal vertebrae known of both types.

Although no mandible is known from the Stretham skeleton and no scapula from *P. brachydeirus* and thus no direct comparison can be made between the two animals in these respects, the associated skeleton of *P. brachyspondylus* has shown that the isolated scapula of a giant Kimeridgian Pliosaur (R. 287) housed in the British Museum (Nat. Hist.) (text-fig. 4*b*) can be placed in the genus *Pliosaurus*. This isolated scapula is expanded medially into a broad flat ventral plate, and its dorsal process projects laterally. It thus differs greatly from the scapula of *Stretosaurus* in which the ventral plate is not greatly expanded and the dorsal process is produced anteriorly. In the present state of knowledge it seems reasonable to assign the isolated scapula R. 287 to a giant individual of *P. brachydeirus*.

Two isolated giant mandibles (39362 in the British Museum (Nat. Hist.) described by Owen (1869), and J. 10454 in the University Museum, Oxford) are known from the Kimeridge Clay. They are both very different from the mandible of *P. brachydeirus*, these mandibles having a short symphysis containing five to six large caniniform teeth in contrast to the symphysis of *P. brachydeirus* which bears ten to twelve teeth, the anterior five to six only being large and caniniform. These two forms of mandible are present in both Oxfordian and Kimeridgian times, and on this basis two possible phylogenetic lineages have been suggested (Tarlo 1958*a*). For the purpose of the present study, however, it is sufficient to establish the existence of giant mandibles different from those of *P. brachydeirus* and I therefore suggest that the two mandibles 39362 and J. 10454 be assigned to *S. macromerus*.

The remains of giant Pliosaurs from the Kimeridge Clay thus clearly fall into two groups which can be recognized on the characters of the mandibles, scapulae, and vertebral columns. Previously all giant-sized Pliosaur remains were included in *P. macromerus* on the basis of size alone but this procedure is now shown to be incorrect, since a detailed examination of these remains has demonstrated the existence of two different Pliosaur genera represented by the species *P. brachydeirus* and *S. macromerus*.

Acknowledgements. I should like to thank Professor D. M. S. Watson and Dr. W. E. Swinton for their helpful criticism of the manuscript, and Dr. P. L. Robinson for valuable discussions. I am pleased to record the generous assistance I have received from Mr. A. G. Brighton and Dr. C. L. Forbes of the Sedgwick Museum, Cambridge; Mr. J. M. Edmonds and Mr. H. J. Hambidge of the University Museum, Oxford; and Dr. W. E. Swinton and Mr. B. H. Newman of the British Museum (Natural History). I should also like to thank Professor A. S. Romer for allowing me a preview of the forthcoming paper on *Kronosaurus*. My thanks are due to the D.S.I.R., as the work embodied in this paper was carried out during the tenure of a Research Studentship.

APPENDIX 1

Dispersed Parts of the Stretham Pliosaur (Stretosaurus macromerus) *recovered in 1956*

In 1952, after some of the material from the Stretham skeleton had been collected by the Sedgwick Museum, Cambridge, the Great Ouse River Board allowed local schools and private collectors to have the remainder. However, in 1956 when the importance of this skeleton was realized, a considerable part of this dispersed material was recovered with the aid of the River Board itself and the local press (*Cambridgeshire Times*, 28 April 1956). I should like to record my particular indebtedness to Miss M. A. Arber, Mr. A. A. Blackmore, Mr. W. Chapman, Mr. M. E. Delanoy, and Mr. H. R. Halls for their assistance in the search for the missing parts of the Stretham Pliosaur.

The specimens recovered are as follows (names of donors in brackets): J. 35990*R*, posterior cervical centrum (Mr. J. Chapman, Ely); J. 35990*S*, dorsal centrum (Mr. M. E. Wicksteed, Wicken); J. 35990*T*, dorsal centrum (Mr. R. A. Taylor, Soham); J. 35990*U*, dorsal centrum (Dr. B. Tilly, Ely); J. 35990*V*, dorsal centrum (Mr. Blaney, Stretham); J. 35990*W*, dorsal centrum (Mrs. J. M. Shrubbs, Lode); J. 35990*X*, symphysial portion of right coracoid (G.O.R.B., Ely); J. 35990*Y*, head of left humerus (Mr. W. E. Doran, Cambridge); J. 35990*Z*, shaft of humerus (Mr. G. W. Dobson, Witchford); J. 35990*AA*, distal end of humerus (Miss W. Foy, Cambridge); J. 35990*BB*, radius (Miss E. M. B. Martin, Littleport); J. 35990*CC*, articular portion of girdle bone in four pieces (Mr. M. E. Delanoy, Ely); J. 35990*DD*, acetabular portion of pubis adjoining *EE* (Mr. R. H. Cory, Newmarket); J. 35990*EE*, acetabular portion of pubis adjoining *DD* (Mrs. G. C. Dimock, Wilburton); J. 35990*FF*, head of right femur (Mr. W. A. Stubbings, Cambridge); J. 35990*GG*, right tibia (Mr. A. W. Gothard, Wilburton). Also numerous fragments of phalanges, girdle bones, and ribs from: Mr. D. S. Allan (Driffield), Mr. M. E. Delanoy (Ely), Miss J. Elsdon (Stretham), Mr. A. Hammond (Prickwillow), Mr. A. Murfitt (Stretham), Misses J. and B. Barber (Stretham), Mr. C. Goodge (Stretham), Miss F. Stevens (Stretham), Mrs. F. P. Horne (Ely), and Mr. D. Robinson (Sutton).

APPENDIX 2

Material now assigned to Stretosaurus macromerus (*Phillips*)

University Museum, Oxford. J. 10441, lectotype vertebra, Shotover railway, Oxfordshire, figured Phillips 1871, fig. 148. J. 10442, 10443, anterior cervical vertebrae, Horspath, Oxfordshire, probably associated with lectotype. J. 10454, mandible, Cumnor, Berks., reconstructed by Mr. H. J. Hambidge, described in this paper. J. 10459, immature scapula, Shotover, figured Tarlo 1958*b*, pl. 36, figs. 3, 3*a*. J. 12499, 1–12, twelve caudal vertebrae, Cumnor, labelled '*P. macromerus*' in Phillips's handwriting.

Not J. 10437, 10438, 10439, listed Phillips 1871, p. 354, *a*, *b*, *c*, which are now provisionally referred to *P. brachydeirus* Owen. Not J. 10460, figured Phillips 1871, fig. 151, also now referred to *P. brachydeirus*.

Sedgwick Museum, Cambridge. J. 29560–2, anterior cervical vertebrae, listed Seeley 1869, p. 97 (84e. 1–3). J. 29570, posterior cervical vertebra, Cottenham, Cambs., listed Seeley 1869, p. 97 (84.f.1) and described p. 104 under *P. brachydeirus*. J. 30057, anterior cervical vertebra, Ely, collected 1893. J. 35990, associated skeleton described in the present paper. J. 46911, immature scapula, Ely, collected 1875, figured Tarlo 1958*b*, pl. 36, figs. 2, 2*a*.

British Museum (*Natural History*). 39362, mandible, Kimeridge Bay, figured Owen 1869, pp. 1–2. 46466*a*, (4)6466*a*, 46466?*a*, anterior cervical vertebrae, Foxhangers, near Devizes, listed Lydekker 1889, p. 135. R. 6, anterior cervical vertebra, from drift, Stanton, Bury St. Edmunds, listed Lydekker 1889, p. 135.

Not 24684, listed Lydekker 1889, p. 134, now referred to *P. brachydeirus*.

Manchester Museum. 3174, immature scapula, Coppock's Pit, Shotover. 3175, immature scapula, same locality, figured Tarlo 1958*b*, pl. 36, fig. 4.

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HYSTRICHOSPHERES FROM THE SILURIAN WENLOCK SHALE OF ENGLAND

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ABSTRACT. Hystrichospheres from samples taken at a single locality and horizon in the Wenlock Shale of Wenlock Edge are described. The assemblage includes thirty-three species and varieties of *Baltisphaeridium*, *Micrhystridium*, *Veryhachium*, *Cymatiosphaera*, *Pterospermopsis*, *Pulvinosphaeridium*, *Leiofusa*, *Leiosphaeridia*, and *Tasmanites*, of which fourteen are new. It most closely resembles an assemblage from the Wenlock of the Montagne Noire.

INTRODUCTION

HYSTRICHOSPHERES are small microscopic organisms having a more or less spherical body usually composed of yellow-brown organic matter. The organic substance of which they are composed may be similar to cutin or sporonin, but this is not certain. Usually the body carries spines or branched processes of various sorts. Hystrichospheres resemble desmid spores in shape, and have been so described by Ehrenberg (1838), Bashnagel (1942), and Timofiev (1956). They appear, however, to be exclusively marine, and were thought by Deflandre (1947) and Eisenack (1954*b*) to be members of the marine plankton whose precise affinities were uncertain.

Hystrichospheres have now been described from a considerable number of localities and horizons in the Lower Palaeozoic. The localities, however, are widely scattered and frequently their stratigraphical position is ambiguous. Consequently an assessment of the stratigraphical value of these microfossils requires a systematic study of their vertical distribution to be carried out in a restricted area, preferably where the age of the rock is determined by other fossil evidence. Because of the absence of metamorphism, and the well-documented stratigraphy, the Shropshire region appears to be most suitable for this study. It is also the type area for a number of stratigraphical divisions of the Lower Palaeozoic. A number of horizons have yielded assemblages of hystrichospheres, sometimes in great abundance, but so far only one from the Tremadocian (Downie 1958) has been described.

There will be described in this paper some of the most commonly occurring hystrichospheres in the Wenlock Shale of Wenlock Edge and this will subsequently form the basis of a fuller account of the distribution of the hystrichospheres within the Wenlock Shale. All the forms described here come from the same locality, an exposure in the lane about 70 yards east of Eaton Church, below Wenlock Edge. The horizon lies about 250 feet below the Wenlock Limestone and can be traced continuously into the Middle Coalbrookdale Beds about five miles to the north-east. These beds belong to the zone of *C. lundgrenni* (Pocock *et al.* 1938).

[Palaeontology, Vol. 2, Part 1, 1959, pp. 56–71, pls. 10–12.]

The rocks yielding the hystrichospheres were slightly calcareous greenish-grey mudstones with an irregular fracture. Marine macrofossils were common. Thin sections showed the rocks to be composed of a clay matrix with sporadic mica and calcite grains, together with abundant quartz about 15 μ in diameter and a few grains of pyrite. The content of organic matter, determined by combustion, was only 1·7 per cent. by weight and the only organic matter visible in thin section was small fragments of chitin and a little bituminous matter diffused in the matrix. No hystrichospheres were visible.

Treatment of material. Three rock samples (WS/A, WS/2a, WS/2b) were collected from points a foot or two apart. A few grammes from each were taken separately, crushed to about pea-size, and dissolved in hydrochloric acid. After decanting the liquid the resulting sludge was heated in hydrofluoric acid for about 48 hours. The residue then consisted of a fine-grained black deposit. When this was washed free from acid, drops were mounted in glycerine jelly for examination under the microscope. Rock sample WS/A was broken into four pieces, each of which was treated separately, so that altogether six independent preparations were made from this horizon. They showed no significant differences in the composition of the hystrichosphere assemblages and it is thought that the total assemblage represents fairly accurately what actually occurs in the Wenlock Shale at this locality. The table (p. 69) summarizes the six assemblages.

Two of the preparations (WS/Ac, WS/Ad) were split after treatment with hydrofluoric acid and one part was put in fuming nitric acid for a few minutes. This treatment had a violent effect. All the remaining clay particles and many of the smaller microfossils, notably *Veryhachium tetraëdron*, disappeared from preparation WS/Ac leaving a concentration of large forms like *Baltisphaeridium digitatum* and thick-walled forms like *Cymatiosphaera pavimenta*. The other preparation, WS/Ad, was treated for a slightly longer time and almost everything was destroyed except very thick-walled forms like *Tasmanites* (see table, p. 69).

All the preparations are now in the collections of the Department of Geology, University of Sheffield. Figured and type material will be deposited in the Geological Survey and Museum, London, the registration numbers of which are quoted.

Abundance of hystrichospheres. The number of hystrichospheres present in the preparations shows that they were not particularly abundant in the rock. There were probably between 1,000 and 10,000 in each cubic centimetre. Similar numbers of microplankton have been recorded in marine sediments by Valensi (1953) from Jurassic flints and Downie (1957) from the Kimeridge Clay. Much greater numbers were found in the Shineton Shales (Downie 1958).

Altogether several thousand individuals were examined, but a large number were unidentifiable and are not included in the figures given on the table. Several distinctive types have been omitted because of their rarity.

Previous research. The only hystrichospheres previously recorded from the British Silurian are *Baltisphaeridium polygonale* and *B. digitatum* from the Wenlock Limestone of Dudley (Eisenack 1954*a*). They have, however, been recorded from the Silurian of the Baltic (Eisenack 1954*a*; 1955), Bohemia (Eisenack 1934; 1958*a*), southern France (Deflandre 1945), Brittany (Deunff 1954*a*), and North America (White 1862; Fisher 1953).

SYSTEMATIC DESCRIPTIONS

Order HYSTRICHOSPHAERIDEA Eisenack 1938

Family HYSTRICHOSPHAERIDAE O. Wetzel 1933, emend. Deflandre 1937

Genus BALTISPHAERIDIUM Eisenack 1958*b*

Type species by original designation: *Hystrichosphaeridium longispinosum* (Eisenack), Ordovician, Baltic.

Diagnosis. A genus of hystrichospheres with round or oval body, surface not divided into fields, carrying more or less numerous, well-separated, hollow processes closed at the end. Processes generally similar, may or may not branch.

Baltisphaeridium longispinosum (Eisenack)

Plate 10, figs. 1, 2, 6

Ovum hispidum longispinosum Eisenack 1931, pl. 5, figs. 6–17.
Hystrichosphaeridium longispinosum Eisenack 1938, pl. 1, figs. 1–9.
Hystrichosphaeridium longispinosum Eisenack 1951, pl. 1, figs. 1–6.

Diagnosis. A species of *Baltisphaeridium* with a more or less spherical test, processes longer than the radius, less than about twenty-five in number.

Occurrence. Shineton Shales, Shropshire (Downie 1958); Ordovician, Baltic regions (Eisenack 1931; 1938; 1951); Ordovician, Rheinischer Schiefer Gebirge (Eisenack 1939); Ordovician, Bohemia (Eisenack 1948); Caradocian, Wales (Lewis 1940); Middle Silurian, Niagara, U.S.A. (Fisher 1953).

Remarks. In redescribing this species Eisenack (1951) emphasized the variation in the size and shape of the processes. Only two of the forms he illustrated appear in the Wenlock Shale. One, comprising about two-thirds of the number present, measures about 30 μ in diameter, with a matt yellow test surface and broad processes often constricted at their base (Pl. 10, figs. 1, 2). It resembles a form illustrated by Eisenack (1951, pl. 1, fig. 6). The second type present is smaller, diameter about 20 μ, the test surface is smooth yellow-green and the processes narrow and cylindrical. It resembles the holotype but is smaller.

Apart from Fisher (1953) this is the only record of *B. longispinosum* from the Silurian. The forms illustrated by Fisher resemble the variety more common in the Wenlock Shale. Eisenack (1939) considered this species to be characteristic of the Ordovician but it is clear that some varieties at least range into the Upper Silurian.

Baltisphaeridium brevispinosum (Eisenack)

Ovum hispidum brevispinosum Eisenack 1931, pl. 5, figs. 3–5.

Diagnosis. A species of *Baltisphaeridium* with a more or less spherical test, processes shorter than the radius, less than about twenty-five in number (in optical section), merging with test at their bases, distal ends rounded.

Baltisphaeridium brevispinosum var. *nanum* Deflandre

Plate 10, fig. 9

Diagnosis. A small variety of *B. brevispinosum*, diameter about 25 μ, processes relatively few, less than twenty in optical section.

Occurrence. Wenlock, France (Deflandre 1945); Middle Devonian, Brittany (Deunff 1954*b*).

Baltisphaeridiun brevispinosum var. *wenlockensis* nov.

Plate 10, fig. 4

Holotype. Mik(P)27001.

Diagnosis. A small variety of *H. brevispinosum*, diameter about 25 μ, processes relatively numerous, about twenty-five in optical section.

Description. The diameter ranged from 16 to 32 μ, the mode being 24 μ. The number of processes ranged from sixteen to thirty-six, the mode being twenty-four, and their length ranged from 20 to 80 per cent. of the test diameter, most of them being shorter than the radius.

Remarks. This variety is distinguished from the typical form by its smaller size and from *H. brevispinosum* var. *nanum* by the greater number of processes. This is one of the most common forms in this assemblage.

Baltisphaeridium brevispinosum var. *granuliferum* nov.

Plate 10, fig. 5

Holotype. Mik(P)22001.

Diagnosis. A small variety of *B. brevispinosum* with relatively numerous processes, the test surface ornamented with small granules 1 μ apart.

Remarks. This variety resembles *B. brevispinosum* var. *wenlockensis* except for its granular surface. It is less common, only eight specimens being found.

Baltisphaeridium ramusculosum (Deflandre)

Plate 11, fig. 13

Hystrichosphaeridium ramusculosum Deflandre 1942, figs. 2–6.
Hystrichosphaeridium ramusculosum Deflandre 1945, pl. 1, figs. 8–16.

Diagnosis. A species of *Baltisphaeridium* with rounded test, processes usually 50 to 100 per cent. of test diameter, test diameter about 20 μ or less, processes branch distally, irregularly, small branches also on trunk of processes. Some processes may be simple.

Occurrence. Wenlock, France (Deflandre 1945); Middle Devonian, Brittany (Deunff 1954*b*).

Remarks. Specimens from Shropshire measured 11 to 21 μ in diameter, process length being 60 to 90 per cent. of diameter, number of processes in optical section from seven to fourteen.

Baltisphaeridium eoplanktonicum (Eisenack)

Plate 10, fig. 3

Hystrichosphaeridium eoplanktonicum Eisenack 1955, pl. 4, fig. 14.

Diagnosis. A species of *Baltisphaeridium* with rounded test, diameter about 20 μ, a few long processes irregularly branching at the tips.

Occurrence. Upper Ludlow, Estonia.

Remarks. Specimens from Shropshire measured 16 to 25 μ in diameter, the process length varied from 100 to 150 per cent. of the diameter; the number of processes was usually four, but five and six were found. According to Eisenack the species belongs to the *B. longispinosum* group, but it also resembles *B. ramusculosum* from which it is distinguished by the smaller number and greater length of the processes.

Baltisphaeridium microspinosum (Eisenack)

Plate 10, fig. 10

Hystrichosphaeridium microspinosum Eisenack 1954*a*, pl. 1, fig. 8.

Diagnosis. A species of *Baltisphaeridium*, test spherical, diameter about 60 μ, processes closely spaced, spines short 1·5 μ long.

Occurrence. Upper Llandovery, Estonia.

Remarks. The specimens from Shropshire ranged in size from 48 to 80 μ, the processes from 2 to 4 per cent. of the diameter. Eisenack's single specimen had processes 2·5 per cent. of the diameter in length. *H.* cf. *microspinosum* from the Upper Ludlow of Estonia (Eisenack 1955) had processes measuring 5 per cent. of the test diameter, but was otherwise similar to the type.

Baltisphaeridium cf. *meson* (Eisenack)

Plate 10, fig. 8

Hystrichosphaeridium intermedium Eisenack 1954*a*, figs. 3–4, pl. 1, figs. 3, 9.
Hystrichosphaeridium meson Eisenack 1955.

Diagnosis. A species of *Baltisphaeridium* with spherical test, diameter about 60 μ, processes well spaced, forked or simple, spikes at tips.

Occurrence. Upper Llandovery, Estonia.

Remarks. B. meson from the Llandovery is intermediate in form between its contemporaries *B. brevifurcatum* (Eisenack), most processes of which bifurcate, and *B. oligofurcatum* (Eisenack), with only a few branching. The specimens from the Wenlock Shale have a few, but indeterminable number of, bifurcating processes. They resemble *B. meson* but are smaller, with diameter 35 to 42 μ. The number of processes in optical section varied from twenty to forty.

Baltisphaeridium robustispinosum sp. nov.

Plate 10, fig. 7

Holotype. Mik(P)9002.

Diagnosis. A species of *Baltisphaeridium* with more or less spherical test, diameter about 30 μ, processes about 10 μ, stout, 4 μ wide at base, 10 to 15 μ apart, about seven seen at circumference, surface of processes granular, terminated by a short hair, sometimes broken.

Remarks. This species does not closely resemble any other.

Genus MICRHYSTRIDIUM Deflandre 1937

Type species by original designation: *Hystrichosphaera inconspicua* Deflandre, Upper Cretaceous, France.

Diagnosis. A genus of hystrichospheres, more or less spherical, diameter generally less than 20 μ.

Micrhystridium stellatum Deflandre

Plate 11, figs. 11, 14

Micrhystridium stellatum Deflandre 1942, figs. 7–8.
Micrhystridium stellatum Deflandre 1945, pl. 3, figs. 16–19.

Diagnosis. A species of *Micrhystridium*, test tending to be polygonal, spines strong, simple, straight or slightly curving, length greater than radius, few in number, about a dozen. Test diameter 11–16 μ.

Occurrence. Wenlock, France (Deflandre 1945), Middle Devonian, France (Deunff 1954*b*), Bajocian, France (Valensi 1953).

Remarks. Test diameter ranged from 9 to 24 μ, process-length from 60 to 120 per cent. of diameter, processes numbered from five to fourteen in optical section. They conform closely in all respects to the typical Wenlock material. The Devonian forms have more numerous, shorter spines. The rare specimens in the Bajocian may be derived.

Micrhystridium stellatum var. *inflatum* var. nov.

Plate 11, fig. 12

Holotype. Mik(P)14002.

Diagnosis. A variety of *M. stellatum* with a spherical inflated test.

Remarks. Diameter 15 to 16 μ, process-length 110 to 130 per cent. of test diameter, number in optical section six to eight. This form could be confused with small individuals of *B. longispinosum*.

Micrhystridium eatonensis sp. nov.

Plate 11, fig. 15

Holotype. Mik(P)15001.

Diagnosis. A species of *Micrhystridium*, walls 1·5 μ thick, red-brown colour usually. Processes stout, 1·5 μ long, 1 μ apart, tips mostly pointed, a few bifurcate.

Remarks. Diameter varied from 12 to 22 μ. This species resembles *B. microspinosum* Eisenack but is less than half the diameter, the spines also are relatively longer and more widely spaced in *M. eatonensis.*

Genus VERYHACHIUM Deunff 1954*d*

Type species by original designation: *Hystrichosphaeridium trisulcum* Deunff, Upper Ordovician, France.

Diagnosis. A genus of hystrichospheres, test shape determined by the number of processes, globose only when a single process is present; processes few (one to eight), long pointed, often curved; body size 10 to 40 μ usually.

Veryhachium tetraëdron Deunff

Occurrence. Middle Devonian, Canada.

Remarks. Deunff (1954*c*) gives no diagnosis or description of this species. The illustration shows it to be tetrahedral, the body measuring 36 μ across, the processes, four in number, also measure about 36 μ. The test surface appears to be granular.

Veryhachium tetraëdron var. *wenlockium* var. nov.

Plate 12, figs. 9, 11

Holotype. Mik(P)23001. *Paratype.* Mik(P)24001.

Diagnosis. A small variety of *V. tetraëdron,* with a smooth test surface and relatively longer processes.

Description. The size of the test varies from 6 to 27 μ, the shape is always tetrahedral, the walls always smooth, yellow-green in colour. The processes range in length from 100 to nearly 500 per cent. of the test diameter.

Remarks. This is one of the commonest hystrichospheres in the Wenlock Shale. It is consistently smaller than the typical Devonian members of the species.

Veryhachium rhomboidium sp. nov.

Plate 12, fig. 10

Holotype. Mik(P)21001.

Diagnosis. Test rhomboidal, surface smooth, walls moderately thick, test size 16 to 23 μ; processes, four or six, arising at corners of the test, simple spines, length 50 to 100 per cent. of test size.

Remarks. This species resembles *V. minutum* Downie but is larger, thicker walled, and has narrower processes. It does not have the long curving processes of *V. staurateroides* Deflandre or *V. crucistellatum* Deunff, nor the broad conical processes of *V. oligospinosum* (Eisenack). The *Hystrichosphaeridium sp.* figured by Fisher (1953, pl. 7, fig. 11) from the Middle Silurian of New York, could belong to this species, but has rather long processes.

Genus CYMATIOSPHAERA O. Wetzel 1933, emend. Deflandre 1954

Type species by original designation: *Cymatiosphaera radiata* O. Wetzel, Upper Cretaceous, Germany.

Diagnosis. Spherical or ellipsoidal tests of brownish organic matter, surface divided into polygonal fields by membranes perpendicular to test surface, no equatorial girdle, no spines.

Cymatiosphaera octoplana sp. nov.

Plate 11, fig. 2

Holotype. Mik(P)17001.

Diagnosis. A species of *Cymatiosphaera*, lemon-yellow colour, test surface granular, divided into eight rectangular, more or less equal sized, areas by membranes about one-third of the diameter in height, height of membrane varies giving a rectangular outline, test diameter about 30 μ.

Remarks. This species closely resembles *C. cubus* Deunff (1954*c*), with which it is associated. *C. cubus*, however, has only six rectangular fields. The extra partitions are usually easily seen but in certain views separation of the species may be difficult.

Cymatiosphaera pavimenta (Deflandre)

Plate 11, figs. 8, 9

Micrhystridium pavimentum Deflandre 1945, pl. 3, figs. 20, 21.

Diagnosis. Test spherical, diameter 10 to 20 μ, walls thick, colour generally deep red-brown, partitions 20 to 40 per cent. of test diameter in height, polygonal fields 5 to 10 μ across, pillars formed where partitions join, nine to fourteen seen around circumference.

Occurrence. Wenlock, France.

Remarks. Deflandre established the species on the basis of two poorly preserved specimens, and it has not been recorded since. His description has been fully confirmed.

Cymatiosphaera wenlockia sp. nov.

Plate 11, fig. 4

Holotype. Mik(P)7002.

Diagnosis. A species of *Cymatiosphaera*, diameter 18 to 35 μ, walls moderately thick, partitions 15 to 20 per cent. of test diameter, polygonal fields 10 to 20 μ across, number variable, always more than eight.

Remarks. This species resembles *C. canadensis* from the Middle Devonian (Deunff 1954*c*) but is smaller with higher crests and smaller polygonal fields.

Genus PULVINOSPHAERIDIUM Eisenack 1954*a*, emend. Deunff 1954*d*

Type species by original designation: *P. pulvinellum* Eisenack, Llandovery, Baltic.

Diagnosis. Hystrichospheres processes of which are broad off-shoots from the central body, no definite boundary between the two; processes with blunt rounded terminations.

Pulvinosphaeridium oligoprojectum sp. nov.

Plate 10, fig. 12; Plate 12, fig. 12

Holotype. Mik(P)12002. *Paratype.* Mik(P)16001.

Diagnosis. Hollow test, walls thin, yellow-brown, surface matt, five broad hollow rounded processes unite to form the ill-defined body, overall size 150 to 250 μ.

Remarks. This species resembles *P. pulvinellum* in size and general appearance, but *P. pulvinellum* has its four projections in the same plane. The only example of *P. oligoprojectum* in the Wenlock Shale with four projections was tetrahedral. *P. oligoprojectum* strongly resembles the 'bodies of unknown affinity' figured by Eisenack (especially 1951, pl. 3, figs. 15 and 16).

Family PTEROSPERMOPSIDAE Eisenack 1954*b*

Genus PTEROSPERMOPSIS W. Wetzel 1952

Pterospermopsis cf. *onondagaensis* Deunff

Plate 12, fig. 8

Diagnosis. A spherical capsule of organic matter, diameter 12 μ, with equatorial flange of thinner organic matter, flange width 50 to 60 per cent. of capsule diameter.

Occurrence. Middle Devonian, Canada (Deunff 1955).

Remarks. The specimens of *Pterospermopsis* found in the Wenlock Shales had capsules ranging in diameter from 15 to 35 μ, and are therefore a little larger than the Devonian form. The flange is a little narrower, usually being about 40 per cent. of the diameter in width. Deunff does not indicate the range of variation shown by Devonian forms.

Family LEIOFUSIDAE Eisenack 1938

Genus LEIOFUSA Eisenack 1938

Type species by original designation: *Leiofusa fusiformis* (Eisenack), Lower Palaeozoic, Baltic.

Diagnosis. Oval or fusiform, hollow test, membrane smooth.

Leiofusa filifera sp. nov.

Plate 11, figs. 6, 7

Holotype. Mik(P)10001.

Diagnosis. A species of *Leiofusa* with the ends drawn out to form long hollow threads, body about one-third of total length, body width about one-quarter of its length.

Remarks. The overall length varied from 30 to 350 μ, it is possible that the small examples (30 to 90 μ) form a distinct species with a mode about 70 μ, but until a greater number of specimens are available it would be unsafe to separate it. *L. filifera* differs from *L. fusiformis* by having a shorter body, the ratio of body to total length being one-third compared with seven-tenths.

Leiofusa tumida sp. nov.

Plate 11, fig. 5

Holotype. Mik(P)28001.

Diagnosis. A species of *Leiofusa* with long terminal processes and rounded central body, overall length about 110 μ.

Remarks. The central body is much more inflated than in *L. filifera* (ratio of width to length being 0·66 to 0·9), but otherwise the species is similar, each processes being about one-third of the total length.

Family LEIOSPHAERIDAE Eisenack 1954*b*

Genus LEIOSPHAERIDIA Eisenack 1958*a*

Type species by original designation: *Leiosphaeridia baltica* Eisenack, Lower Palaeozoic, Baltic.

Diagnosis. Hollow more or less spherical test, often folded by subsequent compression, walls of waxy, yellow to red-brown organic substance, without visible pores.

Remarks. A very large number of specimens were found, apparently belonging to a number of species. But in a genus with so few variable characters species are not easy to distinguish (Eisenack 1958*a*, p. 4). Only the most important groups are dealt with here.

Leiosphaeridia wenlockia sp. nov.

Plate 12, figs. 2–4

Holotype. Mik(P)13003.

Diagnosis. A species of *Leiosphaeridia*, diameter 20 to 50 μ, distinct mode at 30 μ, walls yellow, 1 μ thick, smooth, waxy.

Remarks. Over 1,000 were observed, but it is uncertain just how many, for it overlaps with other species at the upper and lower ends of its size range. It closely resembles *L. baltica* but is smaller, the genotype measuring 80 to 140 μ. It is also smaller than *L. microcystis* (Eisenack) of the Upper Silurian (57 to 72 μ), but *L.* cf. *microcystis* (Deflandre 1945) from the Wenlock of France may belong to *L. wenlockia*.

Leiosphaeridia cf. *microcystis* (Eisenack)

Plate 12, fig. 1

Diagnosis. A species of *Leiosphaeridia*, diameter about 65 μ, range 57 to 72 μ.

Occurrence. Ordovician and Silurian, Baltic (Eisenack 1938); Upper Silurian, Baltic (Eisenack 1958*a*).

Remarks. A number of specimens of *Leiosphaeridia* were found, ranging in size from 40

EXPLANATION OF PLATE 10

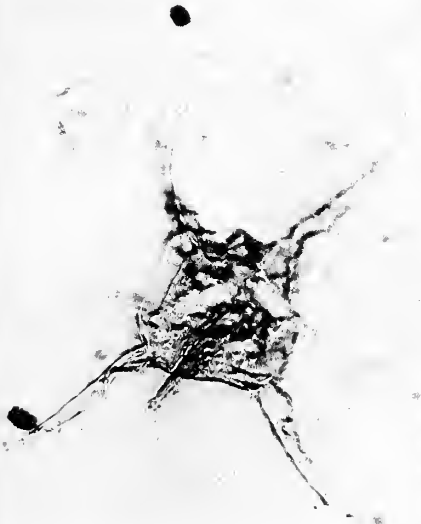
Figs. 1, 2, 6. *Baltisphaeridium longispinosum* (Eisenack). 1, Mik(P)14001, an example of the common form with broad processes. 2, Mik(P)20001, a smaller individual of the same type. 3. Mik(P)29001, a small form with narrow cylindrical processes.
Fig. 3. *Baltisphaeridium eoplanktonicum* (Eisenack), Mik(P)26001.
Fig. 4. *Baltisphaeridium brevispinosum* var. *wenlockensis* nov., Mik(P)27001, holotype.
Fig. 5. *Baltisphaeridium brevispinosum* var. *granuliferum* nov., Mik(P)22001, holotype.
Fig. 7. *Baltisphaeridium robustispinosum* sp. nov., Mik(P)9002, holotype.
Fig. 8. *Baltisphaeridium* cf. *meson* (Eisenack), Mik(P)6002.
Fig. 9. *Baltisphaeridium brevispinosum* var. *nanum* Deflandre, Mik(P)9001.
Fig. 10. *Baltisphaeridium microspinosum* (Eisenack), Mik(P)6001.
Fig. 11. *Veryhachium* cf. *balticum* (Eisenack), Mik(P)19002.
Fig. 12. *Pulvinosphaeridium oligoprojectum* sp. nov., Mik(P)12002, holotype.
All figures are × 500.

EXPLANATION OF PLATE 11

Fig. 1. *Baltisphaeridium digitatum* (Eisenack), Mik(P)12001.
Fig. 2. *Cymatiosphaera octoplana* sp. nov., Mik(P)17001, holotype.
Fig. 3. *Cymatiosphaera cubus* Deunff, Mik(P)26002.
Fig. 4. *Cymatiosphaera wenlockia* sp. nov., Mik(P)7002, holotype.
Fig. 5. *Leiofusa tumida* sp. nov., Mik(P)28001, holotype.
Figs. 6, 7. *Leiofusa filifera*. 6, Mik(P)25001, small specimen. 7, Mik(P)10001, holotype.
Figs. 8, 9. *Cymatiosphaera pavimenta* (Deflandre). 8, Mik(P)13001. 9, Mik(P)13002.
Fig. 10. *Veryhachium bulbiferum* (Deflandre), Mik(P)19001.
Figs. 11, 14. *Micrhystridium stellatum* Deflandre. 11, Mik(P)7001. 14, Mik(P)18001.
Fig. 12. *Micrhystridium stellatum* var. *inflatum* var. nov., Mik(P)14002.
Fig. 13. *Baltisphaeridium ramusculosum* (Deflandre), Mik(P)8001.
Fig. 15. *Micrhystridium eatonensis* sp. nov., Mik(P)15001.
All figures are × 500.

EXPLANATION OF PLATE 12

Fig. 1. *Leiosphaeridia* cf. *microcystis* (Eisenack), Mik(P)14003.
Figs. 2–4. *Leiosphaeridia wenlockia* sp. nov. 2, Mik(P)13003, holotype. 3, Mik(P)14004, specimen with a pylom. 4. Mik(P)5003, specimen with wrinkled surface and pyrite grains within, a common habit.
Fig. 5. *Tasmanites medius* (Eisenack), Mik(P)5002.
Fig. 6. *Tasmanites* cf. *medius* (Eisenack), Mik(P)18002.
Fig. 7. *Veryhachium trispinosum* (Eisenack), Mik(P)11001.
Fig. 8. *Pterospermopsis* cf. *onondagaensis* Deunff, Mik(P)5001.
Figs. 9, 11. *Veryhachium tetraëdron* var. *wenlockium* nov. 9, Mik(P)23001, holotype. 11, Mik(P)24001, paratype.
Fig. 10. *Veryhachium rhomboidium* sp. nov., Mik(P)21001, holotype.
Fig. 12. *Pulvinosphaeridium oligoprojectum* sp. nov., Mik(P)16001, paratype.
All figures are × 500.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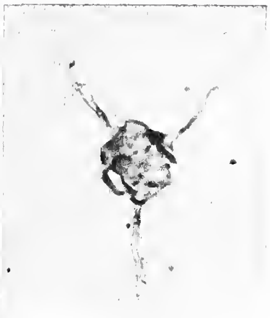
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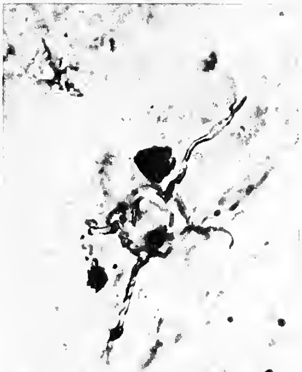
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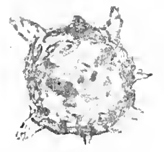
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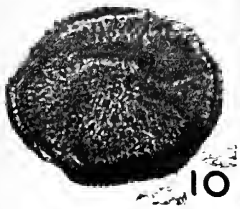
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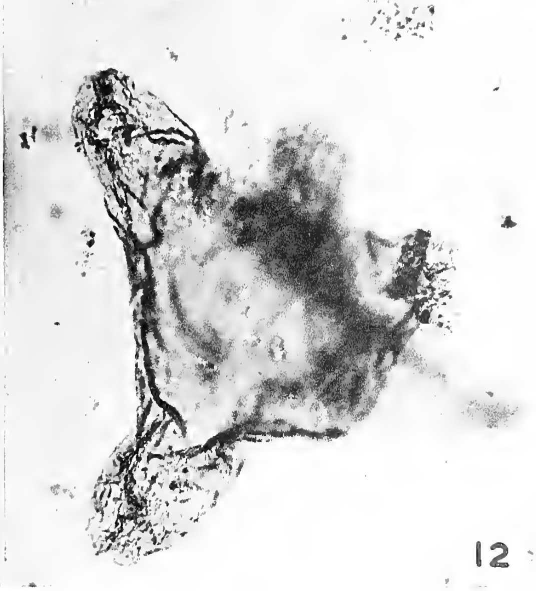
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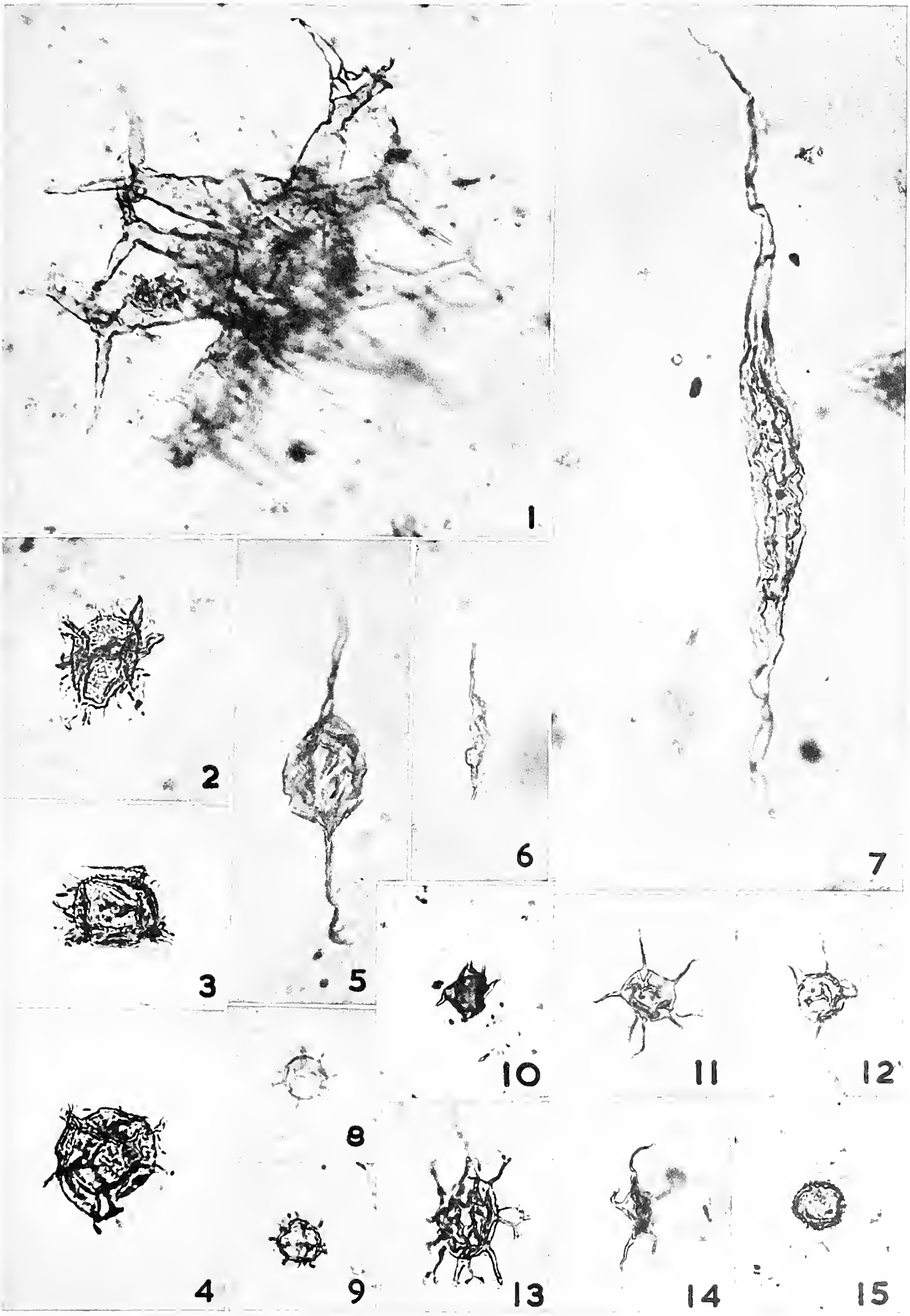
DOWNIE, Silurian Hystrichospheres × 500



DOWNIE, Silurian Hystrichospheres × 500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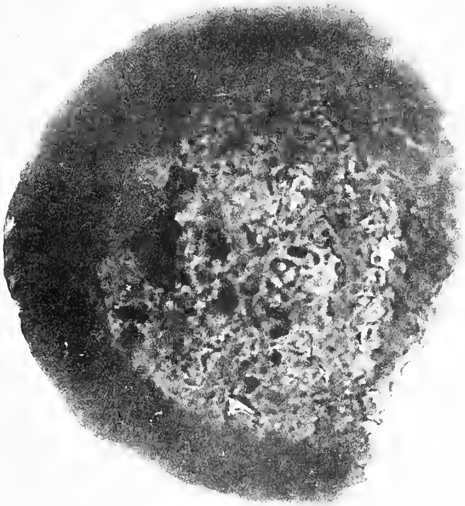
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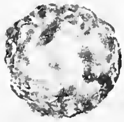
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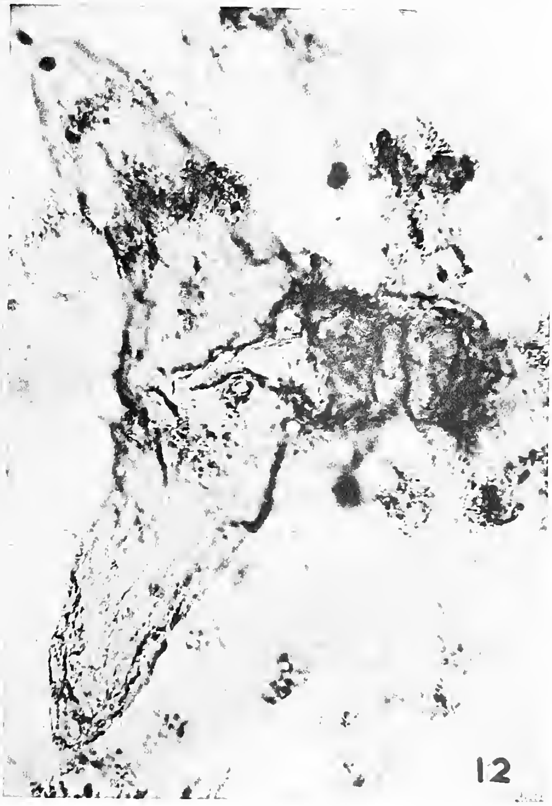
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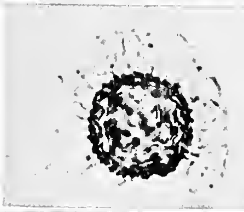
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DOWNIE, Silurian Hystrichospheres × 500

to 60 μ, which were distinguished from *L. wenlockia* by their slightly larger size, thicker (2 to 3 μ) walls and darker yellow or reddish-brown colour. They resemble *L. microcystis* but are slightly smaller in size.

Genus TASMANITES Newton 1875, emend. Eisenack 1958*a*

Type species by original designation: *Tasmanites punctatus* Newton, Permian, Australia.

Diagnosis. Hollow spherical test, wall relatively thick, of yellow to dark-brown colour, radial pores occur but seldom penetrate the whole wall, most often opening outwards.

Tasmanites medius (Eisenack)

Plate 12, fig. 5

Tasmanites medius Eisenack 1958*a*, p. 6.

Diagnosis. A species of *Tasmanites*, diameter a little over 100 μ, wall thickness 25 per cent. of radius, surface smooth, pores occasional, wall not layered, colour yellow to reddish-brown.

Occurrence. Ordovician to Upper Silurian, Baltic (Eisenack 1955).

Remarks. This is the first record from the Wenlock. The diameter ranged from 120 to 150 μ, and the walls from 14 to 16 μ in thickness.

Tasmanites cf. *medius* (Eisenack)

Plate 12, fig. 6

Remarks. Some specimens differed from the typical form of *T. medius* by having a slightly smaller diameter (60 to 100 μ) and relatively thinner walls (6 to 10 μ). No transitional forms have been found and the two groups appear to be quite distinct. The smaller forms have therefore been separated from *T. medius*.

OTHER SPECIES IN THE ASSEMBLAGE

A number of other species were present. Little need be said about them except to record their presence and previously recorded occurrences.

Baltisphaeridium digitatum (Eisenack), Pl. 11, fig. 1, has been recorded from the Wenlock of the Montagne Noire (Deflandre 1945) and the Llandovery and Wenlock of the Baltic by Eisenack (1951) who also noted it in the Wenlock of Dudley.

Micrhystridium imitatum Deflandre has previously been recorded only from the Wenlock of the Montagne Noire by Deflandre (1945).

Micrhystridium parinconspicuum Deflandre has been found in the Wenlock of the Montagne Noire (Deflandre 1945) and in the Middle Silurian of New York State (Fisher 1953). The specimens in the shale from Wenlock Edge appear to have somewhat thinner tests than those figured by Deflandre.

Micrhystridium is also represented by a number of small forms with long processes and thin walls. Since they may be small individuals of *Baltisphaeridium longispinosum* it is not proposed to give them a name here.

Veryhachium bulbiferum (Deflandre), Pl. 11, fig. 10, has previously only been recorded from the Wenlock of the Montagne Noire (Deflandre 1945).

Veryhachium cf. *balticum* (Eisenack), Pl. 10, fig. 11, is a form resembling Eisenack's (1951) species from the Ordovician of the Baltic, but is smaller with thinner walls.

Veryhachium trispinosum (Eisenack), Pl. 12, fig. 7, is found in considerable numbers in this assemblage, ranging in size from 8 to 50 μ, with processes from 50 to 200 per cent. of the test size. Possibly more than one species is represented. *V. trispinosum* has been recorded from the Ordovician of the Baltic (Eisenack 1938), Bohemia (Eisenack 1948), Rheinischer Schiefer Gebirge (Eisenack 1939), the Middle Devonian of Brittany (Deunff 1954*b*), and probably from the Middle Silurian of New York (Fisher 1953, figs. 8, 10; Bashnagel 1942, pl. 1, figs. 6, 7). A similar species, *V. geometricum*, described by Deflandre (1945) from the Wenlock of France, has not been observed.

Cymatiosphaera cubus Deunff, Pl. 11, fig. 3. The only previous record of this species is from the Middle Devonian of Canada (Deunff 1954*c*). The specimens in the Wenlock Shale range in size from 12 to 35 μ, excluding the membranes.

Cymatiosphaera prismatica Deunff has previously only been recorded from the Middle Devonian of Canada (Deunff 1954*c*).

CONCLUSIONS

The examination of about 3,000 hystrichospheres from a restricted horizon in the Wenlock Shales has yielded more than thirty-three different forms. Fourteen of these are new. Of the other forms present, ten have been previously described from the Wenlock. They are: *B. brevispinosum* var. *nanum*, *B. digitatum*, *B. ramusculosum*, *M. stellatum*, *M. imitatum*, *M. parinconspicuum*, *C. pavimenta*, *V. bulbiferum*, *L. microcystis* and *T. medius*. In addition *B. meson* and *B. microspinosum* were previously known only from the Upper Llandovery, and *B. eoplanktonicum* was previously recorded only from the Ludlow.

The remaining forms show links with the Devonian on the one hand and the Ordovician on the other. The species previously known only from the Devonian are *C. cubus*, *C. prismatica*, and *P. onondagaensis*. The Ordovician species are *B. longispinosum* and possibly *V. balticum*. One species, *V. trispinosum*, had been recorded previously from the Ordovician and Devonian, but not from the Wenlock.

The assemblage from Wenlock most closely resembles that described by Deflandre from the Wenlock of the Montagne Noire in south France. Of the fourteen forms noted by Deflandre, nine are found in Shropshire. The Wenlock Shales also have a number of forms in common with Estonia. However, no Wenlock assemblage from there has been described so the closest comparison is with the Upper Llandovery (Eisenack 1954*a*), which has three species in common (excluding leiospheres), and the Ludlow (Eisenack 1955) with three species in common (including leiospheres).

There are even species in common with North America, two from the Middle Devonian of Canada and two from the Middle Silurian of New York.

These observations clearly demonstrate the wide distribution of the hystrichospheres and suggest at the same time that they may have some limited stratigraphical value.

TABLE

DISTRIBUTION OF HYSTRICHOSPHERES IN SIX PREPARATIONS OF WENLOCK SHALE

	Percentage in preparation						
	WS/Aa	*AS/Ab*	*WS/Ac*†	*WS/Ad*	*WS/2a*	*WS/2b*	*Total no.*
HYSTRICHOSPHERES:							
B. longispinosum (Eisenack) . .	8·5	16·7	13·0	6·0	3·0	18·9	49
B. brevispinosum var. *nanum* (Deflandre)	0·4	. .	. .	. .	0·6	. .	2
,, var. *wenlockensis* nov.	11·0	16·7	2·4	12·1	13·6	13·5	66
,, var. *granuliferum* nov.	1·3	. .	. .	2·4	3·6	. .	8
B. ramusculosum (Deflandre) . .	3·4	. .	. .	7·2	1·8	5·4	19
B. eoplanktonicum (Eisenack) . .	3·0	. .	2·4	9·6	1·2	2·7	20
B. microspinosum (Eisenack) . .	2·5	. .	. .	1·2	0·6	. .	8
B. digitatum (Eisenack) . . .	. .	. .	3·5	. .	. .	. .	3
B. meson (Eisenack)	0·8	. .	. .	1·2	. .	2·7	4
B. robustispinosum sp. nov . . .	0·4	. .	. .	. .	0·6	. .	2
M. stellatum Deflandre . . .	11·4	16·7	5·9	9·6	4·3	2·7	49
M. stellatum var. *inflatum* nov. . .	0·4	. .	2·4	2·4	3·6	. .	8
M. parinconspicuum Deflandre . .	3·8	33·2	10·6	. .	7·4	. .	32
M. imitatum Deflandre . . .	0·4	. .	. .	1·2	. .	. .	2
M. eatonensis sp. nov.	. .	. .	14·2	. .	1·2	. .	14
V. bulbiferum (Deflandre) . . .	0·4	. .	. .	1·2	. .	. .	2
V. cf. *balticum* (Eisenack) . . .	. .	. .	. .	1·2	. .	. .	1
V. tetraëdron var. *wenlockium* nov. .	25·4	. .	4·7	19·3	41·3	16·2	144
V. rhomboidium sp.nov. . . .	0·4	. .	. .	2·4	0·6	2·7	5
V. trispinosum (Eisenack) . . .	3·0	. .	. .	3·6	5·5	8·1	22
C. cubus Deunff	2·1	. .	. .	3·6	0·6	. .	9
C. octoplana sp. nov.	2·5	. .	. .	1·2	. .	2·7	8
C. prismatica Deunff	0·4	. .	1·2	. .	0·6	. .	3
C. pavimenta (Deflandre) . . .	0·8	. .	13·0	1·2	. .	. .	14
C. wenlockia sp. nov.	1·3	. .	2·4	1·2	. .	2·7	7
P. oligoprojectum sp. nov. . . .	. .	. .	8·3	1·2	. .	. .	8
Pt. cf. *onondagaensis* Deunff . .	1·2	. .	1·2	. .	1·2	. .	6
L. filifera sp. nov.	4·7	16·7	. .	7·2	3·7	10·8	28
L. tumida sp. nov.	. .	. .	. .	. .	. .	8·1	3
Other identifiable forms (excluding leiospheres)	10·5	. .	14·8	3·8	5·0	2·8	65
TOTAL	*100·0*	*100·0*	*100·0*	*100·0*	*100·0*	*100·0*	*609*
LEIOSPHERES:							
L. wenlockia sp. nov. . . .	62·2	60·9	42·6	68·0	53·3	66·7	1,202
L. cf. *microcystis* (Eisenack) . .	1·2	. .	2·7	3·6	1·4	2·1	37
T. medius (Eisenack)	0·3	. .	. .	1·8	0·3	1·4	12
T. cf. *medius* (Eisenack) . . .	0·6	. .	1·6	1·5	. .	0·7	15
Other leiosphere species . . .	11·2	13·0	617	0·4	1·3	0·4	129
Hystrichospheres (excluding leiospheres)	*24·5*	*26·1*	*46·4*	*24·7*	*43·7*	*28·7*	*609*
Total per cent.	100·0	100·0	100·0	100·0	100·0	100·0	. .
Total number	961	23	183	337	371	129	2,004

† Treated with fuming nitric acid.

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NORMANICYTHERE GEN. NOV. (PLEISTOCENE AND RECENT) AND THE DIVISION OF THE OSTRACOD FAMILY TRACHYLEBERIDIDAE

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ABSTRACT. Taxonomic criteria are examined and a review of the family Trachyleberididae leads to a revised diagnosis of the subfamily Hemicytherinae. One of Norman's specimens is designated lectotype of *Normanicythere leioderma*, the type species of the new genus. The lectotype and a number of syntypes are figured for the first time, together with fossil Pleistocene material. Changes of hinge structure during development are described. The affinities of the genus are discussed and its growth and distribution examined.

INTRODUCTION

Cythere leioderma was first described by the Rev. A. M. Norman (1869, p. 291) from Recent material dredged from 'very deep water in Unst Haaf' in the Shetlands in 1867. These nine specimens, which were never figured, are in the British Museum (Natural History). Brady published the first figures of the species (1870, pl. 19, figs. 11–13) showing a complete female shell seen from the left (fig. 11), above (fig. 12), and behind (fig. 13). This came from the Gulf of St. Lawrence, Canada, where he records this as being the most abundant species in the Canadian dredgings (although the Canadian workers inform me that they have no knowledge of it). From his figures and description Brady's interpretation of the species would seem to be valid enough although the material on which it was based has so far not been traced, and even though at that time he had not seen Norman's type material for he mentions 'the single (?) specimen described by Mr. Norman' (Brady 1870, p. 452). The main features on which recognition of the species was based seem to have been the general shape of the shell, the smooth unsculptured surface, and particularly the 'few very distant punctured papillae' (Norman 1869, p. 291). Brady comments that this latter is probably an optical illusion (1870, p. 451) and Brady and Norman (1889, p. 139) agree that there are a 'few scattered, short and rigid setae, which in some lights look deceptively like small circular papillae'. These early authors do not mention the muscle scar pattern or soft parts and their description of the hinge is confined to generalities. Thus Norman in his original description says 'This species has much more the aspect of a *Cytheridea* than of a *Cythere*, but the hinge margin is not toothed', while Brady, Crosskey, and Robertson (1874, p. 149) note 'hinge teeth strongly developed' and Brady and Norman (1889, p. 139) say 'Hinge . . . processes very strongly developed but not crenulated'.

The only published figure giving a reasonable representation of the adult hinge, and then only in dorsal view, is the male right valve figured by Brady, Crosskey, and Robertson (1874, pl. 9, fig. 6). Müller (1912, p. 377; 1931, p. 30) referred to this species under 'Genera dubia et species dubiae Cytheridarum', and Elofson (1941, p. 304) also had difficulty in placing *C. leioderma* systematically, referring it very doubtfully to *Cythereis*. On the other hand, Blake (1933, p. 239) stated that 'In spite of the remarkable form of the shell, the hinge and appendages show this to be a normal species of *Cythereis*'. Blake, however, took a very wide definition of the genus *Cythereis* even for 1933, and

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reduced *Hemicythere* to the status of a subgenus of the former. In view of the large amount of work done on '*Cythereis*' in the past two decades Blake's comments on the hinge now read rather strangely and the soft parts need re-examination. Specimens showing the soft parts are rare and this is the only allusion to them in the whole literature. Blake's specimens are no longer available for study since the material has been disbanded and is now untraceable.

It is doubtful whether it will ever be possible to define the nature of the soft parts in *Cythereis* s.s. as the type species is a Cretaceous form, although recent techniques developed by Martin (1957) perhaps hold out some slight hope here for the chitinized parts of the animal. The selection of *Cythereis montereyensis* by Skogsberg (1928, p. 9) as the type species for *Cythereis* s.s. is invalid since this is not one of the original species included in *Cythere* (*Cythereis*) by Jones (1849), a point made by Blake (1933, p. 238). Triebel (1940, p. 174), in making *Cytherina ciliata* Reuss 1845 the type species, was the first to select a valid type for the genus, and both his diagnosis, and the later one in English by Sylvester-Bradley (1948, p. 795), show that the hinge of the type differs radically from that of the present species. This is particularly obvious in the case of the right valve where the latter has a stirpate anterior tooth and a reniform posterio tooth while *Cythereis* has dentate anterior and posterior elements.

During an examination of the Pleistocene Sub-Basement Clay at Dimlington on the Yorkshire coast (see Bisat 1939*a*, *b*; 1954 for stratigraphical details) three specimens were obtained and showed a number of interesting features, particularly in the development of the adult hinge structure. These features are paralleled in Norman's type material and are here described for the first time. Hitherto the only figured specimen from this country was the single adult valve noted above from the Bridlington Crag (see Phillips 1875, pp. 86, 163, for stratigraphical details). The new Dimlington material, Norman's type specimens and the three previously unrecorded valves in the Hancock Museum, Newcastle, together with the abundant and excellently preserved Spitzbergen material, now make it possible to describe and figure this species adequately for the first time.

GENERIC CRITERIA

It is a truism that the different approaches of the zoologist and palaeontologist to the problems of taxonomy are governed by the nature of the material available, and that discrimination of fossil species and genera must always be to some extent subjective. The zoologist naturally attaches most importance to the soft parts of the living animal and, in the case of the Ostracoda, bases his differentiation particularly on the nature of the limbs and genitalia. This is abundantly clear in Skogsberg's work (1928) on the genus *Cythereis* for he records (p. 12) that 'the structure of the mandible is, indeed, the most characteristic feature of the genus *Cythereis*' and goes on to state (p. 16) that 'a subdivision of the genus *Cythereis* on the basis of the shape and structure of the shell is, generally speaking impossible. . . . The subdivisions must, on the contrary, be based on the structure of the appendages and of the penis. Especially the structure of the penis appears to be significant.' Blake (1933, p. 238) reiterates this view that a knowledge of the appendages is necessary for the discrimination of subgenera in *Cythereis*. He goes on to note that in *C. leioderma* the hinge is that typical of *Cythereis*—a statement at variance with the hinge structure of the first valid type designated by Triebel (1940) as pointed out above.

The palaeontologist has only hard parts to deal with in the majority of cases, and since 1933 there has been a very considerable splitting of the genus *Cythereis* on this basis. The criteria usually used in the discrimination of species and genera are such features as hinge structure, the shape and ornamentation of the shell, the relationship between the inner margin and line of concrescence, the nature of overlap at the margins of the valves, the nature and distribution of the radial and normal pore canals, and the shape and distribution of the muscle scars. Although important biological differences may occur in the soft parts without any ascertainable differences in the hard parts, the hard parts are by no means completely divorced from the soft structures. Triebel (1941) has pointed out that the various features of the ostracod carapace do in fact bear a close relationship to the morphology of the soft parts, although Malkin (1953) considers that some of these characters may emphasize differences that are relatively insignificant biologically. The rate at which the various characters mature is variable and in her work on the Miocene, Malkin (1953, p. 777) concludes that the order of reaching the adult stage seems to be (1) shape, (2) ornamentation, (3) marginal area, (4) size and shell thickness, (5) hinge. She notes that 'the final complex hinge is the last character to mature, as would be expected, because the hinge must be relatively weak in order that the immature carapace be shed'. The dangers of dealing with immature forms in the fossil state are too well known to need re-emphasizing here.

One of the great difficulties in dealing with the Ostracoda lies in evaluating the taxonomic importance of the varying characters and in this it is particularly difficult to reconcile both zoological and palaeontological practice. On the other hand, while it has been suggested that an independent classification based on hinge structure should be set up by palaeontologists (Beroušek 1952), and that this is more or less the case in the Palaeozoic Ostracoda, such a scheme can certainly not be entertained in the case of the Mesozoic and later Ostracoda. All possible characters should be taken into account and it seems to the author that the most important of these are the nature of the first four pairs of limbs (particularly the mandible), the muscle scars, and the hinge structure. The mandible especially would seem to give a far clearer guide to the genetic relationships than the hinge and the former structure is particularly valuable in enabling a satisfactory division to be made between the Trachyleberidinae and the Hemicytherinae.

Although the hinge structure is important for distinction at the generic level, minor differences seem to have been much over-emphasized in the past and this would seem to be particularly so in the *Cytheridea* group. With further knowledge the genitalia might well prove as important as the limbs, as suggested by Skogsberg. Other features of the carapace noted above—shape, marginal areas, ornament, &c.—are all useful differentiating characters on occasion. Of these, shape, which as Malkin points out is the first feature to show adult characteristics, is the most useful in dealing with immature forms, whilst ornament is of little use at the higher taxonomic levels but is one of the most useful features at the specific level.

THE SUBFAMILY HEMICYTHERINAE

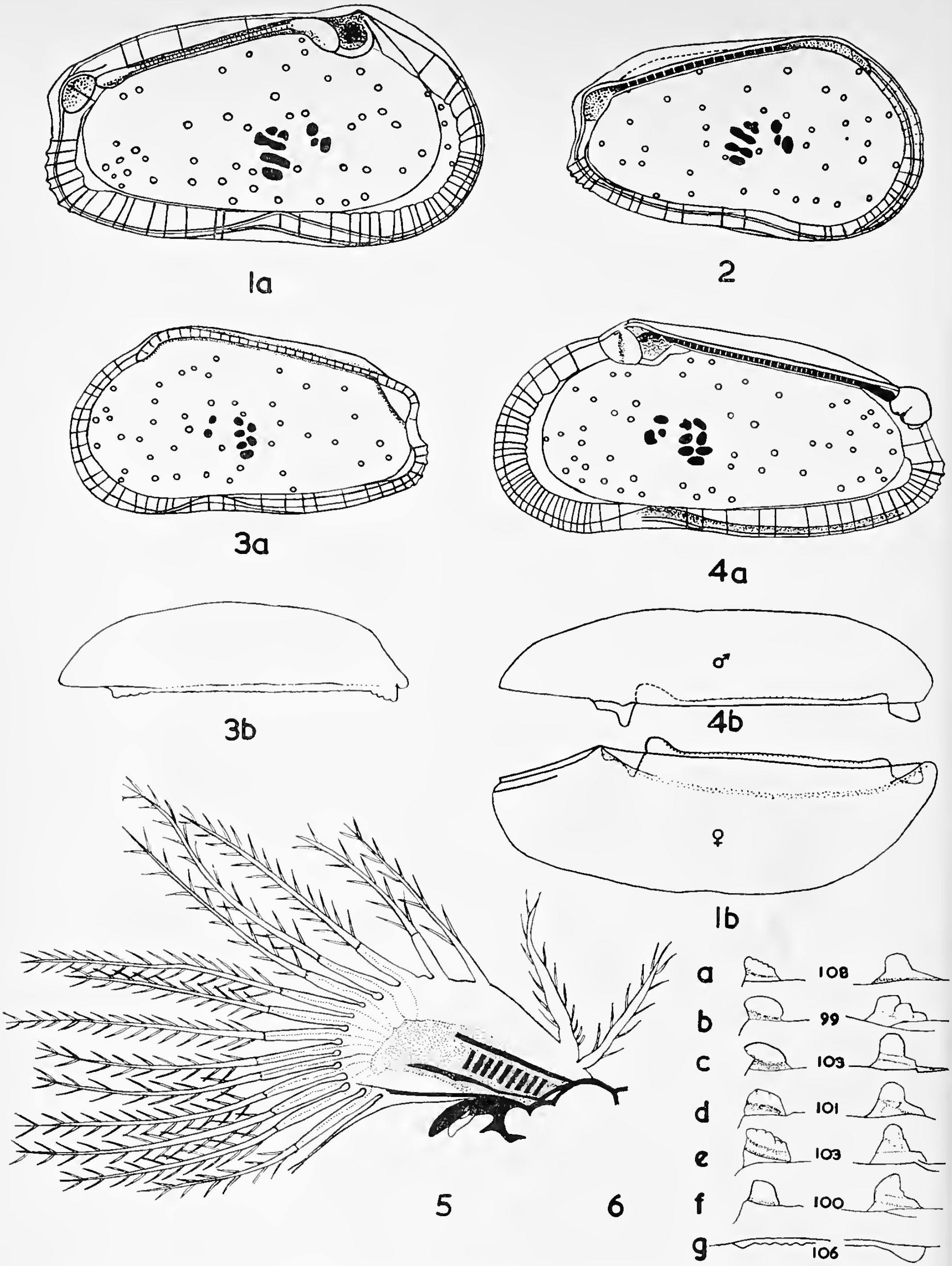
The subfamily Hemicytherinae was formed by Puri (1953) to accommodate the five genera *Hemicythere* Sars 1925, *Procythereis* Skogsberg 1928, *Caudites* Coryell and Fields 1937, *Heterocythereis* Elofson 1941, and *Urocythere* Howe 1951, which he separated from the Trachyleberididae *s.s.* (= subfamily Trachyleberidinae). Puri did not discuss the differences between the Hemicytherinae and the Trachyleberidinae and the most significant statement in his diagnosis was that in the Hemicytherinae there are an 'additional three or four scars in an oblique row situated anteriorly' to the row of four adductor scars (see Pokorný 1955, p. 4, for comment on this). Subsequently Puri added the genus *Hermanites* Puri 1955 (= *Hermania* Puri 1954 preoccupied) to his original five. Pokorný (1955) reviewed the Hemicytherinae as known at the time, and for the first time gave adequate diagnoses and figures of some of the genera. As his paper was in the press he added a footnote to the effect that in the light of the new genera proposed by Hornibrook (1953) and Puri (1954) the limits between the Hemicytherinae and Trachyleberidinae were difficult to draw and that the taxonomy of the genera included in these two units needed further study. After pointing out the anomalies in Puri's original diagnosis Pokorný (1955) gave an excellent key to the genera, and, while regarding *Urocythere* as a doubtful member of the Hemicytherinae, added the genera *Urocythereis* Ruggieri 1950, *Elofsonella*, *Hemicytheria*, and *Aurila* to the subfamily.

While the present paper does not set out to give a detailed analysis of the Hemicytherinae—an impossible task until we know more about some genera—the following remarks may help to clarify the diagnosis and recognition of the subfamily. A study of the genera in which the soft parts are known shows that the subfamily Hemicytherinae Puri 1953 may be recognized as a distinct unit within the Trachyleberididae and may be most satisfactorily differentiated from the subfamily Trachyleberidinae Sylvester-Bradley 1948 on the basis of the soft parts. The soft parts are well known in *Hemicythere*, *Procythereis*, and *Heterocythereis* among Puri's original five genera, and one may single out for mention the five-jointed first antenna, the generally well-developed exopodite of the second antenna, and in particular the single plumose seta (double in the case of *Procythereis*) which forms the exopodite (= epipodial appendage of Skogsberg 1928) of the mandible. On the other hand, in *Trachyleberis* Brady 1898, *Pseudocythereis* Skogsberg 1928, and *Pterygocythereis* Blake 1933—three of the genera included by Sylvester-Bradley (1948) in the Trachyleberididae and not placed in the Hemicytherinae by Puri—the first antenna is six-jointed, the exopodite of the second antenna is much reduced, and the mandible bears a branched exopodite which consists usually of five branches. This latter would appear to provide the easiest means of differentiating between the two subfamilies when the soft parts are available for study. Using the criteria outlined above the following groupings occur:

TRACHYLEBERIDINAE Sylvester-Bradley 1948.
Trachyleberis Brady 1898.
Pseudocythereis Skogsberg 1928.
Pterygocythereis Blake 1933.

HEMICYTHERINAE Puri 1953.
Hemicythere Sars 1925.
Procythereis Skogsberg 1928.
Heterocythereis Elofson 1941.
Eucythereis Klie 1940 (= *Cythereis* s.s. Skogsberg 1928 *non* Jones 1849 invalid).
Elofsonella Pokorný 1955 (= *Paracythereis* Elofson 1941 preoccupied).
Aurila Pokorný 1955.
Normanicythere gen. nov.

In fossil material where the limbs are not available the muscle scars give the best indication of the relationships. The main difference here lies in the muscle scars anterior



TEXT-FIG. 1. *Normanicythere leioderma* (Norman). 1, Left valve of adult female. Recent, Spitzbergen. ×66. *a*, from inside; *b*, from above. R.S. 996. Dissection 6. Slide 17. 2, Left valve of immature female (penultimate instar). Recent, Spitzbergen. ×66. From inside. R.S. 996. Slide 19. 3, Right valve of immature male (penultimate instar). Recent, Portree, Skye. ×66. *a*, from inside; *b*, from above. H.M. 8/79. 4, Right valve of lectotype. Adult male, Unst Haaf, Shetland. ×66. *a*, from inside *b*, from above. B.M. 1911.11.8.M.3210*a*. 5, Vibratory plate of right maxilla. Recent, Spitzbergen. ×195. Composite, based on camera lucida drawings and photographs of Dissections 2 and 7. R.S. 996. Slides 2, 9, 10. 6, Variation in tooth structure of adult carapaces from Spitzbergen, seen from above. ×80. *a–f*, right valves; *g*, left valve. Numbers indicate the length of the valve in hundredths of a millimetre. R.S. 996. Slide 20.

to the row of four adductor muscle scars and is probably connected with the great development of the exopodite of the second antenna and its associated antennal gland in the Hemicytherinae. In this latter subfamily the anterior field consists of two or three rounded muscle scars which lie obliquely to the vertical. In the Trachyleberidinae, on the other hand, this group of muscles is represented by one large and usually horseshoe-shaped muscle. In the vertical row of four adductor muscles there is a distinct tendency in the Hemicytherinae for the individual muscles to split into two and leave a double or 'binodal' scar, while this does not appear to occur in the Trachyleberidinae. Finally, in the Trachyleberidinae the muscle area seems to be sunk in a central pit which is not so well defined in the Hemicytherinae, although this distinction is of doubtful validity. Using the foregoing criteria one may group a number of additional genera whose soft parts are as yet unknown as follows:

TRACHYLEBERIDINAE
Cythereis Jones 1849.
Buntonia Howe 1935.
Isocythereis Triebel 1940.
Platycythereis Triebel 1940.
Oligocythereis Sylvester-Bradley 1948

HEMICYTHERINAE
Urocythereis Ruggieri 1950.
Tyrrhenocythere Ruggieri 1955.
Hemicytheria Pokorný 1955.

Although a number of genera placed in the Trachyleberididae cannot at the present time be placed in their respective subfamilies due to inadequate information on their soft parts or muscle scar pattern, it is suggested that the essential differences between the Trachyleberidinae and the Hemicytherinae lie in the features outlined above, rather than in any general consideration of shape, hinge or ornament.

SYSTEMATIC DESCRIPTION

Family TRACHYLEBERIDIDAE Sylvester-Bradley 1948

Subfamily HEMICYTHERINAE Puri 1953

Revised Diagnosis. Trachyleberididae which differ from the Trachyleberidinae in having a five-jointed first antenna, the second antenna with well-developed exopodite, and the exopodite of the mandible formed of a single (or occasionally double) plumose seta. The muscle-scar pattern differs from that in the Trachyleberidinae in that there are two or three scars in an oblique row anterior to the adductor muscles, and the latter tend to be binodal.

Genus *Normanicythere* gen. nov.

Type Species *Cythere leioderma* Norman 1869

Diagnosis. Third endopodite of the distinctive mandible with seven antero-distal setae and one large postero-distal seta, the latter being smooth proximally and serrate distally and carrying six long hair-like processes. Adult hinge amphidont with stirpate anterior tooth. Posterior tooth usually reniform. Hinge line straight and oblique to dorsal margin of the shell seen from the side. Inner margin and line of concrescence well separated anteriorly and at postero-ventral angle. Radial pore canals simple.

Normanicythere leioderma (Norman)

Plates 13, 14

Cythere leioderma, n.sp.; Norman 1869, pp. 255, 291.
Cythere leioderma, Norman; Brady 1870, pp. 451–2, pl. 19, figs. 11–13.
Cythere leioderma (Norman); Brady and Crosskey 1871, pp. 61–2.
Cythere leioderma, Norman; Brady, Crosskey, and Robertson 1874, pp. 149, 150, pl. 9, figs. 5, 6.
Cythere leioderma, Norman; Brady 1878, p. 254.
Cythere leioderma, Norman; Brady and Norman 1889, p. 139, pl. 15, figs. 12, 13.
Cythere leioderma, Norman; Norman 1891, p. 111.
Cythere leioderma Norm.; Müller 1912, p. 377.
Cythere leioderma, Norman; Stephensen 1913, p. 363.
Cythere leioderma A. M. Norman; Klie 1929, pp. 19, 42.
Cythere (?) *leioderma* Norman; Müller 1931, p. 30.
Cythereis leioderma (Norman) comb. nov.; Blake 1933, p. 239.
Cythereis leioderma (Norman); Stephensen 1938, pp. 10, 17.
Cythereis (?) *leioderma* (Norman); Elofson 1941, p. 304.
non*Cythere lejoderma*, Norman; Seguenza 1884, p. 51.

Types. Nine syntypes in the British Museum (Natural History), London, nos. 1911.11.8.M.3210*a*–*i*, from Unst Haaf, Shetland. Of these, an adult male, right valve, no. 1911.11.8.M.3210*a* is here chosen as the lectotype.

Description

(*a*) *The Carapace.* In lateral view the shape is an elongate oblong, rounded anteriorly with straight dorsal margin and almost straight or slightly sinuate ventral margin. The

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EXPLANATION OF PLATE 13

Figs. 1, 2, *Normanicythere leioderma* (Norman), Recent, Spitzbergen. 1, Adult female seen from the left with all the right side limbs removed. × 115. ag.—antennal gland; 1*a*, first antenna; 2*a*, second antenna; ex.—exopodite ('Spinnborste'); mdp.—mandibular palp; mx.—maxilla; 1wl, 2wl, 3wl.—first, second, and third walking legs; fs.—furcal setae; ts.—terminal seta. R.S. 996. Dissection 4, Slide 4. 2, Male genitalia seen from the front. × 165. mcs.—median chitinous support; pe.—penis; co.—copulatory organ; ode.—opening of ductus ejaculatorius; rc.—rounded corner of co.; fl.—flagella; de.—ductus ejaculatorius; 1fs, 2fs, 3fs.—first, second, and third furcal setae. R.S. 996. Dissection 2, Slide 2.

EXPLANATION OF PLATE 14

Figs. 1–8, *Normanicythere leioderma* (Norman), × 42. 1, Lectotype. Adult male. Right valve. Recent, Unst Haaf, Shetland; (*a*) outside, (*b*) inside, (*c*) dorsal view. B.M. 1911.11.8.M.3210*a*. 2, Syntype. Adult female carapace. Recent, Unst Haaf, Shetland; (*a*) from left, (*b*) from right, (*c*) dorsal view. B.M. 1911.11.8.M.3210*b*. 3, Adult male. Right valve. Sub-Basement Clay, Pleistocene, Dimlington, E. Yorks.; (*a*) outside, (*b*) inside, (*c*) dorsal view. H.U. 1.Q.1.1. 4, Syntype. Immature female. Left valve. Penultimate instar. Recent, Unst Haaf, Shetland; (*a*) outside, (*b*) dorsal view. B.M. 1911.11.8.M.3210*c*. 5, Syntype. Immature female. Right valve. Recent, Unst Haaf, Shetland; (*a*) outside, (*b*) dorsal view. B.M. 1911.11.8.M.3210*d*. 6, Immature female. Left valve. Penultimate instar. Sub-Basement Clay, Pleistocene, Dimlington, E. Yorks.; (*a*) outside, (*b*) inside, (*c*) dorsal view. H.U. 1.Q.1.2. 7, Immature female. Right valve. Penultimate instar. Sub-Basement Clay, Pleistocene, Dimlington, E. Yorks.; (*a*) outside, (*b*) inside, (*c*) dorsal view. H.U. 1.Q.1.3. 8, Immature carapace. Instar 5. Recent, Spitzbergen. (*a*) from left, (*b*) dorsal view. R.S. 996. Slide 21.

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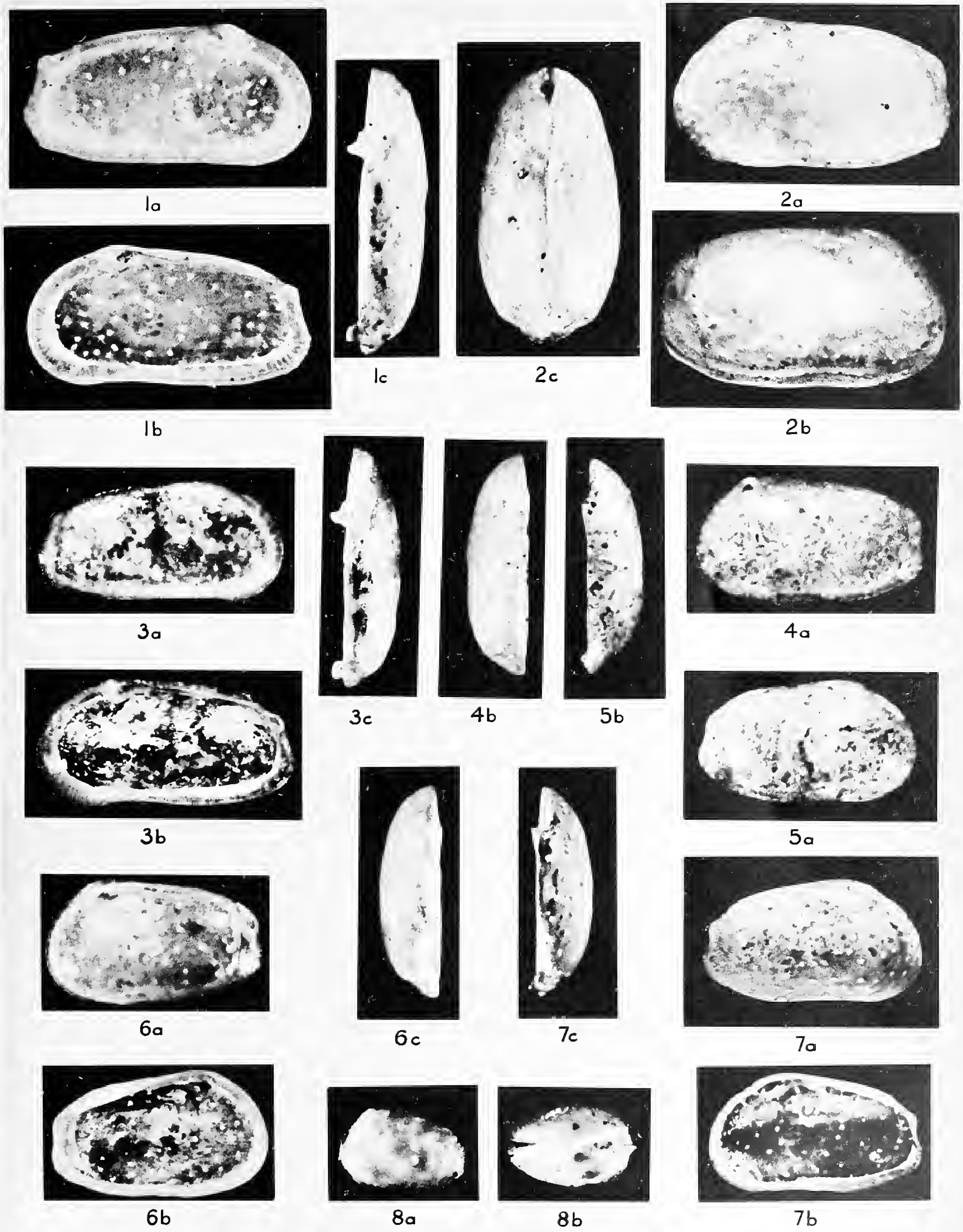
NEALE, *Normanicythere leioderma* (Norman)



NEALE, *Normanicythere leioderma* (Norman)

posterior margin is truncate or sinuate, the sinuation being due largely to the development of the strongly everted posterior tooth in the right valve with its corresponding socket in the left. The carapace is highest anteriorly and the left valve is slightly larger than the right valve, overlapping the latter in the region of the anterior tooth. The greatest height is a little more than half the length and sexual dimorphism is pronounced in the adult, and to a lesser extent in the penultimate instar, the females being higher in proportion to the length than the males (text-fig. 1, figs. 1*a*, 4*a*; Pl. 14). The dorsal hinge line is straight, the shell gradually rising above it posteriorly to form a shallow trough which is deepest at the posterior end. In dorsal view the carapace is more or less evenly rounded with a suggestion of a vertical median sulcus, and is rather parallel-sided in the case of the male, and somewhat pear-shaped and widest posteriorly in the case of the female. In this view the tooth structure (q.v.) is very characteristic (text-fig. 1, figs. 1*b*, 4*b*). The carapace is smooth and unornamented.

In immature forms the line of concrescence and inner margin coincide except at the postero-ventral angle. In the adult the line of concrescence and inner margin are very near or coincident ventrally, but are well separated anteriorly and at the postero-ventral angle. Radial pore canals, which are simple and usually well marked, are densest at the antero-ventral border and postero-ventral angle in which latter position there may be a slightly serrate margin to the carapace (*randzähnchen*). Antero-dorsally and ventrally the radial pore canals are more sparsely distributed. The normal pore canals are large, very distinct and well spaced, appearing as lucid spots under the microscope and sometimes giving the impression of raised papillae (Pl. 14, figs. 1*a*, 7*a*). In immature and thin-shelled specimens these canals are easily seen, but are much less easily seen in the case of some older or thick-shelled specimens. The selvage is well developed in both immature and mature forms and ventrally the left valve fits into a groove in the right valve, the latter overlapping the left valve along the posterior part of the ventral margin. Anteriorly the relative overlap is reversed and the left valve overlaps the right.

The muscle-scar pattern consists basically of a vertical row of four adductor scars with three muscle scars anterior to, and on a level with, the two more dorsally situated scars of the row of four. In the adult two or three small scars are sometimes seen about the same distance above the row of four scars as the height of the row. There is some minor variation in the adult pattern but in the row of four scars: 1, the bottom scar is always single; 2, the ventral central scar is very elongated and narrow and tends to be 'binodal' or form a double scar; 3, the dorsal central scar is not so elongate and is generally binodal; 4, the dorsal scar is a double scar in the adult. In immature specimens the muscle pattern is similar but the scars are more rounded and less elongated. In the adult there are three rounded equidimensional muscles in an oblique row anterior to the vertical row of four. The dorsal and ventral of these are easily seen, the smaller median one less so.

The hinge structure shows a big change from merodont in the penultimate instar to amphidont in the adult (see Sylvester-Bradley 1956 for terminology). The right valve of the penultimate instar (text-fig. 1, fig. 3*a*) has an anterior and posterior tooth joined by a finely denticulate bar, with a groove or shelf below which is open ventrally. The anterior tooth is triangular in dorsal view (Pl. 14, figs. 5*b*, 7*c*), highest anteriorly and in strongly oblique lighting shows a subdivision into three or four crenulations. The posterior tooth is a deep, plate-like, outstanding tooth formed by the everted posterior angle of the right valve. This too shows a subdivision into four or five distinct crenulations. The insetting of the tooth at the posterior corner of the valve gives a very characteristic appearance, especially when viewed from dorsally. The left valve (text-fig. 1, fig. 2; Pl. 14, figs. 6*a–c*) overlaps the right along the hinge margin. The hinge consists of a deep posterior socket, a locellate groove which accommodates the marginal bar of the right valve, and a shallow socket anteriorly for the anterior tooth. Anteriorly the valve has a curiously unfinished look due to this rather ill-defined socket. In the adult hinge the right valve has a large, stirpate anterior tooth with post-jacent socket and faintly locellate groove, the latter being defined above and below by a thin ridge or bar. Posteriorly is a large outstanding tooth which markedly affects the outline of the shell. This tooth is rather rhomb-shaped in the lectotype but reniform in the adult male from Dimlington (Pl. 14, fig. 3*b*). Some of the variations in shape of these teeth in the Spitsbergen material are shown in text-fig. 1, fig. 6. Posteriorly the dorsal bar and groove are slightly modified immediately anterior to the posterior tooth. The bar (which may be faintly denticulate) shows two small crenulations or vestigial teeth which seem to be a relic of the previous instar tooth pattern, while the groove is somewhat enlarged to form a small socket into which fits a complementary expansion of the bar in the left valve. In the left valve the anterior socket shows minor variations in shape corresponding to those seen in the anterior tooth in the right valve, and is succeeded posteriorly by a large tooth and faintly denticulate bar. These denticulations are best seen posteriorly before the slight expansion of the bar to form the posterior tooth (text-fig. 1, figs. 1*b*, 6*g*). A deep socket to accommodate the posterior tooth completes the hinge.

(*b*) *The limbs and soft parts.* Five dissections (three female, two male) and two partial dissections were made and all the line figures were drawn by camera lucida at magnifications of either 390 or 780. These figures were then checked by examination with an oil-immersion lens at ×1,000 when minor details of pilosity and pectination were added freehand. The most recent detailed description of an advanced marine Podocopa is due to Harding (Harding and Sylvester-Bradley 1953) and the terminology used below follows that paper closely. In the present description, however, 'inside' is used in preference to 'median' in referring to the inside surface of the leg, and median is restricted to describing structures occurring on the mid-line of the body. Proportional lengths are not given for the various segments (numbered from proximally to distally) and for these reference should be made to the appropriate figures. As the annulate setae carry hairs at each joint or annulus these are not referred to as hairy in the text but are shown on the figures. All the limbs are bilaterally symmetrical and the absence of any comment on sexual dimorphism indicates that a particular limb is the same in both sexes.

The first antenna consists of five segments. Segment 1 carries a tuft of long spinules on the posterior face near the base, and small spinules at the antero-distal corner. Segment 2 has tufts of spinules both anteriorly and posteriorly. One or two of these spinules are more prominent than the rest. The more prominent spinules anteriorly lie in the proximal position, while posteriorly the most prominent lie about half-way down the segment. A tuft of fine spinules and hairs lies anterodistally and there is a slender, flexible, annulate seta at the postero-distal corner. Segment 3 has a single major seta, which is pectinate on both sides, at the antero-distal corner. Segment 4 corresponds to segments 4 and 5 in *Trachyleberis* and *Pseudocythereis* but shows continuous chitinization posteriorly in which it agrees with *Hemicythere* and *Cythereis* s.s. (*sensu* Skogsberg). It carries two

TEXT-FIG. 2. *Normanicythere leioderma* (Norman). Recent, Spitzbergen. 1, Furcal setae seen from the left-hand side. Female. ×390. R.S. 996 Dissection 4, Slide 4. 2, Right mandible from outside. Male. ×195. R.S. 996. Dissection 2, Slide 2. 3, Right second antenna from outside. Male. ×195. R.S. 996. Dissection 2, Slide 2. 4, Right first antenna from outside, Male. ×195. R.S. 996. Dissection 2. Slide 2. 5, Left maxillary palp and endites from outside. Male. ×390. R.S. 996. Dissection 5, Slide 5. 6, Postero-proximal seta. Third right walking leg (seventh limb). Female. ×390. R.S. 996. Dissection 6, Slide 7. 7, Postero-proximal seta of first right walking leg (fifth limb). Female. ×390. R.S. 996. Dissection 6, Slide 7. 8, Median terminal seta. Female. ×390, seen from left. R.S. 996. Dissection 4, Slide 4.

stout major setae—one antero-median in position, the other antero-distal. The former, which is pectinate on both sides, is associated with two more slender, bristle-like setae—one as long as the major seta lying more posteriorly on the inside of the limb; the other, somewhat shorter, lying above (i.e. proximal to) the main seta. The distal seta, which is pectinate on the anterior side only, is also associated with two bristle-like setae, the longer one again placed on the inside of the limb in a more posterior position, the shorter one again lying above the main seta. In addition there is a very short seta, which is at first cylindrical and then tapers rapidly, placed distally on the outside of the limb (latero-distal spine of Skogsberg 1928, p. 40.). This segment is finely pilose anteriorly. Segment 5 shows a somewhat similar pattern with a single major, distal seta, two bristle-like setae and in addition a somewhat shorter sense club. The middle third of the major seta is pectinate on the anterior side, carrying about ten or eleven hairs, but this is only seen with great difficulty and some specimens appear smooth. It appears to be more obvious in the males than the females. This segment is finely pilose anteriorly.

The second antenna shows distinct sexual dimorphism in the case of the long bristle-like seta on the anterior side of the second endopodite segment. The protopodite of one segment is followed by an endopodite of three segments and a long, slender exopodite, also of three segments.

Endopodite 1 is short with a tuft of spinules anteriorly about the middle of the segment and a hairy seta at the post-ero-distal corner. Endopodite 2 is much elongated and carries a patch of spinules on the anterior side about a quarter of the way down from the proximal end. This segment has two hairy setae posteriorly about two-thirds of the way down, associated with a rather shorter sense club which lies immediately anterior to them on the outer side of the limb. Immediately above these setae the surface has a number of short fine hairs. Anteriorly about three-quarters of the way down the segment are two bristle-like setae. The inner, shorter one reaches to about the middle of the last segment while the outer, longer seta extends level with the distal tip of the terminal seta. In the female this longer seta only reaches about half-way down the terminal seta. There is a short pilose seta at the postero-distal corner with a fringe of hairs lying anterior to it. Endopodite 3 has two setae half-way down the posterior side, a stouter one which is pectinate, carrying about a dozen hairs on the middle third of the posterior (upper) surface and occupying the inner position; the other more slender one lying outside it. There is a stout, terminal seta which is also pectinate in the middle third of the upper surface, carrying eleven or twelve hairs. Skogsberg (1928, p. 44) remarks that in *Cythereis* the distal claws of the female are more strongly pectinate than those in the male. There is some slight suggestion of this in the present species.

The exopodite (*Spinnborste* of Müller, Klie, &c.) contains the efferent duct for the large gland (*Spinndrüse*) which lies on either side of the body near the base of the second antenna (Pl. 13, fig. 1. *ag*., text-fig. 2, fig. 3). This gland appears to be best developed in those marine *Cytheracea* living among seaweeds and large detritus and is much reduced in many of the mud dwelling forms according to Elofson (1941, p. 438). The function of the gland appears to be that of spinning a thread which functions as a climbing or safety rope and Elofson goes on to state 'Oft habe ich in Aquarien beobachtet, wie Individuen einer Anzahl Algenarten (*Cytherura*, *Loxoconcha*-Larven) von ihrem Zweig herunterfielen, aber an den Spinnfäden hängen blieben und wie Spinnen wieder an diesen hinaufkletterten.'

The mandible consists of a strongly chitinized *pars incisiva* and an attached mandibular palp shown in text-fig. 2. The biting edge consists of a row of six main teeth, of which the anterior two are by far the strongest, with a row of six more, slightly less prominent teeth, lying outside it. Between the first two teeth is a bifurcate seta about twice the length of the largest tooth, each arm of the seta being armed with small, fine hairs on the posterior side. In addition there is a small, smooth, tapered seta at the postero-ventral corner, and a hairy, rather carrot-shaped seta on the anterior side of the body of the mandible.

The mandibular palp consists of a protopodite of one segment, which together with an exopodite of one segment is well chitinized, and an endopodite of four segments which is very poorly chitinized except for the most distal segment, segmentation often being difficult to observe in the first three segments. The protopodite carries a series of long hairs along the distal margin. The exopodite carries a single pilose seta which has, in addition, some four pairs of longer hairs. Endopodite 1 has a slender seta posteriorly which is pilose on both sides and has, lying dorsal to it, a hairy seta which shows signs of annulation. Endopodite 2 has two dorsal setae. The proximal is really the largest of a group of four spinules which increase in size distally, while the distal one is annulate. Ventrally there are two long, slender setae lying outside which, near their bases, are two small setae. The inner long seta is minutely pilose on the anterior edge, while the outer long seta is armed with five pairs of rather long hairs. Of the two small setae, the more ventral is a little shorter and more hairy than the dorsal. Endopodite 3 has a few small hairs on the dorsal surface and a felt of long hairs on the ventral. Antero-distally this segment has a bundle of seven setae—four, distributed in two pairs, very long, smooth, and whip-like; the other three, which are about half the length of the latter are pilose on both sides. Postero-distally (ventrally) is the largest seta of the palp which has a short, smooth, slender seta at its base on the outside. The large seta is smooth proximally but is serrate and pectinate for the distal half of the anterior side, and the distal third of the posterior side. There are six long, hair-like processes of which two are placed on the posterior side some distance proximal to the others, which latter often assume a grapnel-like position when mounted.

Endopodite 4 has four distal setae, the antero-distal one annulate, the postero-distal one smooth being cylindrical at first and then tapering rapidly; while the other two setae are about twice as long and are smooth anteriorly and minutely pilose posteriorly.

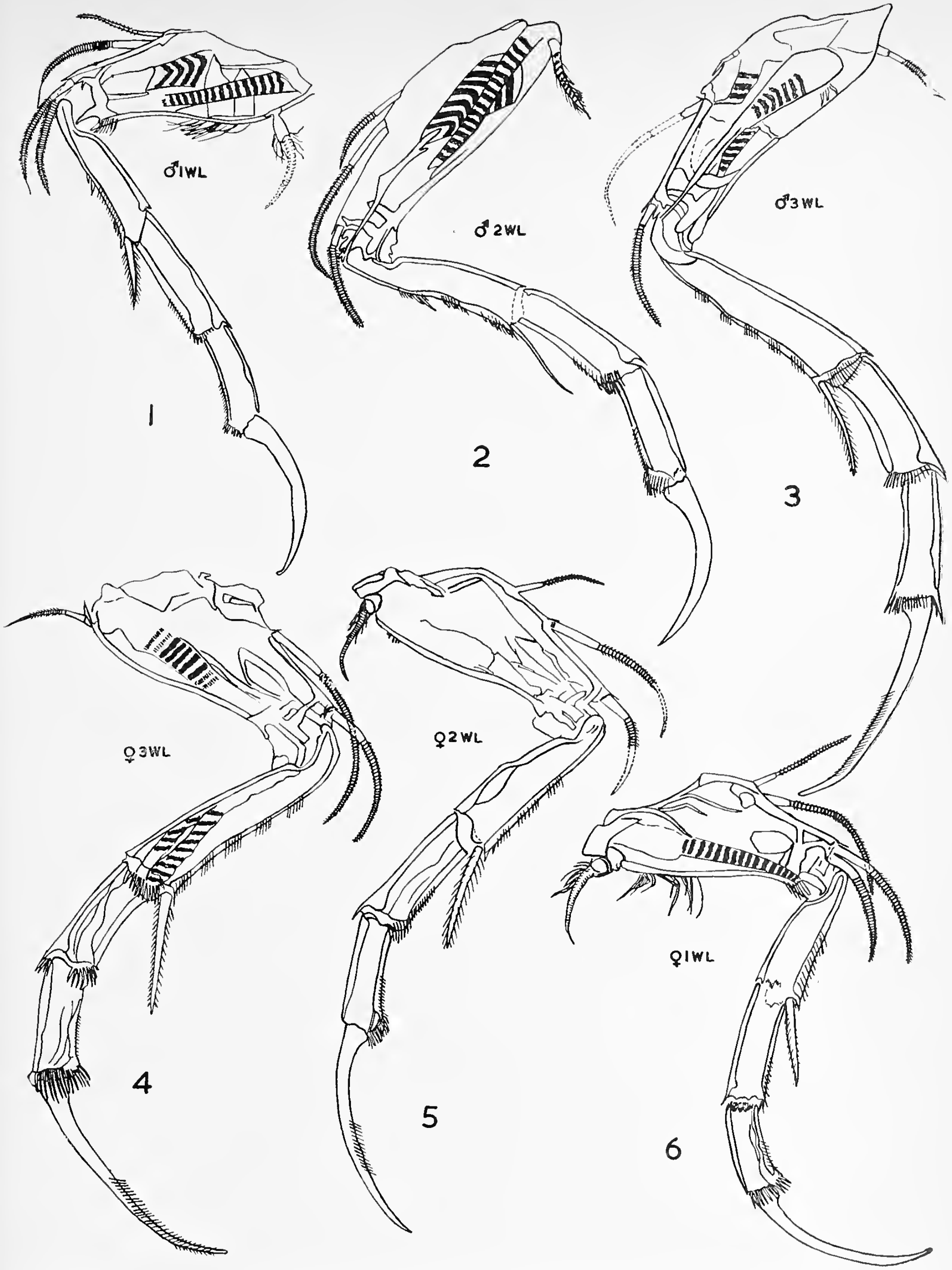
The maxilla consists of a vibratory plate and palp with associated endites. The vibratory plate has eighteen plumose setae whose distribution is figured in text-fig. 1, fig. 5, and which it is unneccessary to describe further. Anterior to this is a palp and three associated endites (text-fig. 2, fig. 5). The palp consists of two cylindrical segments, the first being about twice as long and wide as the second. On the distal edge of the first segment, dorsal to the second segment are three slender annulate setae, the longest of them placed centrally and towards the outside. There is an associated fourth flagella-like, non-annulate seta which is outside, and slightly ventral to, the main annulate seta. Ventral of the second segment, a fifth stout, smooth, curved seta is placed at the ventero-distal corner. The second segment carries three setae—a smooth antero-distal blade-like seta, and two setae postero-distally—the inner one like the latter, the outer one slightly larger and pectinate on the posterior (ventral) side.

Endite 1 nearest the palp carries six smooth, rather similar, tapering setae disposed in an outer and an inner row of three each. Endite 2 is similar, while Endite 3 appears to have seven setae, with, in addition, a larger hairy seta on the outside of the endite.

The first walking leg (fifth limb) (text-fig. 3, figs. 1, 6). Special attention was paid to this leg in view of Harding's remarks on the same leg in *Trachyleberis* but no asymmetry or significant sexual dimorphism could be detected. The leg consists of four segments. Segment 1 has two annulate setae on the anterior margin and two on the antero-distal corner overhanging the 'knee'. The posterior side has a felt of long hairs and spinules and distally there is a hollow with a fringe of hairs. Patches of hairs occur on the outside of this segment particularly in the proximal half and near the base on the posterior side is a hairy, carrot-shaped seta (text-fig. 2, fig. 7). Segment 2 broadens distally and has one non-annulate, hairy seta antero-distally. This occupies the same position in male and female with a tendency to be a little more pilose in the male. The distal two-thirds of the segment has small hairs anteriorly, a patch about the middle of the anterior edge being slightly larger than the rest in both sexes. The third and fourth segments are similar, the distal half of the anterior edge having fine hairs, while antero-distally a fringe of hairs, which shows a slight tendency to be better developed in the female, overhangs the next segment or seta. Distally the fourth segment carries a curved claw or seta which is smooth in both sexes.

The second walking leg (sixth limb) shows marked sexual dimorphism (text-fig. 3, figs. 2, 5). The first segment is similar in both sexes and has two annulate setae on the anterior side whilst a further annulate seta overhangs the 'knee'. At the postero-proximal corner there is a hairy, carrot-like seta which tends to be rather stumpier in the female than in the male, and there is a spinule at the base of the limb in the middle of the outside surface. The second segment broadens distally and has three patches of hairs on the anterior side, the middle patch being the most prominent. The antero-distal corner has a seta which is long, smooth and slender in the male, and more robust and hairy in the female. Segments 3 and 4 carry a number of fine hairs on the distal half of their anterior sides and overhanging the following segment or terminal claw are fringes of hairs which are more prominent in the female than the male. The terminal claw or seta is curved and is longer and more slender in the female than the male. In the male this seta is smooth, while in the female it is pectinate for the middle third of its length on the anterior side where it carries between six and twenty hairs.

The third walking leg (seventh limb) consists of four segments and shows only slight sexual dimorphism (text-fig. 3, figs. 3, 4). The first segment carries a very small seta proximally on the anterior edge and two annulate setae—one midway along the segment and the other overhanging the 'knee'. At the postero-proximal corner there is a slender annulate seta (text-fig. 2, fig. 6), and a few small spinules may occur proximally on the outer surface near the posterior edge. The second segment broadens distally and has five patches of hairs anteriorly, which are more conspicuous in the female than the male. There is a pilose antero-distal non-annulate seta which is rather slimmer in the males than the females. A fringe of hairs occurs distally. Segments 3 and 4 are similar and have a fringe of hairs distally which is again rather more prominent in the females than the males. The terminal claw is long, narrow, and pectinate on the inside curve in its distal half. Pectination is also present on the posterior distal sixth of the claw, although difficult to see in the males. In the female the claw tends to be more incurved distally than in the male.



TEXT-FIG 3. *Normanicythere leioderma* (Norman), Recent, Spitzbergen. All figures × 195. 1, First left walking leg (fifth limb) from outside. Male. R.S. 996. Dissection 2, Slide 2. 2, Second left walking leg (sixth limb) from outside. Male. R.S. 996. Dissection 2, Slide 2. 3, Third left walking leg (seventh limb) from outside. Male. R.S. 996. Dissection 2, Slide 2. 4, Third right walking leg (seventh limb) from outside. Female. R.S. 996. Dissection 6, Slide 7. 5, Second right walking leg (sixth limb) from outside. Female. R.S. 996. Dissection 6, Slide 7. 6, First right walking leg (fifth limb) from outside. Female. R.S. 996. Dissection 6, Slide 7.

The genitalia are extremely complex. It appears to the author that some of the terminology needs revision but for the present purpose that of Skogsberg (1928) has been adopted. In the male (Pl. 13, fig. 2) the genitalia consist of a median chitinized supporting structure (*mcs*) with heavily chitinized paired organs on either side. These paired organs consist of two parts—a somewhat oval muscular 'penis' (*pe*) and a distal triangular 'copulatory appendage' (*co*). The muscular part has a number of chitinous structures which stain heavily. There is a spiral *ductus ejaculatorius* (*de*) which runs from a heavily stained chamber and opens ventrally in a brush-like organ (*ode*) towards the rear of the copulatory appendage. More posteriorly is a two-fingered flagellum (*fl*) and the postero-ventral corner of the appendage is rounded (*rc*). The *vasa deferentia* could not be ascertained. Associated with the genitalia are three pairs of furcal setae—two pairs of which are relatively large, hairy, and carrot-shaped (*fs2*, *fs3*), the third pair (*fs1*) being only a third the length of the others but also armed with hairs. The paired penes were symmetrical and showed no trace of the asymmetry described by Skogsberg in certain species of '*Cythereis*' and Triebel (1956) in *Xestoleberis arcturi*.

The female genitalia did not take stain and were only imperfectly seen and so will not be described. The female differs in that only the two pairs of more prominent furcal setae are developed (text-fig. 1) the small pair (*fs1*) being absent.

Brush-like organs, which generally occur in the male on the ventral side of the body near the fifth pair of limbs were not seen.

The body ends in a minute median, terminal seta (Pl. 13, fig. 1, *ts*).

Affinities and differences

The soft parts are most distinctive and show that the genus is most closely akin to *Heterocythereis* Elofson 1941 (type species *Cythere albomaculata* Baird 1850) and somewhat less closely related to *Elofsonella* Pokorný 1955 (type species *Cythere concinna* Jones 1856). In *Normanicythere* and *Heterocythereis* the first and second antennae are identical to all intents and purposes, and it is only in the mandible that differences occur. We are dependant on Sars's figure (1925, pl. 78, fig. 1*M*) for the nature of this latter in *Heterocythereis* and he does not describe the limb in any detail. The mandibles in the two genera show an obvious general similarity, particularly in the fact that 'the inner distal seta of the penultimate joint [is] remarkably strong and falciform curved' (Sars, p. 169). There are, however, important differences. The distal annulate seta of Endopodite 2 is missing in Sars's figured specimen (probably broken off), while the antero-distal margin of Endopodite 3 carries five long setae in *H. albomaculata* as compared with four long whip-like and three shorter pilose setae in *Normanicythere*. Postero-distally on this segment the main seta also carries six longer hairs which are absent in *Heterocythereis*. The distal segment in the latter genus also carries three instead of four setae, and there are also marked differences in pilosity on the two posterior setae of Endopodite 2. While it is obvious that *Normanicythere* is closely related to *Heterocythereis*, it is equally obvious that there are differences in the structural details and that the soft parts of *Heterocythereis albomaculata* need careful re-examination and redescription. In the hard parts, these two genera differ considerably. Wagner (1957, pl. 24) gives the best figure of the carapace of *Heterocythereis* and while in this genus the hinge follows the arched dorsal margin, in *Normanicythere* the hinge is straight and sinks below the margin of the shell posteriorly. In addition the detailed hinge structure, the marginal areas, and the distribution of the radial pore canals is different. There is, however, a similarity in the large normal pore canals which again suggests a fairly close kinship.

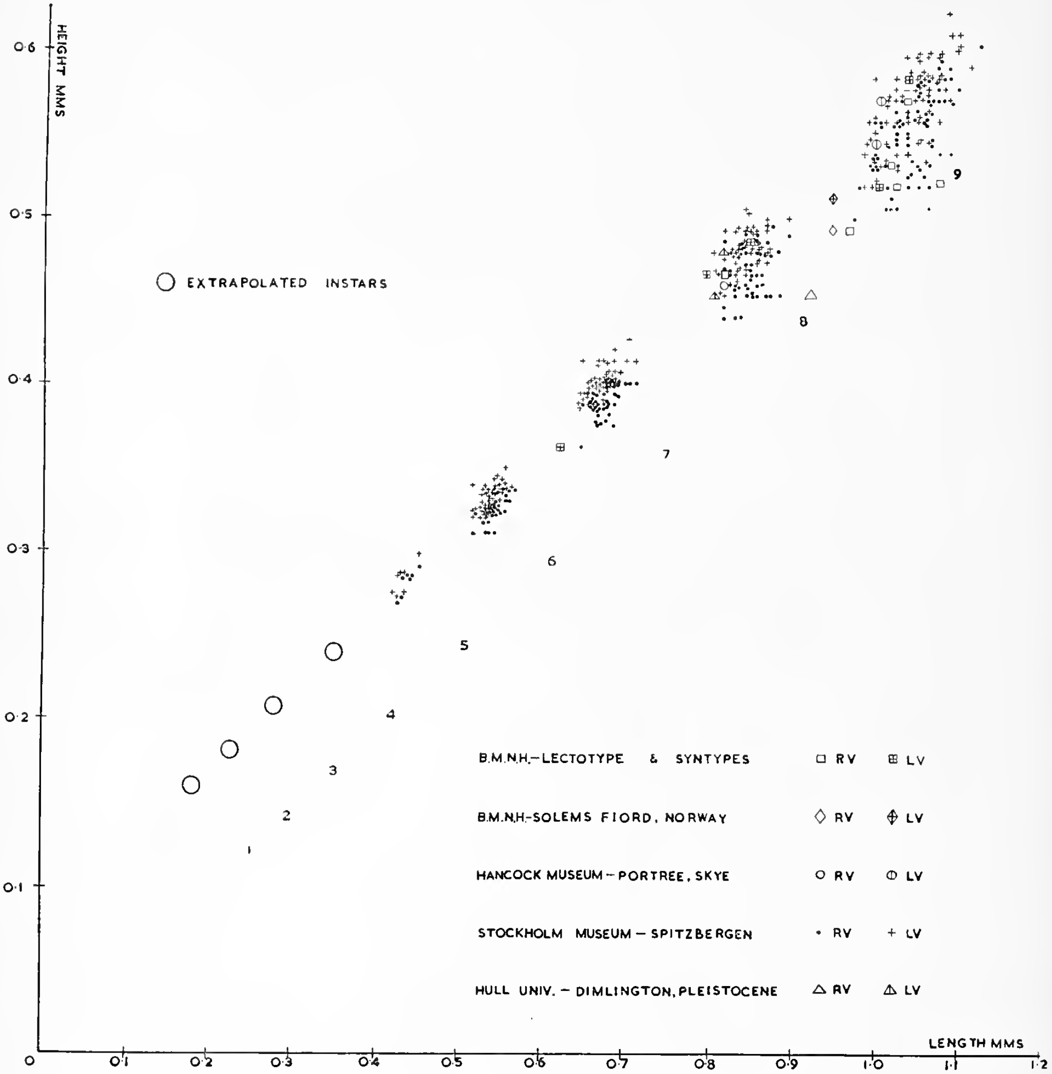
From *Elofsonella* the differences are more marked, both in the antennae—the exopodite of the second antenna is much reduced in *Elofsonella* for example—and in the mandible where the postero-distal seta is less developed.

The hard parts differ markedly from many of the genera placed in the Trachyleberididae and a list would be tedious. The present genus is closest to *Campylocythere*, *Elofsonella*, and *Urocythereis*. While *Normanicythere* agrees with the description of *Campylocythere* (= *Acuticythereis*) Edwards (1944, p. 514) there are striking differences in the hinge structure compared with Edwards's figures (1944, pl. 86, figs. 8–16) and in the soft parts as far as they are known. This is particularly so in the case of the first antenna (= antennule) as figured by Swain (1955, text-fig. 39, fig. 8*b*) in *C. concinnoidea* (not the type species) which has only three endopodite segments instead of four and differs markedly in the setae also. From *Urocythereis* Ruggieri 1950 it differs in the development of the hinge and particularly in the vestibule developed anteriorly and the separation of the inner margin and the line of concrescence at the postero-ventral angle. The differences in the hard parts from those of *Elofsonella* are not so well marked and lie in the insetting of the hinge and the large scattered pore canals of the new genus, the differences being much more marked in the case of the soft parts.

Growth

Growth shows the usual discontinuous pattern associated with Ostracoda and other Crustacea. Ecdysis occurs periodically and is accompanied by a rapid increase in size when a new and larger carapace is formed. There follows a period during which size remains stable (the instar) until ecdysis recurs. Two 'laws' have been postulated to explain the size relationships between instars in this discontinuous type of growth. Brooks (1886) working on the Stomatopoda suggested that there was a constant percentage increase in length of the carapace at each moult, a concept first applied to the Ostracoda by Fowler (1909); and Przibram (1931) working with weight and volume suggested that the volume of the shell roughly doubled after ecdysis. Later work has upheld the general validity of these hypotheses and the position has been summarized by Kesling (1953).

All available specimens of *N. leioderma*, including both left and right valves in complete specimens, were measured and the results were plotted in a simple height: length graph (text-fig. 4). Four hundred and one valves from Spitsbergen were measured and showed the presence of five instars including the final adult stage, disposed in an extremely compact pattern indicating a single interbreeding community. Material from other localities in some cases falls within the size limits of Spitsbergen instars, and in others well outside. This seems to indicate that communities of one species in different localities may have different absolute measurements with regard to a particular instar and that the result of plotting more equal numbers of specimens from different localities would be to blur the sharpness of the graph. By taking the modes of the various instars it is possible to calculate the average increase in length from instar 5 to the adult, this increase being successively 1·254, 1·238, 1·247, and 1·239. The constancy of these values is enough to indicate the general truth of Brooks's Law in respect of this species. The average value for the increase in size at ecdysis is 1·2445 and this figure was used to work out the hypothetical early instar sizes shown in text-fig. 4. It differs slightly from the generalized value of 1·25992 given by Kesling (1953, p. 105).



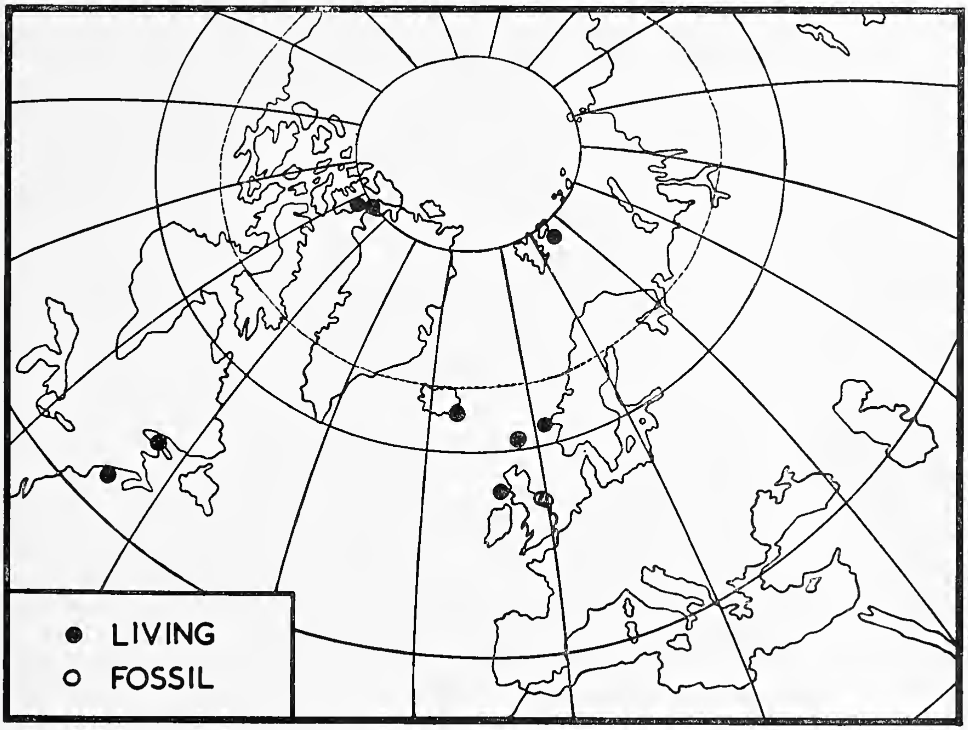
TEXT-FIG. 4. Graph showing the size distribution of carapaces in *N. leioderma*.

It is suggested on text-fig. 4 that altogether there are nine instars in the full life span of *Normanicythere leioderma*. Obviously this conclusion is tentative and can only be verified by breeding living material. There is little data to indicate the average size of the first instar in closely related forms but the value of about 0·18 mm. length postulated here is not inconsistent with the figures given by Elofson (1941, p. 378) for such forms as *Cythere lutea* (0·156 mm.) and *Cyprideis littoralis* (0·150 mm.).

In *N. leioderma*, due to its shape, the volume $\simeq \frac{1}{2}$ length × height^2; and when the values obtained by using this formula are plotted graphically (graph not shown here) there is a close approximation to the curve $V_2 = 2V_1$ (Przibram's Law).

Distribution

N. leioderma is characteristic of marine conditions and Elofson (1941) has recorded that it is unknown where the salinity falls below 26 to 30 parts per thousand. Its distribution (text-fig. 5) shows it to be an essentially cold-water species, and as early as 1891 Norman (p. 120) included it in his list of Arctic species. The living form occurs rather rarely on the eastern side of the Atlantic. Norman (1869) obtained nine specimens (the type material) from 'very deep water' in Unst Haaf, Shetland; and a single specimen (also in the British Museum) from 50 to 60 fathoms in Solems Fiord, Norway (Brady and Norman 1889, p. 111). Norman (1891, p. 111) further localizes this latter as 'Flöro'. A search of the 1:200,000 Ampt maps of Norway revealed no Solems Fiord. There is in fact no Sulen Fjord shown, but Sulen on the north side of Sognesjöen lies just north of Flöro and presumably Norman's locality is in its vicinity. Elofson only found this species at one station in the Skaggerak (58° 18′ N. 10° 49·5′ E.), where he obtained four valves. Hitherto this has been thought to be its southern limit on this side of the Atlantic, but three specimens (mature male and female left valves, and an



TEXT-FIG. 5. Distribution of *Normanicythere leioderma* (Norman).

immature male right valve) from Portree, Skye (57° 25′ N.), have now been found in the Hancock Museum, Newcastle. The slide is labelled '79' (presumably 1879) and as Norman, Brady, and Robertson were all actively working at this time it is puzzling that this record should have been overlooked, particularly in view of Brady and Norman's (1889) meticulous locality lists.

In the western Atlantic, on the other hand, *N. leioderma* has been recorded as the most abundant species in the Gulf of St. Lawrence dredgings described by Brady (1870, p. 452), and it seems common in Iceland and eastern Ellesmereland (Brady and Norman 1889). In the latter region it occurs at Cape Frazer, Grinnell Land (79° 44′ N.), in 50–80 fathoms; off Victoria Head, Bache Island, in 35 fathoms (Brady 1878, p. 254); and in Dobbs Bay (79° 35′ N.) [Dobbin Bay in *The Times Atlas*, 1922 edition] in 46 fathoms. Klie (1929, p. 19) gives Spitzbergen, which Elofson clarifies as König Karl Land (= King Charles Land also known previously as Wiches Land *v.* Conway 1897) and Stephensen (1938, p. 10) also gives west Greenland. Farther south on the west side of the Atlantic it has been recorded from Mount Desert Island, Maine (Blake, 1933, p. 239), where it was found twice in mud in 10 to 40 feet of water.

Fossil records are rare and *N. leioderma* has not yet been found outside Yorkshire. Brady (1870, p. 452) records seeing a single fossil valve from the Scottish glacial clay but there is no reference to this in the Post-Tertiary Entomostraca monograph of 1874 of which he is one of the authors. There is indeed only one single valve in the whole monograph and this is from the 'Bridlington Crag'. However, as the monograph is concerned mainly with the Scottish glacial deposits it seems certain that Brady had this particular specimen in mind in his 1870 reference, and that the locality he gives there represents a slip of the pen. The Dimlington Cliffs some thirty miles south of Bridlington show the most complete section of drift deposits on the Yorkshire coast, and here it occurs in the Sub-Basement Clay which also contains a large fauna of cold-water Mollusca, Foraminifera, and other Ostracoda. This blue sandy clay is the lowest bed of drift seen on the coast. It appears in the cores of a number of small folds or anticlinal flexures and is overlain by Newer Drift (see Bisat 1939*a* for full succession). The 'Bridlington Crag' was seen at Bridlington before the promenade was built but is not now exposed in any convincing section. The term seems to have been applied rather loosely to deposits which were not necessarily of the same age, but which were all overlain by boulder clay. Without entering into a detailed discussion on the correlation between the two areas and the problems involved, it may be said that the deposit which yielded the single right valve at Bridlington is probably identical with the Dimlington bed.

Seguenza (1884, p. 51) recorded a single valve from the Quaternary of Rizzolo in Sicily. Professor Ruggieri kindly informs me that all Seguenza's material was lost during the earthquake of 1908 and that he himself has never found it in the Sicilian Pleistocene or seen any examples of it—fossil or living—from the Mediterranean area. Seguenza's record, if true, would extend the range of this species over a thousand miles south of its present known southern limit on this side of the Atlantic, and in view of this and the information supplied by Professor Ruggieri the Sicilian record is regarded as erroneous.

Blake (1933, p. 239) found this species on a mud bottom, but Elofson (1941, p. 304) dredged his Skaggerak (Koljefjords) specimens from a sand bottom. The specimens from Portree, Skye, were filled with fairly coarse glauconitic sand while those from Unst Haaf had a glauconitic silt infilling and the Dimlington Pleistocene specimens came from a sandy clay which contains a proportion of glauconite. This suggests that while this species prefers a sandy bottom, the nature of the bottom is not critical.

It is proposed to deal with the microfauna of the Pleistocene Sub-Basement Clay at Dimlington in a subsequent paper, but it may be mentioned here that among the associates of *N. leioderma* in this deposit are the typical coldwater ostracods *Cytheridea papillosa* Bosquet, *Krithe glacialis* Brady, Crosskey, and Robertson, *Heterocyprideis sorbyana* (Jones), *Trachyleberis dunelmensis* (Norman) and varieties, and *Elofsonella concinna* (Jones).

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Repositories. B.M.—British Museum (Natural History); H.M.—Hancock Museum, Newcastle upon Tyne; H.U.—Hull University; R.S. 996—Naturhistoriska Riksmuseets Evertebratavdelning, Stockholm. The latter number is followed by the author's dissection and slide numbers.

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ENGLISH APTIAN TEREBRATULIDAE

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ABSTRACT. Terebratulidae from the English Aptian are systematically revised and their external and internal characters investigated, the latter chiefly by means of serial sections and dissections. Some new terms are introduced, notably for the hinge plates, and others redefined. Five new genera are proposed: *Rhombothyris* (type sp. *Terebratula extensa* Meyer), *Platythyris* (type sp. *P. comptonensis* nov.), *Sellithyris* (type sp. *Terebratula sella* J. de C. Sowerby), *Cyrtothyris* (type sp. *Terebratula depressa* var. *cyrta* Walker), and *Praelongithyris* (type sp. *P. praelongiforma* nov.). These genera show some uniformity in the absence of reversed plication and of convex hinge plates, the types of hinge plate present being the horizontal, concave, and virgate. The cardinal process throughout is relatively small and the loop relatively short.

Three main stratigraphical conclusions are drawn: (*a*) Aptian and Albian terebratulid faunas are clearly distinct; (*b*) Upper Aptian and Lower Aptian terebratulid faunas can be distinguished in England; (*c*) the Aptian fauna of England is very distinct from that of north-west Europe.

INTRODUCTION

THIS paper is based primarily on museum collections, especially those of London, Cambridge, and Paris, supplemented where possible by field collecting.

Terebratula sella J. de C. Sowerby (1823) was the first species from the English Aptian to be described. Sowerby (*in* Fitton 1836) also described *T. praelonga*. Little further was done in Britain until Davidson (1852–5; 1874; 1884) published his monograph, which still remains the standard work of reference. Other workers who contributed to the study of the group were Meyer (1864), Walker (1867; 1868; 1870), Keeping (1883), and Sahni (1929).

The techniques used have been based on those of Muir-Wood (1934; 1936; 1953), Buckman (1918), and Elliott (personal communication), and consist of serial sectioning, dissection with needles, grinding and dissection combined, and Buckman's burning method of exposing muscle impressions.

Measurements throughout the paper are given in millimetres. The transverse sections have been selected to illustrate, as far as possible, the diagnostic characters of the cardinal process, hinge plates, crura, and transverse lamella of the loop. Copies of all the complete series of sections have been deposited at the British Museum (Natural History). The sections are numbered to give the distance in millimetres from the ventral umbo.

Repositories of specimens are indicated as follows: BM, British Museum (Natural History); SM, Sedgwick Museum, Cambridge; GS, Geological Survey, London; CWW, C. W. Wright's collection, London.

Terminology. The terminology of Thomson (1927) and Muir-Wood (1934; 1936) is used with certain modifications. Definitions given refer only to terms which are new, or of which the connotation has been slightly altered, or which are thought to require further elucidation.

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Terms relating to the general shell shape

Orientation. All directions are given with the antero-posterior axis vertical, the umbo uppermost.

Anterior and posterior length. The posterior length is that part of the line of maximum length which lies posterior of the line of maximum width; the anterior length is the corresponding part anterior of that line. The ratio posterior length/anterior length is the *P/A ratio*.

Cardinal and lateral slopes. The cardinal slopes are those parts of the ventral profile which lie between the umbo and the line of maximum width. The lateral slopes are those parts of the ventral profile which lie between the line of greatest width and the outer corners of the median plica. (*Arêtes cardinales* and *arêtes latérales* of d'Archiac 1846.)

Folding. When a shell is thrown into longitudinal ridges and furrows it is described as folded. In either valve of the shell the ridges are referred to as *folds* and the furrows as *sulci* (see plication).

Plication. When the anterior commissure of a shell is thrown into undulations it is said to be plicated. An undulation towards the ventral side is a *sinus*, one towards the dorsal side a *plica*. These do not necessarily imply the presence of folds and sulci on the valve.

The terms used for combinations of sinuses and plicae are those of Buckman (1918) as restated by Thomson (1927) and Muir-Wood (1934; 1936), but some need further explanation when applied to Aptian forms:

Sulciplication, parasulcation, and episulcation. According to Buckman the sulciplicate stage consists of a sinus formed in the centre of a uniplica, the parasulcate stage of sinuses formed on either side of a uniplica and the episulcate stage of sinuses formed on either side and also in the centre of a uniplica. These definitions are easy to follow if the lateral commissure is plane but in most Aptian terebratulids it is strongly arched ventrally. In this case the terms parasulcate or episulcate have not been used unless there is a lateral sinus present which can be distinguished from the general arch of the lateral commissure.

Quadriplication. This term is used only where four plicae in the sense defined above can be counted.

Profile. The ventral profile is the outline of the shell in ventral view. The lateral profile is the outline of the shell when viewed from the side.

Terms relating to the beak

Beak. That part of the pedicle valve which lies posterior to the extreme posterior end of the brachial valve.

Beak angle. This has been measured by looking at the lateral profile of the shell, with the *commissural plane* vertical, this commissural plane being defined as the plane containing the dorsal umbo and those points on the anterior commissure which come midway between the summits of the highest plicae and the bases of the lowest sinuses. In this view the line bisecting the beak can be seen to make an external angle with the commissural plane, defined as the beak angle (text-fig. 1).

It has been customary to describe the beak as straight, erect, sub-erect, or incurved according to the beak angle, but these terms have been defined in different ways and used in almost opposite senses by different authors. In specific descriptions the terminology used here for the beak follows that of Thomson (1927) but the terms have been more rigidly defined, thus: *straight*, beak angle 0–20°; *nearly straight*, 20–30°; *sub-erect*, 30–70°; *erect*, 70–90°; *incurved*, more than 90°.

Produced. A produced beak is one that protrudes markedly beyond the posterior end of the brachial valve but is narrow and conical. 'Produced' is not synonymous with 'long', since a long beak may also be broad, but quite a short beak may be produced.

Umbo. The extreme posterior end of a valve. The true umbo is not usually visible in terebratulids, since that of the brachial valve is usually just hidden by the anterior border of the symphytium and that of the pedicle valve is, except in hypothyrid types, perforated by the foramen. It seems permissible, however, to refer to the most posterior visible part of the valve as the umbo.

Angle of Truncation. The angle made by the intersection of the plane containing the rim of the foramen with the lateral profile of the pedicle valve in the umbonal region.

Terms relating to the cardinalia

Hinge plates. The following terms are introduced to describe the types of hinge plates found: *concave*, hinge plate curved, concave towards the pedicle valve; *virgate*, hinge plate V-shaped in cross-section, concave towards the pedicle valve; *horizontal*, hinge plate not curved but flat, more or less parallel to the commissural plane; *keeled*, part of the hinge plate is produced into a sharp edge, projecting dorsalwards; *tapering*, hinge plate becomes thinner inwards, its inner margin sharp; *clubbed*, hinge plate becomes thicker inwards, its inner margin in particular thickened and blunt or rounded; *piped*, hinge plate becomes thinner inwards but its inner margin is finished off with a narrow rounded thickened rim. A virgate hinge plate is divisible into two parts, the outer lamina from the socket ridge to the virgation and the inner lamina on the inner (median) side of the virgation. In text-fig. 1 these terms are illustrated diagrammatically as seen in transverse section.

Flange. In some species the inner lamina of the hinge plate passes anteriorly into the crural process while the outer lamina continues anteriorly along the outer side of the base of the crural process as a *flange*. This flange may not be attached to the base of the crus but slightly above it so that the crus extends below the flange as a *crural keel*. In some species the keel can be traced back into the carinalia, giving a keeled hinge plate, while in others it is developed only in the region of the crura (text-figs. 1 and 14).

GENERAL CHARACTERS OF ENGLISH APTIAN TEREBRATULIDAE

Shell-shape and plication. All species are biconvex in the adult stage, varying from elongated to transverse and from depressed to highly compressed. The shell is usually folded to some extent.

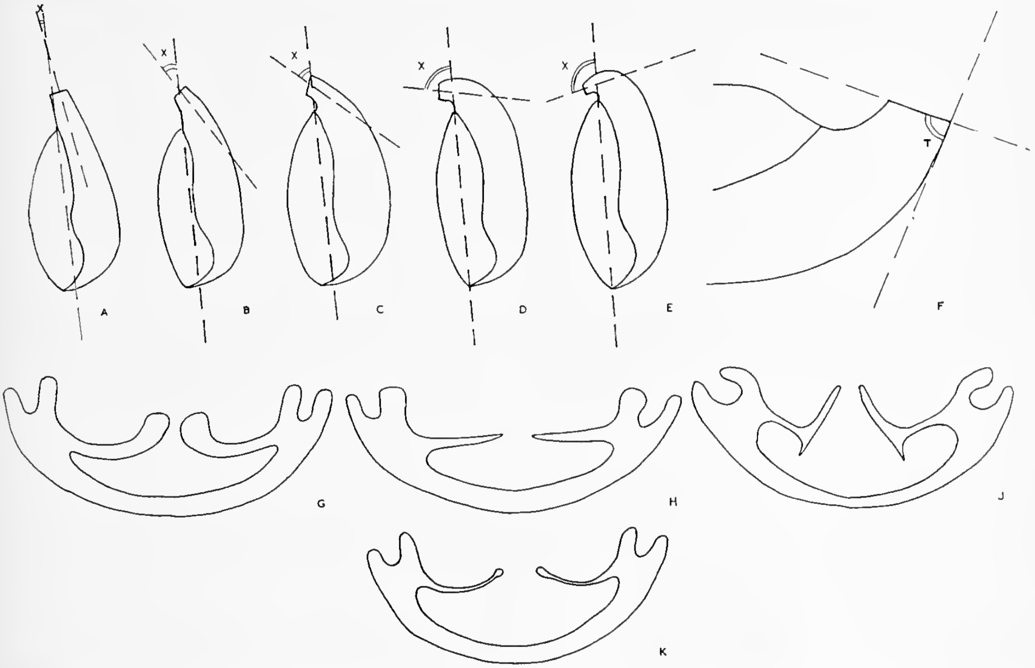
In the anterior commissure reversed plication of the intraplicate, paraplicate, or antiplicate types is never present in British species, although characteristic of a few European Lower Cretaceous species. The types of plication which may occur are the rectimarginate, sulcate, uniplicate, sulciplicate, parasulcate, episulcate, and quadriplicate stages (Thomson 1927, p. 58). The development of the commissure during ontogeny does not always follow the lines indicated by Buckman; for example, he regarded both the sulciplicate and the parasulcate stages as derived through a uniplicate phase but on different lines of development, of which the parasulcate can lead to the episulcate stage by the formation of a sinus in the median plica. In *Sellithyris sella*, however, both sulciplicate and parasulcate stages occur as variants of the one species and are both reached not through a uniplicate stage but directly from the rectimarginate. Muir-Wood (1936) notes a similar case in *Wattonithyris*. The sulciplicate stage is the commonest among the Aptian terebratulids but *Sellithyris* becomes episulcate through the addition of lateral sinuses to the sulciplicate stage. Quadriplication is found only in gerontic individuals of *Sellithyris upwarensis* and even there rarely; it is reached by adding external plicae to the lateral sinuses of the episulcate stage.

The shell is smooth, except for growth lines of variable prominence. Faint closely spaced radial striations are present, not visible on the outside of the shell and hence not to be confused with capillation, but often visible on specimens which have the outermost layer of shell worn away and upon calcite internal casts; these striae are not diagnostic of any particular species but are present in all Aptian species examined.

Beak and foramen. The beak angle lies between straight and erect, the former being rare. The foramen is in nearly all cases marginate but not labiate except in *Praelongithyris* and occasionally in *Cyrtothyris*. Forms with short beaks, such as *Rhombothyris*, have an attrite foramen.

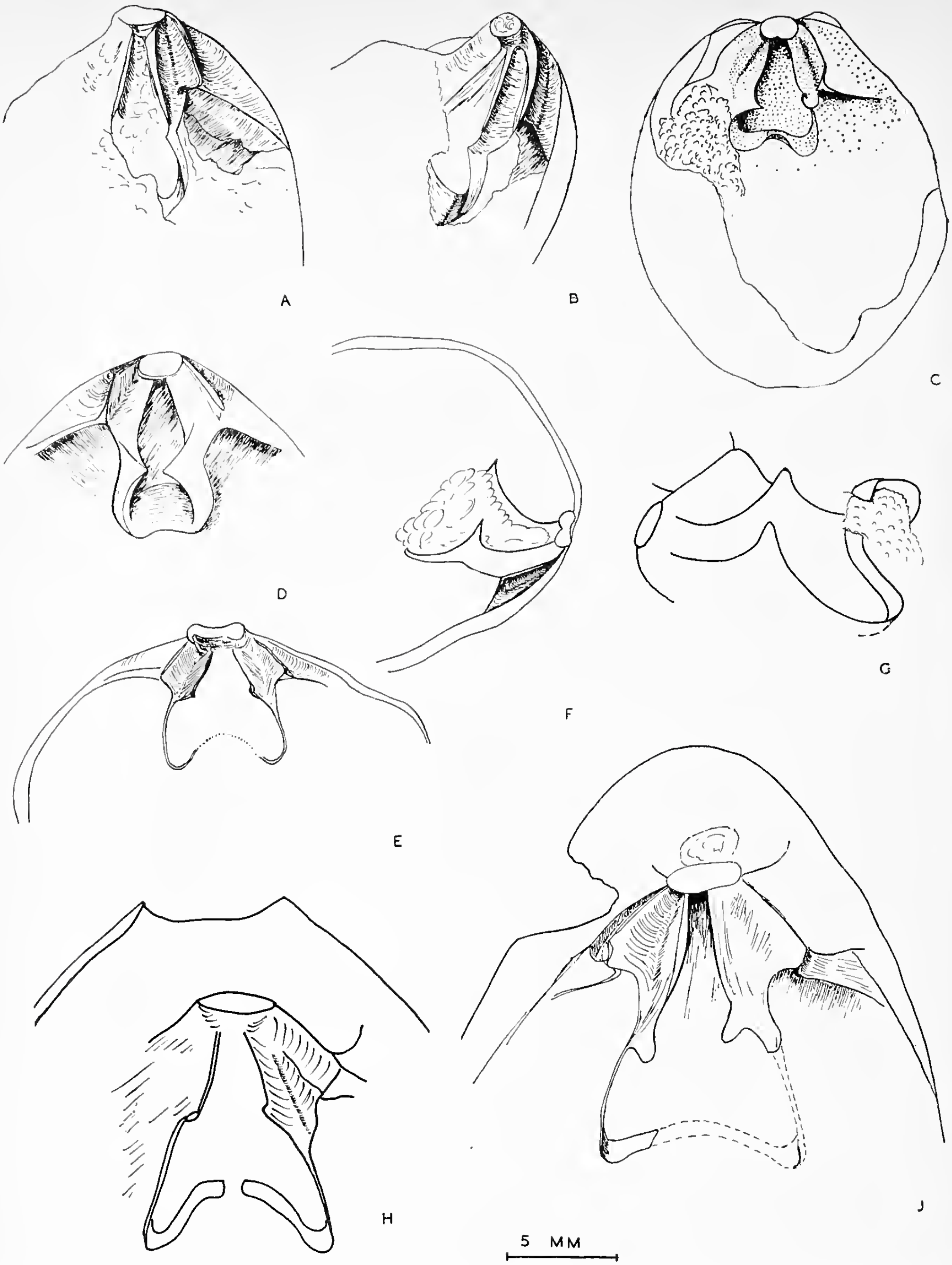
The interior of the brachial valve. The cardinal process is always present but is typically small compared with that seen in some Upper Cretaceous genera. The hinge plates are continuous with the base of the cardinal process and are divided throughout.

Callus is usually deposited at the junction of the cardinal process with the hinge plates and enables the originally small cardinal process to keep pace in growth with the growth of the shell. The callus is punctate, its outward growth taking place in an irregular manner so that the outer boundary of the callus frequently presents an indefinite, furry appearance in section. The cardinal process is thus enlarged by callus deposition so that it comes to enclose the posterior ends of the hinge plates, but since the callus is less dense than the primary shell material the incipient hinge plates and sockets may sometimes be distinguished, enclosed by callus, in the transverse sections (text-figs. 7, 20).



TEXT-FIG. 1. A–E, The Beak Angle (X). A, Straight beak; B, nearly straight; C, sub-erect; D, erect; E, incurved. F, The Angle of Truncation (T). G–K, Terms relating to the hinge plates. Diagrammatic representations of transverse sections through terebratulids with G, concave clubbed; H, horizontal tapering; J, virgate keeled; K, concave piped hinge plates.

The divided hinge plates are in no cases convex and are horizontal in very few species, most forms possessing concave or virgate hinge plates. The crural processes are direct continuations of the hinge plates and are blade-shaped structures, commonly bending inwards and anteriorly towards their pointed distal ends. The loop has the same general shape in all species, directly continuing the crural bases which distally become concave inwards and at their distal extremities become recurved to form the transverse lamella in such a way that the inner surface of the descending lamella is continuous with the outer surface of the transverse lamella, no ascending lamella being present. The loop is short—in all species less than half the length of the shell—the ratio between total length of shell and the distance from the dorsal umbo to distal end of loop varying from 2·09 in *Praelongithyris praelongiforma* to 3·17 in *Sellithyris coxwellensis*. The ratio between the total



TEXT-FIG. 2. Camera lucida drawings of dissections of Aptian terebratulids. A, B, *Rhombothyris extensa* (Meyer), showing cardinalia and part of the loop; B, seen obliquely. SM B.80770, Brickhill, Bucks. C, D, *Platythyris comptonensis* nov., showing cardinalia and loop. C, SM B.80768, Brickhill; D, SM B.80766, Upware. E, F, *Sellithyris sella* (J. de C. Sowerby), showing cardinalia and loop (loop partly restored; F, seen obliquely. BM BB.16206, Ferruginous Sands, Atherfield, Isle of Wight. G, H, *Cyrtothyris cyrta* (Walker), showing hinge plates, crura and loop (incomplete), BM BB. 16242, Upware, Cambs. G, seen obliquely. J, *Praelongithyris praelongiforma* nov., showing cardinalia and loop (incomplete). SM B.80779, Upware.

width of shell and the maximum width of loop varies from 2·60 in *Rhombothyris extensa* and *Cyrtothyris dallasi* to 4·66 in *Platythyris comptonensis*.

The inner socket ridges are continuous at their posterior ends with the cardinal process and tend to be large and massive, especially in *Rhombothyris*. The teeth and sockets are never crenulate; denticula and accessory sockets are sometimes present but are developed to varying degrees within one species. The angle of insertion of the teeth varies within one species according to the proportions of the shell, thicker and more compressed variants having teeth at a greater angle to the commissural plane than thinner, more depressed forms. The median dorsal septum or 'euseptoidum' (Muir-Wood 1934, p. 529) is constantly well developed only in *Platythyris*; where present in other genera it is usually most marked between the widest parts of the dorsal muscle scars. The muscle scars are seldom very clearly visible, especially those in the pedicle valve; the impressions are not deeply incised into the floor of the valve except in *Rhombothyris*, and in nearly every case it is very difficult to distinguish the posterior adductors, as Buckman (1918) remarks apropos of Cretaceous terebratulids.

SYSTEMATIC DESCRIPTIONS

Introductory. Genera. The chief characters used in dividing the Aptian Terebratulidae into genera are internal. The English species are divisible into genera based primarily on the form of the hinge plates, crura and loop and the shape and relationships of the dorsal muscle scars. These characters can in most cases be correlated with external characters such as the form of the beak and the ontogeny of the shell shape, especially of the plication.

The generic classification adopted here was foreshadowed to some extent by Keeping (1883, p. 23) in a table based entirely on external appearance of the species. The grouping shown in his table, which was not intended to be phylogenetic, has been broadly confirmed by study of the internal characters except that Keeping regarded the *microtrema-extensa-meyeri* series (*Rhombothyris*) as closely related to '*Terebratula praelonga*' (*Praelongithyris*).

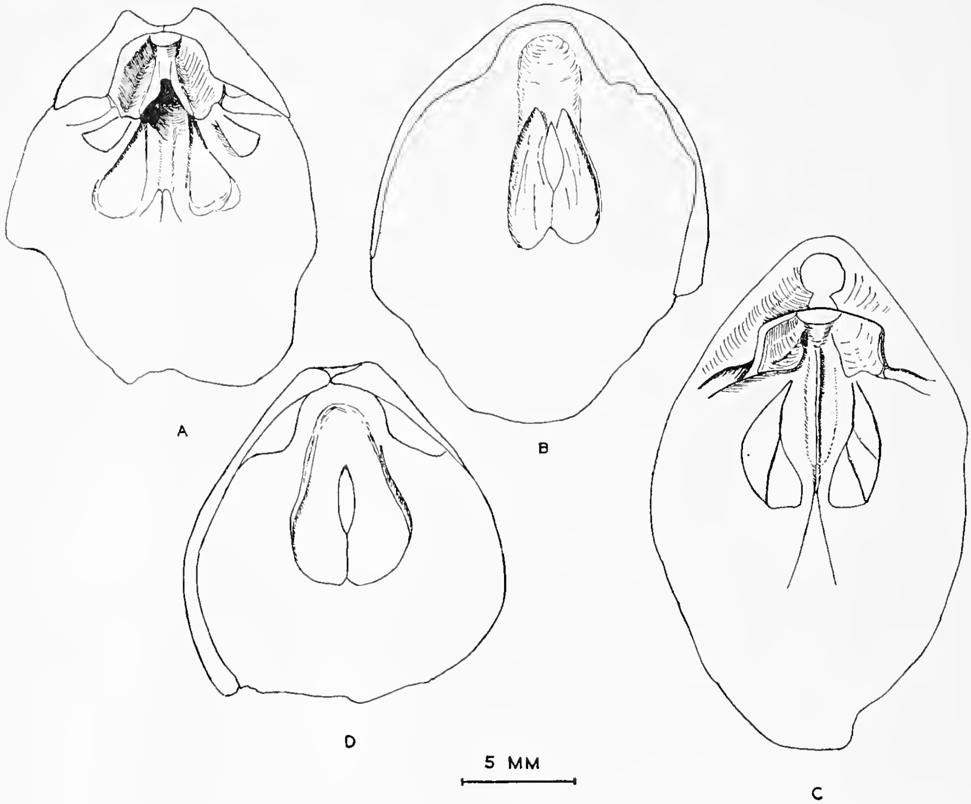
Species. Specific diagnosis is based mainly upon external form, including in particular: characters of the beak, such as length, angle, and degree of production; sharpness of the beak ridges; size, shape, and distinctness of the symphytium; size of the foramen, its position relative to the beak ridges and the angle of truncation; P/A ratio; course of the lateral commissure; development of plication; degree of folding of the shell; type of shell ornamentation.

Internal characters may assist in specific classification, for example the proportions of the hinge plates relative to the size of the shell, the relations of the crural flange and keel to the crura and hinge plates, and the degree of incision of the dorsal muscle scars.

Genus RHOMBOTHYRIS gen. nov.

Type species *Terebratula extensa* Meyer 1864

Diagnosis. Beak very short, nearly straight to sub-erect. Beak ridges poorly defined except immediately adjacent to the foramen. Foramen mesothyrid, attrite, somewhat marginate; angle of truncation 105–110°. Symphytium very short. Shell elongate–oval. Development of anterior commissure rectimarginate to sulcate or rectimarginate to uniplicate, thence to sulciplicate.



TEXT-FIG. 3. Camera lucida drawings of muscle impressions in Aptian terebratulids. A, *Rhombothyris extensa* (Meyer), interior of brachial valve with hinge plates *in situ* but crura and loop removed. The posterior and anterior adductor scars are separate. BM BB.16236, CWW Coll., Bargate Beds, Compton, Surrey. B, *Rhombothyris extensa* (Meyer), interior of pedicle valve, showing adductor, diductor and ventral pedicle adjustor scars. BM BB.16237, CWW Coll., Bargate Beds, Compton, Surrey. C, *Platythyris comptonensis* nov., last stage of dissection showing interior of brachial valve and part of pedicle valve, crura and loop removed and hinge plates incomplete. The strong euseptoidum shows well; the posterior and anterior adductor scars are closely adjoined. BM BB.16238, CWW Coll., Bargate Beds, Compton, Surrey. D, *Platythyris comptonensis* nov., interior of pedicle valve, showing adductor and diductor scars, the latter continuous with the ventral pedicle adjustor scar. SM B.80769, Brickhill.

Hinge teeth inserted at 40–70° to commissural plane; accessory articulation may be well developed. Hinge plates concave, clubbed. Inner socket ridges rather massive. Anterior adductor muscle impressions in brachial valve well incised; elongated pear-shaped. Posterior adductor impressions on postero-lateral sides of anterior adductors but very difficult to see. Euseptoidum absent or weakly developed.

Remarks. The name refers to the rhombic shape of the rim of the foramen in its usual attrite condition, the telate condition being very faintly indicated only in some very young individuals. No species from outside England have been seen which could be referred to this genus.

Rhombothyris extensa (Meyer)

Plate 15, figs. 1, 2; text-figs. 2–4

Terebratula extensa Meyer 1864, p. 252, pl. 12, figs. 1–4.
Terebratula extensa Meyer; Walker 1868, p. 404, pl. 18, figs. 5–5*a*.
Terebratula extensa Meyer; Davidson 1874, p. 43, pl. 5, figs. 22–24.

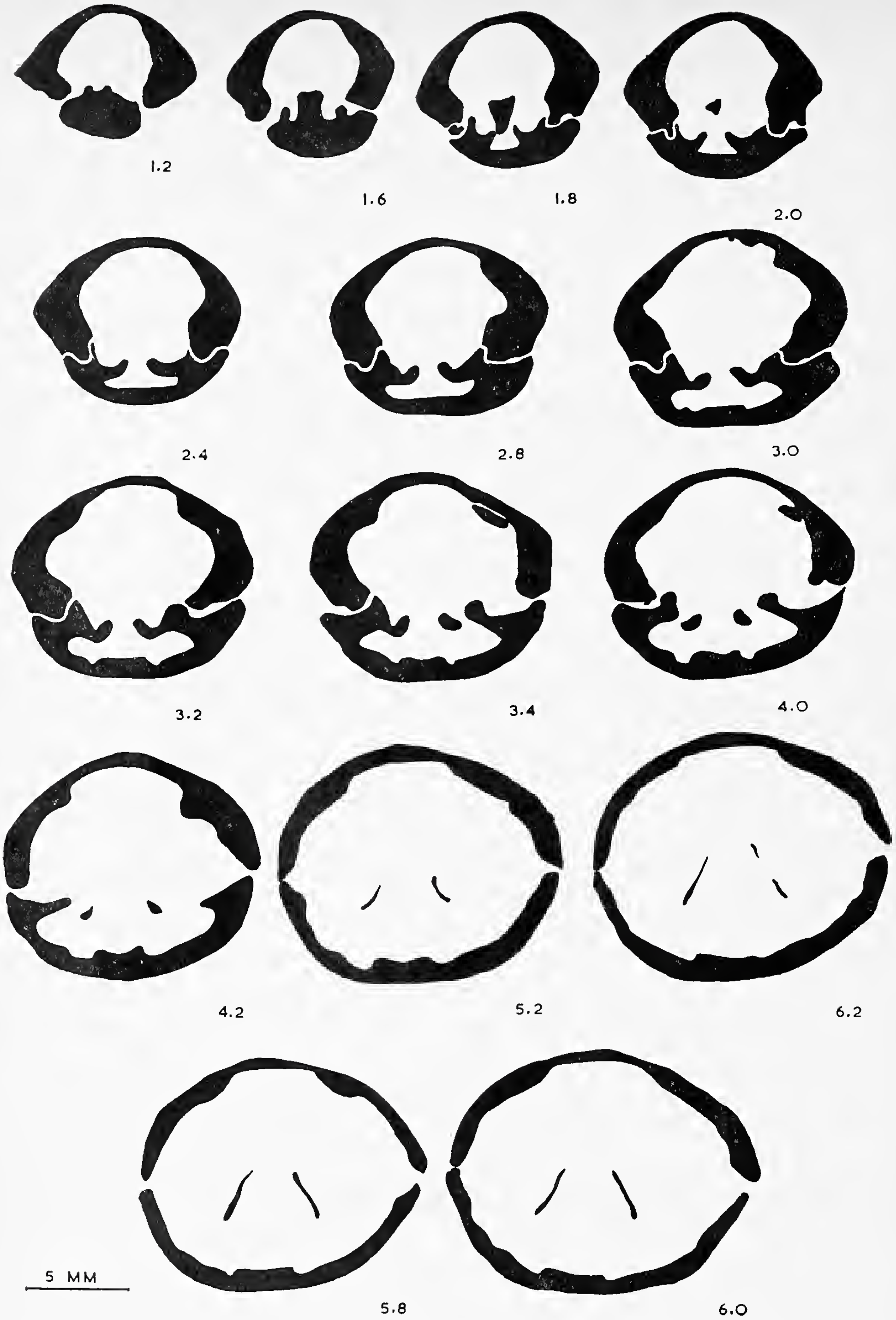
Type. Meyer's three syntypes SM B.16738–40. B.16739, Bargate Pebble Beds, Tuesley, Surrey, is chosen lectotype (dimensions: length 26, breadth 13, thickness 12).

Diagnosis. Elongate oval *Rhombothyris* with P/A ratio about 2. Brachial valve with greatest convexity near to umbo, pedicle valve regularly convex with maximum convexity about the centre. Beak nearly straight. Angle of truncation *c*. 105°; foramen attrite. Symphytium wide but short. Development of anterior commissure sulcate to rectimarginate to uniplicate, and to sulciplicate in some cases. Cardinal process oval. Inner socket ridges massive. In brachial valve anterior adductor muscle scars elongated pear-shaped; posterior portion of them deeply incised. Posterior adductor scars obscure smooth areas on postero-lateral sides of anterior adductors. Euseptoidum absent or poorly developed.

Description. In the typical uniplicate forms the brachial valve usually shows a low but distinct fold extending back about half the length of the valve, but there is no corresponding sulcus in the pedicle valve. On both sides of the fold the surface of the valve appears very slightly concave, giving a pinched appearance; in biplicate forms a shallow sulcus appears in the centre of the fold. A characteristic feature is the strong, sometimes almost bulbous convexity of the brachial valve near the umbo, but a median groove may be developed in this part of the valve; the groove is occasionally well developed, beginning about 1 mm. from the umbo and extending anteriorly about 5 mm. In lateral profile some individuals, particularly from the Bargate Beds, show a concavity in the anterior part of the brachial valve, the pedicle valve being carried down by the uniplication of the anterior commissure to form an overhanging beak.

In ventral profile the pedicle valve may be squarish anteriorly but many specimens are perfectly rounded. In many the pedicle valve is very slightly carinate at and near the umbo which, together with the frequent presence of a groove in the earlier-formed part of the brachial valve, suggests that the neanic stage of this species tends to be sulcate, although in the majority of individuals the sulcate stage is missing.

Remarks. Variation occurs in three main directions: (1) towards biplication by sulciplication—the biplicate forms sometimes resemble *R. microtrema* but differ from it in the feebler development of biplication, the absence of strong lateral compression and the absence of any anterior thickening; (2) towards loss of the uniplicate stage, giving a rectimarginate to slightly sulcate adult shell not easily distinguishable from *R. meyeri* but differing from that species in having a smaller foramen and in being less distinctly sulcate; (3) towards a broad oval form sometimes mistaken for '*Terebratula depressa*'



TEXT-FIG. 4. Transverse sections through *Rhombothyris extensa* (Meyer). The cardinal process (enlarged by callus) is seen in the first four sections, the concave clubbed hinge plates best at 3·0, the deep muscle impressions at 4·0, and the crural processes in the last three sections. BM BB.16235, CWW Coll., Bargate Beds, Compton, Surrey.

in the past but identifiable as *R. extensa* by the deep incision of, and form of, the dorsal muscle scars.

Distribution. Abundant at Upware and Brickhill and the commonest fossil in the Bargate Beds of Surrey. It is rare at Shanklin, in the '*Exogyra*' Beds, which Fitton (Sowerby 1836) correlated with Group XIII of the Atherfield coast section; a crushed specimen from Sevenoaks (BM B.21949) probably belongs to this species.

Rhombothyris microtrema (Walker)

Plate 15, figs. 3–5; text-fig. 5

Terebratula microtrema Walker 1868, p. 401, pl. 19, figs. 7–7*c*, 8–8*a*.
Terebratula microtrema Walker; Davidson 1874, p. 37, pl. 5, figs. 18, 18*a–c*, 21.

Type. Walker figured two specimens, of which that figured as pl. 19, fig. 7 (BM BB.16216), Upware, Cambridgeshire, is designated lectotype (dimensions: length 30, breadth 20·25, thickness 19).

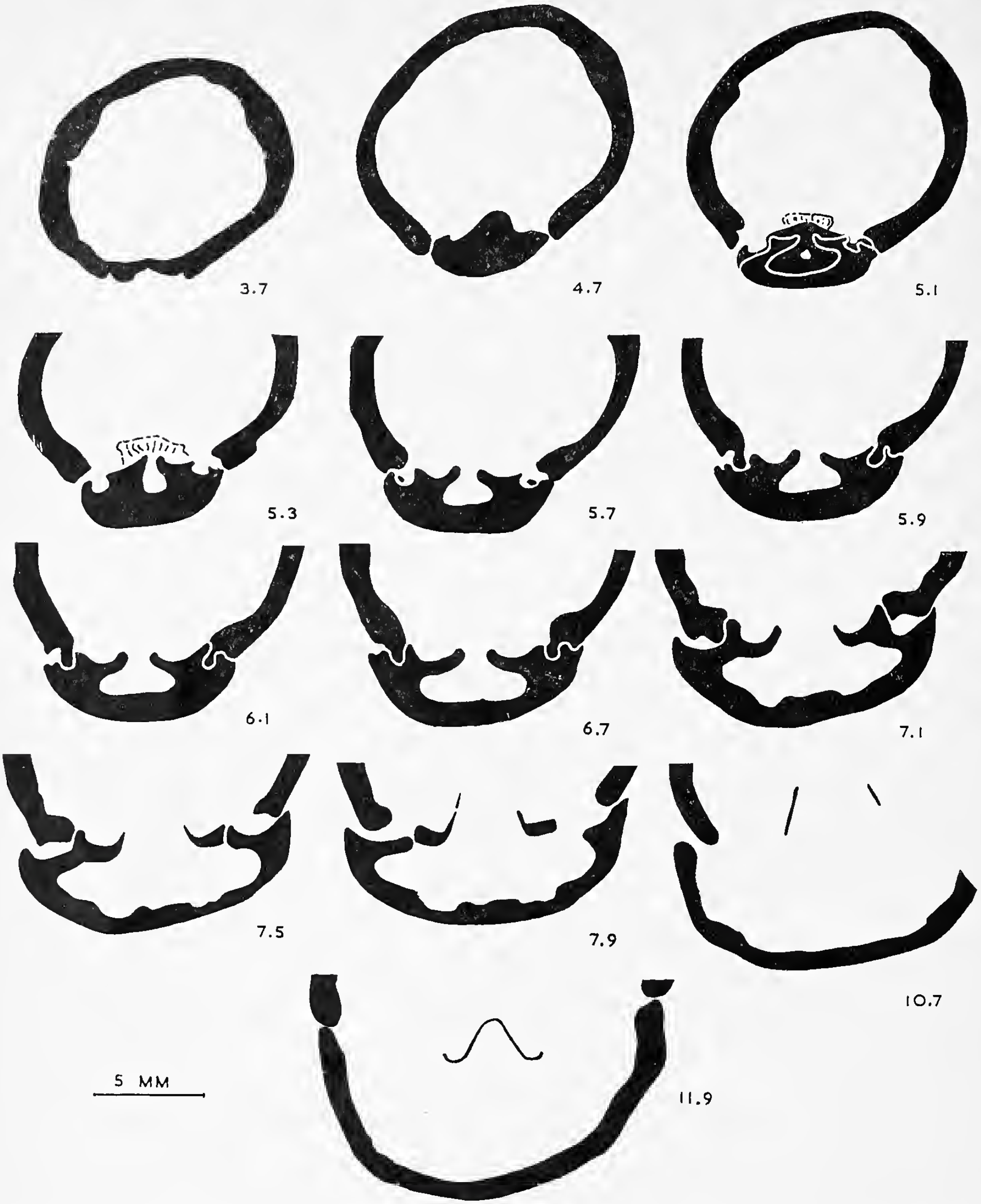
Diagnosis. Rhombothyris with ventral profile oval, truncated anteriorly, to rounded triangular. P/A ratio more than 2. Brachial valve has greatest convexity near umbo, strongly folded anteriorly. Pedicle valve very slightly carinate near umbo, posterior part of valve regularly convex, anterior part strongly folded. Both valves laterally compressed. Beak short, sub-erect. Angle of truncation *c.* 110°. Foramen attrite. Symphytium wide but short. Development of anterior commissure rectimarginate to uniplicate to strongly sulciplicate. Cardinal process oval. Crural processes high, reaching half-way to internal surface of pedicle valve. Loop narrower than space between anterior ends of inner socket ridges. Muscle scars deeply incised.

Description. The laterally compressed appearance, due to the vertical parallel or sub-parallel sides, is characteristic and may be sufficient to make the shell thicker than broad, especially in old individuals, which also show thickening of the anterior region. Young individuals are usually thinner in proportion to their breadth.

Although rare individuals do not pass beyond the uniplicate stage, sulciplication is typically well developed, with the apex of the median sinus reaching to or beyond the level of the lateral commissure. The plication of the commissure is typically reflected to some extent in folding of the shell, but this does not affect a very large part of the valves; thus in adult specimens not more than the anterior third of each valve is affected, usually less; in neanic specimens only the extreme anterior end is affected. Adult individuals are often deformed and asymmetrical.

Since grooving of the posterior convex part of the brachial valve has not been seen it seems that this species does not normally pass through a sulcate stage, if the doubtful premise that all changes during growth are retained in the adult shell be accepted.

Remarks. The chief variation is towards a uniplicate or only very slightly sulciplicate form with a resemblance to *R. extensa*. Some specimens in this condition have a concavity in the anterior part of the brachial valve as seen in lateral profile, giving a projecting beak-like appearance to the anterior end, as in some specimens of *R. extensa*. *R. microtrema*, however, is always thicker in proportion to its breadth than *R. extensa*



TEXT-FIG. 5. Transverse sections through *Rhombothyris microtrema* (Walker). 3·7 shows the symphytium, 4·7 the cardinal process. The hinge plates are enclosed by callus at 5·1 but are concave and clubbed at 6·1–6·7. The crural processes are seen at 7·9 and 10·7 and the transverse lamella of the loop at 11·9. SM B.80771, Brickhill.

and always shows some recognizable sign of the characteristic laterally compressed appearance.

R. microtrema is distinguished from *Praelongithyris praelongiforma* by its laterally compressed appearance and sub-parallel sides, its much blunter and less produced beak, its mesothyrid foramen and smaller angle of truncation. In addition the symphytium is much shorter and the folds and sulci affect a smaller proportion of the surface of the valves in *R. microtrema* than in *P. praelongiforma.*

Distribution. Abundant at Upware and Brickhill. Meyer's (1868*a*) specimens from the Bargate Beds (SM B.16773–8) are regarded as *R. extensa* and those from Shanklin (SM B. 14911–2) as *Praelongithyris praelongiforma* (Davidson 1874). The species has not been found at or from Faringdon, Meyer's record from there being based upon a single valve (Davidson 1874). Keeping's (1883) specimens from Schöppenstedt, Brunswick (SM F4617–18), appear to be long-looped.

Rhombothyris meyeri (Walker)

Plate 15, fig. 6; text-fig. 6

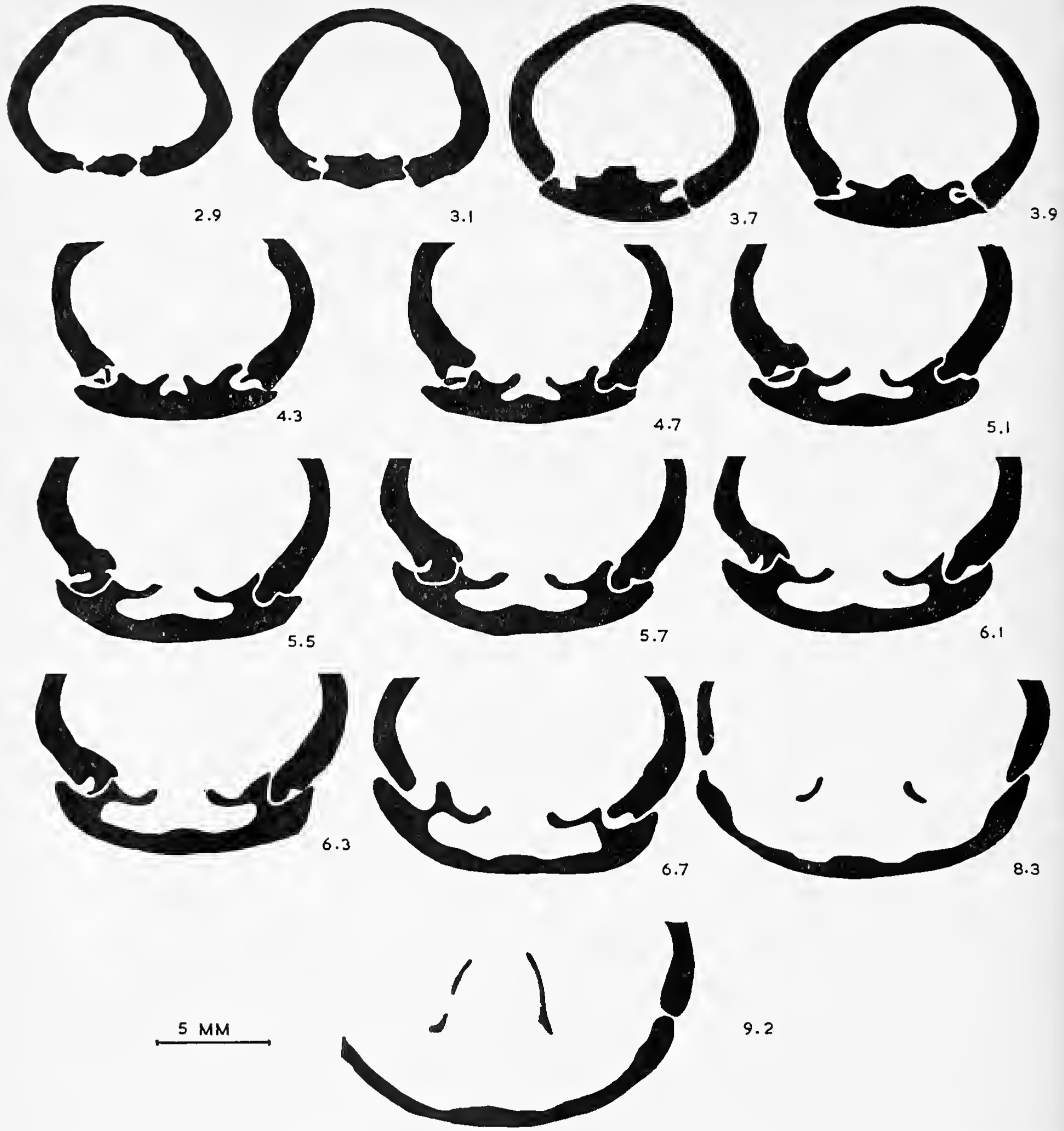
Terebratula meyeri Walker 1868, p. 401, pl. 19, figs, 6–6*b*.
Terebratula meyeri Walker; Davidson 1874, p. 44, pl. 3, figs. 6–8.

Holotype. BM 67598, Upware, Cambridgeshire (dimensions: length 36, breadth 28·5, thickness 20·5).

Diagnosis. Elongate oval *Rhombothyris*, squarely truncated anteriorly; P/A ratio about 1. Valves fairly regularly convex; greatest convexity of brachial valve about the middle, of pedicle valve slightly nearer the umbo. Pedicle valve very slightly carinate near umbo. Beak nearly straight. Angle of truncation *c.* 105°. Foramen large, transverse, attrite. Symphytium wide but very short. Development of anterior commissure rectimarginate to sulcate. Cardinal process prominent, slightly bifid. Loop of rounded triangular shape, width approximately equal to distance between anterior ends of socket ridges.

Description. The foramen is of the same type as that of *R. extensa* and *R. microtrema* but is larger and more transverse. In some ways the shell resembles that of *R. extensa* in reverse; in *R. extensa* the pedicle valve is regularly convex while the brachial valve is most convex near the umbo and develops a fold anteriorly, in *R. meyeri* the brachial valve is regularly convex while the pedicle valve tends to be most convex nearer to the umbo than half-way and develops a fold anteriorly. The brachial valve does not normally show a sulcus corresponding to the sinus in the commissure but more commonly has a fold which runs up into the sinus giving to the anterior end a characteristic 'bull-dog' appearance. Rare specimens may show a sulcus in the extreme anterior part of the brachial valve. The well-developed sulcate condition is seen only in fully adult or gerontic individuals, most specimens being rectimarginate and there is no trace of any grooving of the brachial valve such as is seen in *R. extensa*. Typically *R. meyeri* is marked by prominent concentric growth-lines which cluster at the anterior end of gerontic specimens to give it a blunt and thickened appearance.

Remarks. The typical form is characterized by its large transverse foramen, blunt



TEXT-FIG. 6. Transverse sections through *Rhombothyris meyeri* (Walker). The cardinal process (enlarged by callus) is seen in the first four sections, the concave clubbed hinge plates at 5·5–6·3 (the peculiar tooth structure here is probably pathological). The muscle impressions can be seen at 8·3 and the crural processes at 9·2. SM B.80772, Upware.

sulcate anterior, and well-marked growth-lines. The species is very close to *R. extensa* and an elongated rectimarginate individual of *R. meyeri* may resemble a rectimarginate variety of *R. extensa*, the essential distinction lying in the foramen. Typically, however, *R. meyeri* is broader in proportion to its length than *R. extensa*.

Thickened individuals may resemble *R. microtrema* but never show any biplication; in addition, in *R. microtrema* the foramen is relatively smaller and the sides of the shell more compressed. Blunt-fronted, almost rectimarginate varieties of *Praelongithyris praelongiforma* have been mistaken for *R. meyeri* but the foramen in the former is very different and the beak has quite a different shape. Within the typical forms of *R. meyeri* the relative proportions of length, breadth, and thickness undergo a certain amount of minor variation.

Distribution. R. meyeri was fairly abundant at Upware but has not been found at Brickhill. Specimens recorded by Meyer as rare in the Bargate Beds of Surrey have on re-examination been found to be *R. extensa.*

Rhombothyris conica sp. nov.

Plate 15, figs. 7, 8; text-fig. 7

Holotype. BM BB.16217 (Walker Coll.), Brickhill, Buckinghamshire (dimensions: length 32, breadth 22, thickness 19).

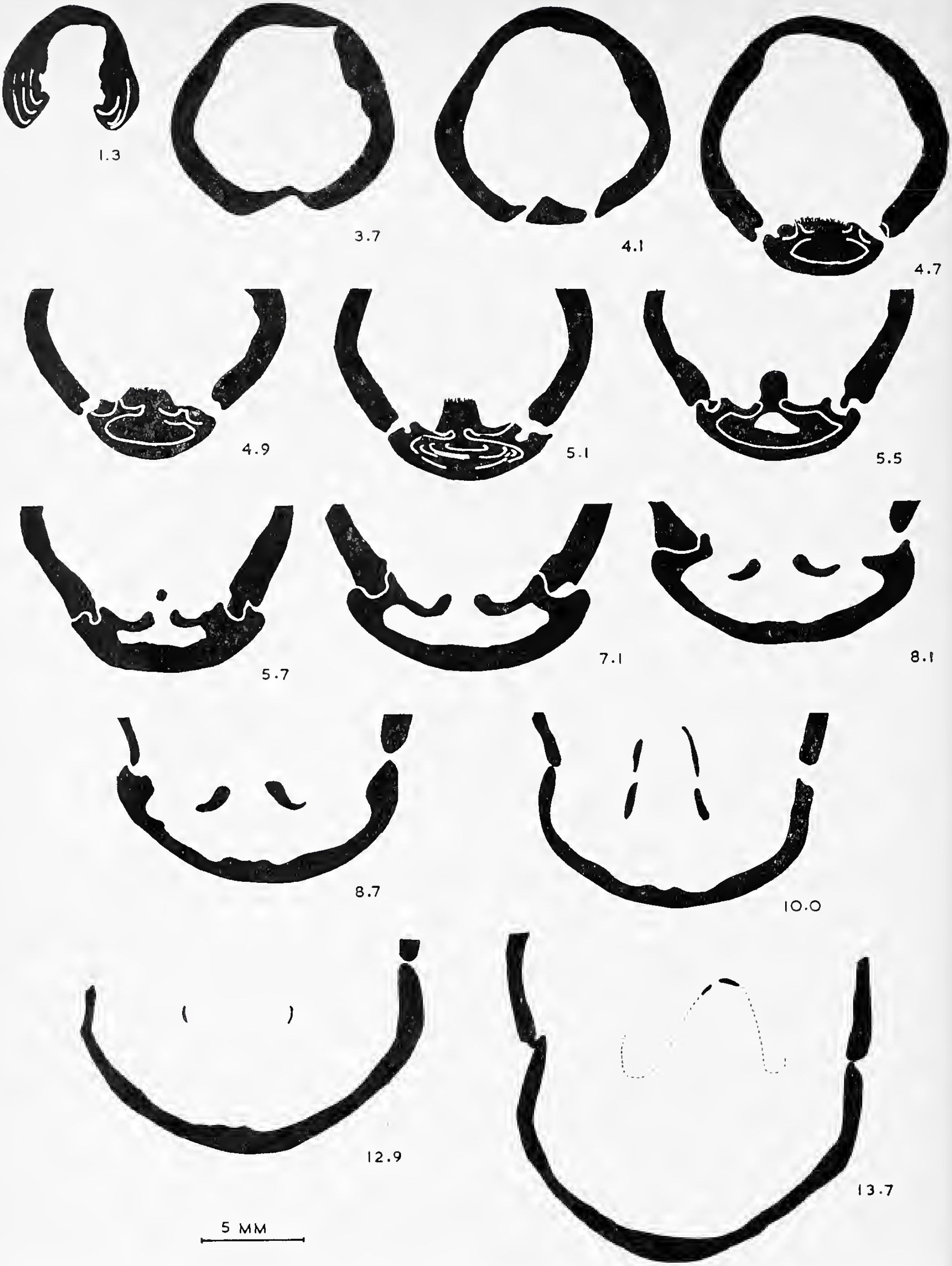
Diagnosis. Rhombothyris of oval ventral profile, more or less elongated. P/A ratio slightly greater than 1. Pedicle valve uniformly convex, brachial valve most convex in posterior half; greatest thickness slightly posterior to mid-line. Anterior commissure sulciplicate with sharp to angular median sinus, apex of which is level with lateral commissure. Beak short, nearly straight, rather narrow and conical; beak ridges rounded but visible. Foramen fairly small, circular, slightly attrite; angle of truncation *c.* 110°. Development of anterior commissure rectimarginate to uniplicate to sulciplicate. Cardinal process small, bifid.

Description. The distinctive characters of this species are those of the beak and foramen and the type of plication. Variation extends in two main directions: (1) towards a broad form, almost as broad as long and rather bluntly truncated anteriorly in ventral profile, tending to become obese in the posterior part of the brachial valve; (2) towards a thick form which may become thicker than wide while retaining the more typical elongated shape; this form tends to possess a more uniformly convex lateral profile in the brachial valve. The characteristics of the beak and the anterior commissure are retained.

Many neanic specimens are distinctly grooved in the posterior part of the brachial valve and carinate in the umbonal region of the pedicle valve, suggesting a nepionic sulcate stage, but no nepionic sulcate specimens have been seen and individuals of about 12 mm. long are uniplicate or rectimarginate; thus the grooving may be a subsequent modification.

Remarks. R. conica differs from *R. extensa* in the narrower and more conical beak and smaller foramen, the well-developed median sinus of the anterior commissure and the tendency to gerontic thickening, giving a slightly compressed appearance, and especially to gerontic thickening of the anterior part of the shell, not seen in *R. extensa.*

R. conica can be distinguished from *R. microtrema* in that the latter is more noticeably compressed, possesses better-developed biplication at an equivalent growth-stage (lacking the sharp emphasis upon the median sinus over the lateral plicae which *R. conica* shows), and has a slightly larger foramen and broader beak. From *R. meyeri* the chief points of distinction are: (1) *R. meyeri* is sulcate, *R. conica* sulciplicate as an



TEXT-FIG. 7. Transverse sections through *Rhombothyris conica* nov. The foraminal margin is shown at 1·3, the symphytium at 3·7, the cardinal process (enlarged by callus to enclose the hinge plates) at 4·1–5·5. The concave clubbed hinge plates can be seen at 7·1, the muscle impressions at 8·7, crural processes at 10·0, descending lamellae of the loop at 12·9, and transverse lamella at 13·7. BM BB.16200, Brickhill.

adult; (2) the shell of *R. conica* shows slight folding in the extreme anterior part, hardly ever seen in *R. meyeri*; (3) the beak is narrower and more conical and the foramen smaller in *R. conica* than in *R. meyeri*. From *Praelongithyris praelongiforma* this species differs in the characters of the beak and foramen and the shape of the anterior commissure.

Distribution. Brickhill only.

Genus PLATYTHYRIS gen. nov.

Type species *P. comptonensis* sp. nov. (= *Terebratula moutoniana* auctt. pars)

Diagnosis. Beak very short to fairly short, sub-erect; beak ridges rounded and ill-defined. Foramen mesothyrid to permesothyrid; angle of truncation 115–120°. Symphytium very short. Shell elongate, oval, or pear-shaped; maximum convexity posterior to mid-line. Development of anterior commissure rectimarginate to uniplicate, thence rarely to sulciplicate. Cardinal process small. Hinge plates horizontal, tapering. Crural processes strongly curved inwards. Loop short and compact, close beneath the crura; arch of transverse lamella low. In brachial valve posterior adductor scars ovoid, with outline concave inwards; anterior adductors triangular, continuous with posterior impressions on inner side of anterior ends of the latter. In pedicle valve adductors form one median elliptical scar. Diductors large, enclosing adductors, not clearly distinguishable from ventral pedicle adjustor scar, which forms a rounded depression. Euseptoidum very well developed and continuous from base of the cardinal process almost to the anterior end of the muscle scars.

Remarks. The name refers to the characteristic horizontal hinge plates. No species referable to the genus are known with certainty from outside England.

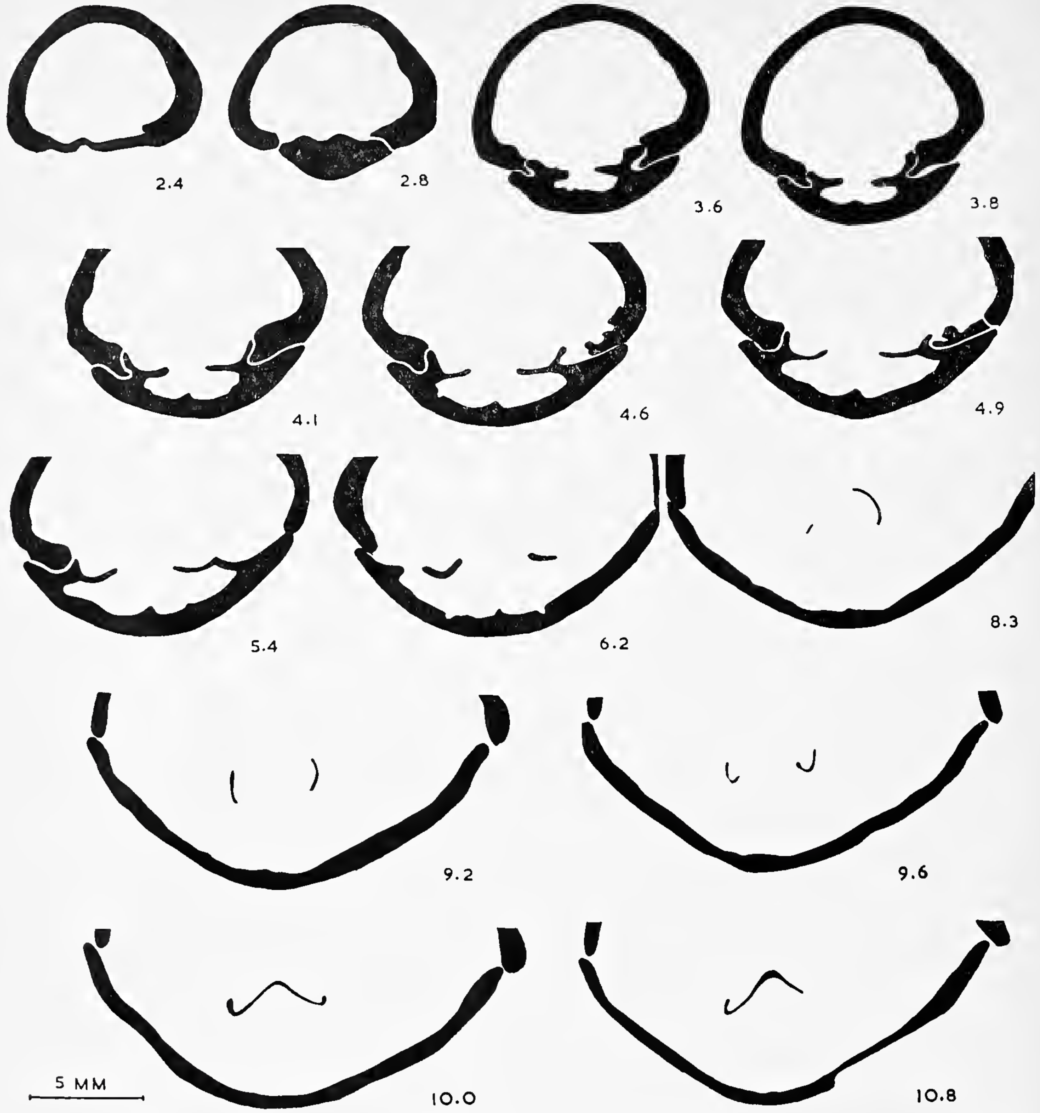
Platythyris comptonensis sp. nov.

Plate 15, figs. 9–11; text-figs. 2, 3, 8

Waldheimia moutoniana (d'Orb.); Meyer 1864, p. 251, pl. 12, figs. 14*a–c*.
Terebratula moutoniana d'Orb.; Walker 1868, p. 403, pl. 18, figs. 6–6*b*.
Terebratula moutoniana d'Orb.?; Davidson 1874, p. 42, pl. 4, figs. 11–13.

Holotype. BM BB.16230, Bargate Beds, Compton, Surrey (dimensions: length 24, breadth 16·5, thickness 13).

Diagnosis. *Platythyris* of elongated pear-shape in ventral profile. P/A ratio more than 1. Apical angle acute; cardinal slopes straight or very slightly convex, ventral profile anterior to line of maximum breadth a parabolic curve. Brachial valve uniformly convex but with a broad median fold in about the anterior third. Pedicle valve has maximum convexity distinctly in posterior half, anterior half somewhat flattened. Brachial valve more obese than ventral. Beak very short. Foramen fairly large, circular, slightly permesothyrid, usually attrite; angle of truncation *c*. 115°. Symphytium short. Lateral commissure much arched and anterior commissure strongly uniplicate. Development of anterior commissure rectimarginate to uniplicate. Cardinal process oval. Loop considerably narrower than space between anterior ends of socket ridges.



TEXT-FIG. 8. Transverse sections through *Platythyris comptonensis* nov. The symphytium is shown at 2·4, cardinal process at 2·8, horizontal tapering hinge plates at 3·6–4·9, strong euseptoidum at 3·8–8·3, incurved crural processes at 8·3, descending lamellae of the loop at 9·2 and 9·6, and the low-arched transverse lamella at 10·0–10·8. SM B.80767, Upware.

Description. This species has a very uniform and characteristic general shape, the main elements of which are: (1) the ventral profile, which is reminiscent of a triangle plus a parabola, representing the posterior and anterior parts respectively; (2) the lateral profile of the pedicle valve, the obese brachial valve seeming almost to enclose the pedicle valve by the strong arching of the lateral commissure; (3) the beak and symphytium characters.

Variations affect the relative proportions of length, breadth, and thickness, not the elements of the general shape just mentioned. Thus Upware and Brickhill specimens tend to be thicker (thickness up to 0·9 of breadth), specimens from the Weald to be wider and flatter. Brickhill specimens tend to be smaller, more elongated and narrower and more compressed anteriorly than those from any other locality.

Very rarely specimens from Upware and Brickhill have a slight median sulcus, giving a gerontic sulciplicate stage.

Remarks. This species has always been identified, with or without a mark of interrogation, with *Terebratula montoniana* d'Orbigny 1849, a species from the Upper Neocomian and Aptian of Western Europe (Lankester 1863; Meyer 1864; Walker 1868; Davidson 1874; Teall 1875; Lamplugh and Walker 1903; Dines and Edmunds 1929; Wright 1939). Nevertheless, this English form seems to be quite distinct from that described by d'Orbigny. Several points in his description refer to characters never seen in English forms; the most important is the statement, borne out by his figure, that the beak is strongly recurved; Schloenbach (1866) also insists on this character. D'Orbigny's statement that the pedicle valve is more convex than the brachial, repeated by Pictet (1872), is also quite out of accord with the English species. The ventral profile is different, d'Orbigny's figures showing a regularly oval shape with the greatest width at about the mid-line and shallow plication; the anterior end is somewhat truncated in the continental form, boldly produced in the English. D'Orbigny's specimens and numerous topotype specimens have been examined and found to differ markedly from the English species in the particulars mentioned above. The English forms are therefore regarded as forming a separate species, *P. comptonensis*, which differs externally from *T. montoniana* as discussed above and internally in having horizontal hinge plates, whereas those of *T. montoniana* are keeled. *P. comptonensis* differs from *Sellithyris sella* externally in having a shorter and less incurved beak and in lacking any true sinuses of the commissure or any sulcus in the pedicle valve; from *Cyrtothyris uniplicata* in having a much shorter beak and symphytium and in having a deeper brachial valve compared with the pedicle valve.

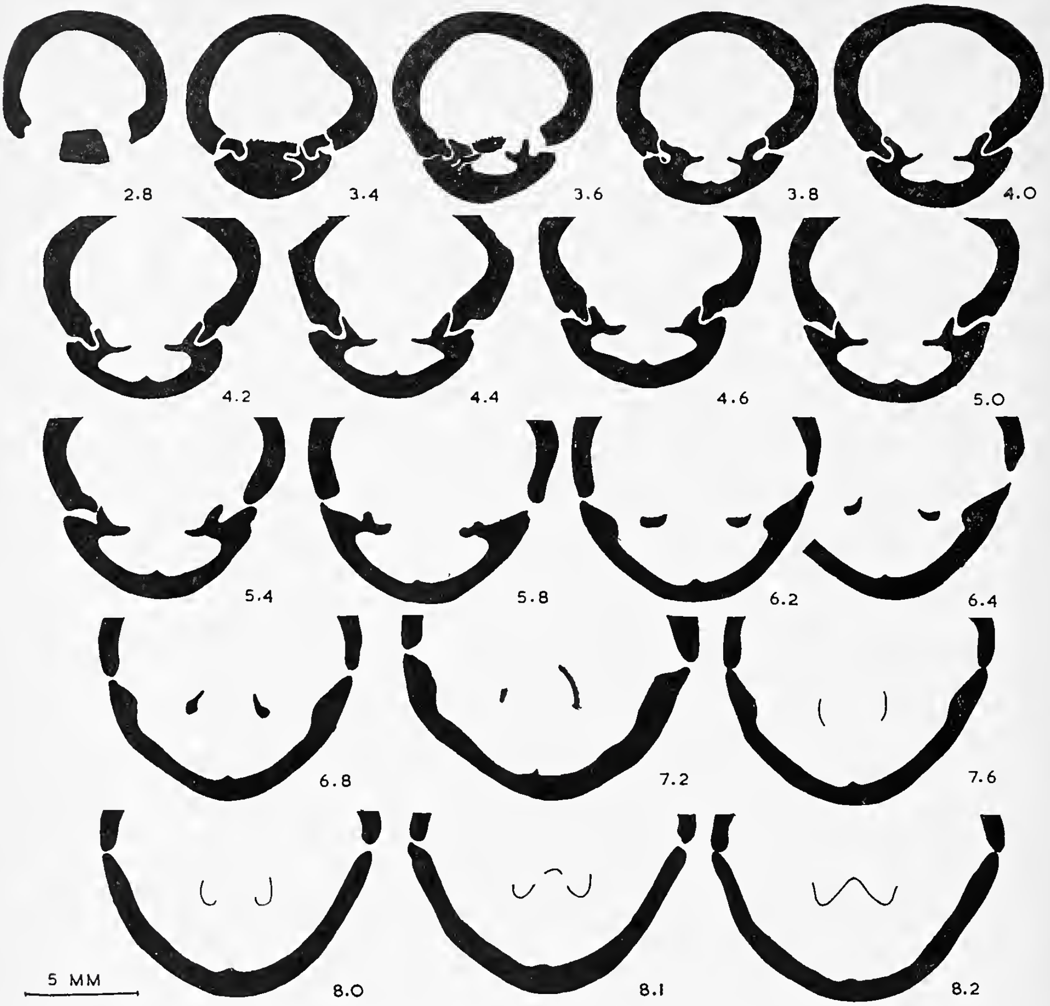
Distributon. Very abundant at Upware and Brickhill and also occurs in the Bargate Beds. At other localities it is rare. Single valves which may belong to the species occur at Faringdon. Meyer (Davidson 1874) recorded it from the Hythe Beds of Hythe, Kent, but his specimens (SM B.58782–5) are varieties of *Sellithyris sella*. It occurs rarely in the upper part of the Ferruginous Sands at Shanklin, Isle of Wight (BM B.25797), and of the Hythe Beds at Maidstone (BM BB.3444 and GS 96848). Forms in the Lower Albian deposits at Leighton Buzzard, Bedfordshire, resembling this species differ from it in beak characters and in internal morphology.

Platythyris minor sp. nov.

Plate 15, figs. 12–14; text-fig. 9

Holotype. BM BB.16220, Walker Coll., Brickhill, Buckinghamshire (dimensions: length 23, breadth 14, thickness 13).

Diagnosis. Platythyris of elongated oval ventral profile, slightly produced at anterior and posterior ends. P/A ratio about 1, or slightly more. Both valves regularly convex,



TEXT-FIG. 9. Transverse sections through *Platythyris minor* nov. The cardinal process is seen at 2·8 and is enlarged by callus to enclose the hinge plates at 3·4 and 3·6. The narrow horizontal hinge plates are best shown at 4·2–5·0, the strong euseptoidum at 3·8–7·6, the incurved crural processes at 7·2, descending lamellae of the loop at 7·6 and 8·0, and low-arched transverse lamella at 8·1 and 8·2. BM B.16201, Brickhill.

with maximum convexity slightly posterior to mid-line. Brachial valve possesses anteriorly a low but often distinct and rather square-cut fold; no sulcus in pedicle valve. Beak fairly short, sub-erect. Beak ridges rounded. Symphytium very short. Foramen mesothyrid to permesothyrid; angle of truncation *c*. 120°. Lateral commissure much arched. Anterior commissure strongly uniplicate but slightly sulciplicate in some specimens; development rectimarginate to uniplicate to sulciplicate. Socket ridges well developed and massive. Hinge plates distinctly narrow.

Description. This is a small species with maximum adult length about 25, width 15; some apparently gerontic individuals do not exceed 21. The most characteristic feature is the strong uniplication combined with some pinching in of the sides of the anterior part of the shell, giving it a distinctly 'nosed' effect. Uniplication develops when the shell is about 10 or 12 mm. in length and strong uniplication at an early stage of growth is characteristic.

Remarks. This species is very close in external characters to *P. comptonensis*, especially to some Brickhill varieties of the latter, but it differs (1) in being smaller, relatively deeper and more compressed; (2) in showing a tendency towards greater incurvature of the beak and towards a permesothyrid rather than mesothyrid foramen; (3) in possessing distinctly narrower hinge plates. Proportions vary a little in *P. minor*; some gerontic (perhaps stunted?) forms with close-set and well-marked growth-lines have thickness as much as two-thirds the length, and a beak approaching the erect condition.

Distribution. Brickhill only.

Genus SELLITHYRIS gen. nov.

Type species *Terebratula sella* J. de C. Sowerby 1823

Diagnosis. Beak short or moderately short; beak angle variable. Foramen mesothyrid to permesothyrid, usually marginate. Angle of truncation 95–110°. Shell squat, not much longer than wide, strongly biplicate in the adult stage. Development of anterior commissure rectimarginate–uniplicate–sulciplicate–episulcate but with a strong tendency towards omission of the two middle stages. Cardinal process small but distinctly bifid. Hinge plates concave, tapering. Crural processes sharp-pointed, inclined towards mid-line, approximately upright in lateral view; lamellae of loop distinctly narrow. Posterior and anterior adductor impressions in brachial valve separate, posterior lying along outer margin of anterior; both rather triangular in shape, diverging from the midline, the posterior at a greater angle than the anterior. Euseptoidum not always present. Adductor scars may be bounded in posterior part by low septum-like ridges.

Remarks. The characters of the beak and foramen cover quite a wide range in the different species but the genus is homogeneous in the general shell shape, type of plication, and characters of the hinge plates, loop, and muscle scars. In addition to the species described below the genus contains some European continental species ranging from the Valanginian to the Cenomanian, including *Terebratula carteroniana* d'Orb., *T. essertensis* Pictet, *Rectithyris tornacensis* d'Archiac sp. (Sahni 1929), and probably *T. campichei* Pictet.

Sellithyris sella (J. de C. Sowerby)

Plate 16, figs. 1–4; text-figs. 2, 10

Terebratula sella J. de C. Sowerby 1823, p. 53, pl. 437, fig. 1.
Terebratula sella J. de C. Sow.; Davidson 1855, p. 59, pl. 7, figs. 4–10.
Terebratula sella J. de C. Sow.; Davidson 1874, p. 78, pl. 202, fig. 19

Holotype. BM B.61547, Sowerby Coll., Hythe, Kent (dimensions: length 27·5, breadth 25·5, thickness 14).

Diagnosis. Rhomboidal to pentagonal *Sellithyris* with P/A ratio more than 1; breadth may almost equal length. Brachial valve regularly convex near the umbo, strongly folded anteriorly. Pedicle valve strongly convex posteriorly, maximum convexity near the umbo, with anteriorly two lateral folds separated by wide sulcus, with, or without a median fold. Beak sub-erect to erect. Angle of truncation *c.* 110°; foramen circular, may be slightly telate; mesothyrid to very slightly permesothyrid. Beak ridges rounded; sometimes well-defined adjacent to foramen. Symphytium wide, moderately short. Development of anterior commissure rectimarginate–uniplicate–sulciplicate–episulcate. Hinge plates thin. Crural processes thin, inclined towards midline at about 20°, slightly incurved at tip, base thickened. Descending lamellae of loop diverge at about 60°; loop wide and triangular. Euseptoidum feeble. Posterior portions of dorsal adductor scars bounded by septum-like ridges.

Description. The posterior lateral angles of the pentagonal ventral profile correspond to the greatest breadth of the shell and to the outer extremities of the lateral sinuses of the commissure. The cardinal slopes are always longer than the other three sides of the pentagonal shape.

The anterior commissure is typically very markedly episulcate, the plicae and sinuses of the commissure reflecting the folds and sulci of the shell. The lateral sinuses are typically wide and strongly arched, giving that winged appearance which is so characteristic of adult individuals from Atherfield and the Kentish Rag. The median sinus is typically smaller and narrower than the lateral. The development of the plications in the anterior commissure can be traced in young individuals from the Atherfield coast. A series of such stages can be observed in BM BB.3591–9 and BB.3577–90, which show that the shell remains rectimarginate up to about 15 mm., when it becomes slightly uniplicate, but by 20 mm. it is already distinctly episulcate, this stage having been apparently reached through a transitory sulciplicate stage. Further development consists of increasing emphasis of the plicae and sinuses and, with them, of the folds and sulci of the valves, so that gerontic individuals of typical form have an acute bi-rostrate appearance, with a great distance from the base of the lateral sinus to the apex of the plica.

EXPLANATION OF PLATE 15

All figures are natural size.

Figs. 1, 2. *Rhombothyris extensa* (Meyer). 1*a–c*, Lectotype, SM B.16739, Bargate Beds, Tuesley, Surrey. 2*a–c*, BM 67592, Upware, Cambs., figured Walker 1868, pl. 18, fig. 5.

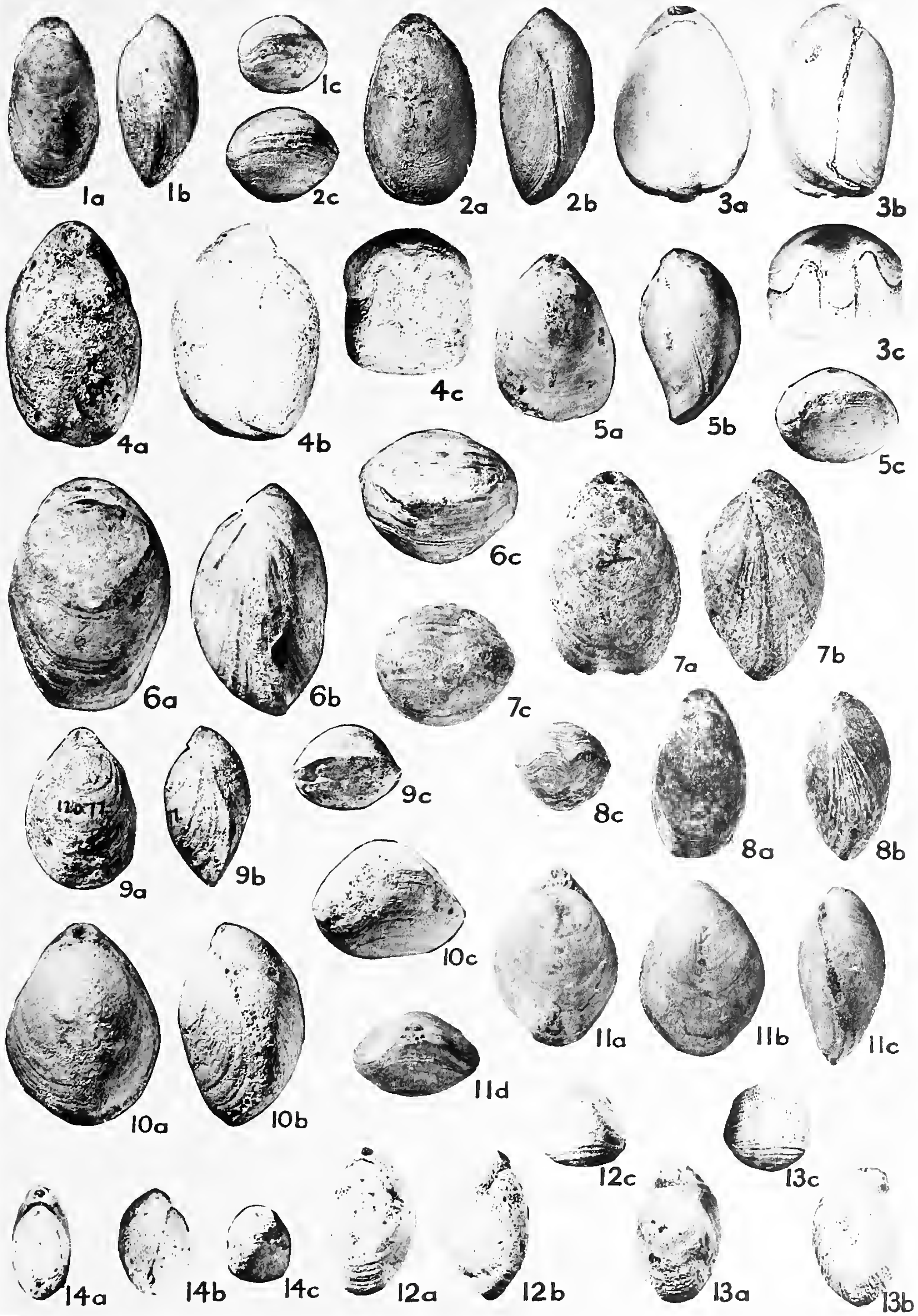
Figs. 3–5. *Rhombothyris microtrema* (Walker). 3*a–c*, Lectotype, BM BB.16216, Walker Coll., Upware, Cambs. 4*a–c*, A thick specimen, BM B.25571, Walker Coll., Upware. 5*a–c*, A specimen showing concavity in the anterior part of the brachial valve, BM BB.16232, Walker Coll., Upware.

Figs. 6*a–c*. *Rhombothyris meyeri* (Walker), Holotype, BM 67598, Walker Coll., Upware, Cambs.

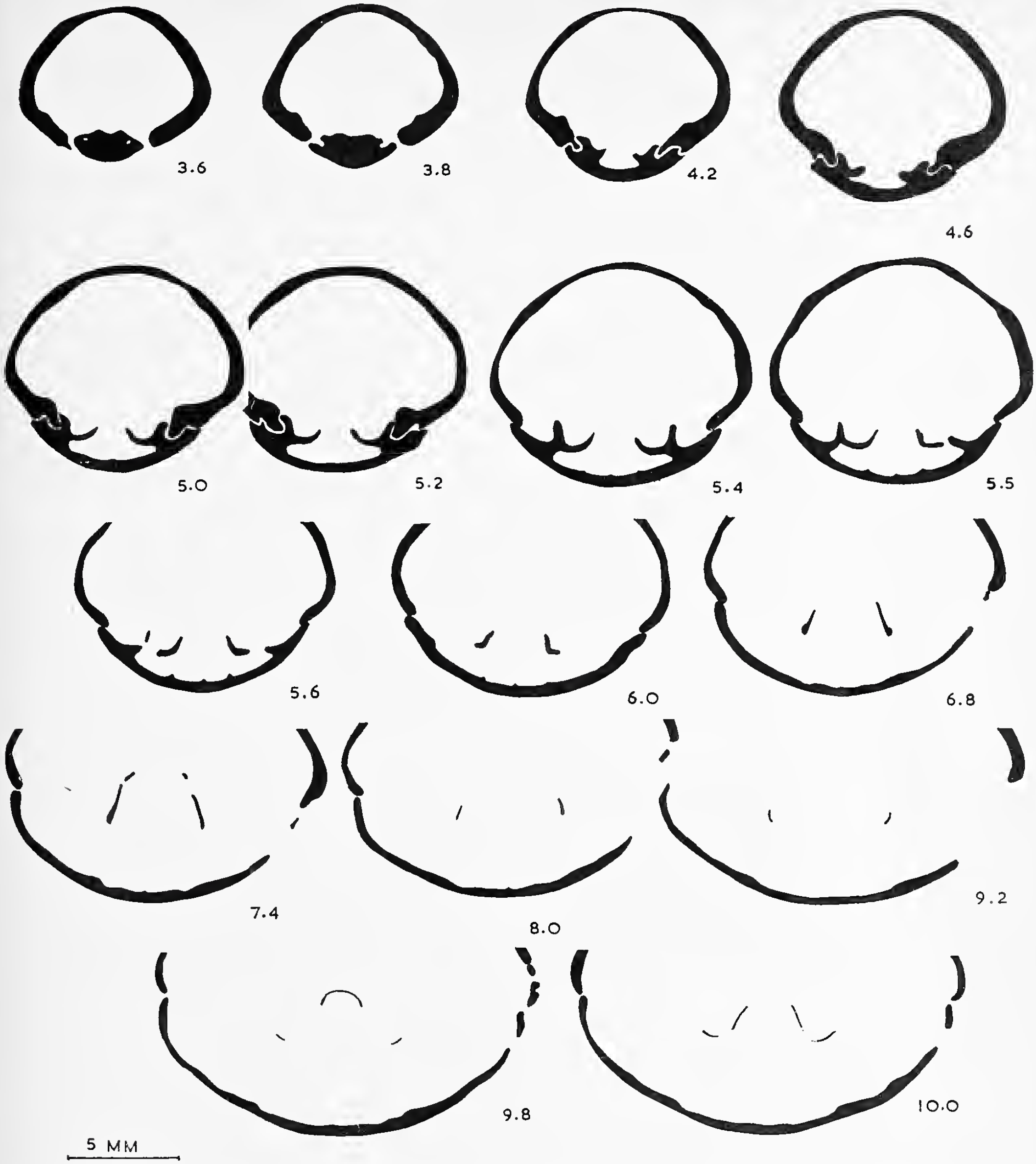
Figs. 7, 8. *Rhombothyris conica* sp. nov. 7*a–c*, Holotype, BM BB.16217, Walker Coll., Brickhill, Bucks. 8*a–c*, A smaller specimen showing well the characteristic shape of the anterior commissure, BM BB.16219, Walker Coll., Brickhill, Bucks.

Figs. 9–11. *Platythyris comptonensis* sp. nov. 9*a–c*, Holotype, BM BB.16230, Bargate Beds, Compton, Surrey (CWW 12077). 10*a–c*, BM BB.16233, Walker Coll., Upware, Cambs. 11*a–c*, BM B.1848, Caroline Birley Bequest, Brickhill, Bucks.; 11*b* shows well the longitudinal striae in the shell (ventral view).

Figs. 12–14. *Platythyris minor* sp. nov. 12*a–c*, Holotype, BM BB.16220, Walker Coll., Brickhill, Bucks. 13*a–c*, BM BB.20444, Brickhill. 14*a–c*, A small compressed specimen, BM B.25466, Walker Coll., Brickhill.



MIDDLEMISS, Aptian Terebratulids



TEXT-FIG. 10. Transverse sections through *Sellithyris sella* (J. de C. Sowerby). The cardinal process and the beginnings of the sockets are seen at 3·6 and 3·8, the concave tapering hinge plates at 5·4 and 5·5 and the ridges bounding the muscle scars at 5·4–6·0. 7·4 shows the maximum height of the crural processes, 8·0 and 9·2 the thin descending lamellae of the loop, and 9·8 and 10·0 the transverse lamella. BM B.16202, Hythe Beds, Hythe, Kent.

Parasulcate adults, lacking the median sinus, are common both in the Hythe Beds and in the Ferruginous Sands of the Isle of Wight. Hythe Bed specimens in particular show considerable variation in the beak angle, some having an erect beak, whereas in typical forms it is sub-erect. The degree of production of the beak also varies. A study of any large collection of *S. sella* from one locality shows considerable variation in the detail of the shape, e.g. the P/A ratio or the degree of development of the 'wings' formed by the lateral sinuses. There is also considerable variation in the ratios of length, breadth, and thickness; in particular there is a tendency, both in the Isle of Wight and in the Weald, for specimens from low horizons, especially those from the *Perna* Bed, to be thinner than those from higher horizons.

In the Bargate Beds *S. sella* is rare and the few specimens known (e.g. Shaw Coll. in GS and BM) are distinctive and might be regarded as a separate subspecies. They show a strong tendency towards the verticality of the lateral commissure characteristic of *S. upwarensis*.

A collection (GS) from the base of the Sandgate Beds of Sellinge, Kent, shows another late Aptian local race of the species. Most of these specimens are rather narrow and elongate, sharply episulcate but with wings less developed than in Atherfield types. The central sinus is small and low; the plicae tend to be angular, the sinuses rounded. There is a tendency towards a vertical lateral commissure, although not as marked as in *S. upwarensis*. Specimens of average size are very slightly globose and the plications are not much reflected in the folding of the shell. Fully adult forms have the anterior third folded. A thoroughly gerontic individual (GS Ca 4622) is thick, angular, with hardly any median sulcus; the lateral commissure turns very sharply into the lateral sinus, almost as in *S. upwarensis*. Another specimen (Ca 4616) is flattened and more like the Bargate Bed specimens mentioned above, although the lateral commissure is rather less vertical and the general shape long and narrow with the front much produced and very little median sinus, i.e. the ventral profile is very different from that in the Bargate Bed material; here again the plicae are angular, the sinuses rounded.

Remarks. It must be emphasized that *S. sella*, although variable, is distinctive, not closely resembling any other English Cretaceous species except some forms of *S. coxwellensis*, but Sowerby's figure and description have been misunderstood by some European authors, who have ascribed other forms to Sowerby's species or vice-versa. The chief European continental species which have been confused with *S. sella* are *Terebratula acuta* auctt., *T. valdensis* de Loriol, and *T. russillensis* de Loriol.

These species occur, along with *S. sella*, in the Lower Cretaceous of the Jura and are all biplicate terebratulids of very similar general external shape. Several other Lower Cretaceous biplicate species of southern Europe and North Africa remain undescribed.

T. acuta is more elongated and has a more acute umbonal angle than *S. sella* but there is a close external resemblance between the two species and Pictet remarked (1872, p. 74) that there is almost a transition between them in the Hauterivian of the Jura and the Hils Conglomerate of Brunswick. There are, however, several differentiating characters:

(1) In *S. sella* breadth is typically not much less than length; in *T. acuta* length is up to $1\frac{1}{2}$ times breadth. (2) In *T. acuta* P/A ratio is much higher than in *S. sella*; the resulting posterior elongation has caused *acuta* to be frequently confused with *T. praelonga* J. de C. Sow. *S. sella*: P/A ratio of twelve specimens, Hythe Beds, near Ashford, Kent, 1·32. *T. acuta*: P/A ratio of twelve specimens, Aptian, La Glappe, Narbonne, 1·94. (3) *T. acuta* usually shows a strong, almost bulbous convexity in the posterior part of the brachial valve, not present in *S. sella*. (4) *T. acuta* possesses strong ventral biplication at a much smaller stage than *S. sella*, the adult form being already developed by a length of 12 mm. (5) *T. acuta*

has a straighter beak and a longer and better-exposed symphytium than *S. sella*. (6) In *T. acuta* the beak ridges are sharper, the cardinal area more clearly defined and the symphytium is bordered by distinct marginal ridges. (7) Internally *T. acuta* differs from *Sellithyris* particularly in its hinge plates, which are deeply concave, almost virgate, and somewhat clubbed. It is hoped to discuss the systematic and nomenclatural position of this species in a later publication.

S. sella differs from *T. valdensis* chiefly in the following:

(1) *T. valdensis* is nearly always considerably longer than broad. (2) *T. valdensis* has a greater P/A ratio so that, like *T. acuta*, it has been mistaken for *T. praelonga*. *T. valdensis*: P/A ratio of twelve specimens, Valanginian, Carrière d'Arzier, Vaud, 1·69. (3) In *T. valdensis* the lateral sinuses are less distinct from the lateral commissure and the lateral sulci of the brachial valve less developed than in *S. sella*. (4) In *T. valdensis* the beak is more incurved, being usually erect, and is more produced in ventral profile; the foramen verges on the permesothyrid condition and the angle of truncation is slightly greater than in *S. sella*. (5) Internally *T. valdensis* differs from *Sellithyris* principally in having piped hinge plates.

T. russillensis differs from *S. sella* chiefly in:

(1) its large, thick, and completely erect beak and short, almost hidden symphytium; (2) its very large foramen with angle of truncation about 130°; (3) in being relatively thicker, lacking well-developed wing-like lateral sulci and bearing only a very small median sinus; (4) in possessing piped hinge plates similar to those of *T. valdensis*, with which it is probably congeneric.

Distribution. In the lower part of the Aptian in England *S. sella* is the typical and most abundant brachiopod which flourished in the Lower Greensand sea before the latter joined with the boreal sea in *Parahoplites nutfieldensis* times. It is common in the *Perna* Bed of the Isle of Wight and the equivalent bed at the base of the Atherfield Clay in Surrey, in the calcareous Hythe Beds of Kent and in the Ferruginous Sands of the Isle of Wight, where it is very abundant in the lower part but apparently dies out before the top of the series. The species becomes much less abundant before or about the beginning of *nutfieldensis* times; it is rare in the Bargate Beds and in the equivalent Sandgate Beds of Kent, in both of which local races, distinct from the Lower Aptian form, occur. Among the specimens from Seend, Faringdon, Brickhill, and Upware which have been referred to *Terebratula sella* there are some which are not easy to distinguish from that species but, nevertheless, these grade imperceptibly into the biplicate forms more typical of those localities, described here as *S. coxwellensis* and *S. upwarensis*, and should be regarded as *sella*-like variants of one or other of these.

On the European continent, too, *S. sella* appears to reach its acme in the Lower Aptian, after which it is not known (Pictet 1872).

Sellithyris sella shanklinensis subsp. nov.

Plate 16, figs. 5, 6

Terebratula sella J. de C. Sow.; Davidson 1874, p. 36, pl. 5, figs. 12–16 (*non* fig. 11).

Holotype. BM BB.16234, Walker Coll., Shanklin, Isle of Wight (dimensions: length 23, breadth 18, thickness 12).

Diagnosis. *S. sella* globose as adult. Plication less developed than in typical forms of species, folding shallower and affecting smaller proportion of shell. Beak nearly straight to sub-erect; symphytium well exposed; beak ridges moderately sharp.

Remarks. That the biplicate terebratulids occurring in the fossiliferous bands of the Ferruginous Sands about Shanklin are distinct from *S. sella* s.s. was realized by Meyer (Davidson 1874, p. 34). In the points of difference set out above, particularly the smaller development of plication which causes the characteristic lateral 'wings' of *S. sella* to be rare in the Shanklin form, the latter approaches *S. coxwellensis*. It was, in fact, upon Meyer's recognition of the similarity between the Shanklin forms and the Faringdon forms that Davidson (1874) based his identification of the latter as varieties of *Terebratula sella*. Nevertheless, there are certain differences between the Shanklin forms and the typical *S. coxwellensis* of Faringdon, the chief of which is the small size and frequent absence of the median sinus among the Shanklin forms. In many ways the latter are morphologically intermediate between *S. sella* and *S. coxwellensis*. The internal structures closely resemble those of the typical *S. sella*.

Distribution. Isle of Wight, in Group XIII of the Ferruginous Sands near Shanklin and Group X near Atherfield.

Sellithyris upwarensis (Walker)

Plate 16, figs. 7–9; text-figs. 11, 12

Terebratula sella, J. de C. Sow.; Walker 1868, p. 403, pl. 18, figs. 7–7*b*.
Terebratula sella var. *upwarensis* Walker 1870, p. 562.
Terebratula sella var. *upwarensis* Walker; Davidson 1874, p. 35, pl. 5, figs. 3–10*a*.

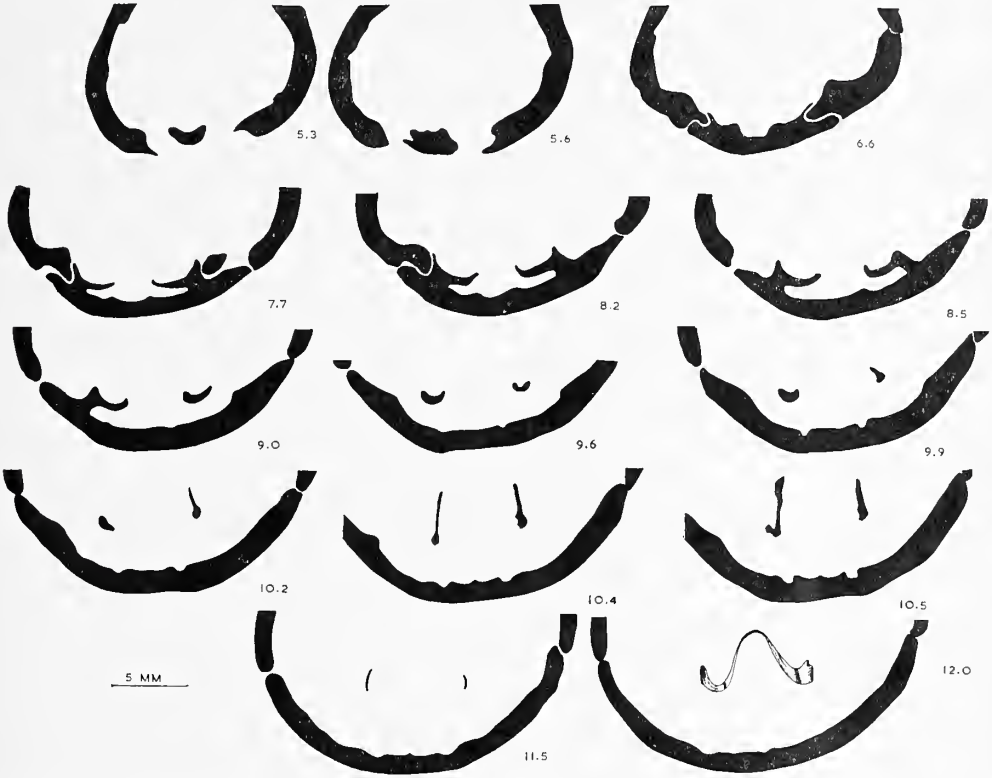
Holotype. BM 67594, Walker Coll., Upware, Cambridgeshire (dimensions: length 27, breadth 20, thickness 21).

Diagnosis. Sellithyris of rounded rhomboidal ventral profile; typical ratio of length to breadth 5:4. P/A ratio slightly more than 1. Brachial valve flattened posteriorly, or slightly grooved in midline near umbo, anteriorly sharply folded with narrow median sulcus and wide and deep lateral sulci. Pedicle valve strongly convex and somewhat carinate posteriorly, with strong folds anteriorly occupying half to two-thirds of length of valve in adults. Anterior commissure strongly episulcate with angular plicae and sinuses, median sinus large. Lateral commissure approximately vertical. Development of anterior commissure rectimarginate–episulcate. Beak sub-erect to erect, usually nearer the latter. Angle of truncation *c.* 110°. Foramen large, circular, may be slightly telate or attrite. Beak ridges rounded, but well defined immediately adjacent to foramen. Symphytium very wide, moderately to very short. Teeth inserted at 30–40° to the commissural plane. Hinge plates thin, close to floor of brachial valve; dorsal umbonal cavity low. Crural flanges present. Loop a wide, somewhat squat triangle. Dorsal adductor scars very large, angular.

Description. Typical specimens of this species, most of which come from Upware, have a highly characteristic appearance: distinctly globose, with thickness three-quarters or more of width (but rarely equalling width), with bold, blunt, angular plication and a laterally compressed appearance.

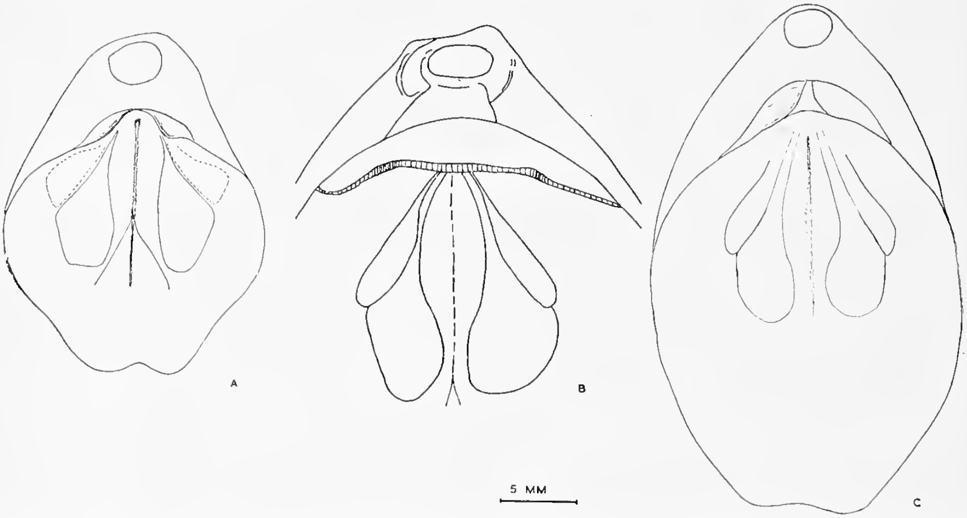
The anterior commissure in many individuals almost reaches the quadriplicate stage by development of an external plica lateral to each lateral sinus. It is characteristic of the species that the lateral commissure is almost vertical in its passage forwards from the umbo and turns abruptly into the lateral sinus through almost a right angle, but in some specimens the commissure turns slightly dorsally before entering the steep turn into the lateral sinus, thus forming a shallow external plica.

The carinate posterior part of the pedicle valve and the frequent occurrence of a groove in the posterior part of the brachial suggest a sulcate nepionic stage but the earliest growth stage actually seen (BM B.25597) is 15 mm. long and rectimarginate. The rectimarginate to episulcate transition seems to be abrupt, the plicae and sinuses appearing at once, without intervening uniplicate, paraplicate, or sulciplicate stages, at about 15 mm., since there are also specimens of that length (BM B.25597) showing all the plication present, although very small. Neanic individuals (18–22 mm.) have well-developed and typical plication, the sub-vertical course of the lateral commissure between the umbo and the lateral sinus being evident, but the whole shell is relatively thin, average ratio of thickness to breadth for ten specimens in that length range from Upware being 0·56 as compared with 0·75–0·85 for adult specimens. In neanic specimens the beak is noticeably straighter than in adults. Growth from the neanic stage results in a relative increase in thickness, coupled with increasing emphasis on the plication and a slight tendency towards incurvature of the beak.



TEXT-FIG. 11. Transverse sections through *Sellithyris upwarensis* (Walker). The cardinal process can be seen at 5·3 and 5·6, the concave tapering hinge plates at 7·7 and 8·5, the crural processes at maximum height at 10·5, and descending lamellae of the loop at 11·5. The transverse lamella has been dissected out at 12·0. SM B.80776, Upware.

Adults of the species vary considerably, even at Upware, the home of the globose type, the chief variable factor being the relative thickness and the consequent depth of the plication, since there is good correlation between these characters well shown in those exceptional specimens which are actually thicker than wide and have extremely exaggerated plication. At Brickhill, although gerontic specimens are globose and laterally compressed with very deep plication, like those from Upware, the majority of the adults resemble rather the neanic stages from Upware in being relatively thin and in not showing strong lateral compression. Average thickness: breadth ratio of ten specimens from Brickhill in the 21–28 mm. length range 0·62; that of ten specimens from Upware in the same length range 0·82. Occasional examples of the Brickhill type occurred at Upware, however. The characters of the commissure remain constant.



TEXT-FIG. 12. Camera lucida drawings of calcite internal casts of three species of Aptian terebratulids in dorsal view, to show muscle impressions. A, *Sellithyris upwarensis* (Walker). The euseptoidum is quite well developed. The posterior and anterior adductor scars are separate. SM B.80775, Upware. B, *Cyrtothyris cantabridgiensis* (Walker), BM BB.16212, Upware. C, *Praelongithyris praelongiforma* nov., BM BB.16213. In B and C the posterior adductor scars lie close against the postero-lateral sides of the anterior adductor scars; the euseptoidum is just visible.

Remarks. S. upwarensis does not resemble any other English species except *S. sella* and *S. coxwellensis*. From *S. sella* this species differs typically in being thicker in relation to breadth, much more globose in appearance and in lacking the prominent 'wings' and the acute produced appearance of the central portion of the anterior margin seen in *S. sella*.

In less typical examples of the two species other characters must be taken into account: (1) The central sinus in *S. upwarensis* is invariably better developed than in *S. sella* and may almost, in rare cases quite, equal in depth the lateral sinuses. In *S. sella* the central sinus is always much smaller than the lateral. (2) In *S. sella*, although the beginning of the lateral sinus is usually formed by a sharp ventral bend of the lateral commissure, the latter drops from the umbo to the lateral sinus at a distinct angle to the vertical, the angle varying with the proportions of the shell but reaching a maximum of 40° in some specimens. In this the species contrasts with *S. upwarensis*.

There are three European continental species which to some extent resemble *S. upwarensis: Terebratula carteroniana* d'Orb., *T. campichei* Pictet, and *T. russilleusis* de Loriol. *T. carteroniana* has a straighter beak, a smaller and narrower median sinus, and characteristically strongly marked growth lines. *T. campichei*, according to Pictet (1872, p. 63), has a much straighter beak. *T. russilleusis* is narrower compared with its length, has a larger and more inflated beak and larger foramen and possesses piped hinge plates; it is no doubt to be referred to a different genus.

Distribution. Upware and Brickhill only, very abundant at the former, slightly less so at the latter.

Sellithyris coxwelleusis sp. nov.

Plate 16, figs. 10–12; text fig. 13

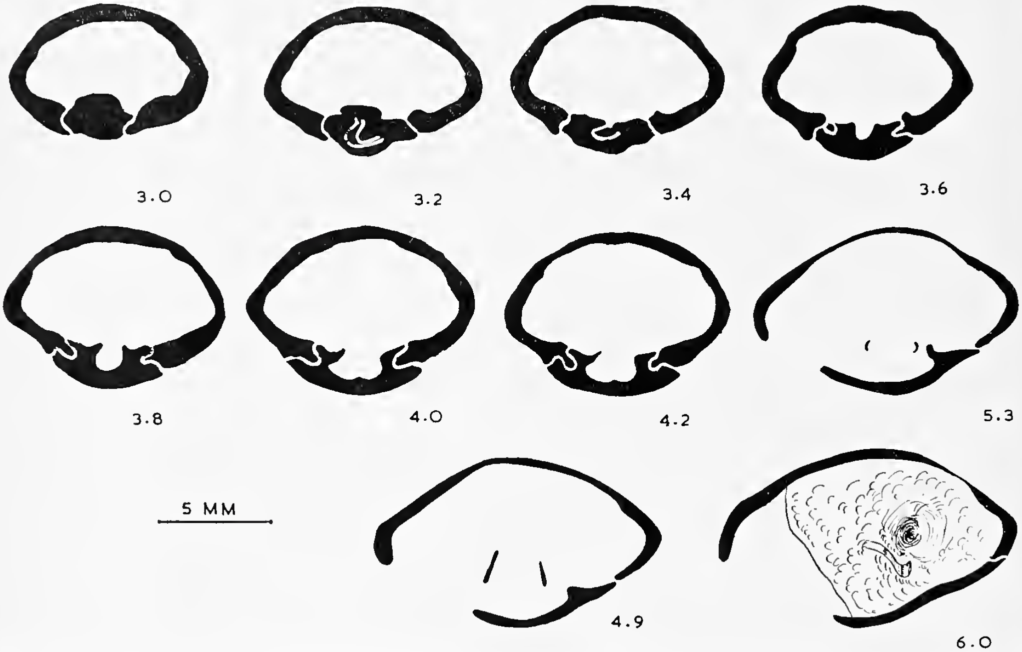
Terebratula tornacensis d'Archiac var. *roemeri* Davidson 1855, p. 61, pl. 7, figs. 11–16; pl. 9, figs. 1–8, 36–37; ?pl. 6, figs. 45–49.

Terebratula sella J. de C. Sow. var.; Davidson 1874, p. 36.

Holotype. BM B.26007, Walker Coll., Faringdon, Berkshire (dimensions: length 20, breadth 18·5, thickness 11).

Diagnosis. *Sellithyris* of pentagonal ventral profile with rounded angles. Breadth typically 0·8–0·9 of length, thickness *c*. 0·6 of breadth. P/A ratio (average of twenty adult specimens from Faringdon) 1·50. Brachial valve has maximum convexity about the centre; pedicle valve more evenly convex but rather inflated near posterior end. Anteriorly both valves folded but this usually affects less than one-third of the shell. Pedicle valve slightly carinate near the umbo. Anterior commissure typically episulcate, the sinuses and plicae gently angular; median sinus well developed, often approaching or equalling the lateral sinuses in depth. Beak sub-erect; symphytium well exposed; beak ridges fairly well defined. Foramen large, circular, precisely mesothyrid. Angle of truncation *c*. 95°. Development of anterior commissure rectimarginate–sulciplicate–episulcate. Teeth inserted at 20–30° to the commissural plane; accessory articulation fairly well developed. Hinge plates narrow. Dorsal umbonal cavity high. Crural flanges present. Loop small and relatively narrow.

Description. Adults are characteristically globose, with the folds affecting the anterior part of the shell only and in some cases even that very little, but the species is variable, the variation affecting chiefly the following characters: (1) the relative proportions of length, breadth, and thickness. Occasional elongated specimens occur and there is a rather distinctive transverse variety, as broad as long, at Faringdon (e.g. Davidson 1855, pl. 9, figs. 5, 7); (2) the development of folding in the shell. Even in those individuals with quite well-developed plications of the anterior commissure both valves usually remain smoothly convex except in the extreme anterior part. The holotype shows about the maximum depth of folding in which approximately one-third of the shell is involved; (3) the anterior commissure. Typically the median sinus is well developed, more so than in *S. sella*, but in some individuals from both Faringdon and Seend it is so large as to equal or even exceed the lateral sinuses in depth and prominence while remaining comparatively narrow. The lateral sinuses are never as well developed as in *S. sella* and may be lacking. There are also variants in which the median sinus is poorly developed or absent; these approach *Cyrtothyris cyrta* in superficial appearance; (4) An obvious character of many individuals from Faringdon is the presence of well-emphasized concentric growth lines or growth halts forming little steps upon the surface of each valve.



TEXT-FIG. 13. Transverse sections through *Sellithyris coxwellensis* nov. At 3·0–3·4 the cardinal process (enlarged by callus) encloses the hinge plates, the concave tapering shape of which is seen best at 4·0–4·2. 4·9 shows the maximum height of the crural process and 5·3 the descending lamellae of the loop, the transverse lamella of which is partly dissected out at 6·0. Sections 3·0–4·2 BM BB.20462, Bowler's Pit, Faringdon, Berkshire. Sections 4·9–6·0 BM B.26019, Faringdon, Berks.

Prominence of these growth lines varies greatly. They seem to be, to some extent, a gerontic character, appearing crowded together near the anterior margin of really large old individuals (21–22 mm.), but they occur even more commonly on comparatively small shells which, from their small size, thinness, and poorly developed plication, appear to be quite young. The deeply cut growth lines seem to be evidence of stunting of the shell by unfavourable conditions.

Remarks. This form has been ascribed to the Tourtia species *Terebratula roemeri* d'Archiac (Sharpe 1854) and *T. tornacensis* d'Archiac (Davidson 1855). The name *T. tornacensis* has been most used for it, in spite of the fact that Davidson later (1874) withdrew his identification, on the advice of Meyer, and described the form instead as a variety of *T. sella* J. de C. Sow.

S. coxwellensis resembles *T. tornacensis* in its well-exposed symphytium and its well-developed median sinus. It differs in several respects: the beak is straighter and the symphytium still better exposed in *T. tornacensis*; in the latter the plicae are angular, the median sinus characteristically rounded, a combination occasionally, but rarely, seen in *S. coxwellensis*. Above all the dorsal profile is different; in *T. tornacensis* the P/A ratio is markedly smaller than in *S. coxwellensis* and it becomes more so as the shell grows older; also the cardinal slopes are concave in *T. tornacensis*, convex in *S. coxwellensis*; these two factors together give a characteristic 'high-shouldered' appearance to *T. tornacensis*, not seen in *S. coxwellensis*.

S. sella resembles *T. tornacensis* in its general proportions and in being episulcate, but in little else. *T. tornacensis* has a straighter beak, much more exposed symphytium and larger foramen than *S. sella*. *S. sella* has a considerably larger P/A ratio; its cardinal slopes are convex; its lateral sinuses are better developed and its median sinus less well developed than those of *T. tornacensis*.

S. coxwellensis and *S. sella* resemble each other considerably and are in rare cases not clearly distinguishable. The essential points of distinction are: (1) *S. coxwellensis* has a straighter beak, a longer and better-exposed symphytium, and sharper beak ridges. (2) In *S. coxwellensis* the median sinus is better developed, the lateral sinuses less well developed, and it lacks the wide lateral 'wings' of *S. sella*. (3) *S. coxwellensis* is more globose as an adult and the folds affect a smaller proportion of the shell. *S. coxwellensis* is, typically, markedly convex with shallow folds affecting the anterior part only, while in *S. sella* the shape is, typically, thinner with deep folds which may affect half or more of the shell. (4) In late adult and gerontic stages *S. coxwellensis* tends to become more and more globose whereas in *S. sella* development tends to be towards emphasis of the folds of the shell.

In both species neanic individuals are relatively thinner than adults and have a straighter beak and better-exposed symphytium, but these latter are more marked in the young of *S. coxwellensis* than in those of *S. sella*. Both species are variable in certain characters, variants of *S. coxwellensis* including some with a slight resemblance to the Brickhill form of *S. upwarensis* imparted by the relatively large median sinus. Young individuals of *S. coxwellensis* at Faringdon may resemble young forms of *Cyrtothyris* but differ in being more transverse and in having much sharper beak ridges.

Distribution. Abundant and varied at Faringdon and Coxwell (Berkshire) and also known at Seend (Wiltshire).

Genus CYRTOTHYRIS gen. nov.

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

Diagnosis. Foramen large, circular, mesothyrid; marginate to slightly labiate. Angle of truncation 110–120°. Beak ridges rounded. Shell depressed, may become more inflated, with or without folding, in later growth stages. Cardinal process essentially small, becoming enlarged by callus deposited around and along posterior parts of hinge plates. Accessory articulation sometimes present but never strongly developed. Socket ridges well developed, hinge sockets deep. Hinge plates virgate, at least in mature condition; clubbed; sometimes keeled. Crural flanges and crural keels typically present. Loop broad, triangular; transverse lamella strongly recurved and high-arched in centre.

Posterior and anterior dorsal adductor scars separate, posterior closely juxtaposed to postero-lateral margins of anterior; posterior elongated, strap-shaped; anterior elongated flask-shaped, with long narrow posterior portion, expanding anteriorly towards mid-line. Euseptoidum not a constant character.

Remarks. Three of the species included here have formerly been ascribed to *Terebratula depressa* Lamarck, now type species of *Rectithyris* Sahni 1929, and between these two genera there are points of resemblance.

The loop is similar in its wide triangular shape and high-arched transverse lamella. The dorsal muscle scars have the same general arrangement and the anterior adductors a similar shape. The socket ridges have the same tendency to bend over laterally so as to enclose the hinge teeth, although this tendency is better developed in *Rectithyris*. Externally there is a close resemblance between some shorter-beaked variants of *Rectithyris depressa* and some longer-beaked variants of *Cyrtothyris uniplicata*, but the latter grades towards the other two Aptian species formerly ascribed to *T. depressa*, namely *C. cyrta* and *C. cantabridgiensis*, and these three species are shown by their internal characters to be closely related to one another and readily distinguishable from *R. depressa*. A further point of resemblance between the two genera is in the ontogeny, during which some species of *Cyrtothyris* are known to pass through a rectimarginate, straight-beaked, rhomboidal stage much resembling *Terebratula viquesneli* d'Archiac 1846 which Davidson (1855, p. 71) regarded as a young stage of *T. depressa*.

The essential differences between the genera lie in the hinge plates and crura. Although both possess virgate hinge plates, those of *Cyrtothyris* form a fairly equilateral V in cross-section and are distinctly clubbed, while those of *R. depressa* form a more open V, with the inner lamina smaller than the outer, and are tapering. Furthermore, the hinge plates in *R. depressa* are keeled for their whole length, which in itself seems sufficient to divide the two genera. In *Cyrtothyris* the keel is typically a crural one, although not always present, and is associated with a flange more or less at right angles to the crus to give the 'golf-club' shape of the crura typical of this genus in transverse section. In *Rectithyris* the keel has moved back to give a keeled hinge plate while the flange resembles rather a curved trough forming an anterior extension of the outer lamina of the hinge plate. As the flange does not extend as far as the region of maximum height of the crural processes there cannot strictly be said to be a crural flange or keel. The crural processes in *Rectithyris* are in fact inwardly curved structures with their curvature parallel to that of the cross-section of the descending lamella of the loop, quite different from those of *Cyrtothyris*. Species of *Cyrtothyris* include variants in which the crural keel had moved back somewhat so that the anterior parts of the hinge plates are keeled, and also variants in which the flange does not extend forwards to the crural process, but the association of fully keeled hinge plates and flangeless crural processes appears to be constant and diagnostic in *R. depressa*. The resemblances suggest relationship between the Aptian *Cyrtothyris* and the Cenomanian *Rectithyris* but the nature of this relationship is obscure in the present state of knowledge of the Albian terebratulids.

The clubbed hinge plate in *Cyrtothyris* often shows a slight double rim on its inner margin and this may just possibly indicate the incipient development of an 'inner hinge plate' such as Sahni described in *R. depressa*. It seems, however, to be a random and inconstant feature and may have no special significance. It may be noted here that no sign of an inner hinge plate has been seen in *R. depressa* during this investigation although numerous topotypes were examined and some sectioned.

Cyrtothyris cyrta seems to occupy a central position in the genus. On either side of it are two main groupings of species; on one hand the depressed forms *C. uniplicata* and *C. seeleyi*, on the other the biplicate form *C. cantabridgiensis*. *C. dallasi* stands apart from the others but its relationship to *C. uniplicata* (then called *T. depressa*) was realized by Walker (1868, p. 404).

Cyrtothyris cyrta (Walker)

Plate 16, fig. 13; Plate 17, fig. 1; text-figs. 2, 14

Terebratula depressa var. *cyrta* Walker 1868, p. 404, pl. 18, figs. 1–1*b*.
Terebratula depressa var. *cyrta* Walker; Davidson 1874, p. 41, pl. 4, figs. 6, 7.

Holotype. BM 67597, Walker Coll., Upware, Cambridgeshire (dimensions: length 44·5, breadth 41, thickness 26).

Diagnosis. *Cyrtothyris* almost as broad as long; in ventral profile sub-circular. In lateral profile maximum convexity distinctly near to posterior end, brachial valve tending to flatten anteriorly. Beak short, nearly straight to sub-erect. Angle of truncation *c*. 120°. Symphytium visible but short and broad. Lateral commissure straight or gently curved. Development of anterior commissure rectimarginate to gently uniplicate.

Description. The distinctive characters of this species are those of the beak and commissure, combined with the broad, depressed shell. Young forms are rectimarginate and distinctly depressed, the rectimarginate stage being retained until the shell is at least 30 mm. in length, in many cases more. Further growth is marked by two main changes in shape: (*a*) the appearance of a uniplicate stage, (*b*) increase in convexity until old individuals have a very rotund appearance compared with juvenile stages, an appearance imparted especially by the strongly marked convexity of the brachial valve close to the umbo, with the symphytium almost overhung by the nearly vertical posterior wall of the obese brachial valve. In young individuals of about 20 mm. the brachial valve may be almost flat and the remarkable increase in the convexity of this valve with growth is a striking characteristic of the species. Accompanying this development of the brachial valve is a reduction in relative length of the symphytium, so that the latter is better-exposed in young specimens than in old. Some very adult individuals from Faringdon are distinctly transverse. Internally the dorsal umbonal cavity varies with growth, being relatively higher in gerontic, thickened specimens.

Remarks. This species differs from *C. uniplicata* chiefly in the much shorter and more erect beak and much shorter symphytium, characters which seem to be constantly associated with the comparatively weak development of uniplication and retention of the rectimarginate condition to a late stage, and also with the tendency to great increase in the convexity of the posterior part of the brachial valve. Uniplication in *C. cyrta* is gerontic but occurs to a varying extent. Really gerontic forms may occasionally be confusable with *C. uniplicata*, especially if crushed.

In some specimens the state of preservation is such that the longitudinal striae appear very prominently and this, together with the short beak, may give a resemblance to *Terebratula capillata* d'Archiac; the specimen of *T. capillata* recorded from the Hythe Beds of Jacket's Hill, Sussex (Kirkaldy and Bull 1940), may possibly have been a *C. cyrta* of this type.

TEXT-FIG. 14. Transverse sections through *Cyrtothyris cyrta* (Walker). Enclosure of the hinge plates by the enlarged cardinal process is well shown at 4·6–5·4, the virgate clubbed hinge plates and euseptoidum at 6·6–8·2, and the keeled and flanged crura at 13·5. The descending lamellae of the loop can be seen at 14·6 and high-arched transverse lamella at 16·6. BM B.25627, Upware, except section 13·5, which is from SM B.80777, Upware.

Distribution. Abundant at Upware, Potton, Brickhill, and Faringdon. Internal casts in the basal Sandgate Beds of Great Chart and Sellinge, Kent, and in the basal Carstone of Hunstanton (e.g. BM B.60975) are probably this species, as are a few silicified forms from the Hythe Beds of Godstone, Surrey (e.g. BM B.85930–2). One or two incomplete and doubtful specimens indicate that it probably occurs rarely in the Bargate Beds of St. Martha's, Surrey (e.g. SM B.16727). Forms which, pending investigation of their internal structures, seem referable to this species occur in the Claxby Ironstone and the Tealby Series of the Lower Cretaceous (Hauterivian) of Lincolnshire.

Poorly preserved specimens probably of this species have been examined from the Aptian of Ste. Croix, Switzerland (BM B.35744), and from the Hils Conglomerate of Berklingen, Brunswick (BM B.35629).

Cyrtothyris uniplicata (Walker)

Plate 17, figs. 2, 3; text-fig. 15

Terebratula depressa Lamarck; Walker 1868, p. 403, pl. 18, figs. 2–2*a*.
Terebratula depressa var. *uniplicata* Walker 1870, p. 561; p. 563, figs. 1, 2.
Terebratula depressa var. *uniplicata* Walker; Davidson 1874, p. 40, pl. 4, figs. 1, 2, 4, 5.

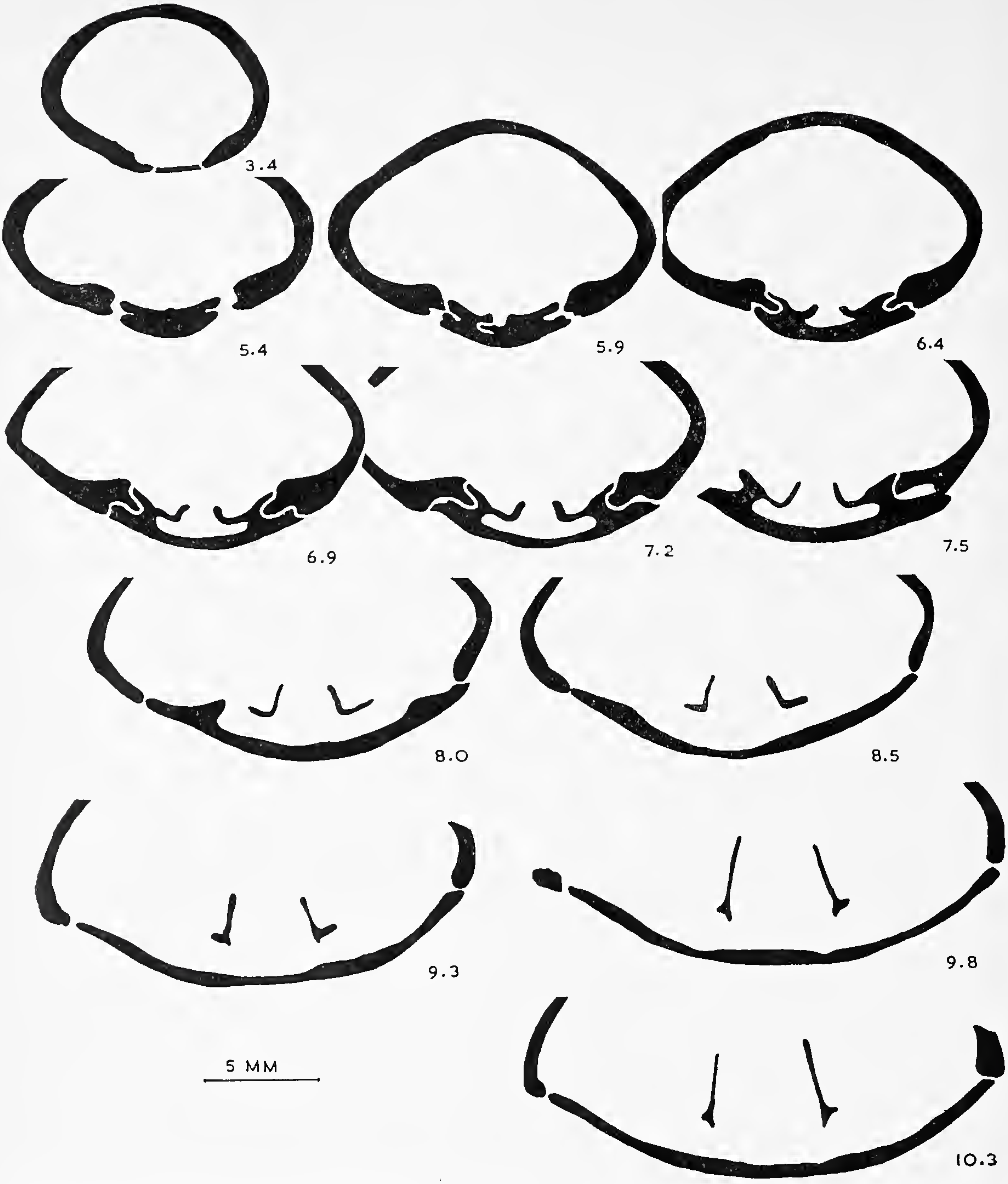
Holotype. BM 67843, Walker Coll., Upware, Cambridgeshire (dimensions: length 61, breadth 52, thickness 28).

Diagnosis. *Cyrtothyris* of rounded ventral profile, oval anteriorly, triangular posteriorly; cardinal slopes straight or very slightly concave, lateral slopes strongly rounded and continuous with front margin. P/A ratio rather more than 2. In lateral profile pedicle valve very regularly convex; brachial valve has maximum convexity about one-third of total length from posterior end and flattens towards anterior margin; pedicle valve somewhat deeper than brachial. Beak straight or nearly straight; symphytium large and well exposed. Foramen slightly telate. Angle of truncation *c*. 115°. Lateral commissure gently arched. Development of anterior commissure rectimarginate to uniplicate.

Description. The wide, depressed shape, ventral profile and characters of the beak and symphytium are the dominant features of this species. Variation mainly affects simple length–breadth–thickness ratios. A more important type of variation is in the length of the beak, e.g. at Upware, although the general form remains reasonably constant. Specimens from Brickhill tend to be thinner and to have shorter beaks than most Upware specimens, while the beak remains straight and the symphytium well exposed. Those from Faringdon tend to be smaller than elsewhere and to have the beak somewhat more incurved, verging on sub-erect, although the symphytium is large and well exposed and the foramen of the same general type. Those from Shanklin, on the other hand, have straight beaks.

The young of this species show a straight beak and well-exposed symphytium. The general form is rhomboidal and the shell tapers in thickness to the anterior margin, which is at first rectimarginate but soon acquires gentle uniplication, the characteristic stage of the adults. The gerontic stage is marked by deepening and squaring of the uniplica, almost into a parasulcate stage, and by increasing obesity of the shell as a whole and especially of the brachial valve, the deepening of which close to the posterior end has the effect of appearing to shorten the beak and symphytium, as in *C. cyrta*.

Remarks. This species includes the 'typical *Terebratula depressa*' and *T. depressa* var. *uniplicata* of Davidson (1874). Some specimens resemble *Rectithyris depressa* (Lamarck) of the Cenomanian Tourtia and on external characters could be confused with that species, the chief differences being that the Tourtia forms are more distinctly rhomboidal in dorsal profile, the beak longer and more produced, and the symphytium longer (in some cases extremely so) and more distinctly concave in lateral profile; the beak ridges are slightly more distinct but the telae formed by them in the foraminal margin rather less so; the umbonal part of the pedicle valve is much more decidedly carinate. The Tourtia species, in late adult or gerontic stages, tends to pass into slight but angular biplication, not seen in *C. uniplicata*, whose gerontic individuals possess massive and



TEXT-FIG. 15. Transverse sections through *Cyrtothyris uniplicata* (Walker). The symphytium can be seen at 3·4 and cardinal process at 5·4. The typical cyrtothyrid inner socket ridges are shown at 6·4–7·2, the virgate clubbed hinge plates at 6·9–7·5, and keeled and flanged crura at 9·3–10·3. BM BB.16211, Upware.

squarish uniplication. It is noteworthy that the characters in which the Tourtia form differs from *C. uniplicata* are in the main possessed also by juvenile forms of the latter.

Distribution. Abundant at Upware, Brickhill, and Faringdon. Occurs at Shanklin, Isle of Wight, in the upper part of the Ferruginous Sands.

Cyrtothyris cantabridgiensis (Walker)

Plate 17, figs. 4, 5; text-figs. 12, 16

Terebratula depressa var. *cantabridgiensis* Walker 1870, p. 561; p. 563, figs. 3–5.
Terebratula depressa var. *cantabridgiensis* Walker; Davidson 1874, p. 41, pl. 4, figs. 8–10.

Holotype. BM 67844, Walker Coll., Upware, Cambridgeshire (dimensions: length 43, breadth 31·5, thickness 25).

Diagnosis. *Cyrtothyris* of oval ventral profile; in lateral profile depressed, juvenile individuals much so. Both valves uniformly convex. Beak short, nearly straight to sub-erect. Angle of truncation *c*. 120°. Symphytium short and broad, but visible. Lateral commissure strongly arched; anterior commissure sulciplicate. Hinge plates concave posteriorly, virgate anteriorly; distinctly clubbed.

TEXT-FIG. 16. Transverse sections through *Cyrtothyris cantabridgiensis* (Walker). The symphytium and dorsal umbo can be seen at 5·4, the cardinal process, enlarged by callus which has enclosed the hinge plates, at 5·8–7·0. The virgate clubbed hinge plates are shown at 9·0–11·0, keeled and flanged crura at 14·2, and high-arched transverse lamella at 17·5. BM BB.16212, except the last section, which is from BM BB.20461 (both from Upware).

Description. The beak resembles that of *C. cyrta* but is rather more erect at all stages of growth. The young stages are depressed but have a general resemblance to those of *C. cyrta* except that they are clearly sulciplicate. In adult individuals the plication becomes the most obvious character and is reflected in considerable folding of the shell; the central sinus is always well developed, with its ventral limit on a level with that of the lateral commissure on each side. The gerontic stage is marked by obesity of the anterior part of the shell, with crowding together of growth-lines. In a few gerontic individuals there is a tendency towards a labiate foramen (e.g. Davidson 1874, pl. 4, figs. 9, 10).

This species does not vary much, perhaps because so few specimens are known. In Brickhill specimens the plication is shallower than in those from Upware, although the relative proportions are the same, including the good development of the median sinus. This difference is retained into old age. Upware forms are rather rhomboidal in ventral profile, the largest specimens (47·5 mm. long) being strongly sulciplicate. Their foramen is large, mesothyrid to slightly permesothyrid, the symphytium exposed but short, the beak nearly straight to sub-erect. In general appearance they resemble *C. cyrta* except for the biplication. Brickhill forms are more ovoid in ventral profile and thinner, with biplication less well developed. The beak is rather more incurved than in the Upware forms, being definitely sub-erect.

Remarks. This species is clearly separate from *C. cyrta* since it is biplicate at an early stage (before 25 mm. in length), whereas *C. cyrta* is rectimarginate at this stage and never attains biplication. Walker (1870) remarks that this species 'approaches *Terebratula praelonga* in the plication', although the resemblance is seen only in older individuals of *C. cantabridgiensis*, in which it may be reinforced by the labiate foremen; nevertheless the two species can be distinguished by the foramen, which is mesothyrid in *C. cantabridgiensis*, permesothyrid in *Praelongithyris praelongiforma* (*T. praelonga* of Walker 1870), by the relatively greater breadth of *C. cantabridgiensis*, and by the early and constant development of biplication in the latter species.

Distribution. Rather rare at Upware, Potton, and Brickhill. A specimen from the Bargate Beds of Surrey probably referable to this species is in the Shaw Collection (GS) and a specimen from Faringdon (SM B.18290) may possibly belong to it.

Cyrtothyris seeleyi (Walker)

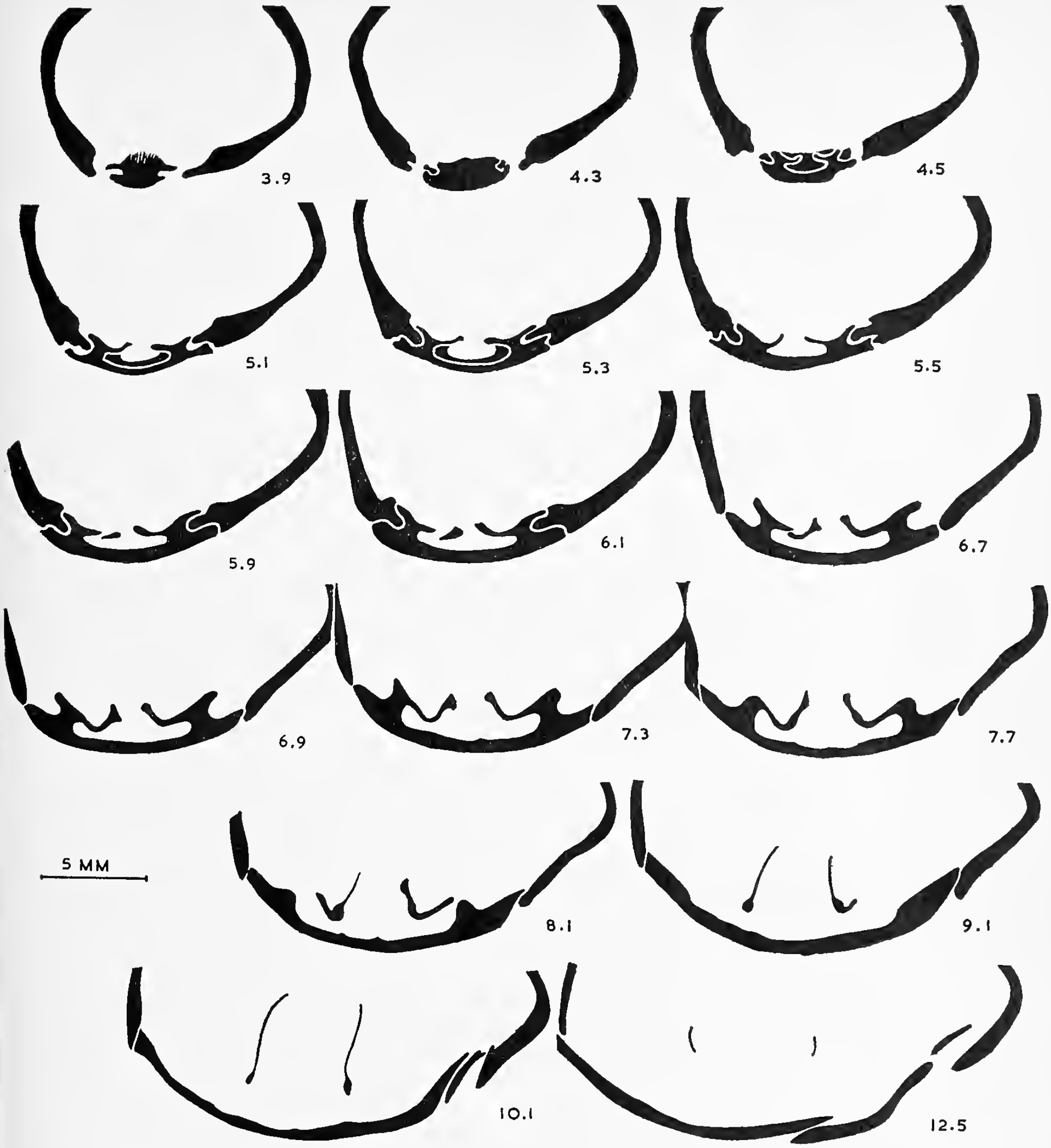
Plate 18, figs. 3, 4; text-fig. 17

Terebratula seeleyi Walker 1870, p. 561; p. 563, figs. 6–8.
Terebratula seeleyi Walker; Davidson 1874, p. 43, pl. 7, figs. 3, 4.

Lectotype. BM 67845, Upware, Cambridgeshire (Walker 1870, figs. 6, 7) (dimensions: length 38, breadth 23, thickness 16).

Diagnosis. *Cyrtothyris* of elongated oval ventral profile; P/A ratio about 1. In lateral profile both valves regularly and gently convex, flattening anteriorly with greatest thickness well posterior to mid-line, shell tapering towards both front and sides. Beak nearly straight to sub-erect. Symphytium large and well exposed. Angle of truncation *c*. 110°. Lateral commissure very gently curved, anterior commissure typically rectimarginate. Hinge plates concave posteriorly to markedly virgate anteriorly.

Description. The ventral and lateral profiles and symphytium characters of this species are its distinctive features. Variation is mainly confined to the length/breadth ratio and



TEXT-FIG. 17. Transverse sections through *Cyrtothyris seeleyi* (Walker). The first three sections show enclosure of the hinge plates by the enlarged cardinal process. The hinge plates can be seen to become clubbed at 5·9 and virgate at 6·7. Sections at 9·1 and 10·1 show the form of the crura and at 12·5 the descending lamella of the loop. BM BB.16214, Upware.

to various asymmetries shown by individuals. Apart from this the most important variable character is the anterior commissure which, although typically rectimarginate, may be incipiently uniplicate or incipiently sulcate.

Juvenile stages are thin, oval, less elongated than the adults, so that, with their fairly straight beak, well-exposed symphytium, and rectimarginate anterior commissure, they much resemble equivalent growth stages of *C. uniplicata*. Further growth is accompanied by relative elongation, while individuals verging on the gerontic tend to develop slight uniplication or sulcation and a slightly more incurved beak. The characteristics of the symphytium and the tapering form of the shell are retained throughout growth.

Remarks. Walker's (1870) and Davidson's (1874) descriptions differ slightly; Davidson describes the beak as 'incurved', Walker as 'very slightly recurved'; Walker describes the anterior commissure as 'not plicated' but Davidson speaks of slight plication. In both of these particulars Walker is the more accurate.

The only species to which *C. seeleyi* bears much resemblance is *C. uniplicata*, to which some younger individuals appear very close externally. Some of the flatter and more elongated varieties of *Platythyris comptonensis* at Upware have been mistaken for *C. seeleyi* in the past but they possess a much shorter symphytium and more definite uniplication.

Distribution. The species is probably confined to Upware and Brickhill and is nowhere abundant, but a crushed specimen, rather juvenile, from the Bargate Beds of St. Martha's, Surrey, could possibly belong to it (BM B.8533).

Cyrtothyris dallasi (Walker)

Plate 18, figs. 5–7; text-fig. 18

Terebratula dallasi Walker 1867, p. 455, pl. 19, figs. 1*a*–*c*, 2*a*–*c*.
Terebratula dallasi Walker 1868, p. 404.
Terebratula dallasi Walker; Davidson 1874, p. 45, pl. 3, figs. 1–5.

Lectotype. BM 62204, Walker Coll., Upware, Cambridgeshire (Walker 1867, pl. 19, figs. 2*a*–*c*) (dimensions: length 27, breadth 20, thickness 25).

Diagnosis. *Cyrtothyris* of short, blunt pear-shaped ventral profile, regularly rounded anteriorly. In lateral profile pedicle valve gently convex for three-quarters or more of postero-anterior distance, whence it bends abruptly dorsalwards at about 80°. Brachial valve gently convex from the umbo to its extreme anterior extension whence it bends abruptly ventralwards and slightly posteriorly at a little more than a right angle to meet downturned portion of pedicle valve. Beak short, sub-erect; beak ridges fairly well defined, especially close to foramen. Symphytium short but visible. Angle of truncation *c*. 115°. Lateral commissure straight; anterior commissure rectimarginate to slightly sulciplicate. Hinge plates almost horizontal posteriorly, more distinctly virgate anteriorly. Crural flanges absent. Loop pear-shaped in plan. Muscle scars large.

Description. The appearance of diverging moderately convex valves connected by a sub-vertical anterior and lateral 'curtain' of shell, together with the short beak and large foramen, makes this species distinctive. It is variable in details of shape and proportion, many individuals showing asymmetry or deformity. The main variable character is the length/breadth ratio, some individuals becoming distinctly elongated while retaining the other diagnostic characters.

The rectimarginate anterior commissure is almost sufficiently constant to be diagnostic, slight development of biplication being rare and essentially gerontic.

The muscle scars are shown by an internal cast (BM B.25607). The principal impressions are broad, pear-shaped, slightly angular in outline and are very large, the impressions of the pallial sinus trunks diverging not from between the adductor scars but from their anterior apices. The diductor scars in the pedicle valve also appear to be very large but are not well preserved.

TEXT-FIG. 18. Transverse sections through *Cyrtothyris dallasi* (Walker). The cardinal process, enlarged by callus, is seen enclosing the hinge plates at 5·8 and 6·6. The clubbed hinge plates become virgate at 8·4. The form of the crura can be seen at 9·9 and the high-arched, strongly recurved transverse lamella can be reconstructed from the sections at 12·9–13·9. SM B.80781, Brickhill.

Remarks. This is a puzzling species in that it exhibits a type of shell growth frequently seen as a gerontic condition in other species, e.g. in *Praelongithyris lankesteri* and *C. cantabridgiensis* and also in *Terebratula biplicata* var. *gigantea* Walker from the Albian (BM B.26146, Shenley Limestone, Leighton Buzzard). It would appear, however, that this shape in *C. dallasi* is a true specific character and not a gerontic development only, since specimens down to 23 mm. in length show it as clearly as larger individuals, if not more so.

Distribution. Largely confined to Upware, Potton, and Brickhill, but not common. A damaged specimen (BM B.25977) from Hythe, Kent (probably Sandgate Beds), may possibly belong to this species. Meyer's record at Faringdon (Davidson 1874) seems to be based only on a doubtful brachial valve (BM B.8317).

Genus PRAELONGITHYRIS gen. nov.

Type species *P. praelongiforma* nov. (= *Terebratula praelonga* auctt. pars)

Diagnosis. Foramen large or very large, circular, permesothyrid, slightly labiate in gerontic stage. Angle of truncation 120–130°. Beak sub-erect to erect; beak ridges rounded. In ventral profile elongated, drawn out posteriorly, truncated anteriorly. Anterior commissure sulciplicate in adult stage but rectimarginate condition retained late. Cardinal process small but enlarged by callus. Pedicle collar sometimes present. Accessory articulation developed. Hinge plates virgate, clubbed. Crural flanges present. Loop broad, triangular; transverse lamella high-arched. Dorsal muscle scars and euseptoidum as in *Cyrtothyris.*

Remarks. The species here ascribed to this genus much resemble internally, and are probably closely related to, *Cyrtothyris.* Evidence on this point may emerge from work on the Hauterivian fauna now in progress. For the time being these species are thought to be sufficiently distinct in external characters, especially of the general shell shape and of the beak and foramen, to justify inclusion in a separate genus.

Praelongithyris praelongiforma sp. nov.

Plate 17, fig. 6; Plate 18, fig. 1; text-figs. 2, 12, 19

Terebratula praelonga J. de C. Sowerby *in* Fitton 1836, p. 339.
Terebratula praelonga J. de C. Sowerby 1837, pl. 14, fig. 14*a*, non fig. 14*b*.
Terebratula praelonga J. de C. Sow.; Davidson 1855, p. 58, pl. 7, figs. 1, 2.
Terebratula praelonga J. de C. Sow.; Walker 1868, p. 403, pl. 19, fig. 1.
Terebratula praelonga J. de C. Sow.; Davidson 1874, p. 37, pl. 3, figs. 12, 13.

Holotype. BM 67590, Walker Coll., Upware, Cambridgeshire (Walker 1868, pl. 19, fig. 1) (dimensions: length 45, breadth 27, thickness 25·5).

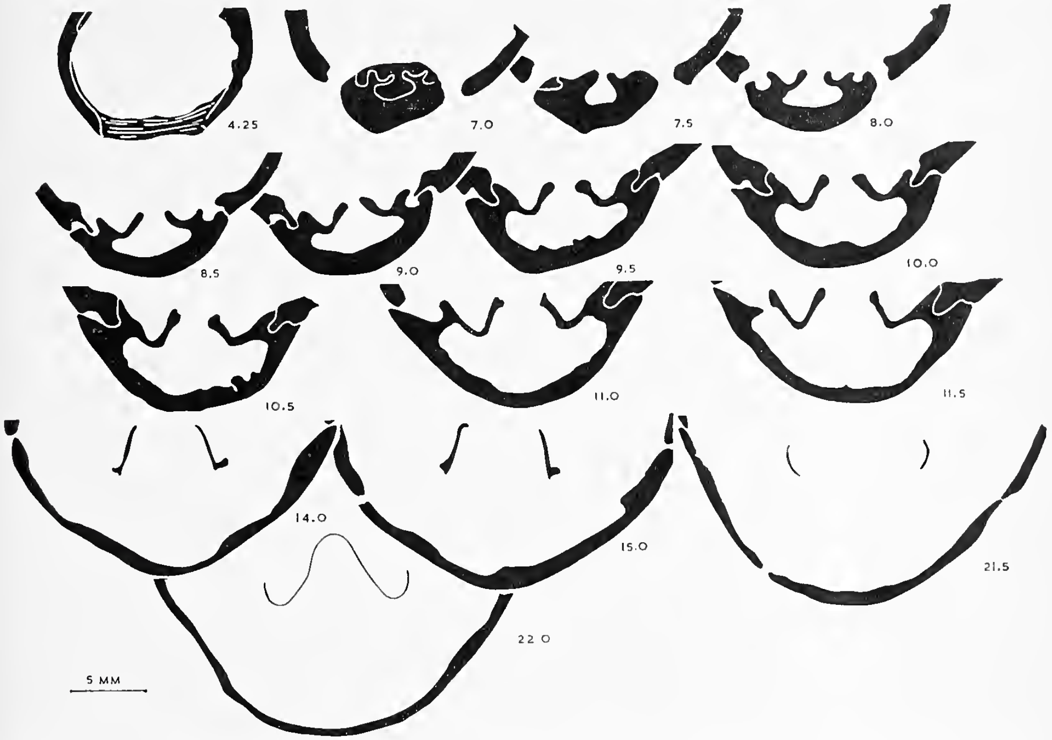
Diagnosis. Praelongithyris with P/A ratio distinctly more than 1. Both valves strongly and uniformly convex in lateral profile. Shell folded anteriorly in adults. Beak moderately long, sub-erect. Foramen slightly labiate in gerontic specimens. Angle of truncation 120–130°. Symphytium large, distinct and well exposed. Dorsal umbonal cavity large. Crural flange and keel present.

Description. In a typical adult the valves are strongly folded to correspond with the plication of the anterior commissure. Davidson aptly described the species as 'scuttle-shaped', to express the appearance given to the shell by the typical drawn out structure of the posterior and the wide, blunt, biplicate truncation of the anterior end. It is a large form, fully adult individuals ranging up to 58 mm. in length, and variable in some of its characters, but the shapes of the beak, foramen, and symphytium are constant. The angle of truncation is unusually high, so that the foramen appears to extend ventrally into the pedicle valve. The symphytium is well exposed not because the beak is remarkably straight, but because it is produced while remaining sub-erect.

Forms of *P. praelongiforma* at Brickhill differ from those occurring at Upware in the biplication, which tends to be very weak or absent at Brickhill but well developed at

Upware, although individuals with weak plication did occur at the latter. Those individuals in which biplication is absent are rectimarginate and not uniplicate. The characters of the beak and foramen remain constant.

Young specimens are thinner than older ones, the increase in obesity continuing into the gerontic stage. Biplication develops comparatively late in life. Out of a number of young specimens of this species from Shanklin (SM B.14903–10) the youngest (13 mm.) are not very clearly distinguishable from the equivalent stages of *Cyrtothyris uniplicata* except perhaps by greater relative thickness; they have the same fairly straight beak, well-exposed symphytium and rather rhomboidal shape with rectimarginate anterior commissure. Some of the larger specimens (20 mm.) show a slight early development of biplication, without intervening uniplicate stage.



TEXT-FIG. 19. Transverse sections through *Praelongithyris praelongiforma* nov. 4·25 shows the large symphytium. Enclosure of the hinge plates by the secondarily enlarged cardinal process is seen at 7·0, the virgate, strongly clubbed hinge plates at 9·0–11·0, the keeled and flanged crura at 14·0, descending lamellae of the loop at 21·5, and the high-arched transverse lamella at 22·0. SM B.80778, Upware.

The development of biplication remains the most variable character, since occasional adult individuals over 40 mm. long remain rectimarginate. The symphytium is variable in length, although always well exposed. There is also a good deal of variation in minor details of shape and proportion.

Remarks. Sowerby described his species *Terebratula praelonga* as ‘ovate, much elongated, gibbose; front slightly elevated, with a depression in its middle; beak prominent, large;

surface smooth' and figured two specimens, giving only one view of each. The first was a dorsal view, taken 'from a drawing by the Rev. G. E. Smith', so that there is no definite indication that Sowerby even saw the specimen, which is presumed to be now lost. This is the figure which has always been taken by authors as the type of *T. praelonga*. As a result, interpretation of the species has always been confused, especially on the European continent, where several distinct species with rather elongated beaks have been referred to it, in particular *T. acuta* auctt. and *T. valdensis* de Loriol.

Sowerby's second figure was a ventral view of a small form which showed nothing of diagnostic value and has apparently been ignored by subsequent authors. The original specimen of this figure is, however, preserved (GS 2008) and, since the original of the first figure is presumed lost, is the sole surviving type specimen. On re-examination it can be seen that this specimen is not the form which has always been known as *T. praelonga* on the basis of Sowerby's first figure but is, in fact, a long-looped form rather close to Walker's '*Waldheimia*' *juddi*. Since this specimen is here chosen as lectotype of *T. praelonga* J. de C. Sow., the form which has usually gone under that name must become a new species for which the name *praelongiforma* is proposed.

T. acuta differs from *P. praelongiforma* in several respects: (*a*) its biplication develops at a much earlier stage; (*b*) its foramen is less strongly permesothyrid; (*c*) it is altogether smaller, really large gerontic specimens reaching little more than 30 mm. in length; (*d*) its symphytium is distinctly 'bordered' (de Loriol *in* Pictet 1872); (*e*) it does not possess the strongly virgate hinge plates and keeled crura of *Praelongithyris*. Pictet (1872, p. 76) discusses the confusion of these two species and concludes that the true *T. praelonga* (*Praelongithyris*) is not present in the Neocomian of Switzerland. *T. valdensis* differs from *P. praelongiforma* principally in its more incurved beak and shorter and more hidden symphytium and in having piped concave hinge plates.

Distribution. The true *P. praelongiforma* is possibly confined to the English area. It occurred fairly abundantly at Upware, more rarely at Brickhill. Elsewhere it is rare but undoubted examples have been found in the Bargate Beds of Surrey, at Maidstone (Davidson 1854, pl. 7, figs. 2–2*c*), and at Shanklin (Upper Ferruginous Sands) (SM B.14903–12). Less typical specimens have been found at Faringdon, at Sandgate, Kent (Sowerby's original figure), in the Hythe Beds of Borough Green, Kent, and Godstone, Surrey (CWW), and at Pulborough, Sussex (BM 9287). A form very similar externally occurs in the Claxby Series of Lincolnshire and the Hils Conglomerate of Brunswick.

Praelongithyris lankesteri (Walker)

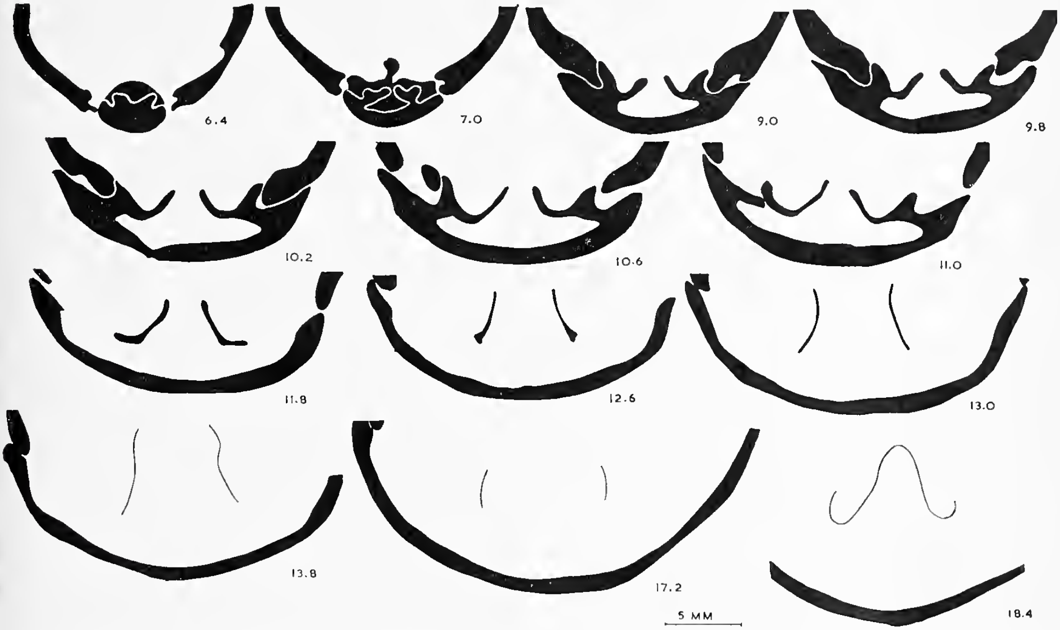
Plate 18, fig. 2; text-fig. 20

Terebratula lankesteri Walker 1868, p. 402, pl. 19, figs. 2–2*b*.
Terebratula lankesteri Walker; Davidson 1874, p. 38, pl. 3, figs. 9–11.

Holotype. BM 67591, Walker Coll., Upware, Cambridgeshire (a deformed individual) (dimensions: length 41, breadth 26, thickness 26).

Diagnosis. *Praelongithyris* of oval ventral profile or slightly truncated anteriorly. In lateral profile both valves very convex. P/A ratio about 1. Maximum thickness towards anterior end, especially in gerontic individuals. Beak moderately short, sub-erect to erect, usually more nearly the latter. Angle of truncation *c.* 120°. Symphytium moderately short but distinctly visible. Anterior commissure sulciplicate but not strongly so; shell little folded. Crural flange present but not crural keel.

Remarks. This species has the same general shape, beak, and foramen structure as *P. praelongiforma.* The chief differences are that in *P. lankesteri*: (*a*) the beak is more incurved and the symphytium shorter; (*b*) the beak is shorter and less obviously produced, although it varies in this respect; (*c*) the shell is globose anteriorly, at least in adult specimens, and little folded; (*d*) the anterior part of the shell becomes increasingly inflated in the gerontic stage, which does not occur in *P. praelongiforma.* Apart from the latter the only species to which any resemblance is shown by certain specimens is *Cyrtothyris dallasi.*



TEXT-FIG. 20. Transverse sections through *Praelongithyris lankesteri* (Walker). Secondary enlargement of the cardinal process by callus is seen at 6·4 and 7·0, the virgate hinge plates at 9·0–10·6, the passage into the crura at 11·0–13·8, descending lamellae of the loop at 17·2, and high-arched transverse lamella at 18·4. SM B.80780, Upware.

Walker laid stress on the fine longitudinal striae said to characterize this species but this is a character seen in any Lower Cretaceous terebratulid in the right condition of preservation. He also quoted the shell structure as a point of distinction from *T. praelonga* (*P. praelongiforma*), the punctations in *P. lankesteri* being smaller and wider apart.

Distribution. Rare at Upware, very rare at Brickhill. Some poorly preserved ferruginous casts from Potton probably belong to this species. It was apparently a local derivation from *P. praelongiforma.*

SUMMARY OF STRATIGRAPHICAL CONCLUSIONS

The stratigraphical value of English Aptian terebratulids is limited partly by the small geographical range of most of the species and partly by their sporadic occurrences, separated by large areas and thicknesses of barren sands, continuous fossiliferous limestone formations being absent.

The Albian and Aptian terebratulid faunas. The distinction between these is most clearly shown on the borders of Buckinghamshire and Bedfordshire where the unfossiliferous Woburn Sands separate the phosphatic deposits of Brickhill, at the base, from the Shenley Limestone, at the top; the former bears an Aptian, the latter an Albian fauna, with hardly a species in common. The Shenley Limestone fauna, never adequately

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EXPLANATION OF PLATE 16

All figures are natural size.

Figs. 1–4. *Sellithyris sella* (J. de C. Sowerby). 1*a–c*, Holotype, BM B.61547, Sowerby Coll., Hythe Beds, Hythe, Kent. 2*a–c*, BM B.61549, Sowerby Coll., Hythe Beds, Hythe. 3*a–c*, BM 31433, Davidson Coll., Ferruginous Sands, Isle of Wight. 4, Ventral view to show the longitudinal striae in the shell, BM B.25970, Hythe Beds, Lympne, Kent.

Figs. 5, 6. *Sellithyris sella shanklinensis*, subsp. nov. 5*a–c*, Holotype, BM BB.16234, Walker Coll., Ferruginous Sands, Shanklin, Isle of Wight. 6*a–c*, Specimen showing well the shape of the anterior commissure, BM B.15126, Slatter Coll., Ferruginous Sands, Shanklin.

Figs. 7–9. *Sellithyris upwarensis* (Walker). 7*a–c*, Holotype, BM 67594, Walker Coll., Upware, Cambs. 8*a–c*, Typical Brickhill specimen, BM B.25468, Walker Coll., Brickhill, Bucks. 9*a–c*, Juvenile specimen, BM B.25594, Walker Coll., Upware.

Figs. 10–12. *Sellithyris coxwellensis* sp. nov. 10*a–c*, Holotype, BM B.26007, Walker Coll., Faringdon, Berks. 11*a–c*, Specimen showing relatively little folding of the valves, BM B.26036, Walker Coll., Faringdon. 12*a–c*, A stunted specimen, BM B.21136, Addison Crofton Coll., Faringdon.

Figs. 13*a–c*. *Cyrtothyris cyrta* (Walker). Holotype, BM 67597, Walker Coll., Upware, Cambs.

EXPLANATION OF PLATE 17

All figures are natural size.

Figs. 1*a–c*. *Cyrtothyris cyrta* (Walker). A relatively juvenile specimen, BM B.25625, Walker Coll., Upware, Cambs.

Figs. 2–3. *Cyrtothyris uniplicata* (Walker). 2*a–c*, Holotype, BM 67843, Walker Coll., Upware, Cambs. 3*a–c*, Typical Faringdon specimen, BM B.26025, Walker Coll., Faringdon, Berks.

Figs. 4–5. *Cyrtothyris cantabridgiensis* (Walker). 4*a–c*, Holotype, BM 67844, Walker Coll., Upware, Cambs. 5*a–c*, A more juvenile specimen, BM B.6256, Davidson Coll., Upware.

Figs. 6*a–c*. *Praelongithyris praelongiforma* sp. nov. Holotype, BM 67590, Walker Coll., Upware, Cambs.

EXPLANATION OF PLATE 18

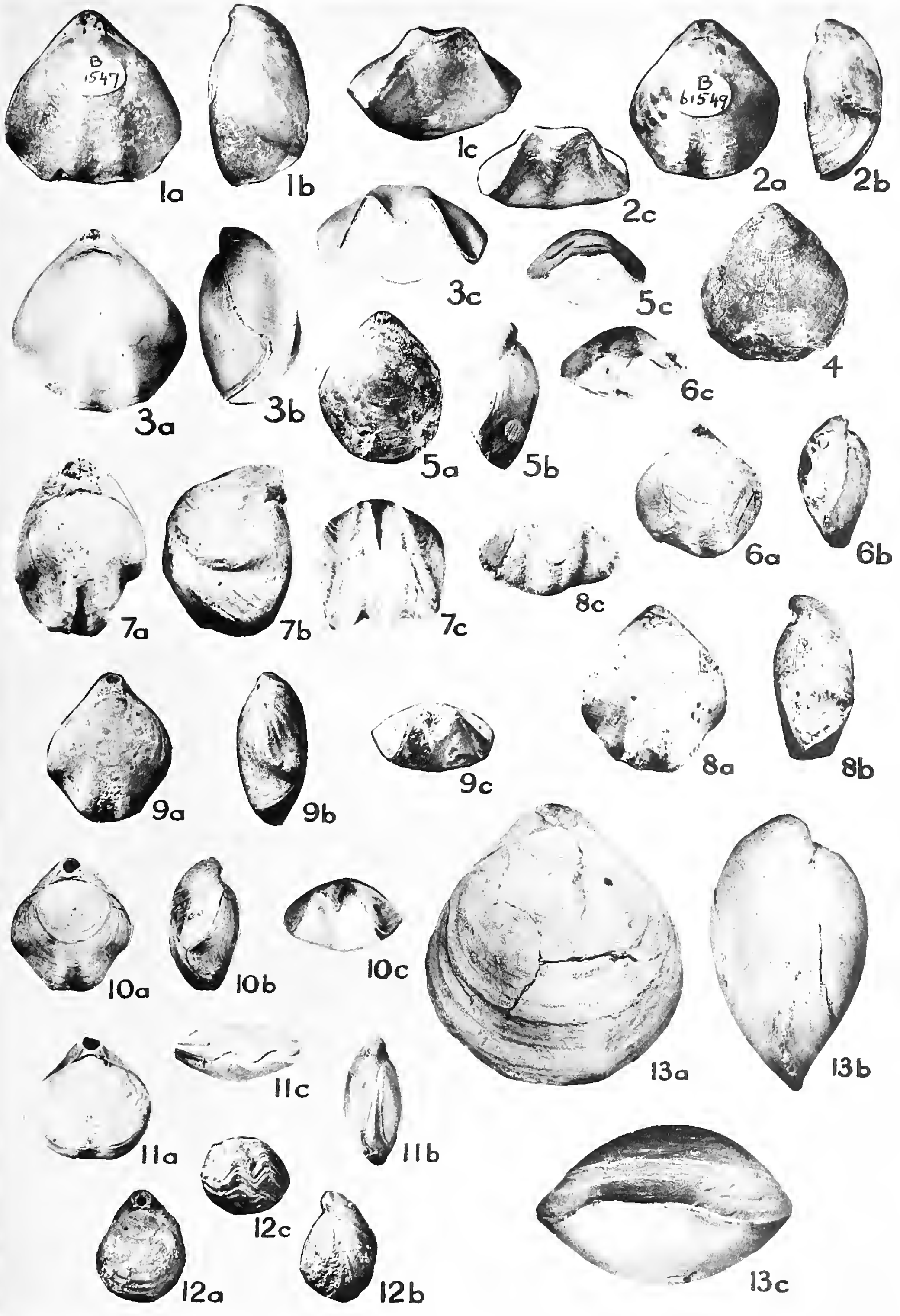
All figures are natural size except fig. 1*d*.

Figs. 1*a–d*. *Praelongithyris praelongiforma* sp. nov. BM BB.16231, Davidson Coll., Upware, Cambs.; 1*d* (slightly enlarged) is an oblique view to show the labiate foramen.

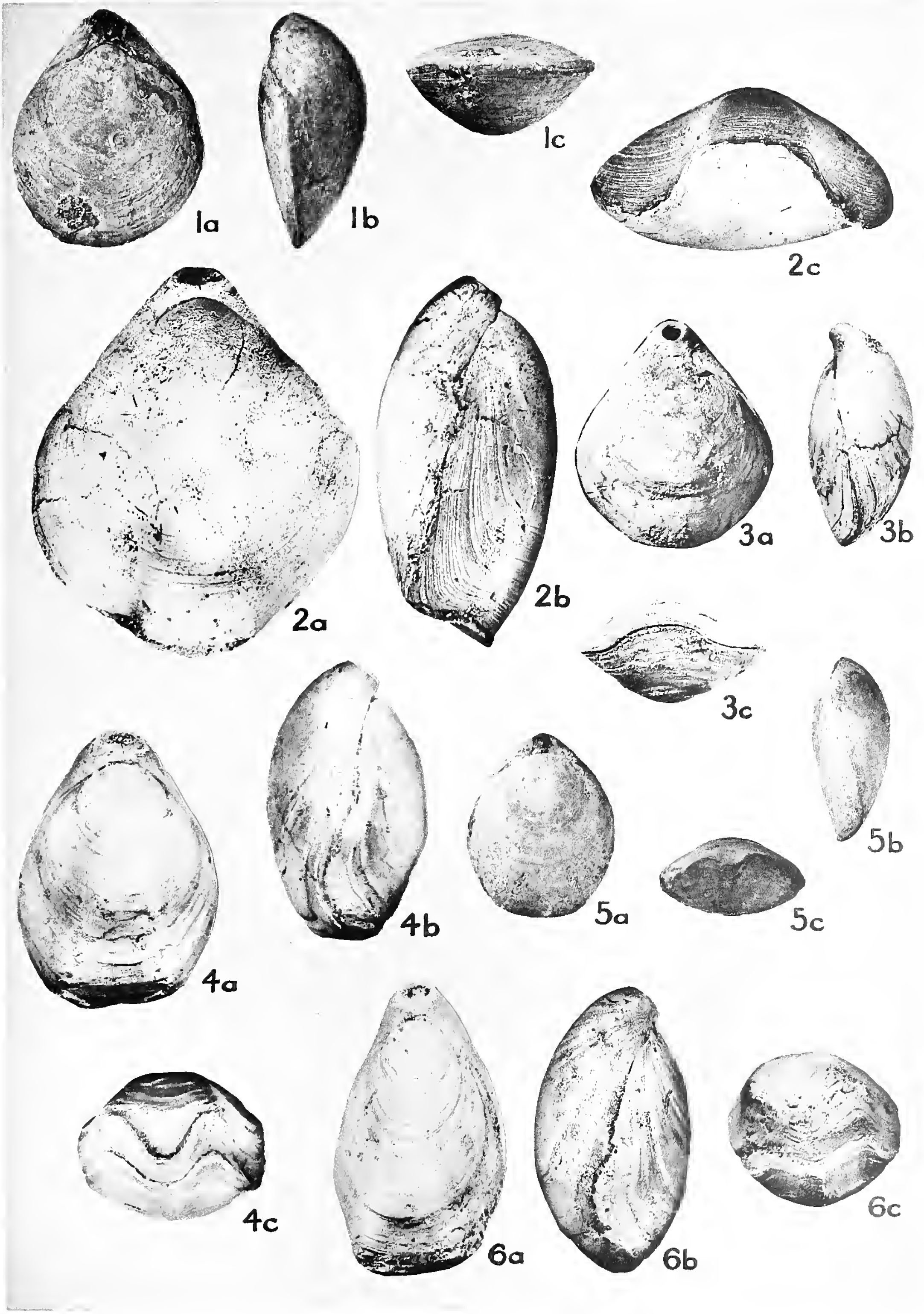
Figs. 2*a–c*. *Praelongithyris lankesteri* (Walker). Holotype, BM 67591, Walker Coll., Upware, Cambs.

Figs. 3–4. *Cyrtothyris seeleyi* (Walker). 3*a–c*, Lectotype, BM 67845, Walker Coll., Upware, Cambs. 4*a–c*, BM B.25462, Brickhill, Bucks.

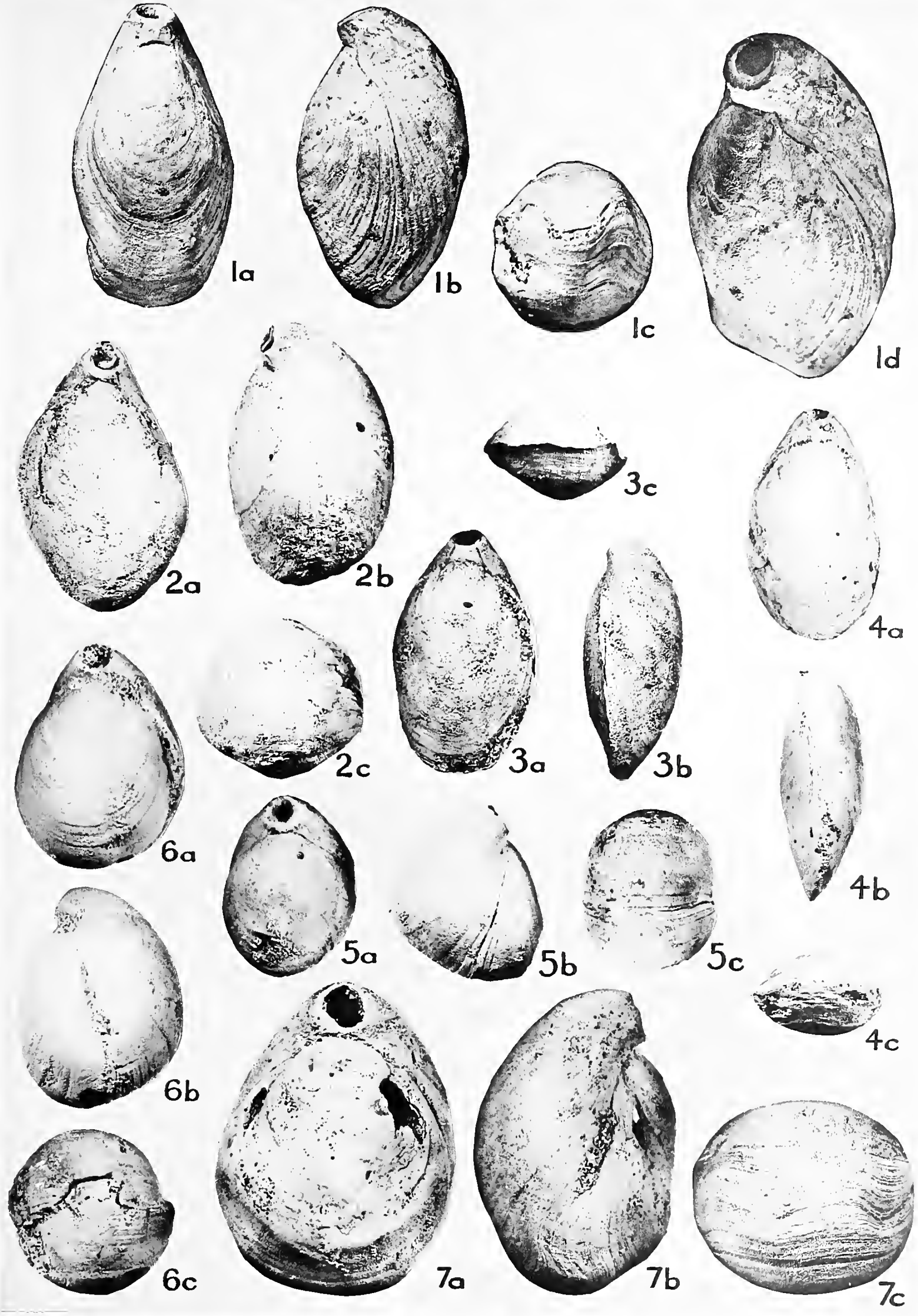
Figs. 5–7. *Cyrtothyris dallasi* (Walker). 5*a–c*, Lectotype, BM 62204, Walker Coll., Upware, Cambs. 6*a–c*, BM 62203, Potton, Beds. 7*a–c*, Gerontic specimen with biplicate anterior commissure, BM B. 25463, Brickhill, Bucks.



MIDDLEMISS, Aptian Terebratulids



MIDDLEMISS, Aptian Terebratulids



MIDDLEMISS, Aptian Terebratulids

described, seems to be essentially of an Albian-Cenomanian type whose affinities with the Cenomanian Tourtias are demonstrated by the abundance of *Terebratula capillata* d'Archiac and of types closely related to *T. dutempleana* d'Orb. and by the presence of *T. robertoni* d'Archiac, *T. boubei* d'Archiac, and *T. ovata* J. Sowerby. This affinity is underlined also by the long-looped terebratuloids and the rhynchonelloids (Lamplugh and Walker 1903; Kitchin and Pringle 1920). A similar brachiopod fauna is found in the remainder of the English Albian (Price 1874; Whitaker and Jukes Browne 1899; Kitchin and Pringle 1922), again with hardly a species which is found in the English Aptian. It should be noted that this English Albian-Cenomanian fauna, unlike that of the Aptian, is closely similar to faunas of the same age in north-west Europe.

The Upper Aptian. This fauna is characterized by the presence of *Rhombothyris* and *Platythyris*, of species and subspecies of *Sellithyris* other than *S. sella* s.s., and of certain species of *Cyrtothyris* (*C. uniplicata*, *C. seeleyi*, *C. cantabridgiensis*).

In the Weald and the Isle of Wight, where Lower as well as Upper Aptian deposits exist, the Upper fauna appears at a definite horizon, corresponding to the Bargate Beds of west Surrey and Sussex, the base of the Sandgate Beds in east Kent, and a glauconitic sand high in the Ferruginous Sands (Group XIII) at Shanklin, Isle of Wight. These three can be correlated also by the presence of the zonal ammonite *Parahoplites nutfieldensis*. Members of the same fauna occur in the upper part of the rag and hassock facies (Hythe Beds) in west Kent, although not until the base of the overlying Sandgate Beds in East Kent, and also in Group X of the Ferruginous Sands in the west of the Isle of Wight, thus the fauna may have entered the area during the deposition of the *Cheloniceras martini* zone, but the evidence is not clear before the succeeding *P. nutfieldensis* zone.

At Faringdon sedimentation commenced with beds containing both *P. nutfieldensis* and an Upper Aptian brachiopod fauna, clearly to be correlated with the Bargate Beds. To the north of London the richly fossiliferous deposits of Brickhill, Potton, and Upware are of more debatable age, lacking indigenous ammonites of precise zonal significance. The indigenous brachiopod fauna is unmistakably Upper Aptian and it can be stated that, on this evidence, there is no ground for assuming the presence of pre-Upper Aptian deposits, although derived Lower Aptian ammonites and derived Infra-Valanginian brachiopods occur. There were two fossiliferous levels at Upware (Keeping 1883), but whether there was any significant difference in fauna between the two is now impossible to say. None seems to have been noted when the sections were visible. Northwards from Upware brachiopods are extremely rare in the Aptian and of no stratigraphical value.

Appended are complete lists of species of Terebratulidae from the principal Upper Aptian localities, together with important species of other groups of brachiopods:

Upware: *Rhombothyris extensa*, *R. microtrema*, *R. meyeri*, *Platythyris comptonensis*, *Sellithyris upwarensis*, *Cyrtothyris cyrta*, *C. uniplicata*, *C. cantabridgiensis*, *C. seeleyi*, *C. dallasi*, *Praelongithyris praelongiforma*, *P. lankesteri*.

Brickhill: As at Upware but without *R. meyeri* and with the addition of *R. conica* and *Platythyris minor*.

Faringdon (Sponge Gravels): *S. coxwellensis*, *C. uniplicata*, *C. cyrta*, *C. cantabridgiensis*, *P. praelongiforma*. The first two species are by far the most abundant.

Significant species of other brachiopod groups common to Upware, Brickhill, and Faringdon: *Gemmarcula aurea* Elliott, *Terebratella fittoni* Meyer, '*Ornithella*' *juddi* (Walker), '*O.*' *pseudojurensis*

(Leymerie), *Rhynchonella antidichotoma* Buvignier, *Rh. depressa* J. de C. Sow., *Cyclothyris latissima* (J. de C. Sow.).

Bargate Beds, West Surrey: Terebratulids: *R. extensa*, *P. comptonensis*, *S. sella* var., *C. cantabridgiensis*, *C. seeleyi*, *P. praelongiforma*. Other groups: *Terebratulina elongata* Davidson, *G. aurea*, *T. fittoni*, *Terebratella trifida* Meyer, *T. davidsoni* Walker (?), '*Ornithella*' *juddi*, '*O.*' *wanklyni* (Walker) (?), *R. antidichotoma*, *Rhynchonella cantabridgiensis* Davidson (?), *R. upwarensis* Davidson (?).

Upper part of Hythe Beds, Maidstone area, west Kent: *R. extensa*, *P. comptonensis* var.; *G. aurea*, *T. fittoni*.

Base of the Sandgate Beds, east Kent: *S. sella* var., *P. comptonensis* (?), *C. cyrta*, *C. dallasi* (?), *P. praelongiforma*; *Terebratella oblonga* (J. de C. Sow.), *Sulcirhynchia hythensis* Owen 1956 (= *Rhynchonella gibbsiana* auctt.), a zeillerid.

Glauconitic sand in Group XIII of the Ferruginous Sands, Shanklin, Isle of Wight: *R. extensa*, *P. comptonensis*, *S. sella shanklinensis*, *C. uniplicata*, *P. praelongiforma*; *T. oblonga*, '*O.*' *juddi* (?), '*O.*' *morrisi* (Meyer), '*O.*' *celtica* (Morris), '*O.*' *tamarindus* (J. de C. Sow.) var., '*O*'. *wanklyni*, *S. hythensis*, *Rhynchonella parvirostris* (J. de C. Sow.), *Lingula truncata* J. de C. Sow.

The Lower Aptian. This fauna is characterized by abundance of *S. sella* s.s. and by occasional forms comparable with *C. cyrta* and *P. praelongiforma*, these being the only terebratulid species. The rest of the brachiopod fauna is scanty: *T. oblonga* (J. de C. Sow.), *S. hythensis* Owen, *R. parvirostris* (J. de C. Sow.), *Lingula truncata* J. de C. Sow.

The Lower Aptian fauna occurs in the lower half of the Ferruginous Sands in the western part of the Isle of Wight (Atherfield), where the upper half is so sparsely fossiliferous that no definite upper boundary to the fauna can be stated. The fauna is also represented in the *Perna* Bed (base of the Atherfield Clay) on both sides of the Isle of Wight and along the northern crop of the Weald, and in the Hythe Beds of Kent, Surrey, and Sussex, especially east Kent, but not to the north of the Weald.

British and continental Aptian faunas. The Aptian brachiopod fauna of England has little in common with that of adjoining countries of Europe, in contrast to that of the Albian and Cenomanian, in which many species are common to Britain and Western Europe.

The Lower Aptian fauna is much poorer in species in England and many of the most characteristic species of the Lower Aptian of the Paris Basin (Corroy 1925), the Jura and north-west Germany do not appear. Such are: *Terebratula essertensis* Pictet, *T. acuta* auctt., *T. russillensis* de Loriol, *T. valdensis* de Loriol, *T. moutoniana* d'Orb., *T. collinaria* d'Orb., *T. moreana* d'Orb., *Terebratella astieriana* d'Orb., *Terebrirostra arduennensis* d'Orb.

The typical southern English Upper Aptian fauna does not appear at all on the Continent; of all the terebratulid species named above as occurring in the English Upper Aptian only *C. cyrta* seems to be known in that of the Continent. Among the long-looped forms, again, the typical English Upper Aptian species *G. aurea* Elliott, *T. trifida* Meyer, *T. davidsoni* Walker, and *T. fittoni* Meyer are not found on the Continent.

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DUFTONIA, A NEW TRILOBITE GENUS FROM THE ORDOVICIAN OF ENGLAND AND WALES

by W. T. DEAN

ABSTRACT. A new phacopid trilobite genus *Duftonia* is described and assigned to the subfamily Acastinae Delo. In addition to the type material from the Ordovician of the Cross Fell Inlier in northern England other specimens related to the same species are described and figured from both North and South Wales.

DURING a recent re-examination of the stratigraphy and shelly faunas of the Caradoc Series in the Cross Fell Inlier, several specimens of what proves now to be a new genus and species of phacopid trilobite, here named *Duftonia*, were collected by the writer from the Pusgillian Stage. Since then another cranidium has been collected from the same horizon at Cross Fell by Mr. M. Mitchell who has kindly made it available for examination. The writer has also traced three other specimens belonging to a closely related form of *Duftonia*, two from North Wales, in the British Museum (Natural History), and one from South Wales, in the Geological Survey and Museum, London. Mr. J. D. D. Smith has kindly facilitated the loan of the last-named specimen.

The Cross Fell material was collected during field-work carried out with the aid of a grant from the Gloyne Outdoor Geological Research Fund, for the award of which I am grateful to the Council of the Geological Society of London. Professor W. F. Whittard has kindly read the manuscript and made several useful suggestions for its improvement. This paper is published by permission of the Trustees of the British Museum (Natural History).

Family PHACOPIDAE Hawle and Corda 1847

Subfamily ACASTINAE Delo 1935

Genus DUFTONIA gen. nov.

Type species *Duftonia lacunosa* sp. nov.

Diagnosis. Glabella of general phacopid outline with three pairs of glabellar furrows, the first or anterior pair of which are only faintly impressed; second and third pairs deep, third pair with apodemes. Three pairs of glabellar lobes, decreasing in size from first to third. Anterior branches of facial suture meet in front of glabella where a pre-glabellar furrow is not developed. In the type species, at least, surface of the glabella is finely granular, but that of the fixed cheeks is pitted. Small fixigenal spines present at the genal angles, and pygidium is mucronate.

Discussion. The type species of the new genus is found in the Pusgillian Stage, comprising the topmost Dufton Shales, Caradoc Series, of the Cross Fell Inlier in Westmorland, but closely related forms occur in strata usually classified with the Ashgill Series in both

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North and South Wales. No other records are yet known, but this may be due to lack of detailed collecting, or to absence of the requisite strata from much of England and Wales. *Duftonia* bears some resemblance to *Phacopidina* Bancroft 1949 but is distinguished by having more divergent axial furrows, eyes set farther from the glabella, deep second glabellar furrows which cut the axial furrows, and much smaller third glabellar lobes of different shape. It is named after the village of Dufton, Westmorland.

Duftonia lacunosa gen. et sp. nov.

Plate 19, figs. 1–3, 5, 6, 8

1948 *Pterygometopus sp.* Bancroft *in* Lamont, p. 468.

Derivation of name. lacunosa (Lat.) = pitted, referring to the pitted surface of the fixed cheeks.

Description. Cephalon roughly semicircular in outline. Glabella expanded anteriorly and attains its maximum breadth, which is about equal to the length, excluding occipital ring, just in front of the first glabellar furrows, though this not apparent in the holotype which is incompletely preserved. Axial portion of frontal lobe occupies about two-fifths of the length of the glabella. Three pairs of glabellar lobes decrease in size from first to third. First glabellar furrows straight, shallow, each extending inwards about one-third of the glabellar width, and diverge anteriorly at an angle of about 140 degrees; first glabellar lobes subtriangular in form, expanding outwards. Second glabellar furrows straight and moderately deep, directed inwards and slightly forwards, parallel to the long axes of the subrectangular second glabellar lobes. Third glabellar furrows deep, directed straight inwards, and expand slightly at their inner ends where apodemes are present, so that in consequence the small third glabellar lobes appear to increase in size outwards. Occipital furrow shallow medially, deepening laterally into apodemal pits; occipital ring long (*sag.*) centrally, but towards the axial furrows it first contracts slightly and then expands to form small occipital lobes. Axial furrows deep, narrow (except in internal moulds), and gently sigmoidal. The externally convex palpebral lobes stand about as high as the top of the glabella; they are sigmoidal in plan, thickened, and with a smooth surface, contrasting sharply with the pitting of the adjacent fixed cheeks from which they are separated by well-defined palpebral furrows. Anteriorly the palpebral lobes meet the axial furrows almost at right angles opposite the anterior half of the first glabellar lobes, after which they first run outwards and backwards, then curve sharply inwards and, finally, turn outwards again before being truncated by the intersection of the palpebral furrows and the outer margins of the palpebral lobes opposite the third or basal glabellar lobes. The eyes themselves have not been found preserved in the specimens from Cross Fell but are discussed later in an account of related Welsh material. Anterior branches of the facial suture run forwards from the eyes towards the widest portion of the glabella, where they cut the axial furrows, and then converge anteriorly to meet medially at the bluntly pointed outline of the frontal lobe. There is no development of a preglabellar furrow. Posterior branches of the facial suture continue the line of the palpebral furrows, curving first forwards and then back to meet the lateral margin just in front of the line of the pleuroccipital furrows which are broad (*exsag.*), straight, and become shallower towards, but do not reach, the lateral margin. Posterior margin of the cephalon transversely straight, and the genal angles are produced into small fixigenal spines, seldom preserved intact; immediately in front of these the cephalic margin is slightly indented, a feature which serves to emphasize the outwardly directed attitude of the fixigenal spines. Corresponding indentations and fixigenal spines of similar type are found in another Ordovician phacopid genus, *Phacopidina* Bancroft 1949, which is typified by the species *P. harnagensis* Bancroft and *P. apiculata* (M'Coy), both from the Caradoc Series of the Anglo-Welsh area.

Hypostoma and thorax are as yet unknown from the Cross Fell Inlier, but the thorax of a related form has been collected from Wales (see later). Several associated pygidia have been found at the type locality, of which one, a paratype, is figured (Pl. 19, figs. 1, 3). Outline is subparabolic and the border is produced posteriorly into a small, thorn-like caudal spine, directed backwards and upwards. Projected length, including spine, is about three-quarters of the maximum breadth. Axis occupies about one-third of the breadth of the pygidium anteriorly and is bounded by moderately deep axial furrows which converge rearwards at 25 to 30 degrees, becoming obsolete before reaching the base of the caudal spine; excluding the articulating half-ring there are five or six axial rings. Each side-lobe is moderately convex and bears four pleural furrows, the first three of which are deeply impressed and the fourth less so, and four faint rib furrows; all these furrows die out laterally without reaching the margin, resulting in the formation of a smooth border.

Surface of the glabella is covered with fine granules, hardly discernible on internal moulds, and the fixed cheeks are finely pitted as seen from the external mould, though appearing granulose in internal moulds owing to the state of preservation. As already stated, the palpebral lobes are quite smooth. One specimen, BM. In.49824B, shows that at least part of the outer surface of the cephalic doublure carries fine granules. Surface of pygidium is smooth.

Measurements (*in mm.*). IM.= internal mould. EM. = external mould.

	In.49821	*In.49824A*	*In.49826*	*In.49920*
	IM.	*EM.*	*IM.*	*IM.*
Length of cranidium	6·2	8·0	7·8	..
,, ,, glabella .	5·3	6·4	6·8	..
Breadth,, ,, .	5·0	7·0	..	..
,, ,, cranidium	12 (estd.)	..	..	..
Length ,, pygidium	..	..	..	6·5
Breadth,, ,,	..	..	..	8·5
Max. breadth of axis	..	..	..	3·0

Holotype. BM. In.49824A (Pl. 19, fig. 6), an external mould of an incomplete cranidium, figured here as a latex cast. *Paratypes*. BM. In.49821 (Pl. 19, fig. 2); In.49826 (Pl. 19, fig. 8); In.49830 (Pl. 19, fig. 5); In.49920 (Pl. 19, figs. 1, 3).

Horizon and localities. The holotype and paratypes were all obtained from a highly fossiliferous band of weathered sandy limestone, average thickness about 2 inches, at the exposure in the eastern bank of Swindale Beck immediately north of the stone bridge 70 yards north-north-east of the barn situated about 820 yards south-south-east of the summit of Knock Pike, Westmorland (National Grid reference 36884/52758). The species occurs also in the western bank of Swindale Beck directly opposite the type locality and at the same horizon. In the section cut through by Pus Gill, about half a mile north-east of Dufton, Westmorland, *Duftonia lacunosa* has been found by Mr. M. Mitchell at the exposure in the north-western bank of the stream 680 feet north-east of Pusgill House (National Grid reference 36980/52577). Other sections from which the species has been recorded are Hurning Lane, one mile due north of Dufton, and Billy's Beck, east of the same village.

All the above occurrences of *D. lacunosa* are in the uppermost part of the Dufton Shales, strata to which Bancroft gave the name Pusgillian Stage. At the type locality the associated fauna includes the trilobites *Atractopyge*, *Cybeloides*, *Flexicalymene*, *Platylichas*, and *Tretaspis*, and the brachiopods *Onniella*, *Sampo*, and *Sowerbyella*.

Discussion. *Duftonia lacunosa* sp. nov. is almost certainly the trilobite recorded by Bancroft on a locality map (*in* Lamont 1948, p. 468) as *Pterygometopus sp.*, though no specimen has been found in his collection at the British Museum (Natural History). The horizon was marked on the same map as '*Pterygometopus* Beds', but this term was never described or defined by him, and the number of individuals occurring there certainly does not warrant the introduction of such a name. The type species of *Pterygometopus*, *P. sclerops* (Dalman), has been redescribed by Whittington (1950, p. 538, pl. 68, figs. 17–20; pl. 69, figs. 1–4) who has preferred to restrict the genus to those forms in which, unlike *Duftonia*, a preglabellar furrow is developed. Another trilobite from the Anglo-Welsh Caradoc Series which is customarily referred to *Pterygometopus* can now be named *Estoniops jukesi* (Salter); the genus *Estoniops* has been erected by Männil (1957, p. 385) on the basis of *Acaste exilis* Eichwald 1857 and, like *Duftonia*, lacks a preglabellar furrow, but other differences are so marked that the two genera are unlikely to be confused, and are placed in different subfamilies.

The phacopid described and figured by Linnarsson (1869, pp. 59, 86, pl. 1, figs. 1, 2) as *Phacops recurvus* from the Trinucleidskiffer of Sweden resembles *D. lacunosa* in the form of the pygidium and, to a lesser extent, of the glabella and eyes, but unfortunately no photographs of the type material have been published and a full comparison is not possible. Kielan (1956, pl. 2, figs. 2–4) has figured what she calls *Pterygometopus recurvus*, the authorship of which species she wrongly ascribes to Olin instead of Linnarsson, from the Ashgill Series of Poland, but her specimen more resembles a typical *Calliops* and is not close to Linnarsson's original figures.

The only British Caradoc phacopid with which *Duftonia lacunosa* might possibly be confused is *Phacopidina apiculata* (M'Coy), which has been redescribed by Harper (1947, p. 169, pl. 6, figs. 6, 9). The glabella of the latter species differs markedly from that of *D. lacunosa* in having eyes situated closer to the glabella, straighter, more closely parallel axial furrows, second glabellar furrows which are curved, only faintly impressed and do not reach the axial furrows, and third glabellar furrows which are less divergent forwards and border larger basal glabellar lobes of 'cat's-ear' form, subtriangular in outline and very narrow (*exsag.*) at their inner ends. Apparently the surface of the glabella and fixed cheeks is smooth. The pygidium of *P. apiculata* is proportionately much larger, has a larger number of well-defined axial rings and, when preserved, a longer, slimmer, better-differentiated caudal spine.

The species described and figured by Reed (1915, p. 53, pl. 9, figs. 1–6) as *Phacops* (*Pterygometopus*) *dagon* from the Upper Naungkangyi Beds of the northern Shan States resembles *Duftonia lacunosa* in several respects such as the plan of the glabella, the presence of granules on the glabella and pitting on the fixed cheeks, and in the possession of a mucronate pygidium. However, there are notable differences, such as the absence of fixigenal spines, the development of a preglabellar furrow and deeper first glabellar furrows; *P.* (*P.*) *dagon* may belong to a new genus.

Duftonia aff. *lacunosa* sp. nov.

Plate 19, figs. 4, 7, 9–11

There are in the older collections of the British Museum (Natural History) two specimens of *Duftonia*, from the Corwen district of North Wales, apparently closely related to *D. lacunosa*. One of these, Thomas Ruddy Collection In.16999 (Pl. 19, fig. 4), is a whole individual with a maximum breadth of 15 mm.; the thorax is flexed but the estimated length, excluding the caudal spine which is broken off, is about 25 mm., though this may be less than the original owing to some distortion. Thoracic axis occupies one-third of the total breadth and is separated from the side-lobes by moderately deep axial furrows. The articulating half-ring and axial ring of each segment are of about the same length medially, separated by a deep, broad (*sag.*) articulating furrow, but the axial ring expands laterally to form a pair of axial lobes directed outwards and slightly forwards. Immediately in front of the axial lobes the articulating furrow deepens to form a pair of apodemal pits situated just inwards from the axial furrows. Inner halves of the side-lobes are flat, but the outer halves then turned down through almost a right angle at the fulcrum. Each pleura carries a broad (*exsag.*), gently sigmoidal pleural furrow which commences just outside the axial furrow where it divides the pleura into a narrow (*exsag.*) posterior band and a broader (*exsag.*) ridged anterior band. Beyond the fulcrum the pleural furrow curves forwards very slightly, at the same time becoming shallower and dying out without reaching the bluntly rounded pleural point which is flexed forwards slightly. The pygidium of the same individual has been slightly distorted, and the caudal spine is missing, nevertheless it can be seen to bear a close resemblance to that of *D. lacunosa*. Axial rings number four, with a suggestion of a fifth, and there are four pleural furrows on each side-lobe.

The eyes are not preserved in the above specimen but, as far as can be ascertained from their remains, they appear to be noticeably shorter than in *D. lacunosa* itself. This conclusion is borne out by an apparently identical form in the British Museum (Natural History), J. E. Lee Collection I. 1301 (Pl. 19, figs. 7, 10), in which the palpebral lobes intersect the axial furrows apposite the anterior half of the first glabellar lobes, as in *D. lacunosa* (s.s.), but then extend rearwards only as far as the level of the second glabellar furrows. The thorax is fairly well preserved, though having undergone some lateral compression, and contains eleven segments apparently similar to those of the preceding specimen. The pygidium is poorly preserved but the axis possesses four rings and each side-lobe four pleural furrows. The eyes themselves are badly preserved but one, the right, exhibits a schizochroal surface which, it is estimated, must have contained about seventeen or eighteen vertical rows of facets, the maximum number in a row being roughly eight.

There is one specimen, JP 3696, of a whole individual of *Duftonia* from the Ordovician of South Wales in the Geological Survey and Museum. The total length, excluding caudal spine, is 21 mm. The cephalon resembles those from North Wales in nearly all respects, particularly in having shorter palpebral lobes than *D. lacunosa* (s.s.), but the first glabellar furrows are slightly different. In *Duftonia* aff. *lacunosa* from the Corwen district the first glabellar furrows are faintly impressed, as in *D. lacunosa*, but diverge anteriorly at just under 130 degrees, compared with 140 degrees in the *forma typica*. The corresponding glabellar furrows of the South Welsh form are slightly deeper than those of the other two trilobites and, forming an angle of about 150 degrees, are more divergent anteriorly. It is not yet clear how much significance should be attached to these variations.

The eyes of the same specimen are not particularly well preserved but there appear to be about sixteen vertical rows of facets, the maximum number in a row being four, and the total number of facets being of the order of fifty-four. The thorax and pygidium of JP 3696 appear to resemble those of the North Welsh specimens though the caudal spine is not preserved.

Horizon and localities. Specimen In.16999 is labelled as coming from 'Blaendinan, 3 miles from Llandrillo'; at the present day this locality is known as Blaen Dinam, a farm 1½ miles south-west of Llandrillo, Merioneth. It is thought that the trilobite may be that recorded by Ruddy (1885, p. 119) from 'Blaendinan' and described by him as 'very rare'. The label gives the horizon as 'Trilobite Zone', a stratum which Ruddy (1885, p. 118) denoted as 'Zone 4', lying above 'Zone 5' which he described as representing the 'Bala crystalline limestone'. Judging by the matrix the specimen probably came from the Ddolhîr Limestone, the lowest member of the Ashgill Series of the district. The second specimen from North Wales, I. 1301, is labelled merely 'Cynwyd, Merionethshire', and the matrix suggests that it, too, derives from the Dholhîr Limestone, outcrops of which are abundant in the Cynwyd District, particularly between the village and Moel Ferna to the east. JP 3696 was collected from the disused quarry by the west side of the Llandilo–Carmarthen road, 1,030 yards almost due north of Dynevor Castle, one mile west of Llandilo, Carmarthenshire (National Grid reference 26152/22350). In recent years the district has been examined by Williams (1953, pp. 195–6, pl. 9) whose

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EXPLANATION OF PLATE 19

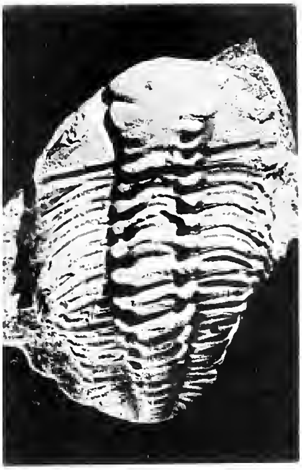
Figs. 1–3, 5, 6, 8. *Duftonia lacunosa* sp. nov. Dufton Shales, Pusgillian Stage, Swindale Beck, near Knock, Westmorland. 1, 3. BM. In.49920, ×4·5. Pygidium, internal mould, showing caudal spine. 2. BM. In.49821, ×3·5. Incomplete cranidium, internal mould. 5. BM. In.49830, ×3. Internal mould of cephalon showing posterior branch of facial suture and fixigenal spine. 6. BM. In.49824A, ×3·25. Latex cast of the holotype, an external mould. 8. BM. In.49826, ×3·25. Incomplete cranidium, internal mould.

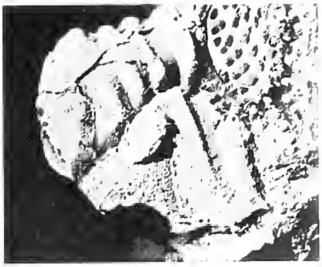
Figs. 4, 7, 9, 10, 11. *Duftonia* aff. *lacunosa* sp. nov. 4. BM. In.16999, ×2·5. Internal mould of whole individual from Ddolhîr Limestone (?), Blaen Dinam, near Llandrillo, Merioneth. 7, 10. BM. In.1301. 7, ×2·8. 10, ×2·4. Plan and side views of whole individual, internal mould, from Ddolhîr Limestone (?), Cynwyd, Merioneth. 9, 11. GSM. JP 3696. 9, ×2·5. Plan and side views of whole individual preserved as internal mould, Ashgill Series, north of Dynevor Castle, near Llandilo, Carmarthenshire.


1 x 4.5

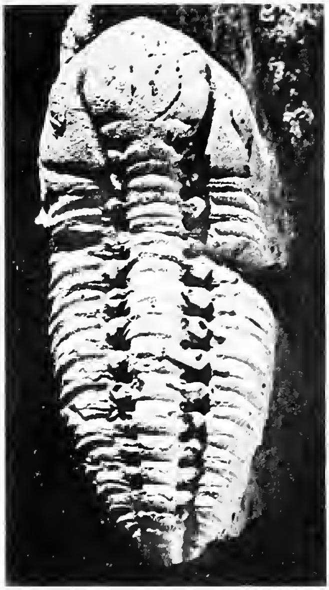

2 x 3.5


3 x 4.5

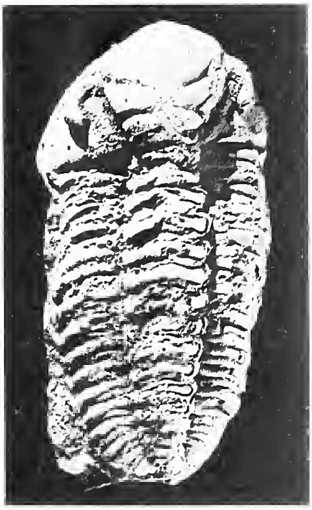

4 x 2.5

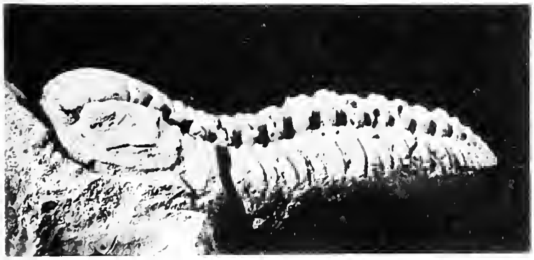

5 x 3


6 x 3.25


7 x 2.8


8 x 3.25


9 x 2.8


10 x 2.4


11 x 2.5

DEAN, *Duftonia* gen. nov.

map shows that the locality occurs in the lower part of the strata which he considers to be of Upper Bala age; Williams has equated at least some of these beds with the *Diacalymene* Beds of Cautley, Yorkshire.

The stratigraphical position of that portion of the Dufton Shales comprising the Pusgillian Stage has been doubtful for some time. The term was introduced by Bancroft (1945, pp. 182, 186) who claimed that it was equivalent to the *Dicellograptus complanatus* zone of the Ashgill, a course which has been followed by other writers, for example King and Williams 1948. It is not proposed to discuss this claim or the position of the Pusgillian in detail here, a topic to be dealt with in a later paper, but in view of a re-evaluation of the correlation between the shelly and graptolitic zones of the Caradoc Series in the Shropshire type area (Dean 1958, pp. 226–30), in which it was shown that the Onnian Stage is no later than the upper part of the *Dicranograptus clingani* zone, it can be argued that the Pusgillian is at least partly equivalent to the *Pleurograptus linearis* zone. The presence of the trilobite *Duftonia* in strata of both the Pusgillian Stage and the lower Ashgill Series should not be taken as conclusive proof of their equivalence. One could equally well argue that the genus may range through a succession of strata at and near the Caradoc/Ashgill junction, and the present lack of material makes it uncertain whether the morphological differences between the English and Welsh specimens are to be attributed to the effects of geographical distribution or of time.

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PHYLLOCRINUS FURCILLATUS SP. NOV., A CYRTOCRINOID FROM THE UPPER JURASSIC OF KAWHIA, NEW ZEALAND

by I. G. SPEDEN

Abstract. *Phyllocrinus furcillatus* sp. nov. is described from Kuritunu Stream, Kawhia, and is attributed to the Middle Kimeridgian. It is the first record of *Phyllocrinus* outside Europe.

In 1957 Mr. W. Sutherland, of Kawhia, presented to the New Zealand Geological Survey several blocks of fossiliferous silty mudstone collected from the bed of Kuritunu Stream, Kawhia, some eighty-five miles south of Auckland. An abundant invertebrate faunule, including lamellibranchs, belemnites, fragmentary ammonites, and the crinoid here described, was obtained from the blocks.

The only known occurrence is at Kuritunu Stream, Awaroa Valley, North Island of New Zealand, collection GS 6933, map reference NZMS1, Sheet N.73, grid reference 465970.

Included in the siltstone blocks are fragments of Ataxioceratid ammonites and abundant *Belemnopsis* cf. *aucklandica* (Hochstetter). In the Jurassic sequence on the south side of Kawhia Harbour, identical ammonites and belemnites to those in the blocks are known (Dr. C. A. Fleming, pers. comm.) to occur between the Lower Kimeridgian at Totara Point (Arkell 1956, p. 455) and beds containing Lower Tithonian ammonites and belemnites identical to those at Puti Point on the north side of the harbour (Arkell 1956, p. 454). Thus the assemblage in the blocks is apparently Middle Kimeridgian in age.

World distribution of Phyllocrinus. The genus ranges from Bajocian to Lower Neocomian (see Moore 1948, p. 51, fig. 17, for a generalized diagram) and prior to its discovery in New Zealand was restricted to Europe where it is found in southern France, Jura Mountains, Switzerland, Lombardy, Apennines, Sicily, Austria, and at Stramberg in the north-west Carpathians. Previously, the most eastern locality with *Phyllocrinus* was Theodosia, on the south side of the Crimean Peninsula, where the Tithonian species *P. verrucosus* Retowski (1893, p. 288) is found. Selected localities have been plotted on a map (text-fig. 1).

The record of *Phyllocrinus* in New Zealand, almost antipodal to southern France where it is so well represented in Bajocian to Neocomian sequences, greatly extends its known distribution. It also fulfils the prediction made by Fell (1952, p. 146) when he wrote 'it now begins to look as if we may expect to find other parallels between the Mesozoic Echinoderms of Europe and New Zealand, despite the present lack of corresponding fossil records from intervening points on the globe'.

[Palaeontology, Vol. 2, Part 1, 1959, pp. 150–5, pl. 20.]

SYSTEMATICS

Numbers with the prefix EC refer to specimens catalogued in the New Zealand Geological Survey's register of fossil echinoderms, while the prefix GS refers to an index of New Zealand macro-fossil collections held at the N.Z. Geological Survey. The classification followed is that elaborated for the Articulata by Sieverts-Doreck in Piveteau (1953).

Order CYRTOCRINIDA Sieverts-Doreck 1953

Family PHYLLOCRINIDAE Jaekel 1907

Genus PHYLLOCRINUS d'Orbigny 1850

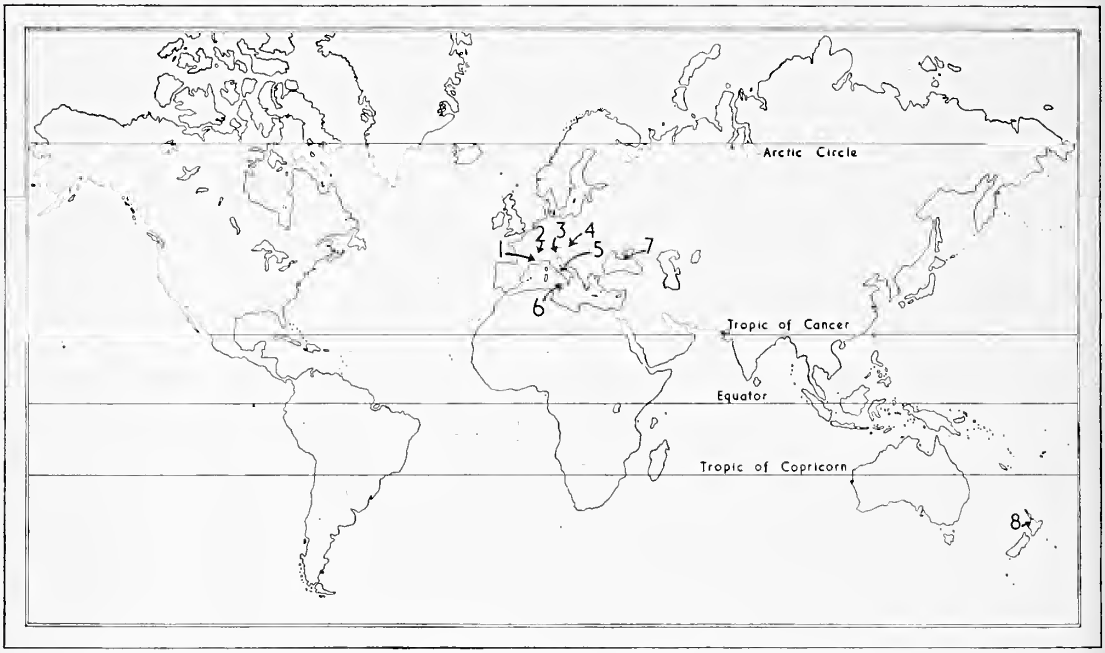
Type species by monotypy: *Phyllocrinus malbosianus* d'Orbigny 1850. Lower Neocomian, southern France.

Discussion. Several different dates have been quoted for d'Orbigny's description of the genus. Zittel (1870, p. 158) gives the year 1851, Bather (1900, p. 197) 1849, and Sieverts-Doreck (1953, p. 756) 1852. Here, the name is attributed to d'Orbigny 1850, the date adopted by de Loriol (1882, p. 160), Sherborn (1928, p. 4931), and Neave (1940, vol. 3, p. 741). The date following the generic name in the *Prodrome de Paléontologie* is 1847, but as explained by d'Orbigny (p. lix) in the introduction to volume one, the date of publication was delayed so that volume two was published in 1850 and not 1847.

By using the words 'C'est un *Pentremites*' in his original description, d'Orbigny clearly thought *Phyllocrinus* was a blastoid. Zittel (1870, pp. 158–64) was first to place the genus in its correct systematic position. He considered that the range of the genus, Upper Jurassic to Lower Cretaceous, indicated it was not rightly placed in the exclusively Palaeozoic Blastoidea, and by a detailed study of specimens of *P. hoheneggeri* Zittel 1870, from the Neocomian of Stramberg, which he compared with the crinoid genus *Eugeniacrinus* Miller, he showed that *Phyllocrinus* is a crinoid. Zittel placed it in the family Eugeniacrinidae and also gave a detailed generic description (p. 162). In 1907 Jaekel (pp. 303–4) established the family Phyllocrinidae in which he included *Phyllocrinus* and his new genus *Apsidocrinus*.

As d'Orbigny included only one species, *P. malbosianus* d'Orbigny in his genus, under Article 30 of the International Rules of Zoological Nomenclature, the genus should be monotypical. However, the rarity of reference to *P. malbosianus* by subsequent authors and, except for Jaekel's (1907, p. 304) brief statement 'Als typische Arten seien genannt der Typus der Gattung d'Orbigny's *P. granulatus* (Fig. 26) und *P. hoheneggeri* Zitt. aus der untersten Kreide,' the lack of mention of a type species by later workers raised doubts in this author's mind as to the validity of d'Orbigny's species. The doubts were increased by Jaekel's (1891) emphasis of the apparent gradation of forms between *Phyllocrinus* and *Eugeniacrinus* and his revision of the placing within these two genera of species described by earlier workers. Through the courtesy of Mme Freneix, Laboratoire de Paléontologie, Paris, M. Roman kindly forwarded a plaster replica of one of d'Orbigny's syntypes (No. 5557*a*) and M. Roger (S.I.G.) sent a photostat copy of Pictet's

(1867, p. 119) redescription of *P. malbosianus*. The replica and text clearly showed *P. malbosianus* to be a valid species and to be correctly interpreted; it is type of the genus by monotypy.



TEXT-FIG. 1. Map showing the distribution of the genus *Phyllocrinus* in Jurassic to Lower Neocomian times. Within the European area the distribution is illustrated by selected localities.

1, Southern France. *P. gauthieri* de Loriol 1882, Bathonian, Bouches-du-Rhône. *P. alpinus* (d'Orbigny 1850), Oxfordian, Chaudon, Basses-Alpes. *P. malbosianus* d'Orbigny 1850, Lower Neocomian, Barrême, Basses-Alpes. 2, Switzerland. *P. sabaudianus* Pictet and de Loriol 1858, Lower Neocomian, Fribourg. 3, Austria. *P. hoheneggeri* Zittel 1870, Jurassic, Dachstein. 4, Czechoslovakia. *P. hoheneggeri*, Tithonian, Stramberg. 5, Italy. *P. nutantiformis* (Schauroth 1865), Tithonian, Monte Catriano (Apennines). 6, Sicily. *P. checchiai* Serra 1934, Neocomian, Boschitello, Licodia Eubea. 7, Russia. *P. verrucosus* Retowski 1893, Tithonian, Theodosia, Crimean Peninsula. 8, New Zealand. *P. furcillatus* sp. nov., Middle Kimeridgian, Kawhia.

Phyllocrinus furcillatus sp. nov.

Plate 20

Holotype. EC 196, N.Z. Geological Survey, Lower Hutt. A complete dorsal cup with one interradial extension slightly displaced by a small fracture.

Material. Holotype, eight paratypes (EC 197–204) and six other specimens.

Diagnosis. Each radial plate with a central, narrow, steep-sided, round-topped ridge which bifurcates about one-third the height of the dorsal cup; branches of ridge continue along ventral prolongations of radial plate. Below level of articulatory facets and between branches of ridge, surface of radial plate concave to flat.

Description. Dorsal cup small, approximately pentagonal in transverse section (figs. 1, 3), composed of five radial plates. Each plate has two ventral prolongations (figs. 2, 4) from the outer margins. Radial plates and prolongations strongly fused to form a cup with five interradial extensions (figs. 1, 2, 4).

Interradial extensions slightly incurved over body cavity (figs. 1, 2). Ventrally extensions triangular in cross-section (fig. 9) with the most acute angle pointing towards body cavity. Internally and just above the level of articulatory facets, the inner edge of extension is grooved by form of body cavity (figs. 5, 7). Side of interradial extensions bordering the socket between extensions straight for dorsal third, but concave for ventral two-thirds, thus forming a prominent angulation at about one-third of their height above the base of socket (figs. 2, 4). Surface of dorsal cup between characteristic ridges deeply depressed (figs. 2, 3, 4), the depression continuing ventrally along the interradial extension as a shallow, narrow groove (figs. 1, 2, 4). Line of fusion of radial plates distinct (figs. 1, 3, 4, 9), situated at centre of depression and groove. Base of socket narrow, constricted medially by interradial extensions; outer part sloping slightly dorsally, inner sloping into body cavity. Articulatory facets not well preserved, situated at base of socket and on external portion. Each facet with four fossae; a central canal between an external, elongated ligament pit and two internal, kidney-shaped fossae (fig. 6).

Depth of body cavity about half height of dorsal cup (exclusive of extensions) (figs. 8, 10). Base of cup with a deep conical excavation, its depth approximately one-third height of cup (exclusive of extensions) (figs. 8, 10), for attachment of stem.

Arms and pelma unknown.

Dimensions

	H	*HC*		*LE*		*D*		*LBC*		*LSD*	
	mm.	*mm.*	%	*mm.*	%	*mm.*	%	*mm.*	%	*mm.*	%
EC 196*	5·2	2·6	50	2·6	50	5·0	95	..	0	..	..
EC 197	11·8	5·4	45	6·4	55	9·2	80	..	..	..	..
EC 198	4·9	2·4	50	2·5	50	4·9	100	..	..	..	..
EC 199	7·3	3·5	45	3·9	55	6·4	90	..	..	..	..
EC 202	5·5	2·4	45	3·1	55	..	..	1·4	60	0·6	25
EC 203	7·0	3·4	50	3·6	50	..	..	1·7	50	1·1	30

H = height of dorsal cup including interradial extensions; HC = height of body of dorsal cup to level of articulatory facets; LE = length of interradial extensions; D = maximum diameter of dorsal cup; LBC = length of body cavity; LSD = length of stem attachment depression.

* Holotype

Remarks. Of the twenty-two species of *Phyllocrinus* that have been traced, nineteen are represented by figures or descriptions in literature available in New Zealand and Australia. In nearly all species the surface of the plates forming the dorsal cup is rounded and lacks the prominent steep-sided central ridge present on the plates of *P. furcillatus*. The only species known to the author with a comparable ridge on each radial plate is *P. sabaudianus* Pictet and de Loriol 1858 (de Loriol 1879, pp. 240–1, pl. 19, figs. 31–32), from the Neocomian of Hivernages, France. However, this species is readily distinguished from *P. furcillatus* as its ridges are not steep-sided and do not branch, but extend ventrally to the level of the articulatory facets. In addition, the interradial extensions of *P. sabaudianus* curve outwards, thus differing markedly from the slightly incurved extensions of *P. furcillatus*.

Acknowledgements. Mr. W. Sutherland, Kawhia, who has collected extensively for the New Zealand Geological Survey, kindly presented the material containing the species described above. The author is indebted to Dr. C. A. Fleming, Dr. J. Marwick, and Dr. D. A. Brown, University of Otago, for advice and information. To Mme S. Freneix and M. Roman, Laboratoire de Paleontologie, Paris, and M. J. Roger, S.I.G., the author wishes to express his gratitude for their assistance in obtaining a replica of *P. malbosianus* and a photostat copy of Pictet's (1867) publication redescribing the species.

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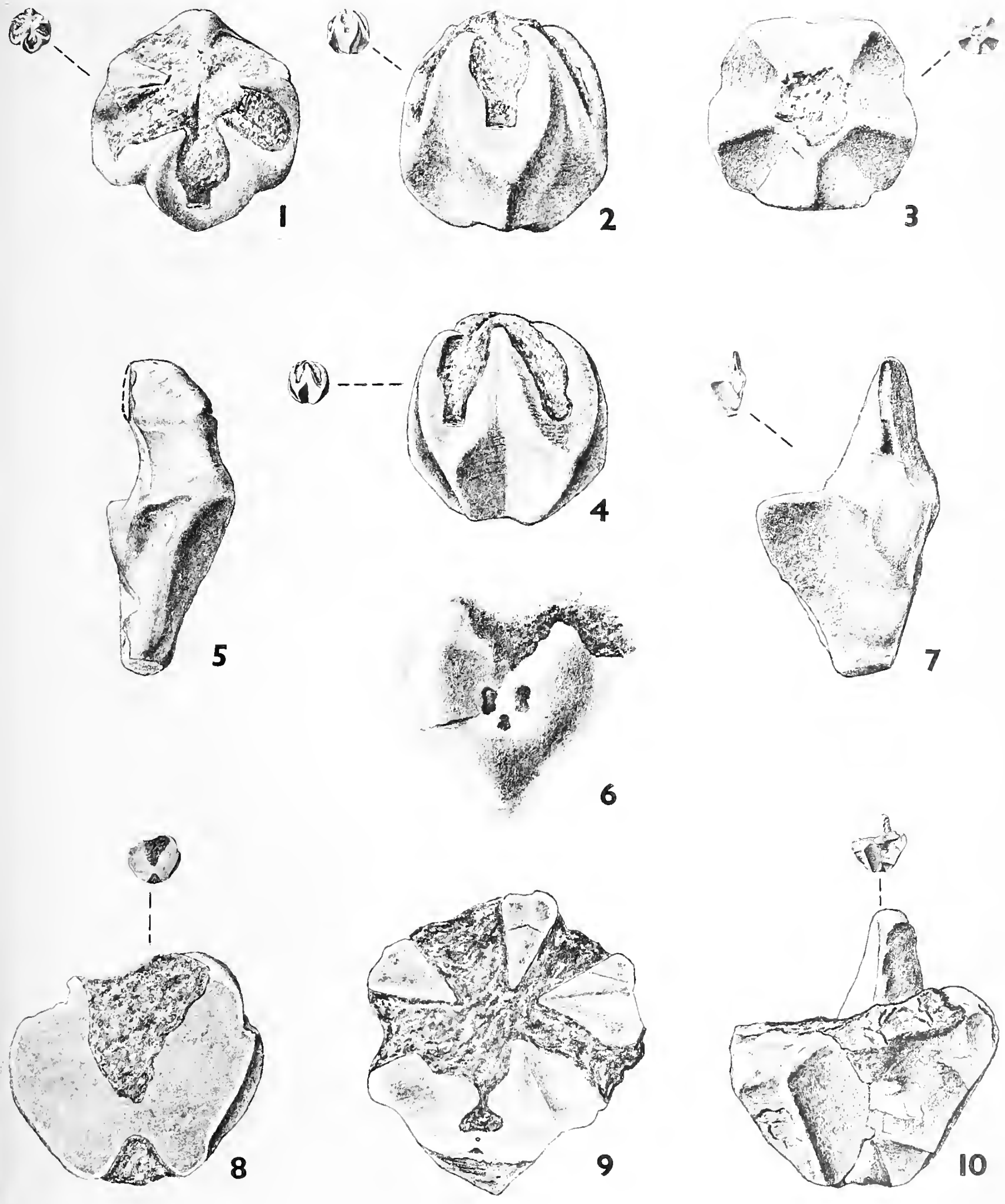
EXPLANATION OF PLATE 20

All figures except fig. 6, ×6; 6, ×12. Small figures show natural size.

Figs. 1–10. *Phyllocrinus furcillatus* sp. nov. 1, Holotype, EC 196, ventral view. Ligament pit exposed at external margin of articulatory facet. 2, Holotype, lateral view. 3, Holotype, dorsal view. 4, Holotype, lateral view. As fig. 2, rotated 45° clockwise. 5, Paratype, EC 204. As for fig. 7, rotated clockwise. Supposed position of upper margin of interradial extension indicated by dotted line. 6, Paratype, EC 200. Enlargement of articulatory facet exposed by distortion of specimen. Ligament pit and central canal almost coalesced; kidney-shaped muscle fossae above. 7, Paratype, EC 204. Fragment with interradial extension showing form of body cavity on dorsal third. Upper two-thirds of internal edge of extension broken away. 8, Paratype, EC 202. Longitudinal section along plane through two interradial extensions. Form of body cavity and stem attachment. 9, Paratype, EC 201. Transverse section oblique to horizontal plane. With shape of interradial extensions at different levels, fusion lines through two extensions, a ligament pit and central canal. 10, Paratype, EC 203. Fragment composed of three radial plates, two of three interradial extensions broken off. Form of stem attachment, body cavity, and internal edge of extension.

R. C. Brazier, del.



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NOTE ON *OPERCULINOIDES* HANZAWA 1935

by Y. NAGAPPA

ABSTRACT. *Operculinoides* Hanzawa as understood now consists of three distinct groups of forms typically represented by (*a*) *Nummulites willcoxi* Heilprin, (*b*) *Operculina ocalana* Cushman, and (*c*) *O. bermudezi* D. K. Palmer. It is shown that (*a*) can justifiably come under *Nummulites*, (*b*) may be regarded as involute *Operculina*, and for (*c*) there is Caudri's genus *Ranikothalia* which is based on valid grounds.

INTRODUCTION

AFTER a critical examination of *Operculina ocalana* Cushman, *Nummulites willcoxi* Heilprin, *O. floridensis* Heilprin, and *O. mariannensis* Vaughan, Hanzawa considered that they 'show peculiar characteristics intermediate between the typical *Operculina* and *Camerina* or *Assilina*' and proposed the generic name *Operculinoides*, with *N. willcoxi* as the type species, for the above and related forms (Hanzawa 1935, p. 18). Grimsdale and Smout (1949, p. 325) suggested that *Operculinoides* is a synonym of *Nummulites*, but later Smout (1954, p. 76) modified this observation and stated that '*Operculinoides* (Hanzawa 1935) is often taken as complanate and partly involute, but the type species, *O. willcoxi* is a typical Nummulite'.

TABLE

Genera / *Characters*	*Nummulites*	*Operculinoides*	*Operculina*	*Ranikothalia*	*Miscellanea**
Shape . .	Lenticular, flat or unevenly globose	Type species evenly low lenticular	Complanate, lenticular in centre only	Evenly low lenticular to nearly flat	Lenticular to nearly flat
Form . .	Involute	Involute mostly, some tending to be evolute	Evolute to partially involute	Involute to partially evolute	Involute; flatter forms tending to be partly evolute
Chamber tops as seen in equatorial sections	Acute angle posteriorly	Type species as in *Nummulites*	As in *Nummulites*	Bluntly round generally	Bluntly round
Whorl wall .	Single, not differentiated, canaliculate	Type species as in *Nummulites*	As in *Nummulites*; spiral canals tend to be more numerous	Double; inner simple, outer coarsely canaliculate, 'degenerate'	As in *Ranikothalia* but often more 'degenerate'
Whorls . .	Many, variable	Few to many	Generally few	Generally few	Few to many

* *Miscellanea* has no marginal cord which is present in all the others.

[Palaeontology, Vol. 2, Part 1, 1959, pp. 156–60, pls. 21–23.]

There are a number of American forms described under *Operculinoides* which are distinctly 'operculine' while others are as distinctly 'nummulitic'. A solution of the problem can only be arrived at after reconsidering firstly, the characters of the type species of *Operculinoides vis-à-vis* other forms included in this genus and, secondly, the nature of the differences between the forms now included in *Operculinoides vis-à-vis* true *Nummulites* on the one hand and true *Operculina* on the other. A summary of the characters, based on the study of actual specimens as well as published descriptions and figures, of the five genera *Nummulites*, *Operculinoides*, *Operculina*, *Ranikothalia*, and *Miscellanea* as understood now, is given in the table. Another genus, about which there was some confusion, was *Pellatispirella* Hanzawa; but Cole (1956*b*) has since demonstrated that this genus is not related to any of the above genera but is more allied to *Elphidium*.

DISCUSSION

Nummulites willcoxi Heilprin, the type species of *Operculinoides* Hanzawa, is a low lenticular completely involute form with a clear marginal cord. The septa in equatorial sections are straight for the most part, slightly oblique and sharply curved backwards where they meet the outer whorl wall. The chambers are slightly higher than broad with a clear acute angle formed in the upper posterior end. Apart from a little loose coiling there is nothing in this species which could not suggest placement in the genus *Nummulites*. Other forms included by various authors under the genus *Operculinoides* may conveniently be grouped under (*a*) *Operculinoides bermudezi* type, or (*b*) *Operculinoides ocalanus* type. These will be discussed below.

(*a*) *Operculinoides bermudezi* type.

Sachs (1957) has made a detailed study of *O. bermudezi* (D. K. Palmer) and related forms. As pointed out earlier by Caudri (1944, p. 17), there are two important characters in which this group of forms differs from *N. willcoxi*, viz. (*a*) the chambers have generally rounded tops and the acute angle formed by the septa on the upper posterior corner of the chambers as seen in *Nummulites* and *Operculina* is usually absent; (*b*) there is a distinct inner lining on the roofs of the chambers which separates the coarsely canaliculate whorl wall above. This latter character is an important one and readily helps in distinguishing this group of forms from typical *Nummulites* and *Operculina*. Cole, who is quite familiar with *O. bermudezi* and related forms, stated: 'American species which were assigned formerly to *Miscellanea* and which are considered here to be *Operculinoides* uniformly possess a coarse marginal cord. At the beginning of this study it was thought that this structure might be of generic significance' (Cole 1953, p. 10). Although, as he states, the marginal cord in *Nummulites* s.l. is extremely variable, forms of the *O. bermudezi* group do exhibit a coarseness in the marginal cord which is not present in any of the true *Nummulites*. According to Vaughan, the American forms of the type *O. bermudezi* 'are intermediate between typical *Miscellanea* and typical *Camerina*' (Vaughan 1945, p. 25). Davies is also of the same view (Davies 1949, p. 113).

The type species of *Ranikothalia* Caudri is *Nummulites nuttalli* Davies. *Operculina sindensis* Davies is a closely related form and, as Davies (1949, p. 113) has pointed out, there is every gradation from one to the other. However, they can generally be distinguished by the following characters:

	Nummulites nuttalli	*Operculina sindensis*
(*a*)	Whorls gradually increasing in width.	Whorls rapidly increasing in width.
(*b*)	Test generally slightly convex.	Test usually flat or most flat.
(*c*)	Marginal cord usually strong on the last whorl.	Marginal cord generally strong on all whorls.
(*d*)	Megalospheric form lenticular; rather inflated.	Megalospheric form not much different from the microspheric form, though slightly more biconvex.

EXPLANATION OF PLATE 21

Fig. 1. *Nummulites beaumonti* d'Archiac and Haime, microspheric form from the Crab Marls (M. Eocene), Bugti, Baluchistan, West Pakistan; equatorial section showing thick whorl wall and nearly straight septa, × 5.

Fig. 2. *Nummulites pengaronensis* Verbeek, megalospheric form from the Kopili Stage (U. Eocene), Jaintia Hills, Assam; equatorial section showing curved septa, × 68.

Fig. 3. *Nummulites irregularis* Deshayes, microspheric form from the Tarkhobi Shales (*Irregularis* Bed), L. Eocene, Tarkhobi, West Pakistan; equatorial section showing irregular coiling and delicate, strongly curved septa, × 5.

Fig. 4. *Nummulites sp.*, microspheric form from the Khirthar Shales (L. Eocene), Kirta, Baluchistan, West Pakistan; equatorial section showing delicate, curved septa, × 22.

Fig. 5. *Nummulites intermedius* d'Archiac, microspheric form from the Nummulitic Limestone (Oligocene), Cutch; equatorial section showing thick whorl-wall and delicate, widely spaced septa, × 30.

Fig. 6. *Nummulites willcoxi* Heilprin; section showing septa nearly straight, slightly oblique, reproduced from Cole 1953, pl. 1, fig. 12, × 12·5.

EXPLANATION OF PLATE 22

Fig. 1. *Operculina sp.* from the Upper Chocolate Clays (U. Eocene), Rakhi Nala, West Pakistan; equatorial section showing septa initially straight and normal, sharply curved at the end, × 45.

Figs. 2, 3. *Operculina sp.* from the Kopili Stage (U. Eocene), Dareng River, Garo Hills, Assam; 2, equatorial section showing delicate and strongly curved septa, × 30; 3, same specimen, portion of whorl-wall × 200 to show canal system (note the numerous spiral canals).

Figs. 4, 5. *Ranikothalia sindensis* (Davies), equatorial sections; 4, microspheric form from the Zinda Pir Limestone (Palaeocene), Zinda Pir, West Pakistan, × 10; 5, megalospheric form from the Lakadong Stage (Palaeocene), Khasi and Jaintia Hills, Assam, × 15.

EXPLANATION OF PLATE 23

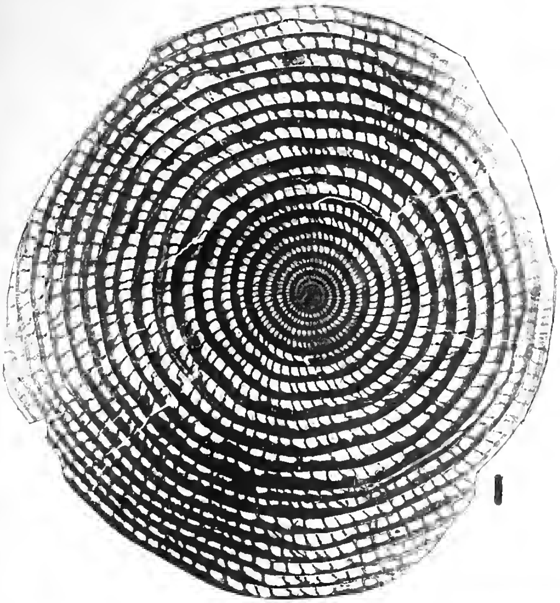
Fig. 1. *Ranikothalia sindensis* (Davies), equatorial section of megalospheric form from the Khairabad Limestone (Palaeocene), Salt Range, West Pakistan, × 15.

Figs. 2, 3. *Ranikothalia nuttalli* (Davies), equatorial sections; 2, microspheric form from the Zinda Pir Limestone (Palaeocene), Zinda Pir, West Pakistan, showing wall structure and nature of septa, × 4; 3, megalospheric form from Baluchistan, West Pakistan, showing rounded-top chambers, × 15.

Fig. 4. *Ranikothalia sp.* from the Brecciated Limestones and Shales (Palaeocene), Tarkhobi, West Pakistan; equatorial section showing double layer of whorl-wall, × 68.

Figs. 5, 6. *Ranikothalia bermudezi* (D. K. Palmer), equatorial sections; reproduced from Cole 1953, pl. 3, figs. 4 and 12, × 20.

Figs. 7, 8. *Miscellanea miscella* (d'Archiac and Haime), equatorial sections; 7, megalospheric form, Zinda Pir Limestone (Palaeocene) Zinda Pir, West Pakistan, × 10; 8, microspheric form from the lower part of the Tarkhobi Shales (Palaeocene), Tarkhobi, West Pakistan, × 10.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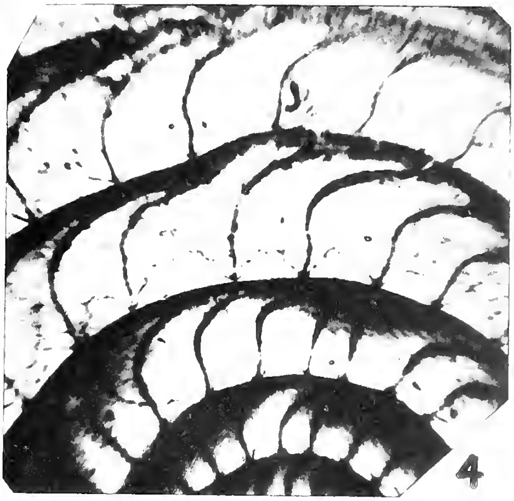
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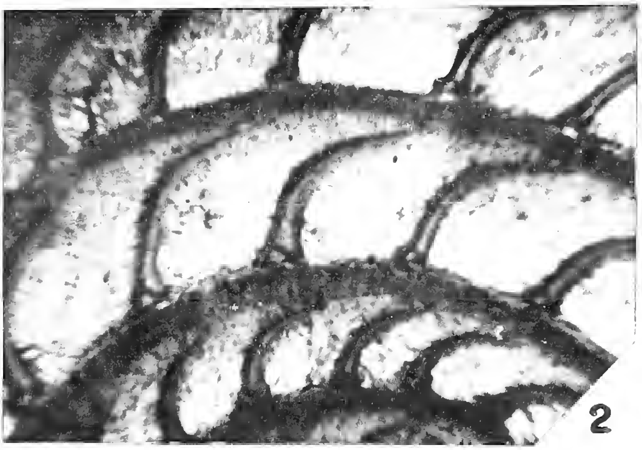
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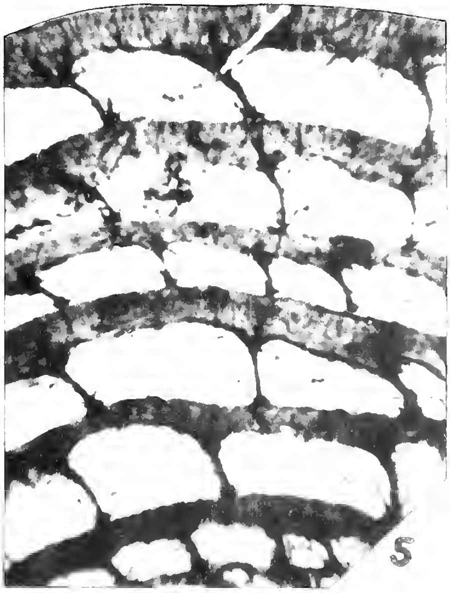
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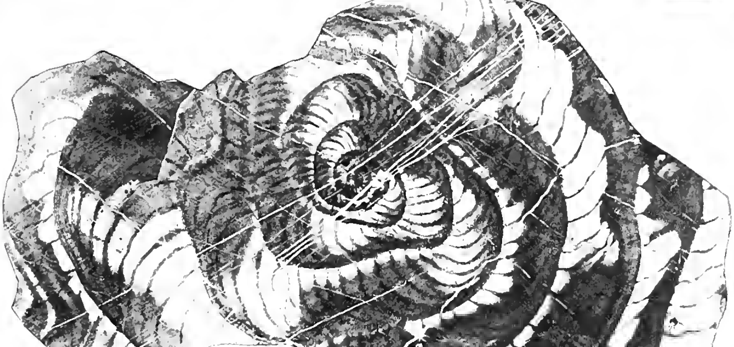
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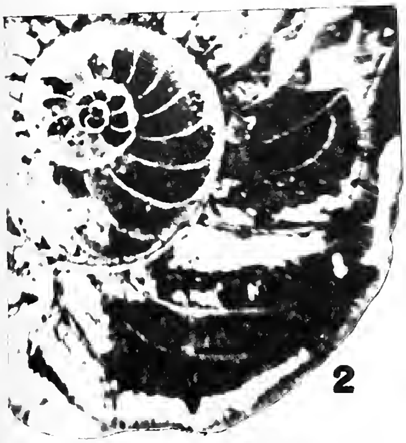
6

NAGAPPA, *Nummulites*


1


4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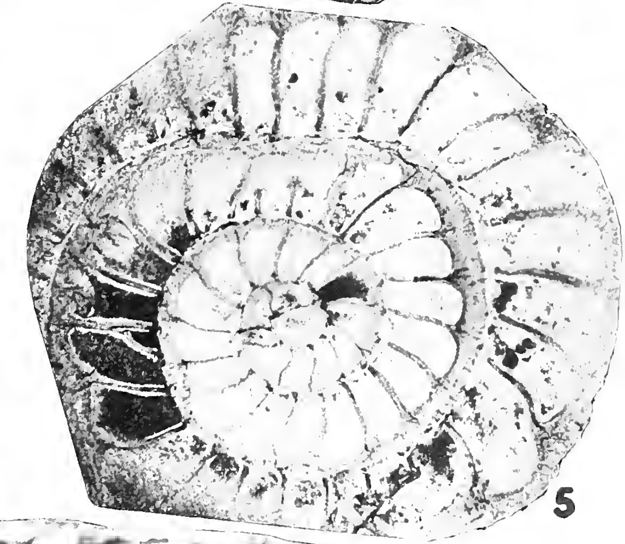
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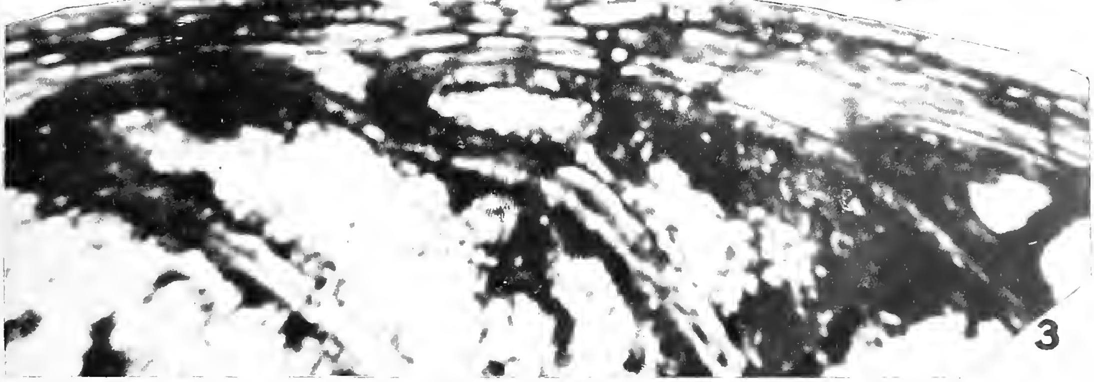
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NAGAPPA, *Operculina* and *Ranikothalia*


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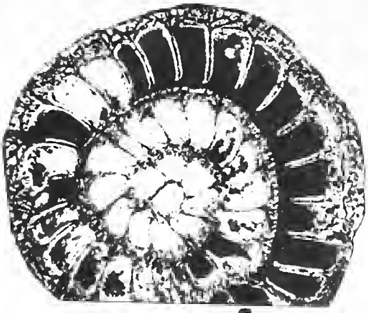
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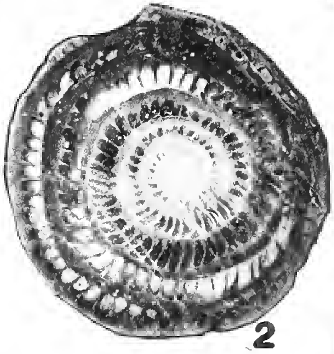
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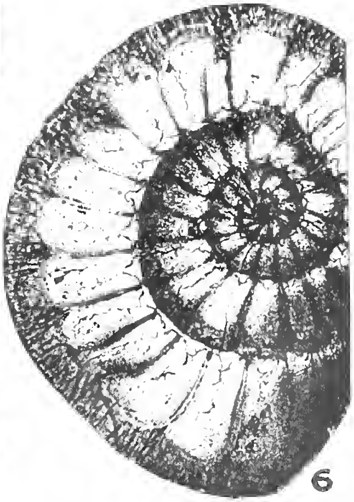
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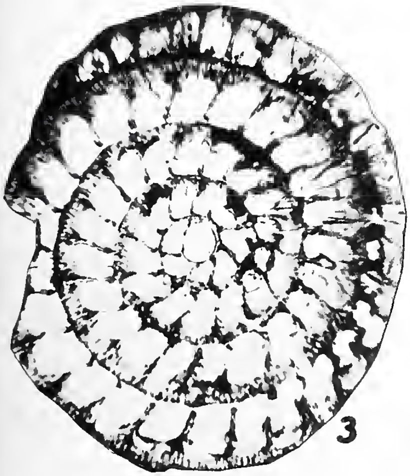
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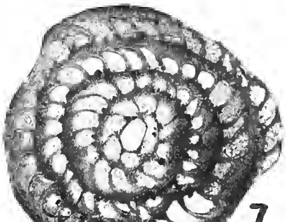
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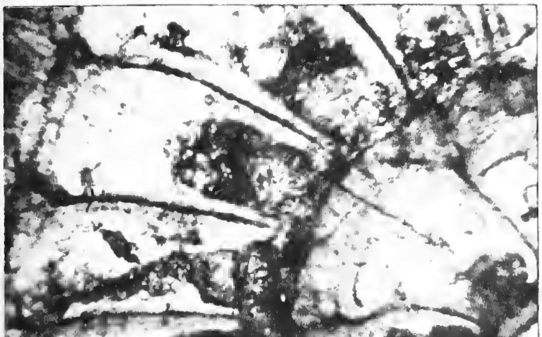
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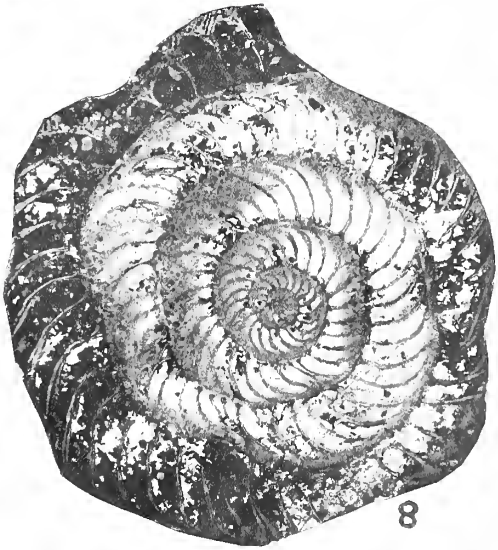
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NAGAPPA, *Ranikothalia* and *Miscellanea*

In India and Pakistan these forms are restricted to the Palaeocene (perhaps rarely extending into the basal Lower Eocene) and since they also exhibit characters different from both *Miscellanea* and *Nummulites*, Caudri's erection of the genus *Ranikothalia* appears justified. Both *Nummulites nuttalli* and *Operculina sindensis* have the typical round topped chambers and there is also the inner lining on the roof of the chambers. The rest of the whorl wall is perhaps less 'degenerate' as compared with *Operculinoides bermudezi*. In spite of such differences from *Nummulites*, Smout (1954, p. 75) has suggested that the type species of *Ranikothalia* is a Nummulite. Hanzawa (1957) has recently placed *Ranikothalia* as a synonym of *Miscellanea*. This is unacceptable, for *Miscellanea* lacks the marginal cord so characteristic of the other nummulitid genera while this forms a very important feature in *Ranikothalia*; the marginal cord in the type species is very strong and forms one of the diagnostic characters of the species. It thus appears that recognition of *Ranikothalia* as a valid genus provides not only a link between *Miscellanea* and *Nummulites* but also enables a clearer and more comprehensive grouping of the forms generally referred to *Operculinoides* in America and the West Indies. It is also of interest to note that forms of the *O. bermudezi* group are all confined, as the related forms *Nummulites nuttalli* and *Operculina sindensis* in India and Pakistan, to the Palaeocene rarely extending into the basal Lower Eocene.

Ranikothalia can thus be shown to be a useful genus both stratigraphically and palaeontologically. Its geographical distribution extends from western part of Burma through north-east India and Tibet into West Pakistan and from thence westwards through Middle East into French West Africa (Davies 1949, p. 114; 1952, pp. 155–7); it is next known from the British West Indies and southern U.S.A. Palaeocene rocks are known to occur in North Africa from the evidence of echinoids and *Assilina*, although at present *Ranikothalia* is not known from this area. Davies (op. cit.) has suggested a possible link with India.

(*b*) *Operculinoides ocalanus* type

As regards forms of the *O. ocalanus* type which show typical operculine septa and mode of coiling, it is clear that they too show considerable differences from *N. willcoxi*. As pointed out earlier, *N. willcoxi* is a typical nummulite and loose coiling is not uncommon in *Nummulites*. Bannink (1948) has already demonstrated that most operculines are in fact involute in the early stage and, in some, this character extends in part to the later stage also. It seems to be purely a case for stretching this point a little farther to include forms which are completely involute but which are operculine in all other respects. Sachs (1957) has demonstrated the existence of considerable variation from completely involute forms to partially evolute forms in the *O. bermudezi* group and, if only the same latitude is conceded to *Operculina*, forms of the *O. ocalanus* type can easily be accommodated under this latter genus. They do not resemble the *N. willcoxi* group of forms in their mode of coiling, in the nature of their septa, or in the shape of chambers. It seems therefore logical to exclude such forms from *Operculinoides* s.s. and if indeed a separate grouping for these completely involute operculinids is considered necessary, they may be regarded as a subgenus of *Operculina*.

With regard to *N. willcoxi* and related forms there is really no need to consider them as anything but what they are, *Nummulites*. It would thus appear that the genus *Oper-*

culinoides Hanzawa becomes superfluous since, if the arguments submitted in this note are accepted, forms now under this genus can be allocated to *Nummulites*, *Operculina*, or *Ranikothalia*.

Acknowledgements. The author is grateful to C. M. B. Caudri for the reprint of her paper on the Venezuelan larger foraminifera wherein she erected the genus *Ranikothalia*, to W. Storrs Cole, Cornell University, Ithaca, N.Y., for giving facilities for the study of typical American nummulitid fossils during the author's visit in late December 1954, and to T. F. Grimsdale for reading through the paper and for his helpful remarks. Hans Thalmann, Stanford University, California, has also read through the manuscript. The paper is published by kind permission of the Assam Oil Company Limited.

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THE LOWER PALAEOZOIC ECHINODERM FAUNAS OF THE BRITISH ISLES AND BALTO-SCANDIA

by G. REGNÉLL

Annual Address, delivered 11 March 1959

INTRODUCTION

A GREAT many difficulties are involved in dealing with the relations between the British and the Balto-Scandian echinoderm faunas in Early Palaeozoic times. It is obvious that this is due mainly to two circumstances: the imperfect knowledge of the original composition of the faunas in different areas, and the insufficient exactitude in stratigraphic correlation between the British Isles on the one hand and Scandinavia, Estonia, and the Leningrad district on the other. It is not necessary to review here the various factors which in the course of time have acted upon the consecutive marine biota of different ecological niches and which have been decisive of the nature of the fossil record now available to us. Even Charles Darwin in his *Origin of Species*, the centenary of which is celebrated this year, devoted a special chapter to these questions which have subsequently received much attention in the literature. The essence of the dilemma was formulated by Wachsmuth and Springer (1897, p. 167) as follows: 'The trouble is that all our generalizations are necessarily based upon the Crinoids as they are represented in *our museums*, and not upon the Crinoids as they actually existed in geological time, which is a very different thing.' The term 'Crinoids' may of course be substituted by the name of any other group of echinoderms, or by the name of almost any other fossil group.

Wachsmuth and Springer introduced the human factor which should certainly not be neglected. It is a fact that some fossil groups have been subject to a more extensive collecting and a more penetrating study than other groups. Rather trivial matters have played a role in this respect. Henbest (1952, p. 304) observed, for instance, that the 'location of fossil records in relation to centres of education, research, industry, and mining is an important factor in the discovery and description of faunas'.

LITERARY BACKGROUND

Much basic knowledge of Palaeozoic echinoderms has come from London—in the first place I refer to the brilliant work of F. A. Bather. However, apart from the carpoids and cystoids from the Ashgillian Starfish Bed of Ladyburn near Girvan described in his magnificent and very important memoir of 1913, no British material of Old Palaeozoic echinoderms was treated monographically by Bather. But we are indebted to him for short but valuable papers on certain British edrioasteroids (Bather 1900, 1915). The work on the Silurian crinoids which he planned was never executed except for a series of minor

[Palaeontology, Vol. 2, Part 2, 1960, pp. 161–79.]

contributions (Bather 1890–2; 1896; 1906; 1907). Much useful information about British forms can, however, be obtained from the only part published of his monograph of the Crinoidea of Gotland (Bather 1893). The non-crinoid Pelmatozoa have thus attracted relatively slight attention after the middle of the nineteenth century when they were described by Edward Forbes (1848) in a memoir which was very good for its time. A certain number of species of the abundant crinoid fauna in the Wenlock Limestone were illustrated by Murchison (1839) in *The Silurian System* and briefly described by Phillips. In spite of Bather's papers just referred to there is no doubt that the crinoids still offer a fertile field of research, as evidenced by the recent publications by Dr. Ramsbottom (1950, 1951, 1952, 1958).

The only Ordovician and Silurian echinoderms included in the monographs of the Palaeontographical Society are the Asterozoa. These have been treated in a comprehensive volume—unfortunately not completed—by W. K. Spencer, published between 1914 and 1940. It tells us much about the difference in character between the British and the Balto-Scandian echinoderm faunas of the Old Palaeozoic that a corresponding work could not have done on the basis of Balto-Scandian material. For fossil remains of asteroids and ophiuroids are met with only occasionally in the deposits of Scandinavia and of the East Baltic area.

On the other hand, where Balto-Scandia is concerned, cystoids have clearly been a conspicuous element in certain Middle and Upper Ordovician faunas. Crinoids have been found in great abundance particularly in the Silurian of Gotland. A first orientation as to the diversification in each group was presented by Angelin's classical work, edited posthumously in 1878. Through his monograph of the crinoids of Gotland, Bather (1893) made a skilful and badly needed revision of the inadunate forms. The articulate crinoids of Gotland (and of Britain) were accounted for by Springer, in 1920, but the camerates have had to wait much longer. Lately, however, Professor Ubaghs, of Liège, has taken up their study. The work is well under way, and three parts have been published (Ubaghs 1956–8). Other recent contributions to the knowledge of the Old Palaeozoic echinoderm fauna of Scandinavia mainly concern different non-crinoid groups. It should be mentioned that even Jaekel drew on material in the Swedish Museum of Natural History in Stockholm when preparing his great monograph of the Pelmatozoa (1899).

The Ordovician of Estonia and of the Leningrad district is famous for excellently preserved and, in part, unique echinoderms, first and foremost non-crinoid pelmatozoans. Many of these were early described in the classic works of Pander (1830), Leuchtenberg (1843), Volborth (1846, &c.), Eichwald (1860, &c.), and Friedrich Schmidt (1874, &c.). Fresh light has been thrown on the morphology and taxonomy of many remarkable forms by the eminent investigations of Professor Hecker (1923, 1940, 1958, &c.), of Moscow. Two interesting genera of Ordovician crinoids have been commented upon by Professor Öpik (1934, 1935), then in Tartu, but the crinoids of the East Baltic Palaeozoic are comparatively poorly known so far.

What has been said now is of course in no way a complete review of the available literature on Old Palaeozoic echinoderms in Britain and Balto-Scandia. My intention has only been to give a rough sketch of the literary background of our subject. It may be added that summaries of the regional distribution of some groups of pelmatozoans are included in general works, as those of Barrande (1887) and Jaekel (1899). Special mention is due to the *Thesaurus siluricus* by J. J. Bigsby (1868), which is a bold attempt to indicate the main traits of Cambro-Silurian palaeobiogeography on the basis of an extensive compilation of data in the relevant literature.

FACTORS IN THE DISPERSAL OF ECHINODERMS

At a British Association meeting in 1938 a discussion was held on 'The Distribution and Migration of certain Animal Groups in the British Lower Palaeozoic Faunas'. The opening contribution, published subsequently in the *Geological Magazine*, was given by Dr. Stubblefield. It gave most valuable details on the behaviour of trilobites in this respect. Dr. Stubblefield (1939, p. 49) observed that 'any conclusions made at the present stage are tentative and are offered as an incentive to research'. Twenty years have passed since these words were uttered. But they are just as true now as then and will for many years to come stand as a motto for all discussions of this kind, irrespective of the group of animals dealt with.

In addition, Dr. Stubblefield drew attention to the fact that trilobites are favourable objects for the study of migration-paths, because they were presumably characterized by ecdysis. As a result, the number of potential fossils were several times greater than the number of individuals. The adult echinoderms, on the other hand, produce only one skeleton during their lifetime. It may be remembered, however, that the echinoderms have a remarkably high capacity of regeneration, which enables a rapid substitution of lost or cast-off parts of the body. Theoretically, this may have contributed to augment their share in the fossil record but in practice it may have been a rather negligible factor.

Another drawback is that the adult stages were capable of no, or a very restricted, shift of position. Like their recent representatives, the great majority of the early echinoderms were bottom-dwellers, either sedentary, as the bulk of the pelmatozoans, or moving sluggishly on the sea-floor or in the bottom ooze, or hiding in crevices of coral-reefs, and so forth. These habits may have been an advantage to potential fossils but did not favour a rapid distribution over wide areas by means of adult individuals. However, echinoderms have an extremely wide range of distribution in modern seas. The fossil record tells us that this was true also of echinoderm faunas from the Palaeozoic onwards. The explanation is, as in so many other cases where the adult generation is practically passive, that the migration to new areas of distribution and their colonization is chiefly performed by larvae. We do not know anything about the behaviour and resistibility of the larvae of primitive echinoderms. But it is reasonable to imagine that, in principle, they were much the same as those of the larvae of recent forms.

Because pelmatozoans predominated strongly among the echinoderms in the Old Palaeozoic faunas, attention should in the first case be given to their only existing representatives, the crinoids, which are likely to demonstrate conditions most nearly comparable to those of their Palaeozoic predecessors. The stage of active swimming is short in the crinoids, its duration being necessarily restricted by the fact that the larvae have no mouth and, accordingly, cannot take any nourishment. This stage lasts generally two or three days but may exceptionally be prolonged to twelve days (cf. Dawydoff 1948, p. 351). In the latter case especially the allotted time is enough for the spreading of a given species over great distances.[1] The larvae of certain other echinoderm groups,

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[1] The transport of marine animals by sea currents has been discussed by Born (1920).

which were yet subordinate in Cambro-Silurian times, lead a pelagic life which may last for months.

There are very few examples of a pelagic, maybe epiplanktonic, habit in adult echinoderms; the most well known of fossil forms is the Upper Cretaceous crinoid *Uintacrinus*. In Middle Ordovician times no echinoderm reached a more universal distribution than the hydrophorid genus *Echinosphaerites*. The spherical thecae of *E. aurantium* or closely related forms are found in many parts of the world. Bather (1928, pp. lxxviii et seq.) tried to account for its relative ubiquity by the alternative explanation that the thecae were occasionally torn off from their tiny stems and swept away by waves and currents. Bather also set forth the hypothesis that thecae of dead individuals floated in the plankton to be ultimately washed ashore. It goes without saying that a nekroplankton could not contribute to the dispersal of the living *Echinosphaerites*. In view of the fact that the *Echinosphaerites*-beds give the impression of being autochthonous, Bather's theory seems to be supported by little actual evidence (see also Regnéll 1945, p. 146).

It should be mentioned, finally, that in the free-living groups of echinoderms, dispersal may to some extent be due to active migration by adult individuals. Schindewolf (1950, p. 54) quoted an instance where marked specimens of asteroids had been stated to migrate more than a thousand kilometres in a remarkably short time.

On the whole, the ways in which echinoderms spread and which have secured them a prominent position in practically all types of biotopes in recent seas all over the world, are of little help to the sleuth who seeks to follow their track through the ancient seas. But the echinoderms have a quality which is much to their credit as potential fossils, that is to say the heavy skeleton characteristic of most of their representatives. This armour, which was in many cases disintegrated after the death of the animal, was no doubt extremely resistent to destructive agencies. Thus, we have reason to suppose that the quota of echinoderm remains in the fossil record is greater, rather than the reverse, than the quota of echinoderms in the faunal assemblages once living. This leads us to the conclusion that the numerous occasions in which a species is represented in our collections by a very small number of specimens, or maybe by a unique specimen, reflect an original condition: the species will have been of very scarce occurrence in the biota to which it belonged.

EDRIOASTEROIDS

Edrioasteroids have never played any conspicuous role in the faunas inhabiting the Cambro-Silurian seas which covered the areas now under discussion. From the Cambrian there are only one or two isolated finds of *Stromatocystites balticus* Jaekel. This species has unfortunately not been encountered in the solid rock but in erratic boulders in north Germany. According to Jaekel (1899, p. 42), these boulders originate from the Middle Cambrian *Paradoxissimus* Sandstone of the Baltic Basin exposed on Öland. Previously the specimens were in museums in Germany, but it is to be feared that they have been lost. *Stromatocystites*, which has not been found in Britain, seems to be of North American origin, since it has been recorded in the Lower Cambrian of Newfoundland.

The evolution of the edrioasteroids reached its acme during the Middle Ordovician. This is due almost exclusively to the prolificity of the North American stock, mainly the Hemicystitidae. The very scanty material from the East Baltic area includes mainly

Lower Ordovician forms. The peculiar *Pyrgocystis* is represented by three species, the age of which is not precisely known, but the specimens seem to originate from beds corresponding to the Arenig (Hecker 1939, p. 245). It is possible that *Pyrgocystis* was present in the Ordovician of the Oslo region as well. Unfortunately, it has not been possible to locate the specimen referred to incidentally by Jaekel in 1927 (cf. Regnéll 1948, p. 39, footnote 2). Dr. G. Henningsmoen has kindly informed me that there is nothing of that kind in the collections of the Paleontologisk Museum in Oslo.

In Great Britain *Pyrgocystis* has been found in the Ashgillian Starfish Bed in Girvan, and in the Wenlock Shales of Shropshire (Bather 1915, p. 16). By which migration routes *Pyrgocystis* arrived at the British area is not entirely evident, because the genus has also been found in Blackriveran beds of Minnesota, which may be correlated broadly with the basal Caradoc. But it is justifiable to state that the Ordovician centre of dispersal of *Pyrgocystis* was located in the East Baltic area. As has just been mentioned, the genus is represented in the Wenlock of England. Other Silurian localities exist on Gotland and in the State of New York. Whether the Silurian forms are descendants of their Ordovician predecessors within the respective regions, or whether they have been introduced by a new faunal invasion, is not known.

There is other evidence of the Baltic origin of the turret-shaped edrioasteroids. This is supplied by *Cyathotheca*, which is known from the Vaginatum Limestone, on the Arenig–Llanvirn boundary, and from the top of the Ordovician in Dalecarlia, North-Central Sweden. In addition, the Middle Ordovician of Estonia has yielded two species of *Cyathocystis*. Like *Cyathotheca* this genus is absent in the British fossil record, but there are two species of *Cyathocystis* in the American Ordovician (*C. americana* Bassler 1936, *C. oklahomae* Strimple and Graffham, *in* Strimple 1955). This would indicate a faunal interchange in Ordovician times between the Baltic area and North America via the Polar Basin.

It is interesting that the disk-shaped type of edrioasteroids, which is the predominating type in North America and Central Europe, is almost unrepresented in the areas now under discussion. The only exception is *Edrioaster buchianus* from a Bala sandstone in Denbighshire, North Wales.[1] This find is remarkable also from the point of view that the four other known species of *Edrioaster* occur in the Trenton of North America. It is unadvisable to give any opinion of the direction of the migration, since *E. buchianus* and the American species seem to have been roughly contemporaneous.

In another context (Regnéll 1950, pp. 10–12) I have commented briefly on the biogeographical significance of edrioasteroids in general.

CARPOIDS

The stratigraphical and geographical distribution of the carpoids[2] neatly display—or seem to do so—the existence of four subsequent faunas, each with a characteristic

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[1] The exact locality was given by Bather (1900, p. 194) as 'two miles west of Ysputty Evan [Yspytty Ifan, acc. to the Geol. Surv. "Quater-Inch" map, sheet 9 & 10]; that is to say, about two miles south of Pentre Voelas [Pentre Foelas], and therefore in Denbighshire and not in Caernarvonshire as stated by J. W. Salter—and by R. Etheridge, sen.—'. The present writer has not been able to find out if the 'Caradoc beds', referred to by Bather, are Caradoc in the modern sense of this term or if they belong to the Upper Bala or Ashgill.

[2] The carpoids are here taken in the conventional sense of the term, thus including aberrant forms as *Lingulocystis* Thoral (cf. Chauvel 1941, p. 172).

regional localization. For the sake of convenience, these faunas will be designated by the names of predominating carpoid genera, as follows: 1, The Middle Cambrian *Trochocystites* fauna; 2, the Ordovician *Dendrocystites* fauna; 3, the Silurian *Placocystites* fauna; and 4, the Lower Devonian *Anomalocystites–Australocystites* fauna. Faunal hiatuses occur in the Upper Cambrian, in the basal Silurian, and in the Ludlow, but these blanks are outstepped by some genera.

The oldest fauna, which comprises two or three genera beside *Trochocystites*, is likely to have originated in the Bohemian Basin but rapidly invaded the waters over south France, Spain, and Morocco. The *Dendrocystites* fauna occupied a much larger area, and the number of genera were multiplied. This fauna represents a high-watermark in carpoid evolution. From the faunal province inhabited by the Middle Cambrian forms, carpoids spread to Estonia in early Ordovician times and reached North America in Chazyan times (Llanvirn-Llandeilo). This presumably took place via a Polar route, as there are no records at all from Ireland, and only from Caradocian-Ashgillian deposits in Scotland and England. All carpoids from Estonia described so far belong to *Rhipidocystis*. This genus, which seems to be endemic to the East Baltic area, comprises six or seven species, probably ranging from the Arenig to the Caradoc.

Carpoids are practically unrepresented in the Ordovician faunas of England. The only published record seems to be a species from the Middle Ashgillian *Dalmanitina robertsi* Beds in the Cautley District, Yorkshire, which, with a question-mark, was referred to *Ateleocystites*[1] by Marr (1913, p. 4).

The famous Starfish Bed of Ladyburn in Girvan has yielded two species of *Cothurnocystis* and one species which was described by Bather (1913) as *Dendrocystis scotica* but which was later given the rank of an independent genus called *Dendrocystoides*. These are among the last survivors of the Middle European *Dendrocystites* fauna. *Dendrocystoides* developed from *Dendrocystites*, and the remarkable *Cothurnocystis* has an early representative in *C. primaeva* of Languedoc which is probably of early Arenig age (Thoral 1935, p. 100). It should be mentioned that remains of carpoids are practically non-existent in the Ordovician rocks of Scandinavia. There is an isolated record of a stem-fragment in a boulder—probably Ashgillian—found on Öland. This has been assigned to *Dendrocystites* (Regnéll 1945, p. 194).

The next younger carpoid assemblage, the *Placocystites* fauna, is of particular interest to us, being restricted to England on the one hand and Gotland on the other. Two species have been described from the Wenlock Limestone in Dudley, namely *Placocystites forbesianus* Koninck 1869 (syn. *Ateleocystis gegenbauri* Haeckel 1896), and *Ateleocystites fletcheri* Salter 1873. According to Woodward (1880, p. 195), the species mentioned are identical, as was also stated by Barrande (1887, p. 90). No recent authors seem to have commented upon *Ateleocystites fletcheri*, but the species has been entered under this name in the well-known *Bibliographic and Faunal Index* by Bassler and Moodey (1943, p. 132). Unfortunately, I have not seen any actual fossil material either of the so-called *Ateleocystites fletcheri*, or of the Caradocian *Ateleocystites huxleyi* Billings type of the genus, from the Trentonian of Canada. But a comparison between the North

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[1] When studying material in the collections of the Geological Survey and Museum, London, the present writer noticed, many years ago, two specimens from Shoalshook (presumably from the Lower Ashgill Shoalshook Limestone), one of which is labelled '*Ateleocystites oblongus* Ms.' and the other '*Ateleocystites* n.sp.'. The specimens have not been examined.

American type species as figured by Miss Alice E. Wilson (1946, pl. 2, figs. 1–4), and *Ateleocystites fletcheri* as figured by Salter (1873, p. 128), makes it clear that the two forms cannot possibly be congeneric. Instead, *Ateleocystites fletcheri* has to be transferred to *Placocystites*. It may well be that it is in fact identical with *P. forbesianus*, as suggested by Woodward and Barrande. If this is true, there is only one carpoid species from the English Wenlock.

If there be some doubt about the species erected by Salter, we have, so far, no substantial knowledge of the member of the *Placocystites* fauna found on Gotland. It is represented by one specimen. It is not known exactly from which stratigraphic unit it comes, but it is reasonable to assume that the specimen originates from a stratum equivalent to some part of the Wenlock Limestone. According to information received from the late Professor T. Gislén, of Lund, it should be assigned to a new species related to *Placocystites forbesianus* (cf. Regnéll 1945, pp. 196–7).

As mentioned, this uniform carpoid fauna seems to have occupied a well-defined marine province in west and north-west Europe, no Silurian carpoids being known from any other part of the world. It is a ticklish question to say from where the *Placocystites* fauna was introduced. Among pre-Silurian carpoids there is not one which can be safely referred to *Placocystites*. It is true that *Anomalocystites bohemicus* Barrande from Ashgillian beds of Bohemia belongs to this genus according to Chauvel (1941, p. 215), but Caster (1952, p. 88) believes it may prove to be an Ateleocystitidae. Be that as it may, the Bohemian form is the only member of the Placocystitida in the Ordovician of Europe, while these enjoyed a certain flourishing in North America. Taking into view the considerable difference in age between the Silurian *Placocystites* and their plausible Ordovician progenitors, we must leave the question whether the *Placocystites* fauna was of an easterly or of a westerly origin unanswered. The fauna appeared rather abruptly. Its closest affinity is with Lower Devonian forms. We are thus entitled to assume that England was the prime centre of dispersal of the widespread fourth carpoid fauna (the *Anomalocystites–Australocystis* fauna), of early Devonian age, which meant a remarkable revival of the carpoid stock before its final extinction.

EOCRINOIDS AND PARACRINOIDS

An analysis of the stratigraphic and regional distribution of the eocrinoids leads us to conclude that the mainly Middle Cambrian *Eocystites* fauna originated in North America in early Cambrian time. No members of this fauna have been traced in the areas now under discussion, although they were present in the Bohemian Basin and France. An interesting find of a new eocrinoid of late Middle Cambrian or early Upper Cambrian age from the Lena Basin in east Siberia was recently announced by Yakovlev (1956).

The eocrinoids rapidly colonized new marine provinces, however, and the *Macrocystella–Mimocystites* fauna seems to have been distributed nearly all over the world in Tremadocian time. But it is worth noticing that Balto-Scandia, which was later to become a refuge of the declining eocrinoid stock, does not seem to have been inhabited by the fauna just mentioned. In England this fauna is represented by *Macrocystella mariae* in the Shineton Shales, the only eocrinoid recorded so far from the British Isles.

The *Macrocystella–Mimocystites* fauna had laggards right up to the close of the Ordovician but was largely substituted by a fauna containing *Cryptocrinites*, *Bockia*, *Ascocystites*, and *Polyptychella*, at the same time as the centre of eocrinoid distribution was shifted to Balto-Scandia, and especially to the East Baltic area. There several species of *Cryptocrinites* and *Bockia* are found, ranging from the Arenig to the Lower Caradoc.

In Europe the eocrinoids became extinct before the opening of the Silurian. They definitely terminated with two species of the inadequately known *Lysocystites* in the upper Niagaran (Wenlock). This is, moreover, a strangely isolated occurrence of eocrinoids in North America, since *Lysocystites* is separated from the next-older eocrinoids by a time-gap extending to the Middle Cambrian.

The paracrinoids are an almost negligible quantity in the Lower Palaeozoic faunas outside east North America. Whereas there are a dozen American genera, ranging from the Chazyan Crown Point Formation (inclusive) (approximately on the Llanvirn–Llandeilo boundary) to the Trentonian Kirkfield Formation (Caradoc), the genus *Achradocystites* is unique in Estonia and in Europe as a whole. Thanks to a recent revision by Hecker (1958) based on fresh material, *Achradocystites* is now known in some detail. Its main affinities are with *Comarocystites* which belongs to the geologically youngest among American paracrinoids. The Estonian species—there are two of them, one in Keila (D_{II}) beds, the other in Vasalemma (D_{III}) beds—are probably slightly younger than *Comarocystites*. It follows from the regional and stratigraphical distribution pattern of the paracrinoids that *Achradocystites* may well be an Appalachian immigrant in the Middle to Upper Ordovician fauna of Estonia.

HYDROPHORIDS

Hydrophorids, or cystoids in a restricted sense, are a conspicuous element in the Lower Palaeozoic faunas of both the British Isles and Balto-Scandia. There is a difference, however, in that the Ordovician hydrophorid faunas of Balto-Scandia were abundant and prolific compared with those of the British Isles, whereas the reverse was true of the Silurian hydrophorid faunas.[1]

The most ancient faunal assemblage of hydrophorids in Balto-Scandia appeared in late Arenig time after having been preceded by a few very early forms. Characteristic of this fauna are *Cheirocrinus* and *Echinoencrinites*, and, in addition, in Sweden, *Sphaeronites pomum*. The sequence on the east side of the Baltic is notable for a number of morphologically and phylogenetically remarkable genera, like *Asteroblastus*, *Asterocystis*, *Mesocystis*, *Blastocystis*, *Protocrinites* (cf. Hecker and Hecker 1957), and others. A corresponding fauna is not present in the British fossil record.

The highest peak of the curve illustrating the representation of hydrophorids in the Ordovician of Balto-Scandia falls within the Llandeilo and the Lower Caradoc and is

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[1] The basis of a comparison between the British Isles and Balto-Scandia would have been firmer, had the hydrophorids of the former region been the subject of a modern revision. My personal acquaintance with the actual material is fairly limited. About ten years ago I had an opportunity to skim over the collections kept in the Museum of the Geological Survey in London, and in the British Museum (Nat. Hist.). In addition, material from Girvan has been placed at my disposal by the kind agency of the late Mr. J. L. Begg, of Glasgow. Mr. M. V. O'Brien and Mr. G. J. Murphy have permitted me to study all the cystoids from the Irish Ordovician present in the collections of the Geological Survey of Ireland in Dublin. It is true that generally the material is not very attractive from a palaeontological point of view because of the poor state of preservation in many cases. But I hope that, in spite of this, somebody will take the trouble to make a general revision which will very likely prove to be worth while. Until such a revision is available we cannot go much beyond some rather generalized statements and assumptions.

caused by the *Echinosphaerites aurantium–Heliocrinites* fauna. There is a certain lagging of the Scandinavian forms in relation to the Estonian ones, which indicates a trend towards the west of the early Middle Ordovician hydrophorids. This migration wave probably carried East Baltic faunal elements into the waters covering parts of Wales and Ireland. As far as I have been able to find out, the fossil record of the Caradoc hardly substantiates a similar statement as regards England. The Tramore Limestones in Co. Waterford and more or less equivalent strata in Co. Wexford, south-east Ireland, have yielded a fairly rich harvest of hydrophorids. According to personal information from Mr. G. J. Murphy, of Dublin, the Tramore Limestones may be considered as being of *Nemagraptus gracilis* age. Main constituents of these oldest hydrophorid faunas of the British Isles are members of the genera *Echinosphaerites*, *Heliocrinites*, and *Cheirocrinus*. It may be objected that these are rather cosmopolitan in distribution, and that few species are common to the British Isles and Balto-Scandia. But the idea of a gradual migration in a westerly direction fits well into the general pattern of distribution of the Balto-Scandian Ordovician hydrophorids, which seem themselves to have come from the Far East (cf. Regnéll 1948*c*, p. 29). In this connexion it will be appropriate to recall that, as demonstrated by Stubblefield (1939, pp. 58–60), the Caradocian trilobite faunas of south-east Ireland and Girvan have both North American and Scandinavian affinities. In the case of the bulk of the hydrophorids, an American origin is inconceivable, but, as we shall see, such an origin is evinced by the presence of representatives of *Pleurocystites*.

There is no main difference between the faunas just referred to and the Ashgill faunas in Wales and England. The most fertile collecting-grounds have been Shoalshook in South Wales and the Bala Country in North Wales.[1] A list of fossils, including seven species of hydrophorids, has been published by Miss Elles (1922, p. 172).[2] The correct interpretation of some species is still obscure. But I take it almost for granted that '*Caryocystites davisi*' M'Coy is identical with *Heliocrinites balticus* of the East Baltic area. It is probable that this is true also of '*Caryocystites granatum*' of Forbes and several subsequent authors. Further, it is likely that *Echinosphaerites granulatus* M'Coy is closely related to *Echinosphaerites aurantium*. Both these species appear in the East Baltic area in lower horizons than in the British Isles. There is a third easterly element in the British Ashgill faunas, namely *Cheirocrinus interruptus* recorded by Bather (1913) in the Drummuck Group in Girvan. According to Jaekel (1899, p. 220), two specimens of *Cheirocrinus interruptus* available to him came from the vicinity of Leningrad, the stratigraphic horizon being unknown.

The East Baltic aspect of the faunas now under discussion cannot be disputed. But there are also threads leading to the western part of the European continent. Thecal plates similar to those of *Oocystis rugata* (Forbes) (syn. *Hemicosmites rugatus* Forbes, *Hemicosmites pyriformis* Forbes), a species recorded from Ireland, Wales, and England, have been found in Ashgillian beds in Belgium (Regnéll 1951, pp. 21–22) and Languedoc

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[1] Both Shoalshook (Shole's Hook) and Bala were exploited for hydrophorids at the beginning of the nineteenth century by officers of the Geological Survey. The fossil-bearing strata at these localities were first classified as 'Llandeilo Flags'; this designation was used, e.g., by Forbes (1848). The Shoalshook Limestone and the Rhiwlas Limestone and Mudstones are now ranged with the Lower Ashgill.

[2] A couple of errors have crept into this list. It is not evident if '*Caryocystites granulatus* Forbes' refers to *Echinosphaerites granulatus* M'Coy, or to *Caryocystites* (i.e. *Heliocrinites*) *granatum* (Wahlenberg). For '*Sphaeronectes*', read *Sphaeronites*.

(Dreyfuss 1939, pp. 129–30). And *Echinosphaerites* (‘*Sphaeronites*’) *arachnoideus* (Forbes) may have a certain affinity to *Echinosphaerites barrandei belgicus* (cf. Regnéll 1951, p. 30).

A few words may be said about ‘*Caryocystites*’ *litchi* Forbes 1848 (see Regnéll 1951, pp. 34–35). According to my notes on the original material in the Geological Survey and Museum in London, the specimen pointed out by Salter (1866, p. 286) as the ‘true’ ‘*Sphaeronites*’ *litchi* can hardly be determined (Forbes 1848, pl. 21, fig. 2*c*; Mus. no. 7431). Other specimens associated with it recall the genus *Haplosphaeronis* with regard to the nature of the thecal pores. But in contradistinction to *Haplosphaeronis* they seem to be many-plated and approach in this respect *Eucystis*. ‘*Caryocystites*’ *litchi* was tentatively assigned to *Eucystis* by Jaekel (1899, p. 406). The original of the specimen figured by Forbes (1848) in his pl. 21, fig. 2*b* (Geol. Surv. Mus. London no. 1430) is possibly a *Sphaeronites*. ‘*Caryocystites?*’ *munitus* Forbes 1848 should possibly be referred to *Eucystis*. The genera *Eucystis* and *Haplosphaeronis* are found in Middle and Upper Ordovician rocks in Scandinavia. *Haplosphaeronis* has also been recorded in the Gembloux Shales in the Brabant Massive in Belgium (Regnéll 1951, p. 31).

The Caradoc and Ashgill of Girvan are, if not exactly unique, so very characteristic among contemporary deposits in the British Isles in having yielded a hydrophorid fauna which has in part a definitely North American stamp impressed upon it by members of the genus *Pleurocystites*. Bather (1913) described four species from the Upper Ashgillian Drummuck Group and reviewed all species of *Pleurocystites* known up to then. Two species had previously been recorded from the British Isles, namely *P. rugeri* Salter and *P. anglicus* Jaekel.[1] The precise horizon of the former is not known, but it has been collected at various Caradoc localities in Wales. *Pleurocystites anglicus* was so named by Jaekel, because he thought that it came from Scotland or, possibly, from South Wales! Bather (1913, p. 475, §§ 466, 468) demonstrated that it comes from Bardahessiagh, Co. Tyrone, Ireland, and concluded that it is a little younger than *P. rugeri* and a little older than the Girvan species from the Starfish Bed.

Subsequently, I have studied echinoderm material from the Caradoc Craighead Mudstone, of the Balclatchie Group, collected in Craighead quarry, Girvan, by Mr. R. P. Tripp. This material which has not yet been published, includes a new species of *Pleurocystites*.

All species of *Pleurocystites* older than those in the Caradoc and Ashgill of the British Isles are North American, with the exception of a somewhat doubtful species from China, *P. bassleri* Sun (1948, p. 6), of Llanvirn age. In North America *Pleurocystites* survived in older Richmond (i.e. older Ashgill) times. But we must conclude that one part of the stock migrated eastward so as to reach European waters in Caradoc times. As emphasized by Foerste (*in* Slocom and Foerste 1924, p. 358), the ‘direction of migration of *Pleurocystites* into the British Isles is unknown’. Records of doubtful *Pleurocystites* in Ashgill rocks of Belgium indicate the extreme eastward extension of the American influence (Regnéll 1951).

If we take a general view of the European Middle Ordovician hydrophorid faunas two main geographical provinces can be recognized: one characterized by the predominance of Aristocystitidae; and a second one characterized by the absence of genera

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[1] Jaekel (1918, p. 95) proposed a new genus, *Dipleurocystis*, for the reception of *P. rugeri* and *P. anglicus*. In my opinion, *Dipleurocystis* is weakly founded and should be rejected.

belonging to that family. The province first mentioned, which conforms with the 'province à Amphorides' of H. and G. Termier (1952, p. 381), occupied the sea south of the hypothetical Scottish–Hungarian barrier and extended to Bretagne, the south-west of Europe, and Morocco. The other province comprised the Balto-Scandian area. The hydrophorid faunas of both provinces undoubtedly originated from the Far East.

No Aristocystitidae have been found in the Lower Palaeozoic deposits of the British Isles. Nevertheless, a certain influx of Mid-European forms may have taken place, especially to the Girvan area, as demonstrated by its carpoid fauna. On the whole, Girvan has been the meeting-place of faunal elements of different origin: Balto-Scandian, Mid-European, and North American. The Bohemian element in the Upper Ordovician faunas of Britain and Ireland is borne out very strikingly by certain trilobites, as observed by several authors, most recently by J. A. Weir (1959, p. 382).

As is the case with several other echinoderm groups, the early Silurian marks a period of decline for the hydrophorids. The Wenlock Limestone in Dudley confronts us with a hydrophorid fauna of an entirely different and much more uniform aspect. Six genera have been recorded, namely *Apiocystites*, *Lepocrinites*, *Pseudocrinites*, *Staurocystis*, *Schizocystis*, and *Prunocystites*. Of these, the last two are Echinoencrinitidae, while the four others belong to the family Callocystitidae. Apart from two species in the Upper Silurian of Balto-Scandia, the English genera are the only representatives outside North America of that family, which arose in late Ordovician times. The European Callocystitidae may be descendants of North American forms. During the deposition of the Wenlock Limestone the Callocystitidae flourished in Dudley whence they wandered to Gotland and to the Island of Ösel (Regnéll 1948*c*, p. 42). It would seem as if a few of the immigrants returned to North America. For, both in the case of *Lepocrinites* and of *Pseudocrinites*, the former of which has two, the latter eight species in the Lower Helderberg (Lower Devonian), the oldest representatives are those present in the Wenlock Limestone.

Prunocystites and *Schizocystis* are specialized morphologically and isolated geographically. They have no doubt a north-easterly origin, however, because all other members of the Echinoencrinitidae are Balto-Scandian.

Except *Lovenicystis* (Callocystitidae) there is only one hydrophorid in the Silurian of Gotland, viz. *Gomphocystites gotlandicus*. Its affinities are exclusively North American.

BLASTOIDS

I shall not here discuss the taxonomic position of certain Lower Palaeozoic genera, which are considered by some authors to be blastoids while others define them in a different way. I am referring to the so-called Coronata. I agree with Jaekel in placing them among the blastoids. Coronate blastoids are very scarce in the fossil record of the areas with which we are now concerned. In fact, only three genera have been mentioned in the literature, each of them containing one or two species. From Sweden there are the Middle Ordovician *Paracystis* and the Upper Ordovician *Tormoblastus*, from Britain there is the Silurian *Stephanocrinus* (see Regnéll 1945, p. 193; 1948*c*, pp. 30, 32, 39). Additional material both from England and Sweden is in the hands of Dr. Ramsbottom.

The oldest coronate blastoid known is *Mespilocystites* which appeared in the Llanvirn in Bohemia. It is possible that the Swedish *Paracystis* and *Tormoblastus* were derived from the Bohemian form. It is more difficult to give an opinion of the relations between the English and the North American species of *Stephanocrinus* which were roughly contemporaneous, that is to say mainly of Wenlockian age.

CRINOIDS

The crinoids are by far the most comprehensive of all pelmatozoan groups. But they will be dealt with very cursorily, chiefly because of my insufficient personal experience of at least the Silurian forms.

We are still unable to point out the ancestors of the crinoids. Accordingly, we have no idea of the place of origin of the group. But we can say that a differentiation into principal branches must have taken place at an early date. For, it is a fact that the most ancient crinoids in Eurasia and North America were already specialized into camerate, inadunate, and flexible forms. Crinoid evolution in relation to major palaeogeographic changes has been summarized and illustrated by diagrams in a paper by R. C. Moore (1950).

To the inadunates belong crinoid remains in Lower Arenig rocks (Lower Tremadoc of Hicks) at St. David's and on Ramsey Island, South Wales, described by Hicks (1873, p. 51, pl. 4, figs. 17–20) under the name of *Dendrocrinus cambriensis*. The generic determination is hardly correct, but, though fairly imperfect, the fossil is of great interest in being probably the oldest genuine crinoid recorded so far.[1] The Ramsey Island material has not been subject to a modern revision. On the whole, little information on the Ordovician crinoids of the British Isles can be gathered from the literature. It would be fortunate indeed if this deficiency could be made up, and I think there is reason to expect that it will be so in the comparatively near future.

As a matter of course, crinoid ossicles are frequently met with in various rocks of the Ordovician sequence in the British Isles. A common Welsh Caradoc fossil is that generally referred to as *Glyptocrinus basalis* M'Coy. Marr (1883, p. 126) gives its horizon as 'Middle Bala'. The species should be assigned to *Rhaphanocrinus* whose oldest known member has been recorded in the upper Chazyan of New York. Also *Merocrinus salopiae* Bather (1896), from Llandeilo rocks in Shropshire, has North American affinities, but in this case the British species is the older one. It is possible that '*Actinocrinus*' *wynnei* Baily and *Periechocrinites laevis* (Portlock, *non* Angelin) provide other examples of an interchange between the Ordovician crinoid faunas of North America and the British Isles, but their generic status must be verified.

The Ordovician seas of Balto-Scandia were inhabited by a group of inadunates called the Hybocrinida. These are remarkable in so far as they demonstrate a retrograde evolution of the brachial apparatus (Regnéll 1948*a*). The oldest representative of the Hybocrinida, *Baerocrinus parvus*, appears on the Arenig-Llanvirn boundary in Estonia, followed by *Revalocrinus* in the upper Llanvirn. *Hoplocrinus* sets out in the Llandeilo and reaches Sweden in early Caradoc time. *Cornucrinus*, finally, appears in the middle Caradoc and ranges to the Ashgill, inclusive. Outside Balto-Scandia, Hybocrinida have

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[1] *Trichinocrinus* from the Table Head Limestone of Newfoundland was supposed by Moore and Laudon (*Amer. J. Sci.* **241**, pp. 262–8) to be 'older than any other yet known' (p. 262). This is probably not correct. In the correlation chart of the Ordovician published by the Geological Society of America (Twenhofel *et al.*, 1954), the Table Head Formation is placed on the level with the Llanvirn (chart, column 3; text p. 284).

been found in North America only (*Hybocrinus*, *Hybocystites*). The oldest of these originates from late Chazyan rocks in Ottawa, and it is possible, therefore, that the North American Hybocrinida are immigrants from Balto-Scandia.

Very few crinoid cups have been collected in the Ordovician of Sweden. This explains why its crinoid fauna is largely unknown. This applies also to other parts of Balto-Scandia, though to a minor degree to Estonia. A number of genera seem to be endemic, namely *Esthonocrinus*, *Metabolocrinus*, *Pentamerocrinus*, *Perittocrinus*, *Tetractocrinus* (all of Jaekel, 1902, 1918), and the morphologically remarkable *Ristnacrinus* Öpik (1934), while *Carabocrinus esthonus* Jaekel (Vasalemma, Middle Caradoc) is a member of an otherwise exclusively American genus. According to Jaekel (1918, p. 43), *Porocrinus*, which first appears in the Blackriveran of Illinois, is evidently a derivative of *Perittocrinus* (see also Foerste, *in* Slocom and Foerste 1924, p. 358).

In his monograph of the inadunate crinoids of Gotland, Bather (1893, p. 7) remarked that out of forty species treated by him only six are common to Gotland and England. But it should be pointed out that of ten genera recognized on Gotland, six have also been found in England. In addition, all Gotland genera but two are represented in North America, and four species are even common to these two areas. One species, *Myelodactylus* ('*Herpetocrinus*') *ammonis* (Bather), has been recorded from both Gotland (the Slite Group: Upper Middle Wenlock), Dudley (the Wenlock Shales), Tennessee, and Indiana (Laurel, Waldrom, Beach River: Lower and Middle Wenlock). In a subsequent paper, Bather (1906) discussed species of *Botryocrinus* from Gotland, Dudley, North America, and Australia;[1] and in another paper (Bather 1907), he commented on a *Scyphocrinites* from west Cornwall which has Bohemian affinities.

I am not going to give further details but will restrict myself to stating that a number of recent papers tend to show that the Silurian crinoid faunas of Europe had a largely North American origin, and that many genera and several species had a very wide regional distribution (Bouška 1942, 1943, 1946, 1956*a*, 1956*b*; Lowenstam 1948; Ramsbottom 1950, 1951, 1952, 1958; Ubaghs 1958; see also Regnéll 1948*c*, pp. 43–44). As a matter of course more or less provincial crinoid faunas had developed, but it is apparent that conditions were favourable for an interchange of faunal elements between North America, Britain, Sweden, and Bohemia.

The apogee of Silurian crinoid development in England is marked by the prolific fauna in the Wenlock Limestone. As pointed out quite recently by Dr. Ramsbottom (1958, p. 106), this gave place to a much impoverished fauna in Ludlow times.

ELEUTHEROZOA

Eleutherozoa are very subordinate in the Lower Palaeozoic rocks of Balto-Scandia, while asterozoans are remarkably abundant in the Ordovician and Silurian sequences in the British Isles. 'Starfish Beds' occur in the Ashgillian Drummuck Group in Girvan; in Wenlock beds of Gutterford Burn, Pentland Hills; in Lower Ludlow shales at Church Hill, Leintwardine in the Welsh Borderland, and near Kendal, Westmorland; and in the Upper Ludlovian Kirkby Moor Flags in the Lake District, &c. Thanks to the monograph by W. K. Spencer (1914–40) we have an excellent knowledge of the Ordovician

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[1] The Melbournian Series, in which *Botyocrinus longibrachiatus* has been found, is placed by T. W. E. David (*The Geology of the Commonwealth of Australia*, London 1950, 1, tab. xi facing p. 224; see also p. 186) in the Wenlock and Lower Ludlow.

and Silurian asterozoans of the British Isles. On two occasions Spencer (1938, 1950) discussed the palaeobiogeographical aspects offered by these forms. The main facts found to be relevant for the British asterozoan fauna can be summarized as follows: the scanty Arenig and Llanvirn fauna from Wales and the Welsh Borderland 'shows a distinct affinity with that of Bohemia' (Spencer 1950, p. 396). The Middle Ordovician asterozoans covered a very wide area extending from Turkestan to the St. Lawrence valley. This was literally true of the Welsh and Irish *Stenaster*, and of *Protopaleaster*, from the Welsh Borderland. Other genera occurring in the British Isles have also been met with either in the west or the east of this vast marine province. 'The centre of much of the new differentiation appears to be to the west of Britain' (Spencer 1950, p. 398). The basic difference between Welsh Ashgillian faunas and contemporary faunas of Girvan is apparent also from the fact that the latter have abundant starfish while the former have none. Spencer (1950, pp. 401–2) recognized four elements in the Girvan starfish fauna, namely forms derived from Middle Ordovician ancestors in the same basin; new forms derived from one or two centres, which supplied immigrants to North America as well; new forms derived from the Arenig faunas of South France; and 'immigrants with untraced ancestry, found also in the Silurian of Australia'. The affinity to Australian faunas persisted during the Silurian.

Turning to Balto-Scandia we find that no information whatsoever about Ordovician asterozoans can be derived from the literature. I can add but little to this, but would like to mention that available to me is a poor specimen of an asterozoan (undescribed) from Upper Ordovician *Tretaspis* beds in Vestrogothia (Västergötland), Sweden. In an erratic boulder of a rock from the Caradoc *Coelosphaeridium* zone in the Oslo area, Norway, Dr. G. Henningsmoen has detected remains of starfish (undescribed).

Three species have been recorded from the Silurian of Gotland. These are *Neopalaeaster hesslandi* H. W. Rasmussen (1952) from Upper Llandovery beds near Visby; *Urasterella ruthveni leintwardinensis* Spencer (1918, p. 147) from Wenlock beds; and *Palasterina antiqua* (Hisinger) (see Spencer 1922, p. 229) from Upper Ludlow beds of south Gotland. Notable among material which still remains to be described is a magnificent specimen of an ophiuroid from the so-called *Pterygotus* Beds at the top of the Högklint Group (Lower Wenlock), Visby.

Rasmussen (1952, p. 23) is inclined to derive *Neopalaeaster* from the Ordovician *Siluraster*, represented in Bohemia and North Wales (*S. caractaci* (Gregory)). *Urasterella* is first found in the Middle Ordovician of North America (Spencer 1918, p. 136). It is also present in the Ashgill of Girvan, in the Wenlock of the Pentland Hills, and in the Upper Ludlow of the Lake District. *Palasterina*, finally, has been found in the Middle Silurian of Australia and England, and in the Upper Ludlow of the Lake District (Spencer 1950, p. 402; see also Regnéll 1948*c*, p. 44).

The remaining eleutherozoic groups do not require any time-consuming comments.

No remains of undoubted holothurians have been recognized in the Lower Palaeozoic rocks of our areas.[1] We may expect, however, that sclerites of holothurians will be found in the residue of samples treated with acetic acid, or in wash samples.

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[1] *Eothuria beggi* MacBride and Spencer 1938, from the Ashgill of Girvan, described as a holothurian has by most subsequent authors been considered to be an echinoid. Gutschick (1954) evidently accepted the original interpretation as a holothurian. Durham and Melville (1957, pp. 262–3) classify the Megalopoda (order containing *Eothuria* only) as 'Incertae sedis'.

Both Britain and Balto-Scandia have yielded forms which have a bearing on the early phylogeny of the echinoids. From the Ashgill of Girvan come the remarkable *Aulechinus* and *Ectinechinus*, while Durham and Melville (1957, pp. 243–4) have recently presented evidence of a Silurian age of *Myriastiches*, possibly from the Welsh Borderland. In any case, the Scottish genera mentioned are the most ancient of the Lepidocentroida. It would seem that this order had a centre in Britain. Silurian representatives are '*Wrightia*' *phillipsiae*, *Lepidocentrus? sp.*, *Echinocystites pomum*, and *Palaeodiscus ferox* (listed by MacBride and Spencer 1938, p. 93; cf. Regnéll 1956, p. 156). The only Silurian species from outside the British Isles is *Koninckocidaris silurica* from the State of New York. This species was approximately contemporaneous with '*Wrightia*' (Upper Llandovery) which is the oldest of the British species.

In their paper just referred to, Durham and Melville (1957, pp. 242–4) argue that the much-disputed *Bothriocidaris*, from the upper Middle Ordovician and Upper Ordovician of Estonia, is a genuine echinoid. A common ancestor of the geographically isolated *Bothriocidaris* and the lepidocentroids is not known. Irrespective of which interpretation we adopt for *Bothriocidaris* we cannot doubt that this very singular unit ended in a blind alley.

A more prosperous line of development, namely that of the Melonechinoida, can be traced back to the Silurian (probably the Lower Ludlow) of Gotland. *Gotlandechinus* described recently (Regnéll 1956) is the most ancient member of this order. In addition, spines of cidaroids and other echinoid remains not safely assigned to definite higher categories, have been found in the Silurian rocks of Gotland. We have no idea of the common source—if there was any—of the lepidocentroids and the melonechinoids, nor, in consequence, of their breeding ground.

Much of the early history of the echinoids seems to have been enacted in the Old Palaeozoic seas of Balto-Scandia and Britain. This is true also of the *ophiocistioids*, very rare eleutherozoic forms which unite traits of several echinoderm groups. It is possible that they evolved in the East Baltic area, for the genus *Volchovia* appeared there as early as in Arenig times. Two species have been described from the Leningrad province (Hecker 1938, 1940), and a slightly younger one from the Oslo district, Norway (Regnéll 1948*b*). There is a great discontinuity in the development of the Ophiocistioidea as known to us, as the next younger representative of the class, *Euthemon*, is not met with until in the Wenlock Limestone of the Malvern district (Sollas 1899, p. 696). Two more genera, each with one species, have come from British Silurian rocks, namely *Eucladia* from Sedgley, near Dudley (Woodward 1869, p. 241), and *Sollasina* (genotype: *Eucladia woodwardi* Sollas 1899) from Leintwardine (Sollas 1899, p. 695). Both are probably Lower Ludlovian of age. A last survivor of the Ophiocistioidea (*Rhenosquama* R. Richter 1930) has been traced in the Middle Devonian of the Rhine Valley, Germany. The group became extinct without leaving any descendants.

INCERTAE SEDIS

Finally, a few words shall be said of *Cyclocystoides* and *Bolboporites*, echinoderms of problematic nature.

As regards *Cyclocystoides* it may suffice to refer to a diagram published by me (Regnéll 1948*c*, p. 41), showing the regional distribution and approximate stratigraphic range of the known species of *Cyclocystoides*.[1] It is apparent that *Cyclocystoides* originated in North America in early Middle Ordovician time. Migrants moving in an easterly direction turned up in Caradoc faunas in England, and in Ashgill faunas in Girvan. The genus entered Gotland in the Wenlock.

Bolboporites has a very narrow stratigraphic range in Balto-Scandia, occurring in Arenig-Caradoc beds. It has been recorded both from the East Baltic area, Sweden, and Norway. A faunal interchange with North America is evidenced by the fact that *Bolboporites* has been found in the Chazyan and Blackriveran of Canada and the State of New York. The only additional record of *Bolboporites* relates to the Tramore Limestones (Caradoc) of south-east Ireland (Reed 1899, p. 732).

EPILOGUE

The various facts presented here will serve to illustrate the points of contact, and the differences, between the echinoderm faunas of the Lower Palaeozoic rocks in the British Isles on the one hand and in Balto-Scandia on the other. To be sure, it is no easy task to recognize the individual threads in this entangled web. An oversimplification would perhaps make us believe that much of the faunal migrations were directed towards the west in Ordovician times and towards the east in Silurian times. But the pictures of palaeobiogeographical features in remote times which we endeavour to envisage are poor in details, on account of scanty information—not least of the role played by ecological factors—and vague in outline, on account of our inability to reproduce the subject in a correct perspective. Some few future finds may have far-reaching consequences. But isn't it so that what makes Palaeontology such a fascinating study is, in part, the very fact that so much of the Past remains to be revealed in the Future?

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[1] Additional Devonian material published subsequently by Dr. Hertha Sieverts-Doreck (1951) does not affect the distributional pattern outline in the diagram.

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THE TETHYAN JURASSIC STROMATOPOROIDS *STROMATOPORINA*, *DEHORNELLA*, AND *ASTROPORINA*

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ABSTRACT. Certain Tethyan Jurassic stromatoporoids, some formerly allocated to the Palaeozoic genus *Stromatopora*, are described with new morphological terms, and grouped in the family Parastromatoporidae (superfamily Milleporellicae). *Dehornella* Lecompte 1952 is reassessed and *Stromatopora choffati* Dehorne 1917, sometimes erroneously allocated to *Stromatoporina* Kühn 1928 (Stromatoporinidae Kühn 1928) of which the type species *Stromatopora tornquisti* Deninger 1906 is redescribed, is allocated to it. *Stromatopora harrarensis* Wells 1943 is also allocated to *Dehornella* and specimens from Oman, Sinai, and Israel are described. Newly founded species are *Dehornella omanensis* from Oman and *D. crustans* from Israel.

Astroporina gen. nov., characterized by a coenosteum consisting almost entirely of conjoined astrosystems, includes *A. stellifera* sp. nov. and *A. stellans* sp. nov. from Somaliland, and *A. orientalis* sp. nov. and related forms from the Lebanon, Somaliland, and Oman.

INTRODUCTION

SOME of the Jurassic clinogonal stromatoporoids, in which both reticulum and astrosystems are tabulate and dominantly vertical, have been variously allocated to the genera *Parastromatopora*, *Tosastroma*, and *Dehornella*: the continued allocation of others to the genera *Stromatopora* Goldfuss or *Stromatoporina* Kühn is, in the opinion of the author, erroneous. Such forms are abundant in the Upper Jurassic of the Middle East, particularly in the Beni Zaid Limestone, Musandam Limestone Group, of the Jebel Hagab area, Trucial Oman. It is to facilitate the naming of some of these that the genera *Stromatoporina* and *Dehornella* are here redefined and a new genus erected.

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Registration numbers preceded by the letter H are those of specimens in the collection of the Department of Palaeontology, British Museum (Natural History), London; those preceded by the letter F are of specimens from the Sedgwick Museum, Cambridge.

STRATIGRAPHY AND LOCALITY

Eastern Arabia. The specimens (H 4833 to H 4869) described in this paper, mainly as *Dehornella harrarensis* (Wells) and *D. omanensis* sp. nov., are from the Musandam Limestone (Jurassic-Cretaceous), which is well exposed in the Jebel Hagab area of the Ruus al Jibal, the northern peninsula of the Oman Mountains, eastern Arabia (Hudson

[Palaeontology, Vol. 2, Part 2, 1960, pp. 180–99, pl. 24–28.]

et al. 1954). In this limestone series the Beni Zaid Limestone Formation, 77 metres thick, is of Oxfordian s.s. age, its type section being along the south bank of Wadi Bih in the Jebel Hagab area (Hudson and Chatton 1959). The top of the formation is a light-grey, massive, pseudo-oolitic limestone, 2·5 metres thick, containing abundant stromatoporoids: it was from this uppermost limestone that the above specimens were collected by Z. R. Beydoun and the author.

Sinai. The Jurassic succession exposed in Jebel Moghara, Sinai (Arkell 1956, Said and Barakat 1958) was measured by the geologists of the Standard Oil Company of Egypt: the fossil collections of the Iraq Petroleum Company, made by S. Nasr, were keyed to that succession. The uppermost part of the succession is as follows:

	metres
9. Shale with *Knemiceras* (Albian)	5·7
8. Sandy limestone	4·5
7. Shale with marl bands. Abundant *Choffatella decipiens* (Aptian) at base (*det.* P. V. Rabanit)	30·5
Non-sequence	
6. Light-grey and white limestone with abundant stromatoporoids as *Shuqraia*, &c. (Argovian)	24·0
5. Chalky limestone (Argovian)	5·0
4. Limestone with marl. Abundant stromatoporoids as *Shuqraia*, *Promillepora*, &c. (Argovian)	31·0
3. Shale, gypsiferous	5·0
2. Limestone, light grey, hard, with flint. Stromatoporoids as *Dehornella* and *Parastromatopora* in upper part. *Pachyceras sp.* (as Douvillé 1916, pl. 8, figs. 4, 5) and *Euaspidoceras*, *det.* Spath. (Oxfordian s.s.)	104
1. Limestone, white, soft, with *Phylloceras* (Rhacophyllitid) and *Binatosphinctes* cf. *schlosseri* Krenkel, *det.* Spath. (Upper Callovian)	10

Both the lithological and faunal successions agree well with those of neighbouring areas. Beds 1 and 2 are the equivalent of the upper part of the Bihen Limestone of Somaliland and that of the Tuwaiq Mt. Limestone of Central Arabia. Beds 3 to 6 are the equivalent of the Gahodleh Shales of Somaliland and the Hanifa Formation of Central Arabia. The non-sequence cuts out the Sequanian, Tithonian, and Neocomian as at Kurnub, Palestine. Said and Barakat (1958) give a totally different stage allocation to the Jurassic of Moghara, an allocation with which the author can in no way agree.

Israel. The fauna of the Jurassic exposed in Maktesh Hathira (Kurnub Anticline) has recently been summarized by the author (Hudson 1958). The stromatoporoid formations are the Shuqraia Limestones-with-Marls of Argovian age. They contain *Shuqraia spp.*, *Promillepora kurnubi* Hudson, *P. pervinquieri* Dehorne, *P. douvillei* (Dehorne), *Steineria somaliensis* (Zuff.-Com.), *Actostroma damesini* Hudson, *A. nasri* Hudson, *A. kuehni* Hudson, *Dehornella crustans* sp. nov., and *D.* cf. *harrarensis* (Wells).

British Somaliland. In this area the Jurassic includes the Bihen Limestone (Callovian and Oxfordian), 83 metres thick, with, above it, the Gahodleh Shales (Argovian), 113 metres thick. The upper part of the Bihen Limestone (= Tuwaiq Mt. Limestone of Central Arabia, the Shuqra Limestone of southern Arabia, and the Beni Zaid Limestone of eastern Arabia) contains corals and stromatoporoids, mostly *Shuqraia zuffardiae* (Wells) (Thomas *in* Macfadyen *et al.* 1935). It was from the upper part of the Bihen Limestone that *Astroporina stellans* sp. nov. and *A.* cf. *orientalis* sp. nov. were collected. The exact horizon of *A. stellifera* sp. nov. is not known.

STROMATOPOROID SKELETAL MORPHOLOGY

Fenestrate and cellular vertical lamellae. In morphological early forms the lateral processes arising from the pillars were usually transversely aligned and thus formed an open mesh of transverse lamellae, important structural elements in the reticulum and often as equally developed as the vertical pillars. In later forms, trending to verticality, the transverse lateral processes functioned differently since they occurred more or less vertically continuously on opposite sides of a pillar and linked one pillar to the other, thus forming vertical lamellae. In some forms the lateral processes may be still occasionally aligned giving sporadic transverse lamellae. Vertical lamellae so formed are often fenestrate (Hudson 1959) due to the intermittent vertical discontinuity of the lateral processes joining the pillars. Such openings are no more than temporary coenospaces between adjacent pillars and show as such in transverse section.

In morphologically advanced forms vertical lamellae are formed by the direct lateral welding of the pillars without the intervention of lateral processes. In such forms transverse structures other than tabulae and tabular laminae are absent. This joining of the pillars may proceed farther so that the vertical lamellae are two or more layers of pillars across or are compact vertical blocks of pillars. Such compound lamellae may not, however, be completely compact. They may enclose one or more small coenospaces, usually vertically elongate and thus form cellular vertical lamellae.

Astrocorridors. In morphological early forms the astrosystem may consist of an axial astrotube from which radiate out at regular or irregular vertical intervals single or groups of transverse astrotubes. In the forms described in this paper astrosystems do not include axial astrotubes and the transverse astrotubes are vertically extended so that they form a group of narrow radial spaces extending vertically throughout the reticulum and usually bounded by vertical lamellae which meet more or less at the axis of the astrosystem. Such vertical spaces, normally tabulate, are here called astrocorridors: they are the superimposed astrorhizae of other authors.

SYSTEMATIC PALAEONTOLOGY

The systematic position of the Mesozoic 'stromatoporoids' is a matter of argument, the main point of issue being the structural, and hence systematic, independence, at both family and order level, of the Palaeozoic and Mesozoic genera. To a less degree there is the same doubt of allocation of certain Mesozoic genera to groups which are essentially Tertiary-Recent. Thus there is no certainty of allocation of the various Mesozoic genera to one or more of the variously proposed orders such as the Stromatoporoidea Nicholson and Murie, Sphaeractinoidea Kühn, Hydroida Dana *not* Johnston, Spongiomorphida Alloiteau, Milleporina Hickson, or Stylasterina Hickson and England.

In 1956 the author agreed with Kühn (1939) that the Milleporidiidae were morphologically more closely comparable to the Hydroida Dana than to the Stromatoporoidea Nicholson and Murie, and allocated them to the former order. Whatever their relation to the Hydroida, the family is closely linked to the Milleporellidae and the Parastromatoporidae, and is here grouped with them in the superfamily Milleporellicae. The Mesozoic forms show little stratigraphical continuity with the Palaeozoic Stromatoporoidea or the Tertiary-Recent Hydroida; the three groups are also more or less morphologically independent. It may be that they evolved independently, their generally similar structural pattern being based on common ancestry: it may be, therefore, that they should be allocated to independent orders. It is, nevertheless, convenient to refer to most of the Mesozoic forms as stromatoporoids rather than hydroids or sphaeractinoids and they are therefore, purely for a matter of convenience, provisionally grouped in the Stromatoporoidea.

The systematic position of the genera discussed in this paper is shown in the part-list of Jurassic and Cretaceous stromatoporoids given below.

- STROMATOPOROIDEA Nicholson and Murie 1878 (order)
  - ACTINOSTROMARIICAE Hudson 1959 (superfamily)
    - ACTINOSTROMARIIDAE Hudson 1935 (family)
      - *Actinostromaria* Munier-Chalmas *in* Haug 1909
      - *Actinostromarianina* Lecompte 1952
      - *Actinostromina* Germovšek 1954
      - *Astrostylopsis* Germovšek 1954
    - ? STROMATORHIZIDAE Hudson 1957 (family)
      - *Stromatorhiza* Bakalow 1906
      - *Actostroma* Hudson 1958
    - SIPHOSTROMIDAE Steiner 1932 (family)
      - *Siphostroma* Steiner 1932
  - MILLEPORELLICAE Hudson 1959 (superfamily)
    - MILLEPORELLIDAE Yabe and Sugiyama 1935 (family)
      - *Millestroma* Gregory 1898
      - *Milleporella* Deninger 1906
      - *Stromatoporellina* Kühn 1928
    - MILLEPORIDIIDAE Yabe and Sugiyama 1953 (family)
      - *Milleporidium* Steinmann 1903
      - ?*Myriopora* Volz 1904
      - *Promillepora* Dehorne 1920
      - *Shuqraia* Hudson 1954
      - *Sporadoporidum* Germovšek 1954
      - *Steinerina* Hudson 1956
    - PARASTROMATOPORIDAE Hudson 1959 (family)
      - *Ceraostroma* Kühn 1926
      - *Parastromatopora* Yabe and Sugiyama 1930
      - *Tosastroma* Yabe and Sugiyama 1935
      - *Dehornella* Lecompte 1952
      - ?*Steinerella* Lecompte 1952
      - *Astroporina* Hudson gen. nov.
    - ? STROMATOPORINIDAE Kühn 1928 (family)
      - *Stromatoporina* Kühn 1928
      - ?*Syringostromina* Lecompte 1952

Previous assessment of Stromatoporina. In 1928 Kühn considered that the allocation by Dehorne, Osimo, Vinassa, Deninger, and others of a number of Mesozoic Tethyan stromatoporoids to the genus *Stromatopora* was an error for, in his opinion, all such Mesozoic forms had simple vertical elements whereas all species of *Stromatopora* from the Palaeozoic had compound vertical elements. He therefore founded a new genus *Stromatoporina* for the Mesozoic forms including in the genus *Stromatopora tornquisti* Deninger 1906, *S. choffati* Dehorne 1917, *S. costai* Osimo 1910, *S. franchi* Osimo 1910, *S. moluccana* Vinassa 1915, *S. virgiloi* Osimo 1910, choosing the first of these as his type species. He also considered that the straight and parallel course of the vertical elements of the reticulum was a characteristic feature of his new genus. Unfortunately the description and illustration by Deninger of *Stromatopora tornquisti* is inadequate and possibly Kühn's conception of the species was based on a redescription by Osimo in 1910, not from the holotype. This is the more probable since in 1939 he defines *Stromatoporina* as having vesicular structure like *Stromatopora* and having astrorhizae well developed, illustrating the genus by reproducing Osimo's figure (1910, pl. 1, fig. 1*c*) of *S. franchi* Osimo. It is also evident from Deninger's description and illustration of *S. tornquisti*, inadequate as they are, that the vertical elements in the reticulum of that species are not straight and parallel as they are in the other species of *Stromatoporina* cited by Kühn, especially in *Stromatopora choffati* Dehorne. *Stromatoporina* was therefore, as admitted by Kühn (1939, p. A46), a genus of convenience to which various species of differing character could be allocated, the species having only one feature in common, that they were not *Stromatopora*.

In 1952 Lecompte redefined the genus *Stromatoporina* Kühn, unfortunately basing his definition on *Stromatopora choffati* Dehorne and ignoring the type species *S. tornquisti* Deninger. This practice he also followed in 1956 illustrating the genus by figures of *S. choffati* Dehorne. The author in 1955 attempted to avoid this misconception by redefining the genus on the basis of the type species. He failed to find the holotype and redefined the genus on the basis of the topotype figured by Osimo (1910, pl. 7, figs. 7*a*, 7*b*) as *S. tornquisti*, a specimen he made a neoholotype. Fortunately, from information supplied by E. Flügel, the holotype has now been found in the collections of the Geologisch-Palaeontologisches Institut of the University of Freiburg and has been lent to the author. It is redescribed in this paper: it has no similarity to *S. choffati* and thus the concept of the genus *Stromatoporina* based on that species must be abandoned, and *Stromatoporachoffat* and related forms be allocated to other genera (see also Flügel 1958, work which did not come to the attention of the author until after this paper was written).

Order STROMATOPOROIDEA Nicholson and Murie 1878

Family STROMATOPORINIDAE Kühn 1928*b*

Nominate genus. Stromatoporina Kühn 1928*a*. *Other genus.* ?*Syringostromina* Lecompte 1952.

Diagnosis. Stromatoporoidea in which rods or short pillars, often joined by lateral processes to form lamellae, are linked to form a fine, irregular, approximately evenly meshed reticulum in which the lamellae may have no dominant direction or may be generally vertical. Reticulum traversed by regular, parallel, transverse laminae. Astrosystems, variously developed, of vertical and radially grouped lateral astrotubes, usually much wider than the coenospaces: may be very indefinite. Reticulum and astrosystems variously tabulate. Structure of skeletal tissue not definitely known.

Genus STROMATOPORINA Kühn 1928*a*

Stromatoporina Kühn 1928*a*, p. 550; 1928*b*, p. 90; 1939, p. A47; Lecompte 1952, p. 19; 1956, p. F137; Alloiteau 1952, p. 393; Hudson 1955, p. 236; Flügel 1958, p. 179.

Type species (by original designation). *Stromatopora tornquisti* Deninger 1906.

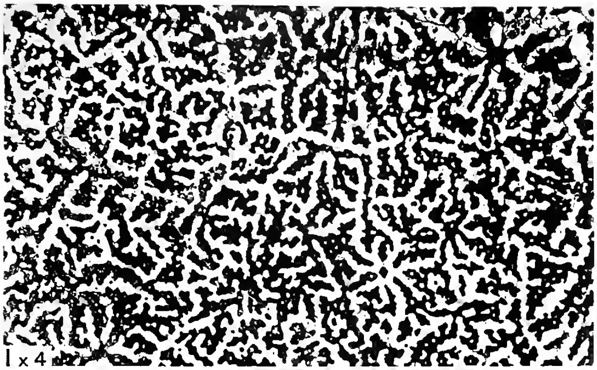
Diagnosis. Stromatoporoid with reticulum of fine rods linked to form a fine, subequla irregular angular mesh which, radially, tends to be open but not reticulate, and, trans-

EXPLANATION OF PLATE 24

Thin sections of *Astroporina* gen. nov., photographed by transmitted light and untouched. Figs. 1, 2, ×4; figs. 3–7, ×8.

Figs. 1–5. *Astroporina stellifera* sp. nov., all of holotype, F 1775, Upper Jurassic, Ahankon Tug, Inda District, British Somaliland. 1, 3, Tangential section, F 1775*b*, showing stellate astrocorridors with bounding vertical lamellae enclosing coenotubules. 2, 4, Radial section, F 1775*c*, mainly parallel to astrocorridors, showing tabulate astrocorridors, tabulate coenotubules, and alignment of tabulae. The larger spaces are along astrocorridors. 5, Oblique radial section, F 1775*a*, mainly across astrocorridors. Note pillars joined to form compound vertical lamellae bounding astrocorridors.

Figs. 6, 7. *Astroporina stellans* sp. nov., all of holotype, F 1774, Bihen Limestone (Upper Jurassic), Daghani Section, Bihendula, British Somaliland. 6, Radial section, F 1774*c*, mainly parallel to astrocorridors. The larger spaces are along astrocorridors. 7, Tangential section, F 1774*a*. Note interlacing astrosystems and merging of astrocorridors and vermiculate coenospaces. Note compound vertical lamellae with coenotubules.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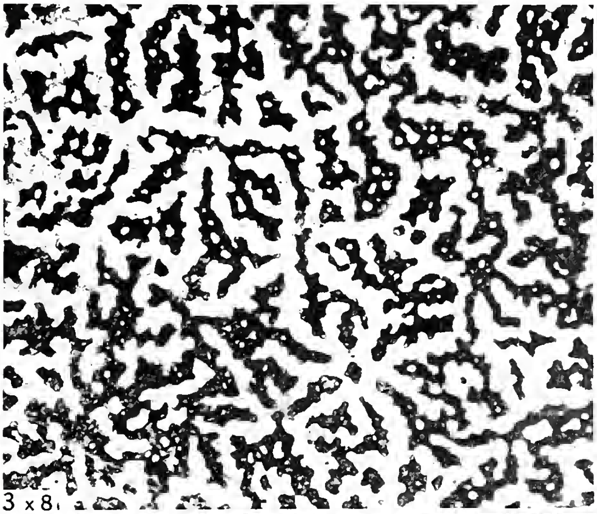
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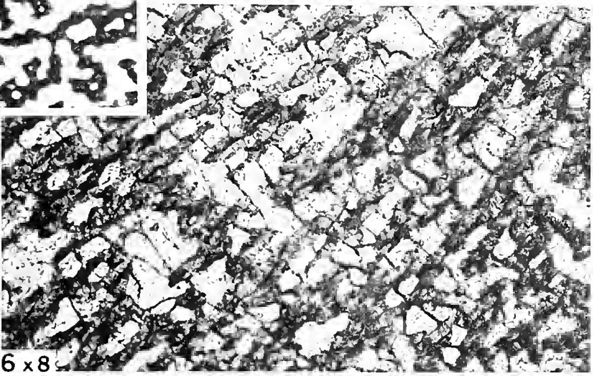
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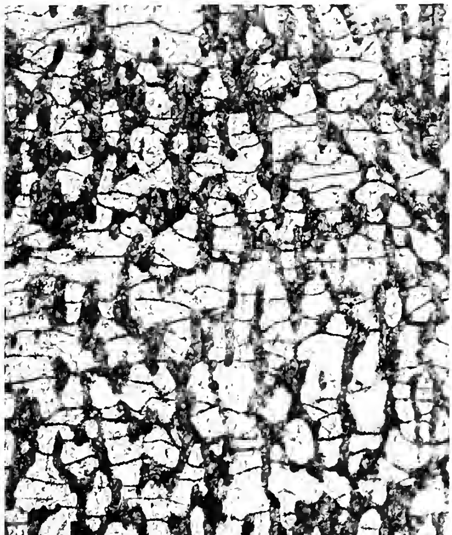
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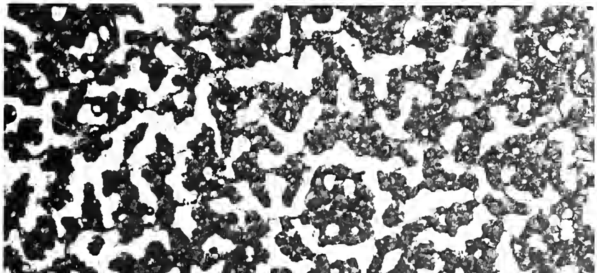
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HUDSON, Jurassic stromatoporoid *Astroporina*

versely, to be closed and irregularly polygonal. Abundant entire transverse laminae, regular, and approximately parallel and even-spaced. Ill-defined astrosystems of groups of irregular, wider tubes, approximately vertical, and occasional inclined lateral tubes. Astrotubes slightly tabulate.

Remarks. The definition of the genus is strictly based on the type species. To have widened it to include the related species *Stromatopora franchi* Osimo and *S. tornquisti* Osimo *non* Deninger (see later) would probably have relegated the genus *Syringostromina* Lecompte 1952 to the status of a junior subjective synonym.

Stromatoporina tornquisti (Deninger)

Plate 27, figs. 3–5; text-fig. 1

Stromatopora sp. Tornquist 1901, p. 19.
Stromatopora tornquisti Deninger 1906, p. 66, pl. 7, figs. 7*a*, 7*b*; Steiner 1932, p. 81; Yabe and Sugiyama 1935, p. 162; Flügel 1958, p. 179. *Not* Osimo 1910, p. 286, pl. 1, figs. 2, 2*a*, 2*b*; Dehorne 1920, p. 82.
Stromatoporina tornquisti Kühn 1928*a*, p. 550; 1928*b*, p. 90.

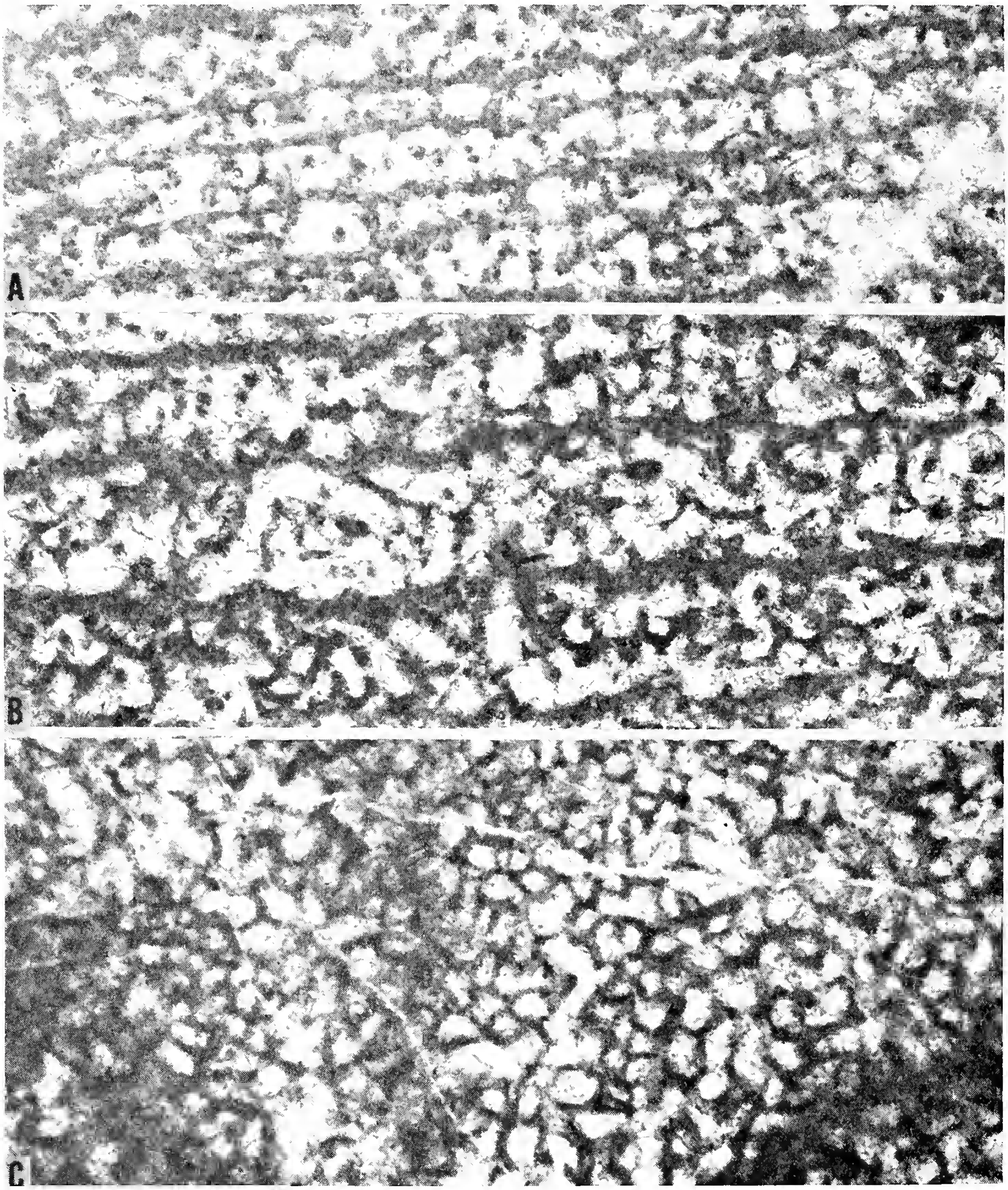
Holotype (only recorded specimen). Sections a (Deninger 1906, pl. 7, fig. 7*b*; Hudson, this paper, Pl. 27, fig. 3, and text-figs. 1A, 1B), b, and c (Deninger 1906, pl. 7, fig. 7*a*; Hudson, this paper, Pl. 27, figs. 4, 5, and text-fig. 1C). Coll. Geological-Palaeontological Institut, University of Freiburg, Austria. ??Keuper (Tornquist 1901), or Bathonian (Deninger 1906); Monte Zirra, Nurra, north-west Sardinia.
Neoholotype (chosen Hudson 1955 and here abandoned). Specimen from Bathonian of Sardinia figured Osimo (1910, pl. 1, figs. 2, 2*a*, 2*b*) as *Stromatopora tornquisti* Deninger.

Diagnosis. Stromatoporina with nodular coenosteum. Reticulum of linked rods (0·04–0·075 mm. across) forming an irregular monomorphic mesh which, transversely, is either open and vermiculate or closed and approximately polygonal (0·06–0·1 mm. across); vertically the reticulum mesh is irregularly open and continuous. Regular, entire, and parallel transverse laminae are of approximate constant thickness (*c.* 0·05 mm.) and *c.* 0·2–0·5 mm. apart. In parts of the coenosteum, the laminae are conically raised (concentric-circular in cross-section). Astrosystems very ill-defined with slightly tabulate axial and lateral astrotubes (*c.* 0·1– 0·15 mm. across). Laminae cross the astrosystems.

Remarks. The reticulum of *Stromatoporina tornquisti* shows no evidence of pillars or pillar-lamellae as generally understood in stromatoporoid morphology. The reticulum apparently consists of rods angularly linked, mainly laterally, so that in transverse section they form an irregular polygonal mesh, but in vertical section there is no regular pattern and many of the rods show isolated cross-sections. Each of these rods consists of dark-coloured small rounded 'nodes' (*c.* 0·02–0·05 mm. across) linked by lighter-coloured lateral processes. These 'nodes' usually form the angles of the polygonal mesh. The reticulum is therefore a close scaffolding of rods which tend to have a lateral linkage.

Comparisons. The form from the Bathonian of Sardinia figured by Osimo (1910) as *Stromatopora tornquisti* Deninger and redescribed from the figures by Hudson (1955, p. 236) has a tabulate reticulum in which the rods tend to be dominantly vertical, and common and well-developed astrosystems, each confined to a space between laminae. The species is not '*tornquisti*' nor is it considered to be a *Stromatoporina*, as defined above. It is here named *Stromatopora osimae* new name (holotype: specimen figured Osimo 1910, pl. 1, figs. 2, 2*a*, 2*b*).

Stromatopora franchi Osimo (1910, pl. 1, figs. 1*a*, *b*, *c*), also from the Bathonian of Sardinia, differs even more from *Stromatoporina tornquisti* since both its reticulum and



TEXT-FIG. 1. *Stromatoporina tornquisti* (Deninger). Thin sections, a and c, ×40, of holotype. Bathonian, Mt. Zirra, Nurra, north-west Sardinia. A, Part of vertical section a, showing area of close laminae. B, Part of vertical section a, showing vertical and transverse astrotubes. C, Part of transverse section c, showing astrosystem. Darker areas laminae, secondary after pillars.

abundant astrosystems have a dominant verticality, and thickened laminae are not common. Nevertheless, the similarity of the fineness and general pattern of the reticulum of both Osimo's forms to that of *S. tornquisti* suggests that they too belong to the Stromatoporinidae.

The general pattern of the reticulum and its fineness when compared with the coarse astrosystems is not unlike the general coenosteal pattern of *Syringostromina pruvosti* Lecompte gen. *et* sp. (1952, pl. 1, figs. 2, 2*a*) and it may be that *Stromatopora osimae* nom. nov. and *S. franchi* Osimo should be allocated to that genus. They, with *S. pruvosti*, may be expressions of a trend to verticality within the Stromatoporinidae.

Superfamily MILLEPORELLICAE Hudson 1959

Stromatoporoids with clinogonal-fibrous skeletal tissue

Family PARASTROMATOPORIDAE Hudson 1959

Nominate genus. Parastromatopora Yabe and Sugiyama 1930. *Other genera. Dehornella* Lecompte 1952; *Tosastroma* Yabe and Sugiyama 1935; *Astroporina* gen. nov.; ?*Steinerella* Lecompte 1952.

Milleporellicae with reticulum mainly of fenestrate vertical lamellae formed by pillars joined directly or by lateral extension. Lamellae variously bound coenospaces, enclose coenotubes, or outline astrocorridors. May be some subordinate transverse lamellae. Astrosystems, variously developed, generally composed of astrocorridors, variously stellate or irregular; no transverse astrotubes. Tabulae common or abundant, may be closely spaced vertically in coenospaces, coenotubes, and astrocorridors; may be aligned. Laminae generally absent. Not markedly latilamellate.

Morphological trends within the Parastromatoporidae. The similarity linking the various forms in this family is the verticality of both reticulum and astrosystem: the differences separating them are partly the relative proportion in the coenosteum of reticulum and astrosystem and partly the extent to which verticality has become dominant in these structures. The structure of the morphological ancestral form seems to be that of *Stromatopora choffati* in which the coenosteum is almost equally composed of reticulum and astrosystem and in which the reticulum retains some element of horizontality. A closely related form is *Dehornella hydractinoides* in which the thinly encrusting coenosteum has an even more horizontally lamellate reticulum. Parastromatoporidae with this approximately equal division between reticulum and astrosystem may persist throughout the Upper Jurassic and Lower Cretaceous, in which latter they may be represented by *Steinerella* in which the astrosystems are better though not more abundantly developed and tend to be divided into vertical astrotubes.

From such forms as *Stromatopora choffati*, structure seems to evolve in two directions. The one is represented by *Parastromatopora* and *Tosastroma* in which the coenosteum consists mainly or wholly of reticulum, astrosystems being absent or more probably not distinguishable; the other is represented by forms, here grouped as *Astroporina* gen. nov., in which the coenosteum tends to be wholly of conjoined astrosystems.

Genus DEHORNELLA Lecompte 1952

Dehornella Lecompte 1952, p. 16; 1956, p. F133.

Type species (by original designation). *Stromatoporella hydractinoides* Dehorne 1920.

Diagnosis. Parastromatoporidae usually nodular and encrusting reticulum of pillars and vertical lamellae, often composite and thick, bounding irregular labyrinthine tabulate coenospaces. Lateral processes may be aligned to form intermittent transverse lamellae. Common and well-developed astrosystems of irregularly vermiculate tabulate astrocorridors, irregularly radial, often bounded by thick vertical lamellae. Tabulae common, may be aligned to form occasional laminae. Skeletal tissue clinogonal or not known.

Family allocation. The genus *Dehornella*, like so many of the Mesozoic stromatoporoid genera, was founded as a one-species one-specimen genus. Its foundation was the more unfortunate since the one-type specimen of the species is a thinly encrusting form and, like all such forms, has a specialized reticulum in the first few millimetres of upward growth. The diagnostic features of the genus, as stated by Lecompte (1952, 1956), are here summarized as follows: (*a*) stellate astrosystems forming mamelons, (*b*) continuous vertical pillars and discontinuous transverse lamellae beneath mamelons, and continuous transverse lamellae and discontinuous vertical pillars between mamelons, (*c*) skeletal tissue possibly originally chitinous. It is now generally accepted that the occurrence of mamelons is specifically but not generically diagnostic. That the pillars were originally chitinous was first tentatively suggested by Dehorne (1920) who considered that growth stages of the skeletal tissue (Dehorne 1920, text-fig. 9) showed a similarity to those of the Recent hydroid *Hydractinia echinata* Fleming in which the skeleton may be in part chitinous. This suggestion was adopted by Lecompte on the grounds that the pigmented core of the pillars seen by transmitted polarized light showed single extinction, a very doubtful assumption that certainly cannot be used as a diagnostic character. The distinction between the vertical structure of astrosystems consisting of astrocorridors and that of the reticulum occurring between them is mainly expressed by the presence of transverse lamellae continuous in the reticulum but limited to between the vertical lamellae in the astrosystem. This is generally the case in those Parastromatoporidae which have transverse lamellae though it is most marked in the initial stages of encrust-

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EXPLANATION OF PLATE 25

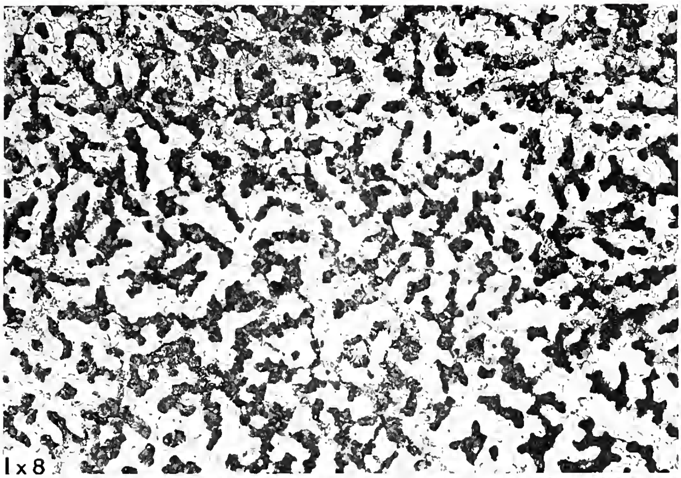
Thin sections (except fig. 6) of *Astroporina* and *Dehornella* photographed by transmitted light.

Figs. 1–3. *Astroporina* cf. *orientalis* sp. nov., F 1773, ×8. Bihen Limestone (Upper Jurassic), Daghani Section, Bihendula, British Somaliland. 1, Transverse section, F 1773*b*; note merging of astrocorridors and coenospaces, and lack of individuality of astrorhizal systems. 2, Oblique section, F 1773*a*, in general across astrocorridors. 3, Radial oblique section, F 1773*c*; note general alignment of tabulae.

Fig. 4. *Astroporina stellans* sp. nov., oblique section, F 1774*b*, from holotype, ×8. Bihen Limestone (Upper Jurassic), Daghani Section, Bihendula, British Somaliland. Note coenotubules within vertical lamellae.

Figs. 5–7. *Dehornella crustans* sp. nov. Upper part of Shuqraia Limestones-with-Marls (Argovian), Maktesh Hathira, Israel. 5, Radial section, H 5618*a*, ×4·5. Encrusting on fine stromatoporoid on coral. 6, Polished tangential surface (photographed reflected light), H 5168, ×7. Note formation of walls of astrocorridors by closely compacted coenosteal pillars. Large circular openings are subsequent borings. 7, Radial section, H 5170*d*, ×7 (as Pl. 26, fig. 1), mainly along astrocorridors and vertical lamellae.

Fig. 8. *Dehornella choffati* (Dehorne). Upper Jurassic (Lusitanian–Pterocerian), Cezimbra massif, Arabida, Portugal. Tangential section, 25*a*, ×9·5, of holotype, specimen 25, Stromatoporoid Coll., Geol. Lab., Sorbonne, Paris (as Dehorne 1917, text-fig. 1; 1920, text-fig. 26 and pl. 13, fig. 2; 1923, pl. 1, fig. 1*c*).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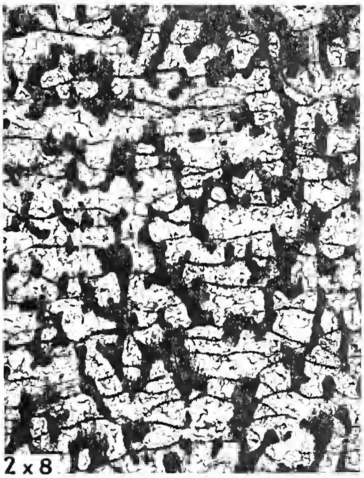
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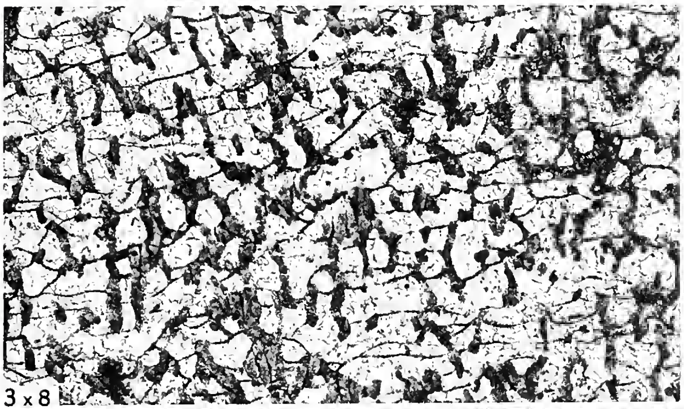
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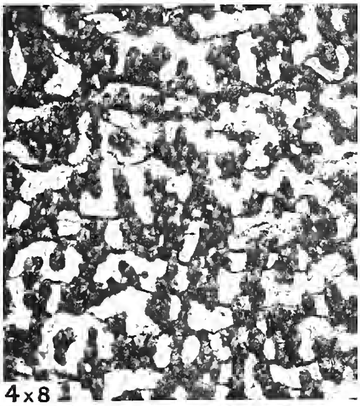
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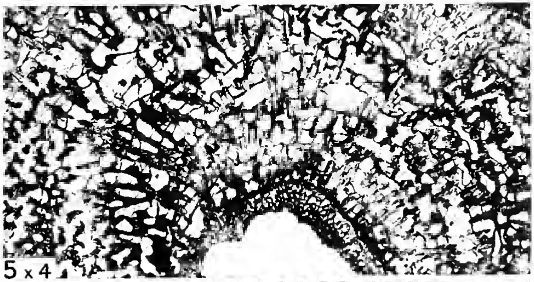
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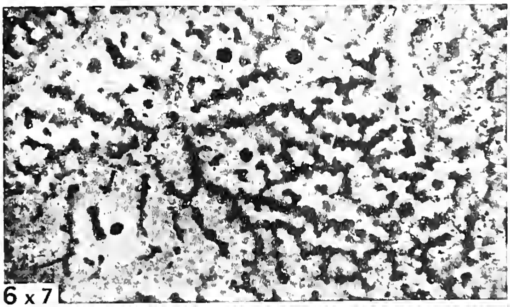
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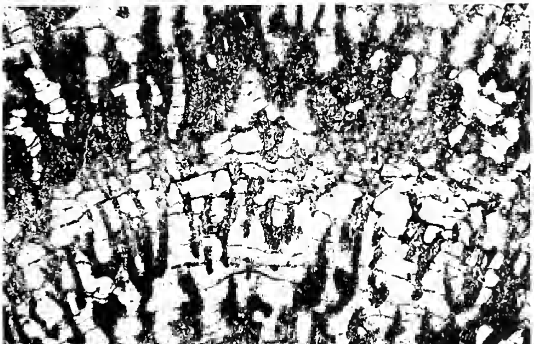
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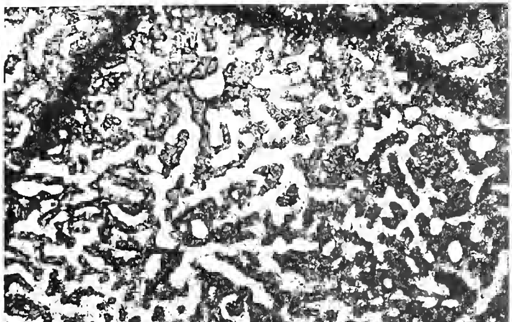
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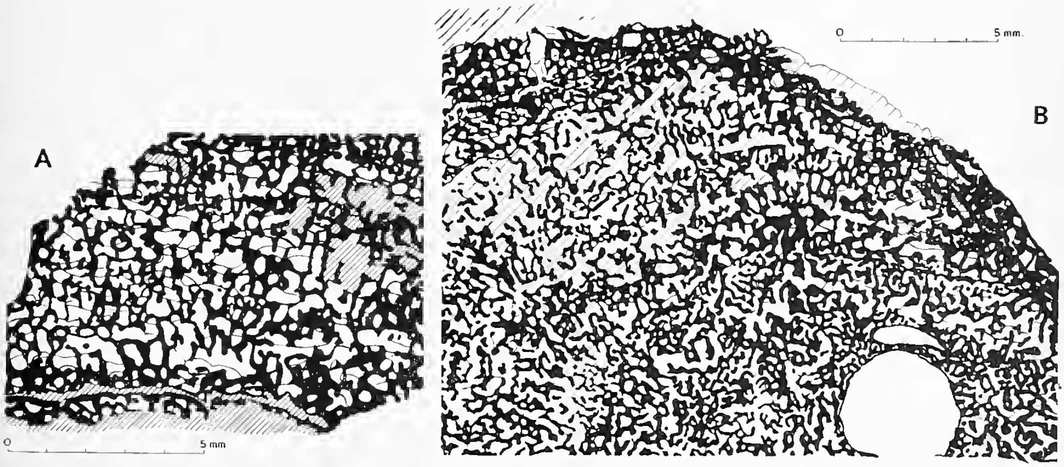
HUDSON, Jurassic stromatoporoids

ing forms where transverse lamellae tend to be more developed than in the rest of the reticulum.

The main features of *Dehornella* such as the abundant astrosystems of radial tabulate astrocorridors, and the dominant vertical pillars or vertical lamellae enclosing irregular, tabulate coenospaces or bounding the astrocorridors are characteristic of certain of the Parastromatoporidae such as *Stromatopora choffati* Dehorne and *S. harrarensis* Wells and it is therefore included in that family.

Morphological range. Dehornella Lecompte could therefore remain as a genus with an eccentric limited diagnosis which would apply only to the type species. In which case the numerous similar forms such as *Stromatopora choffati* Dehorne and *S. harrarensis* Wells must be allocated to a new genus since there is no other genus within the Parastromatoporidae suitable for them. To avoid the creation of only slightly differing genera, *Dehornella* has been more redefined as above and is thus available for many species other than the type.

The various species which can be allocated to *Dehornella* can be mainly grouped into those with a fine reticulum with lamellae about 0·1–0·2 mm. across and coenospaces up to about 0·3 mm. across, and those with a coarse reticulum with lamellae up to 0·3 mm. across and coenospaces up to 0·5 mm. across. The former group includes *Stromatopora choffati* Dehorne, *S. kurtchensis* Wells, *Dehornella hydractinoides* (Dehorne), *D. crustans* sp. nov., and *D. omanensis* sp. nov.; the latter group includes *S. harrarensis* Wells. There are other species, some with an even coarser reticulum and some with a very fine, encrusting reticulum. When these species occur in the same fauna, they are often intergrown or encrust each other. Otherwise many of them encrust crinoids, corals, or gastropods.



TEXT-FIG. 2. *Dehornella choffati* (Dehorne). Sections of holotype. Oblique lines represent areas infilled with mud. A, Oblique section 25*b*, wider spaces are across or along astrocorridors. Note lamellate character of initial reticulum after cessation of growth due to mud deposition. B, Section 25*c*, encrusting? coral. Section around coral is tangential, that of outer part is oblique. Note irregular lamellate character of initial reticulum.

Dehornella hydractinoides (Dehorne)

Stromatoporella hydractinoides Dehorne 1920, p. 77, text-fig. 9, pl. 6, fig. 2, pl. 17, fig. 3 (not pl. 15, fig. 3); 1923, p. 19, pl. 1, figs. 2*a*, *b*.
Stromatoporellina hydractinoides Kühn 1928*a*, p. 550; Kühn 1928*b*, p. 39.
Stromatoporella hydractinoides Steiner 1932, p. 80.
Dehornella hydractinoides Lecompte 1952, p. 16, pl. 2, figs. 1, 1*a*; 1956, p. F133, text-fig. 109, 5.

Holotype (only recorded specimen). Specimen (Dehorne 1920, pl. 6, fig. 2; 1923, pl. 1, fig. 2*a*) and thin sections a (Dehorne 1920, text-fig. 9, pl. 17., fig. 3; 1923, pl. 1, fig. 2*b*), b (Lecompte 1952, pl. 2, fig. 1; 1956, text-fig. 109, 5), and c (Lecompte 1952, pl. 2, fig. 1*a*). Stromatoporoid coll., Geological Laboratory, Sorbonne, Paris. From Abbadia Marls (upper Lusitanian), 150 metres north-west of Silveiras, Arrabida massif, Portugal.

Diagnosis. *Dehornella* with encrusting lamellate coenosteum with conical mamelons about 5·0 mm. across at base and about 7·0 mm. apart. Reticulum with irregularly developed vertical pillars (0·1–0·2 mm. across) and lamellae, and irregular transverse lamellae. Astrosystems common, with well-developed but tortuous astrocorridors, about 0·25–0·3 mm. across, often with thick (*c.* 0·1–0·25 mm. across) bounding vertical lamellae.

Dehornella choffati (Dehorne)

Plate 25, fig. 8; Plate 26, figs. 7, 8; text-fig. 2

Stromatopora Choffati Dehorne 1917, p. 117, text-fig. 1, 2; Dehorne 1920, p. 83, text-figs. 12, 18, 25, 26, pl. 5, fig. 6, pl. 7, fig. 1, pl. 13, figs. 1, 2 (not pl. 6, figs. 3, 4); Dehorne 1923, p. 15, pl. 1, figs. 1*a–c*, pl. 2, fig. 1; Steiner 1932, p. 82.
Stromatoporina Choffati (Dehorne), Kühn 1928*a*, p. 550; 1928*b*, p. 90.
Stromatoporina choffati (Dehorne), Lecompte 1952, p. 20; Lecompte 1956, text-fig. 109 (3*a*, *b*).
Not *Syringostomina choffati* (Dehorne), Lecompte 1956, text-fig. 106 (4*a*, *b*).

Lectotype (Chosen Lecompte 1952, p. 20). Specimen 25 and sections 25*a–e* cut from it, Stromatoporoid coll., Geological Laboratory, Sorbonne, Paris. Nerinea elsgaudiae Limestones (Upper Jurassic; Lusitanian–Pterocerian), Pedreiras, Cezimbra massif, Arabida, Portugal. Figured Dehorne 1917, text-fig. 1, 2; 1920, text-figs. 12, 25, 26, pl. 5, fig. 6, pl. 13, figs. 1, 2; 1923, pl. 1, figs. 1*a–c*, pl. 2, fig. 1; Lecompte 1956, text-figs. 109 (3*a*, *b*); Hudson, this paper, Pl. 25, fig. 8, Pl. 26, figs. 7, 8, text-figs. 2A, 2B.

EXPLANATION OF PLATE 26

Thin sections of *Astroporina* and *Dehornella*, photographed by transmitted light and showing clinogonal microstructure of coenopillars, all ×100.

Fig. 1. *Dehornella crustans* sp. nov. Radial section H 5170*g* (as Pl. 25, fig. 7). Shuqraia Limestones-with-Marls (Argovian), Maktesh Hathira, Israel. Medial strands with groups of dark-rimmed circles (transverse sections) and elongate tubes (longitudinal sections), both with clear centres.

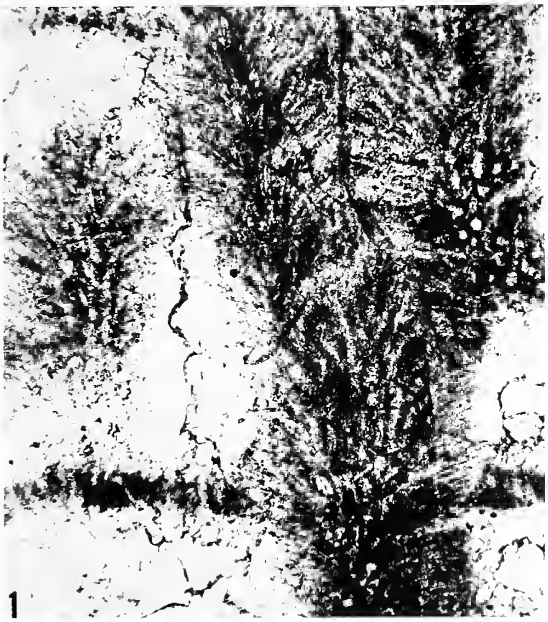
Figs. 2. 3. *Astroporina* cf. *orientalis* sp. nov., F 1773, Bihen Limestone (Upper Jurassic), Daghani Section, Bihendula, British Somaliland. 2, Radial section, F 1773*a*. Section does not pass through medial strand. 3, Transverse section, F 1773*b*, medial strand present though faintly shown.

Fig. 4. *Astroporina orientalis* sp. nov. Radial thin section H 4850*b*. Cladocoropsis Limestones (Sequanian), near Ain Safra, Yanta, Lebanon.

Figs. 5, 6. *Astroporina stellans* sp. nov., both of holotype, F 1774. Bihen Limestone (Upper Jurassic), Daghani Section, Bihendula, British Somaliland. 5, Radial section, F 1774*a*, showing medial strand. 6, Longitudinal section, F 1774*b*, not through medial strand.

Figs. 7, 8. *Dehornella choffati* (Dehorne). Both part of thin section, 25*c*, of holotype. Note clear tubules at position of origin of clinogonal fibres. 7, Radial section. 8, Transverse section. Upper Jurassic, Arabida, Portugal.

PLATE 26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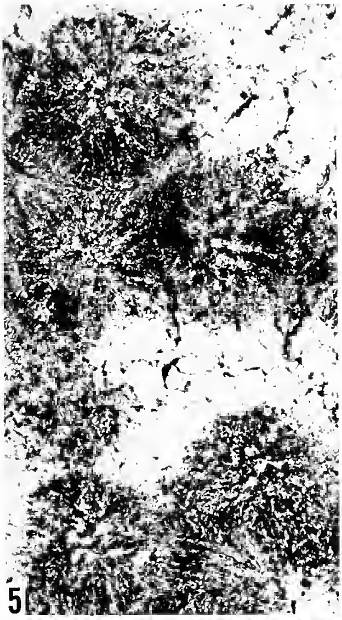
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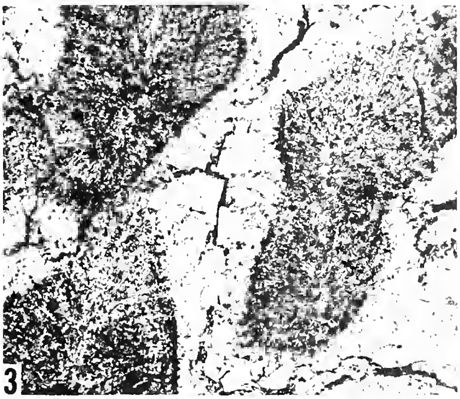
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HUDSON, Pillar clinogonal structure, *Astroporina* and *Dehornella*, x100.

The uncut lectotype (Dehorne 1920, pl. 5, fig. 6) was a thin slab about 1·5 cm. thick, a fragment from across the centre of a concentric encrusting nodule of about 4 cm. diameter. The sections cut from it consist of *a*, a tangential (Dehorne 1920, pl. 13, fig. 2; Lecompte 1956, text-fig. 109 (3*a*); this paper, Pl. 25, fig. 8), *b*, an oblique radial (Lecompte 1956, text-fig. 109 (3*b*); this paper, text-fig. 1A), *c*, a tangential with outer part radial (this paper, text-fig. 1B), *d*, a radial (Dehorne 1920, pl. 13, fig. 1) and *e*, an oblique radial (Dehorne 1920, text-fig. 18). The last two are now missing.

Dehorne (1920) gave the magnifications of her figures of the type specimen as follows: text-fig. 20, ×5; pl. 5, fig. 6, ×1; pl. 13, fig. 2, × ?7: they should respectively be ×8·2, ×1·5, ×12. In her 1923 paper the magnification of pl. 1, fig. 1*c*, is ×10.

Diagnosis. *Dehornella* with encrusting nodular coenosteum with vertical pillars (*c*. 0·1 mm. thick) joined directly or, at intervals, by transverse pillar-outgrowths to form vertical lamellae (0·1 mm. thick). Prominent astrosystems (centres 3–4 mm. apart), often conjoined, of irregularly stellate branching astrocorridors (0·2 mm. across). Reticulum of irregular and usually narrow elongate coenospaces and irregularly shaped coenotubes (0·12–0·15 mm. across) bounded by vertical lamellae, and occasionally crossed, for varying distances, by transverse lamellae formed by aligned transverse pillar-outgrowths. Occasional isolated pillars. Tabulae common in both coenospaces and astrocorridors.

Dehornella crustans sp. nov.

Plate 25, figs. 5–7; Pl. 26, fig. 1

Holotype. H 5168, two pieces (Pl. 25, fig. 6) and section a (Pl. 25, fig. 5). *Paratypes*. H 5170, one piece and sections *a–c*, d (Pl. 25, fig. 7), e, f, g (Pl. 26, fig. 1). H 5166, one piece and section *a*. All from the upper part of the Shuqraia Limestones-with-Marl (Upper Jurassic, Argovian), Maktesh Hathira, Israel (Hudson 1958).

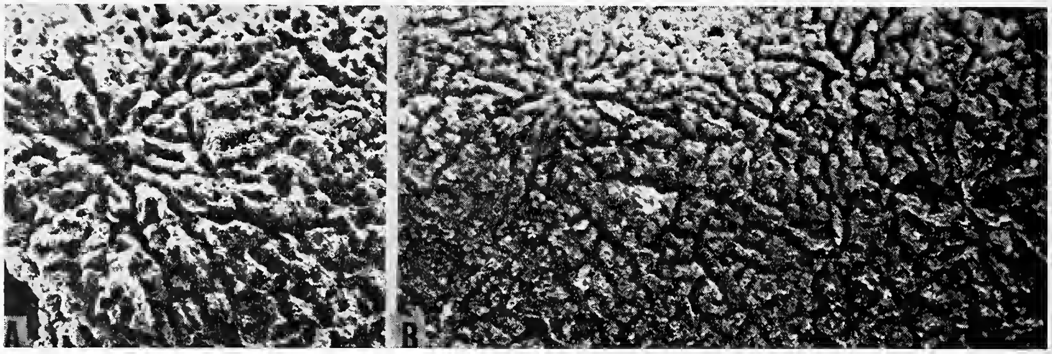
Diagnosis. *Dehornella* with small, nodular, and encrusting coenosteum consisting of abundant astrosystems separated by small areas of irregular reticulum. Vertical lamellae (*c*. 0·1–0·2 mm. across) which bound astrocorridors of astrosystems and coenospaces of reticulum, formed of vertical pillars (*c*. 0·15 mm. across) linked by transverse processes which, occasionally, may be aligned. Vertical lamellae, generally vermiculate, may be fenestrate and compound. Coenospaces (*c*. 0·2–0·3 mm. across) irregular and elongate. Astrosystems abundant, about 0·5 mm. apart, of irregularly radial astrocorridors (*c*. 0·2–0·3 mm. across). Tabulae abundant, irregularly aligned.

Dehornella omanensis sp. nov.

Plate 28, figs. 1, 2, 5–8; text-figs. 3B, 4, 5

Holotype. H 4833 (one piece, text-fig. 3B). *Paratypes*. H 4834 (one piece, Pl. 28, fig. 6), H 4835 (two pieces, Pl. 28, fig. 8), H 4836, 4838–43, 4845–7 (each one piece), H 4837 (one piece and section *a*, text-fig. 5), H 4844 (four pieces, Pl. 28, fig. 1, and sections a, Pl. 28, fig. 1, b, and c, Pl. 28, fig. 7), H 4848 (one piece, Pl. 28, fig. 5), and H 4849 (three pieces and sections a–c). All from Beni Zaid Limestone (Oxfordian), Wadi Bih, Ruus al Jibal, Trucial Oman, Arabia.

Description. Coenosteum nodular, concentric, often an aggregate of several independent concentric growth nodules (only fragments known; greatest diameter 80 mm.; greatest height, 80 mm.). May be encrusting (as H 4844, Pl. 28, figs. 1, 2, grown around a coral). Surface even, no mamelons, ostia-mesh mainly vermiculate. Surface astrosystems, about 0·4 mm. across, consist of irregularly radial and irregularly dichotomizing astrocorridors, commonly 0·2 mm. wide. Reticulum of dominant vertical lamellae and occasional transverse lamellae, the former both transversely and longitudinally vermiculate so that the reticulum pattern is loose and irregular. In the vertical lamellae which are commonly 0·12–0·15 mm. thick and generally discontinuous, it is possible to recognize the component pillars. The transverse lamellae, formed of joined transverse processes, are widely spaced, and may be continuously aligned across a number of coenospaces. These are commonly 0·2–0·25 mm. wide, vermiculate and generally not completely enclosed; coenotubes are not common. Widely spaced simple tabulae cross the coenospaces but are not abundant. Latilamellation which is mainly due to variation in thickness of the vertical lamellae and to the varying occurrence of the transverse lamellae is never very strong. Basal holotheca present. Astrorhizal systems entirely composed of tabulate astrocorridors of the same width as the coenospaces and therefore not discernible in vertical section.



TEXT-FIG. 3. Coenosteal surfaces of *Dehornella* from Beni Zaid Limestone, Oman, showing astrosystems. A, *D. harrarensis* (Wells), H 4865, ×4. Surface slightly mammelate. B, *D. omanensis* sp. nov., holotype, H 4833, ×4·5. Surface worn smooth.

Specific differences of Dehornella choffati *group.* There is so little difference between the members of this group, of which *D. choffati* is the senior species, that their distinction is probably infraspecific. That they were not designated subspecies is due to the author's dislike of departure from the binominal system of nomenclature, a dislike based on the general lack of agreement as to the meaning and function of a subspecies in invertebrate palaeontology.

The type of the genus, *D. hydractinoides*, is mamellate and its astrosystems are more

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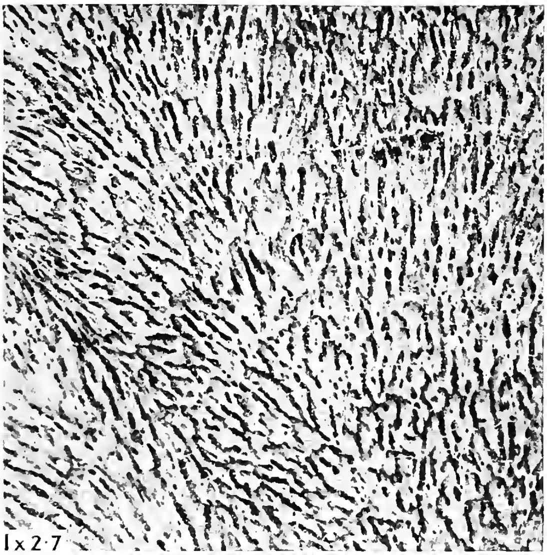
EXPLANATION OF PLATE 27

Figs. 1, 2. *Astroporina stellifera* sp. nov. Polished surfaces (radial and transverse) of holotype, H 3657, ×2·7. Upper Jurassic, Ahankon Tug, Inda District, British Somaliland. Note tendency to latilamellation and, in fig. 1, columnar grouping of reticulum.

Figs. 3–5. *Stromatoporina tornquisti* (Deninger). Thin sections A, C, ×8, from holotype. Bathonian, Monte Zirra, Sardinia. 3, Vertical section A. Wider tubes between laminae belong to astrosystems. 4, 5, Transverse sections C. Tangential in fig. 4 and in upper part of fig. 5. Lower part of fig. 5 across ? mamelon. Note slightly wider lateral tubes of astrosystems.

Figs. 6, 7. *Astroporina orientalis* sp. nov. Thin sections of holotype, H 4850, from Cladocoropsis Limestones (Sequanian), near Ain Safra, Yanta, Lebanon. 6, Radial section, H 4850*b*, ×8. Note conjoined pillars and aligned tabulae. Wide spaces are along astrocorridors. 7, Transverse section, H 4850*a*, ×4.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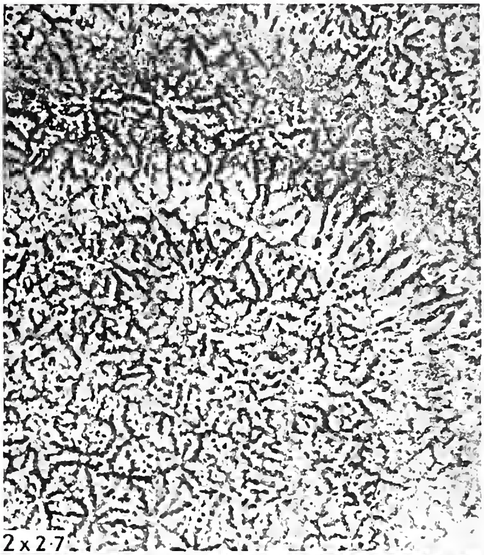
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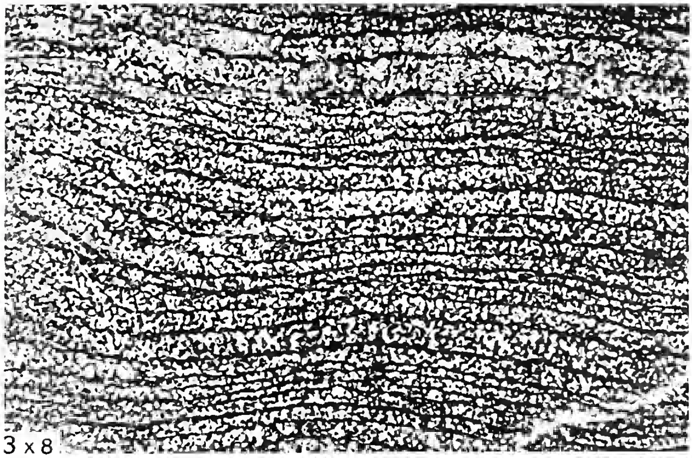
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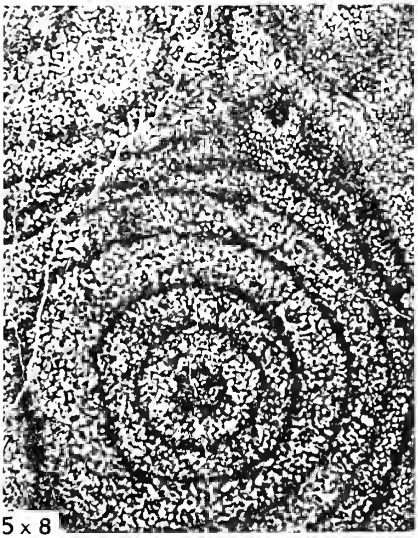
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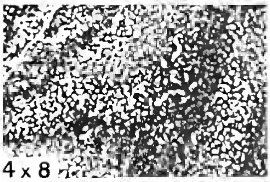
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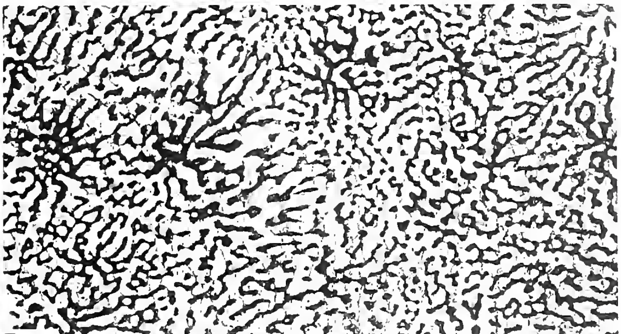
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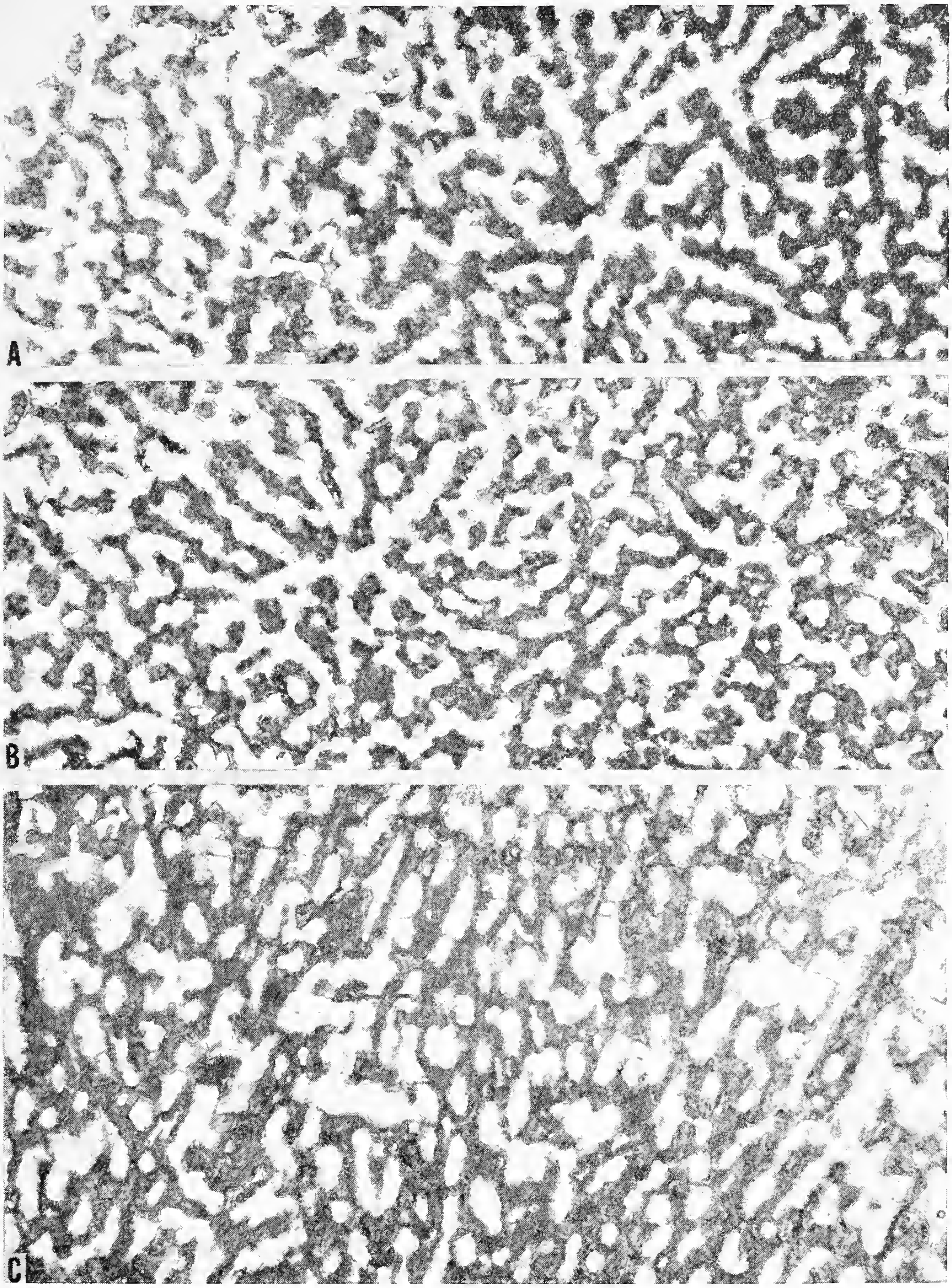
HUDSON, *Astroporina* and *Stromatoporina*.



TEXT-FIG. 4. *Dehornella omanensis* sp. nov. Thin sections of H 4844, × 12, from Beni Zaid Limestone, Oman, eastern Arabia. A and B, Transverse section H 4844*c*, showing astrosystem and vermiculate reticulum. C, Vertical section, H 4844*b*, slightly oblique. Wide spaces are along astrocorridors. Note fewness of tabulae.

common and coarser than in *D. choffati*; otherwise there is no significant difference between them since in both the vertical lamellae are irregular, transverse lamellae are sporadically developed especially in early growth, and tabulae are common. *D. crustans* differs from them in that transverse lamellae are rare and the reticulum is generally more vertical; it also is not mamellate.

D. omanensis, as befits its stratigraphical position, is morphologically simpler than the above species. It is generally finer and much more evenly meshed, has smaller astrosystems with narrower astrocorridors, and, generally, less tabulae. *D. kurtchensis* (Wells) is a mamellate form which is otherwise apparently similar to *D. omanensis*. It may have the same relationship to that species as *D. hydractinoides* has to *D. choffati*.

Dehornella harrarensis (Wells)

Plate 28, figs. 3, 4, 9, 10; text-fig. 3A

Stromatopora harrarense Wells 1943, p. 50, pl. 8, figs. 1–5.
Stromatopora harrarensis Wells, Hudson 1954, p. 219, pl. 7, fig. 4.
Stromatopora cf. *harrarensis* Wells, Hudson 1955, p. 318.

Holotype. Amer. Mus. Nat. Hist., Spec. 25285, Wells 1943, pl. 8, figs. 1, 2. Upper Jurassic, Kurtcha, Harrar Province, Eastern Ethopia.

Middle East material. H 4851 (one piece and sections a–c), H 4852–6, 4858–60, 4863, 4867, 4869 (each one piece), H 4861 (one piece and sections a, b), H 4862 (one piece and sections a, Pl. 28, fig. 4, and b), H 4864 (two pieces, Pl. 28, figs. 3, 9, 10), H 4865 (one piece, text-fig. 3A, and section *a*), H 4866 (one piece and section a), and H 4868 (three pieces and sections a, b). All from Beni Zaid Limestone (Oxfordian), Wadi Bih, Ruus al Jibal, Trucial Oman, Arabia. H 4832 (one piece and section a, text-fig. 6). Oxfordian, Jebel Moghara, Sinai, Egypt.

Description. Nodular (largest specimen, fragmentary, 14 cm. across), usually a confluent aggregate of either concentric coenosten or coenosteal columns, about 8–12 mm. across, each with axial and peripheral reticula; often encrusting or intergrown with other species. Surface undulant with low rounded basses (not mamelons). Coenosteum may be lightly latilamellate due to alternation of layers (*c*. 40 mm. thick) in which vertical lamellae are thick and closely joined or thinner and separate. Reticulum with dominant vertical lamellae of conjoined pillars, transversely vermiculate, and, vertically, tending to be

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EXPLANATION OF PLATE 28

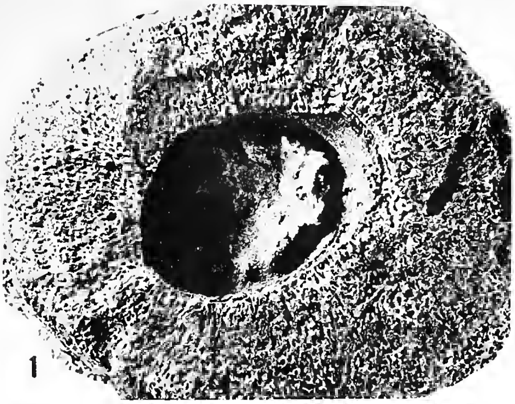
Dehornella spp., all from Beni Zaid Limestone (Oxfordian s.s.) of Wadi Bih, Jebel Hagab area, Ruus al Jibal, eastern Arabia. All specimens are partly silicified.

Figs. 1, 2, 7. *Dehornella omanensis* sp. nov., H 4844, encrusting coral. 1, Weathered upper surface, ×1·7, showing holotheca at base of coenosteum. 2, Thin section a, ×1·7, across coenosteum, showing vertical pattern of reticulum. Photographed by reflected light. Note holotheca at base of coenosteum and lamellate pattern of initial reticulum. 7, Tang. thin section c, ×3, photographed by reflected light, showing astrocorridors.

Figs. 3, 9, 10. *Dehornella harrarensis* (Wells) H 4864. 3, Coenosteal surface, ×1·1, showing astrosystems and intervening reticulum. 9, Polished surface, ×1·1, across middle of nodular coenosteum showing adjoining coenosteal columns and latilamellae. 10, Radial polished surface, ×1·7, showing latilamellae.

Fig. 4. *Dehornella harrarensis* (Wells), tangential thin section H 4862*a*, showing astrocorridors.

Figs. 5, 6, 7. *Dehornella omanensis* sp. nov. 5, Weathered radial surface, H 4848, ×1·5. 6, Polished surface across middle of coenosteal nodule, H 4834, ×2. 7, Radial polished surface, H 4835, ×2. Compare fineness of texture with that of *D. harrarensis* Wells, fig. 10. Note indefinite latilamellation.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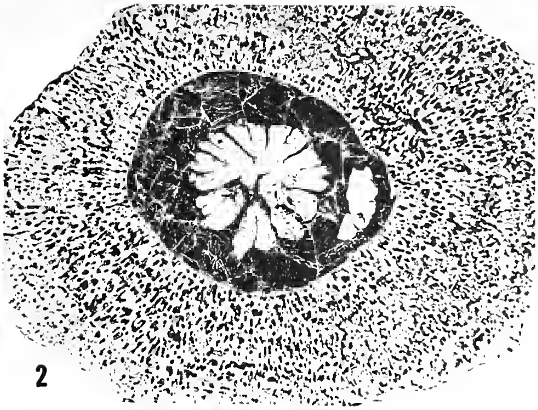
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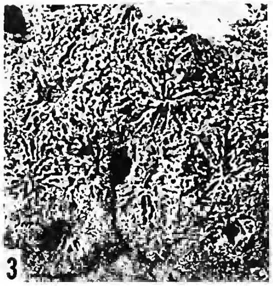
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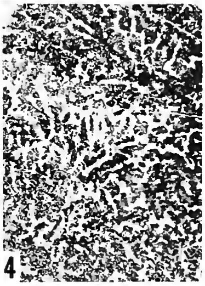
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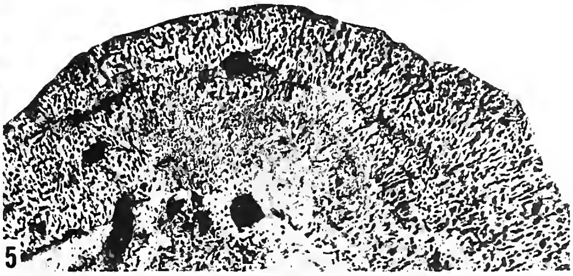
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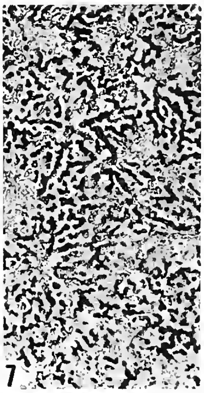
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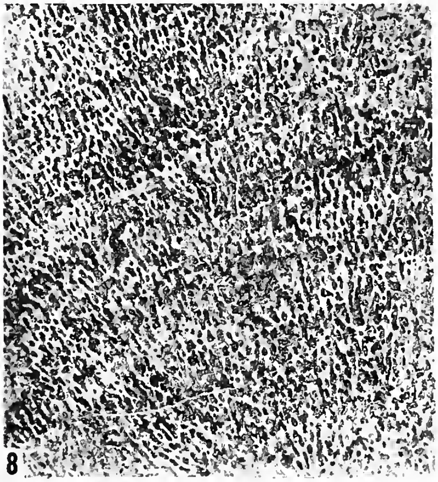
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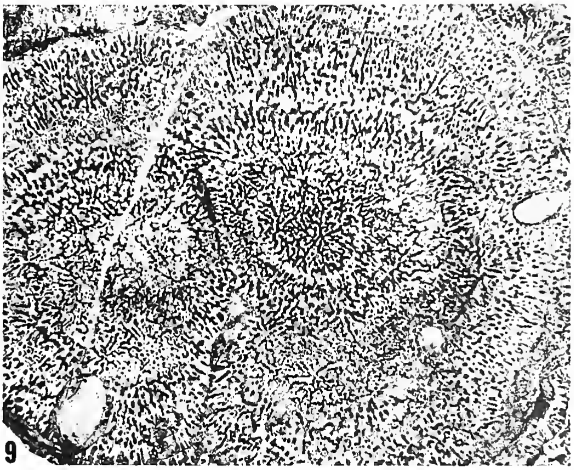
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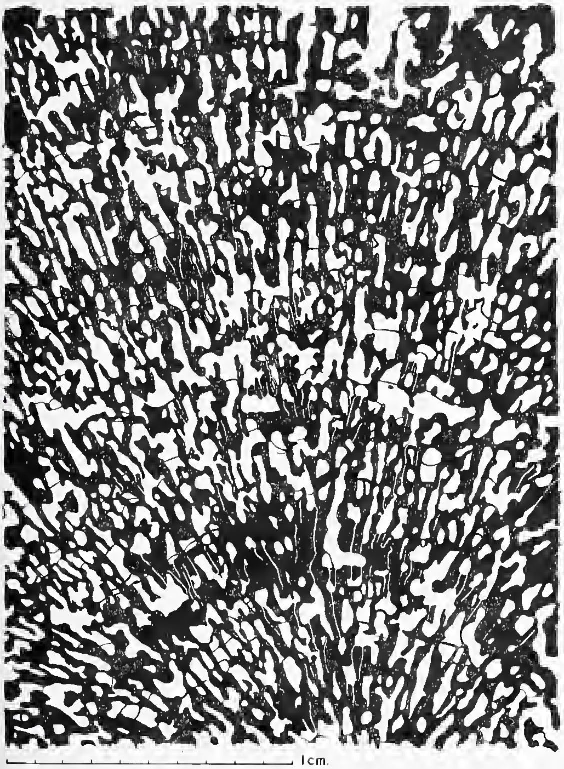
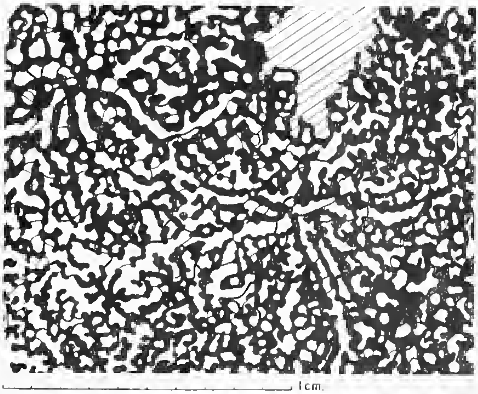
10

HUDSON, *Dehornella.*

irregular in thickness (generally 0·2–0·3 mm. across) and direction. Lamellae enclose elongate vermiculate coenospaces, generally 0·4 mm. across, or, less common, smaller coenotubes. Transverse processes arising laterally from the vertical lamellae may occur and join to link two lamellae. Aligned transverse lamellae are occasionally present usually at wide intervals; they show better in weathered specimens than in sections.



TEXT-FIG. 5



TEXT-FIG. 6

TEXT-FIG. 5. *Dehornella omanensis* sp. nov. Vertical thin section, H 4837*a* from Beni Zaid Limestone, Oman, eastern Arabia. Wide spaces are along astrocorridors. Thin white lines in vertical lamellae indicate junction of adjoining pillars. Note slight latilamellation.

TEXT-FIG. 6. *Dehornella harrarensis* (Wells), H 4832*a*, from Upper Jurassic (Oxfordian s.s.) of Jebel Moghara, Sinai. Note plan of astrorhizal systems and reticulum as those of *Dehornella choffati* (Dehorne). In *D. harrarensis* the vertical lamellae are thicker and astrocorridors wider.

Coenotabulae not uncommon. Abundant astrosystems, about 5–6 mm. across, occasionally contiguous, but centres usually about 7–9 mm. apart, consist of irregularly radial, long, dichotomizing, tabulate astrocorridors, generally 0·4 mm. across, and bounded by vertical lamellae joining at or near the astrosystem axis.

Many of the Oman specimens, such as H 4852, 4854, 4858, 4869 are encrusted on or by a form with much coarser skeletal elements than *D. harrarensis*: others as H 4859, 4866, 4867 are encrusted on or by *D. omanensis*.

Dehornella aff. *harrarensis* (Wells)

Material. H 5159, H 5169 (each one piece and a thin section), H 5160–2, H 5165, H 5167 (each one piece), and H 5164 (two pieces and a thin section). All from Shuqraia Limestone-with-Marl (Upper Jurassic, Argovian). Maktesh Hathira, Israel (Hudson 1958).

Description. Dehornella with small nodular coenosteum (up to 6 cm. across) encrusting (usually small phaceloid corallites) and with irregular slightly nodose surface. Coarse reticulum with thick vertical lamellae (*c.* 0·2–0·5 mm. across) of pillars joined directly or by short lateral processes, and enclosing irregular coenospaces (*c.* 0·2–0·3 mm. across), often irregularly vermiculate and joining each other. Astrosystems of coarse irregular astrocorridors (0·2–0·3 mm. across) joining coenospaces. Tabulae fairly common. Skeletal tissue largely replaced by silica and hence specimens not preserved well enough for illustration or definite identification.

The skeletal elements of these forms have generally the same dimensions as *D. harrarensis*. They differ in that their lamellae are generally more vertical and perhaps thicker (more compound) and there are few or no transverse lamellae.

ASTROPORINA gen. nov.

Type species *Astroporina stellifera* sp. nov.

Diagnosis. Parastromatoporidae with coenosteum of abundant conjoined or interlaced astrosystems of well-developed tabulate astrocorridors, variously radial or irregular and indefinite, bounded by vertical lamellae, often composite with cellules. Reticulum of coenospaces and coenotubes, if present, very subordinate. Tabulae abundant and irregularly aligned.

Astroporina stellifera sp. nov.

Plate 24, figs. 1–5; Plate 27, figs. 1, 2

Holotype. F 1775, one piece and sections a (Pl. 24, fig. 5), b (Pl. 24, figs. 1, 3), and c (Pl. 24, figs. 2, 4) and H 3657, two pieces (Pl. 27, figs. 1, 2) and sections H 3658–9 (cut from H 3657). Upper Jurassic, Ahankon Tug (11° 01′ N., 48° 26′ E.), Inda District, British Somaliland.

Diagnosis. Astroporina with nodular coenosteum of conjoined distinct astrosystems (centres 3·5–5 mm. apart) consisting of astrocorridors (0·25–0·30 mm. wide), irregularly stellate and well branched, bounded by vertical lamellae (pillars 0·15 mm. across) enclosing abundant coenotubules (0·12 mm. across).

Astroporina orientalis sp. nov.

Plate 26, figs. 1, 2; Plate 27, figs. 6, 7

Holotype. H 4850, one piece and thin sections a (Pl. 26, fig. 1; Pl. 27, fig. 7) and b (Pl. 27, fig. 6; Pl. 26, fig. 2). Cladocoropsis Limestones (Sequanian), near Ain Safra, Yanta, Lebanon.

Diagnosis. Astroporina with coenosteum of vertical pillars, occasionally isolated but mainly joined laterally to form extensive vertical lamellae (*c.* 0·15–2·0 mm. across), vertically fairly straight, occasionally enclosing ?coenotubes. Interlaced astrosystems of astrocorridors (*c.* 0·3–0·4 mm. across) bounded by vertical lamellae joining at or near the axis. In parts of the coenosteum the corridors are intermingled and lose their identity as astrocorridors. Tabulae abundant, close (about 7 to 2 mm.), and irregularly aligned.

Astroporina cf. *orientalis* sp. nov.

Plate 25, figs. 1–3; Plate 26, figs. 2, 3

Material. F. 1773, three pieces and sections a (Pl. 25, fig. 2; Pl. 26, fig. 2), b (Pl. 25, fig. 1; Pl. 26, fig. 3), and c (Pl. 25, fig. 3; Pl. 3, fig. 3). Upper Jurassic, Bihen Limestone, Daghani Section (10° 09′ N., 45° 10′ E.), Bihendula, British Somaliland.

Description. Astroporina with nodular coenosteum of vertical lamellae (constituent pillars 0·13–0·19 mm. across), vertically and transversely irregular, occasionally enclosing coenotubes, and bounding interlacing corridors (0·22–0·38 mm. across). The general plan of this specimen is that of *Astroporina orientalis.* The vertical lamellae are, however, more irregular and the astrocorridors are more indefinitely radial: the overall transverse plan is that of the more indefinite parts of *A. orientalis.*

Astroporina stellans sp. nov.

Plate 24, figs. 6, 7; Plate 25, fig. 4; Plate 26, figs. 5, 6

Holotype. F 1774, one piece and sections a (Pl. 24, fig. 7; Pl. 26, fig. 5), b (Pl. 25, fig. 4; Pl. 26, fig. 6), and c (Pl. 24, fig. 6). Upper Jurassic, Bihen Limestone, Daghani Section (10° 09′ N., 45° 10′ E.), Bihendula, British Somaliland.

Diagnosis. Astroporina with nodular coenosteum. Reticulum of thick irregular vertical lamellae (*c.* 0·2–0·5 mm. across) formed of joined pillars (*c.* 0·2 mm. across). Lateral processes not common. Lamellae occasionally enclose coenotubes (*c.* 0·125–0·2 mm. across) but generally bound irregular vermiculate conjoined coenospaces (*c.* 0·2–0·3 mm. across). Astrosystems, centres about 2·5–4·5 mm. apart, of irregularly branching astrocorridors (*c.* 0·25–0·33 mm. across) bounded by irregular vertical lamellae. Tabulae common (about 0·4–0·6 mm. apart).

Astroporina sp.

Material. H 4857, four pieces and sections a–d. Beni Zaid Limestone (Oxfordian s.s.), Wadi Bih Jebel Hagab area, Ras al Khaima, Trucial Oman, Arabia.

Description. Astroporina with nodular coenosteum of intergrown coenosteal columns forming low bosses at surface. Astrosystems dominant, of long radial astrocorridors (*c.* 0·4 mm. across), bounded by irregular but continuous vertical lamellae (*c.* 0·25 mm. across). Reticulum between astrosystems not extensive, of isolated vertical lamellae and pillars, and wide joined coenospaces similar to astrocorridors. Occasional transverse lamellae. Tabulae not common, mainly aligned.

Specific distinction in *Astroporina*

Species of *Astroporina*, as species of *Dehornella* and *Parastromatopora*, include those with fine structural elements as *A. stellifera* and *A. orientalis* (compare *D. choffati* and *D. omanensis*) and those with coarse structural elements as *A. stellans* and *Astroporina* sp. (compare *D. harrarensis*): it seems probable that fine and coarse structural forms are independent lineages. The difference between *Astroporina* and *Dehornella* and the distinction between the species of *Astroporina* is based on the progressive elimination of the normal reticulum within the coenosteum. In *A. stellifera* the astrosystems remain about the same size (*c.* 5 mm. across) but so increase in number and completely occupy the coenosteum, the reticulum being represented by the cellular skeletal blocks between the astrocorridors. The coenosteum is therefore a complex of short corridors.

In *A. orientalis* the astrosystems increase in width up to 12 mm. across, the astrocorridors widening, lengthening, and increasing in number. The single tubes enclosed by the lamellae and usually in an astrocorridor wall have as far as is known no special significance; they appear to be normal coenotubes. Otherwise there is no remnant of the reticulum. The general pattern is therefore a mesh of wide and comparatively straight radial astrocorridors. Occasionally the walls of the astrocorridors break up into pillars or small lamellae and the astropattern is lost. This is especially the case in *A.* cf. *orientalis.*

The coenosteum of *A. stellans* consists of a mesh of close short branching corridors, many of which have a radial arrangement and all of which are considered to be astrocorridors. The astrosystems are small, with few astrocorridors and closely intermingled. The astrocorridors are separated by thick short vertical lamellae and columns enclosing coenotubes. *A. stellans* is thus more closely similar to *Dehornella.*

Astroporina sp. occurs with and has the dimensions of *Dehornella harrarensis.* It differs from that species in that astrosystems are more numerous, have long astrocorridors, and occupy a much greater part of the coenosteum.

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HENGESTITES, A NEW GENUS OF GAULT AMMONITES

by RAYMOND CASEY

ABSTRACT. *Hengestites applanatus* gen. et sp. nov., described from the Upper Gault (Lower Cretaceous, Upper Albian) of south-east England, is a primitive member of the Placenticeratidae, a family of ammonites not previously recorded from Britain. It is a characteristic fossil of the *Mortoniceras inflatum* Zone (*Callihoplites auritus* Subzone) but has hitherto escaped notice owing to homoeomorphy with *Anahoplites planus* (Mantell). Its occurrence points to a polyphyletic origin for the Placenticeratidae.

DURING the sixteen years that have elapsed since the completion of the late L. F. Spath's 'Monograph of the Ammonoidea of the Gault' (Spath 1923–43) there have been many additions to knowledge of the ammonite fauna of the English Albian. One of the most notable is the genus *Falciferella*, a characteristic ammonite of the Lower Gault whose small size and resemblance to the common *Anahoplites planus* (Mantell) caused its presence to be undetected until as late as 1954 (Casey 1954*b*). The present paper draws attention to the existence in the Gault of yet another ammonite novelty. This is an Upper Gault form, by no means rare, widely distributed in south-east England, and, like *Falciferella*, is a homoeomorph of *Anahoplites planus*. It is described below as *Hengestites applanatus* gen. et sp. nov. and is assigned to the Placenticeratidae, a family of ammonites well known in Cretaceous rocks in many parts of the world, especially North America, though not hitherto recorded from Britain. It is remarkable that specimens of *Hengestites* were long ago collected at Folkestone, Kent, the type locality of the Gault formation, and have lain unrecognized in the cabinets of our museums for nearly a century.

I am indebted to Mr. A. G. Brighton of the Sedgwick Museum, Cambridge, and to Mr. R. A. Milbourne and Mr. C. W. Wright for the loan of some of the specimens used in this account. The paper is published with the permission of the Director of the Geological Survey and Museum.

SYSTEMATIC ACCOUNT

Family PLACENTICERATIDAE Hyatt 1900

Type genus *Placenticeras* Meek 1870, Upper Cretaceous, U.S.A.

The Placenticeratidae have been classified with the heterogeneous group of ammonites known as 'pseudoceratites', i.e. shells in which the septal suture tends to break up into a long series of sub-equal, simplified elements arranged in a gentle curve. Commonly this type of sutural pattern is correlated with an involute lenticular shell having a narrowly truncated or grooved venter, though it is also found in some evolute and inflated forms (e.g. *Stantonoceras* Johnson, *Diplacmoceras* Hyatt). A point of contrast between the Placenticeratidae and typical pseudoceratite families such as the Engonoceratidae and the Sphenodiscidae is that simplification of the individual elements, especially the saddles, is less advanced, both lobes and saddles being minutely frilled or even deeply dissected.

[Palaeontology, Vol. 2, Part 2, 1960, pp. 200–9, pl. 29.]

The family is circum-global in its distribution and is particularly well represented in the U.S.A. Unlike the Engonoceratidae it was not concentrated in the equatorial or 'Tethyan' region and is found in latitudes as far apart as Alaska and Patagonia. Stratigraphically it does not become important until high in the Upper Cretaceous, a single genus only (*Proplacenticeras*) extending down to the Cenomanian. Rare examples of *Hypengonoceras warthi* (Kossmat) in the Upper Albian of southern India (Kossmat 1895) and Madagascar (Boule, Lemoine, and Thévenin 1907) are the only occurrences of the Placenticeratidae in the Lower Cretaceous hitherto recorded. After J. P. Smith (1900) and Hyatt (1903), the principal students of the family are Spath (1926), Reeside (1926; 1927), and Wright (1957).

Genus HENGESTITES nov.

(*Hengest, Saxon chieftain and ancient King of Kent*)

Type species. Hengestites applanatus gen. et sp. nov., Upper Gault (Upper Albian, *Mortoniceras inflatum* Zone), south-east England.

Generic characters. High-whorled, involute platycone with angular umbilical rim and narrow venter. For a brief period in early youth the sides have faint flexuous riblets that terminate in marginal clavi alternating on opposite sides of the venter. Subsequently the shell becomes quite smooth, the venter sulcate and with carinated edges, later tabulate. Body-chamber unknown. The suture-line has a shallow, squat ventral lobe, a broad bifid or asymmetrically subtrifid principal lobe and a very narrow bifid dorsal lobe. The saddles have a phylloid tendency and are also bifid, and the tops of the auxiliaries are aligned in a gentle forward-facing convexity. A deep, bifid adventitious lobe splits the external saddle into two unequal parts, the ventral part being much the smaller.

Remarks. The Placenticeratid affinities of *Hengestites* are clearly demonstrable both in shell-form and in sutural characters. Consideration may be given first to the chief points of difference between this ammonite and members of the Hoplitidae, especially *Anahoplites*, with which it has been confused.

1. Shell-form. The whorls are more compressed, flatter and more involute than in any described species of *Anahoplites*, and the only other smooth, thinly discoidal Hoplitid that is at all like *Hengestites*, namely *Neosaynella* (Casey 1954*a*), has a different type of ventral development, the venter being non-sulcate in early youth and acute in maturity. The very narrow, sulcate and bicarinate venter of *Hengestites* is common enough in the Placenticeratidae (see, for example, Hyatt 1903, pl. 36, fig. 3; pl. 43, fig. 8; pl. 46, fig. 2) but cannot be matched in the Hoplitidae. An apparently similar venter, but without sharp edges, seen in some specimens of *Anahoplites planus* (Mantell) (Spath 1925, p. 137, text-fig. 39*d*) is due to an internal ridge-like thickening of the test in the region of the siphuncle, reproduced as a furrow on internal moulds. In *Hengestites*, which is known only by internal moulds, the ventral sulcus is impressed on the dorsum of the succeeding whorl, proving that it was a corrugation of the test and was not due to differential deposition of shell-substance. *Anahoplites* is further distinguished by the presence of umbilical bullae and of ventral clavi that are lost only in 'gerontic' specimens. Lastly, I know of no Hoplitid in which the sculpture is fully developed at diameters less than 10 mm., though this is not unusual in the Placenticeratidae (compare *P. meeki* Boehm, as described by Reeside 1927, p. 30).

2. Suture-line. It is in the characters of the suture-line that *Hengestites* exhibits the widest divergences from the Hoplitidae (text-fig. 2B). The long series of auxiliary saddles with their tops aligned in a gentle curve convex forwards is typical of the Placenticeratidae and is in contrast to the condition seen in *Anahoplites* (text-fig. 2C). In the latter genus, as in all the Hoplitidae, the auxiliaries are fewer in number and are arranged in a straight line descending obliquely backwards to the umbilical seam. A broad, open, strongly asymmetrical first lateral lobe, approaching that of *Hengestites*, occurs in some of the Transcaspian forms of *Anahoplites* and *Epihoplites* figured by Sinzow (1909, pls. 3, 4), but in general this lobe is much narrower necked in the Hoplitinae. So far as I am aware, no Hoplitid possesses a dorsal lobe that is bifid, nor one that is shallower than the adjacent lobe, though this feature of *Hengestites* is met with frequently in the Placenticeratidae. Another Placenticeratid character unknown in the Hoplitidae is the presence in the external saddle of a deep adventitious lobe, in this instance even exceeding the ventral lobe in depth. Small irregularities are sometimes seen in the ventral lobe (Pl. 29, fig. 4) but the marked displacement of this lobe to one side—a consistent peculiarity of *Anahoplites planus* and its allies—is not found in *Hengestites*. Conversely, the ontogenetic change in the principal lobe from bifid to subtrifid, seen in *Hengestites* (text-figs. 1A–C), is alien to the Hoplitidae. In the bifid nature of the principal lobe the immature *Hengestites* shows better agreement with young *Placenticeras*, as illustrated in text-figs. 1A and D.

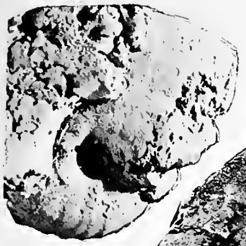
The Desmoceratid ammonite *Beudanticeras beudanti* (Brongniart), for which *Hengestites* has also been mistaken in a crushed condition, has a rounded venter, a slightly wider umbilicus with blunter rim, and a more complex suture-line of different pattern.

Among the Placenticeratidae *Hengestites* finds its nearest morphological parallel in the group of *Placenticeras meeki* Boehm, well illustrated by Hyatt (1903, pl. 45, figs. 3–16; pl. 66; as *P. whitfieldi*) from occurrences in the Upper Cretaceous Montana Group of South Dakota and Nebraska, and by Boule, Lemoine, and Thévenin (1907, pl. 12, figs. 5, 5*a*) from beds of about the same age in Diego-Saurez, Madagascar. Usually, however, both *Placenticeras* and *Proplacenticeras* have umbilical tubercles and other ornament which persist to a relatively late stage of growth. Also, in these two genera, as in *Hypengonoceras* and *Pseudoplacenticeras*, multiplication and equalization of the sutural elements is so far advanced that the identity of the primitive lateral lobe is lost in the mature shell. *Hengestites*, with clearly identifiable principal lobe, thus compares more closely with the genera *Metaplacenticeras* Spath and *Hoplitoplacenticeras*

EXPLANATION OF PLATE 29

All figures are natural size unless otherwise indicated.

Figs. 1–4. *Hengestites applanatus* gen. et sp. nov. 1, Holotype (Sedgwick Museum B 81598), Upper Gault, *inflatum* Zone, *auritus* Subzone (horizon inferred), Folkestone, Kent. Rev. T. Wiltshire Coll. 2, 2*a*–*b*. Fragmentary pyritic nucleus showing sculptured stage of the young, enlarged × 2 in figs. 2*a*, *b*, Upper Gault, *inflatum* Zone, *auritus* Subzone, Aylesford Brick and Tile Works, Aylesford, Kent. R. A. Milbourne Coll. 3, 3*a*. Portion of phosphorite nucleus showing the ventral sulcus of the adolescent, Upper Gault (not *in situ*), Aston Clinton, near Aylesbury, Bucks. C. W. and E. V. Wright Coll. 7075. 4. Part of external suture-line at 160 mm. diameter, from venter to middle of first lateral lobe. Upper Gault, condensed *auritus-aequatoriale* Subzones, cutting for by-pass road in Horish Wood, two-thirds of a mile north-east of the Chiltern Hundreds Inn, north-east of Maidstone, Kent. Geological Survey Museum Ca 7250.



2a

1

2b

3a

2

4

3

CASEY, *Hengestites.*

Spath, both of high horizon in the Upper Cretaceous and quite different in sculpture from the present genus. A unique feature of *Hengestites* that serves as a ready means of separation from all other genera of the Placenticeratidae is the dwarfing of the ventral portion of the external saddle.

Hengestites applanatus gen. et sp. nov.

Plate 29, figs. 1–4; text-figs. 1A–C, 2A–B

1875 *Ammonites splendens*, Sow., grooved var.; De Rance (in Topley), p. 436 (pars).
1882 *Ammonites splendens*?; Norman, table facing p. 440.
1887 *Ammonites splendens* (?); Norman, p. 77.
1900 *Ammonites splendens*, Sow.; Jukes-Browne, pp. 141, 256, 458 (pars).
1923 *Beudanticeras beudanti* (Brong.); Spath, p. 76 (pars).
1939 *Anahoplites planus* (Mant.) (sulcate form); Wright and Wright, p. 116.
1947 *Anahoplites planus* (Mant.) (sulcate form); Wright, p. 188.

Holotype. Sedgwick Museum No. B 81598, Upper Gault (Bed XI), Folkestone, Kent (Rev. T. Wiltshire Coll.).

Description. Shell compressed, strongly involute; whorl-section high and lanceolate, widest near the umbilical margin, the sides subparallel below, converging more rapidly above to a narrowly truncated venter. The narrow umbilicus is limited by a flat, subvertical wall, angular at the rim.

At the earliest observed diameter (7–10 mm.) the ammonite is ornamented by very faint primary riblets, numbering four to one-third of a volution, which commence at the umbilical margin and lean slightly forwards to traverse the flattened sides in a feeble S-bend. Secondary riblets take origin from near mid-flank and are intercalated among the primaries singly or in pairs. Every riblet ends at the peripheral margin in a compressed, hoplitoid clavus directed forwards and inwards at an angle of 30° to the smooth siphonal line, the alternation of the clavi of opposite sides giving the suggestion of a zigzag pattern on the venter.

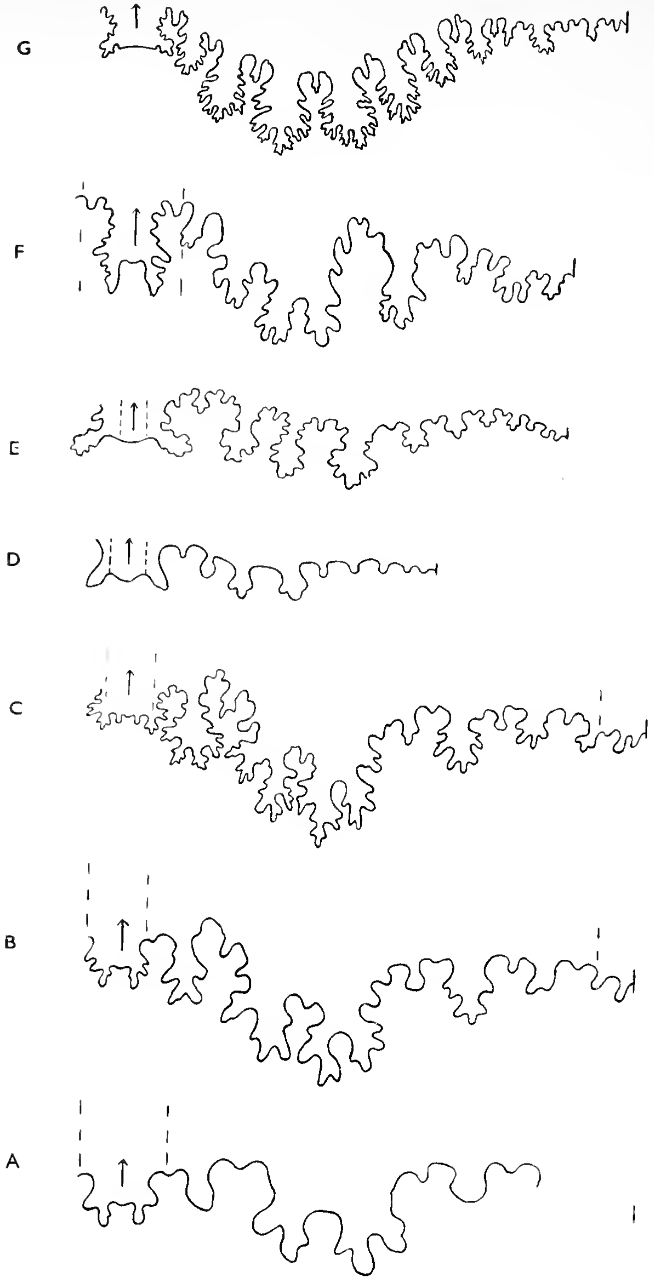
With subsequent growth the sculpture degenerates, the whorls become increasingly compressed, flat-sided and involute, the venter increasingly narrow. Already at 15 mm. diameter the riblets have almost disappeared and the clavi are reduced to gentle waves along the edges of a sulcate venter; at 20 mm. diameter the shell is smooth to the naked eye, the ventral edges sharp and entire. After about 45 mm. diameter the ventral sulcus is lost, the venter then becoming tabulate, though maintaining well-angulated margins until at least 160 mm. diameter.

The sutural characters have been outlined in the foregoing description and discussion of the genus.

Measurements

	Diameter	*Whorl-height*	*Whorl-thickness*	*Umbilicus*
Holotype	163	89 (0·54)	?	18·5 (0·12)
R. A. Milbourne Coll. 1752	*c.* 40	23	10	?
	18	9·5 (0·53)	5 (0·28)	2·7 (0·15)

(Dimensions are in mm. Figures in parentheses are dimensions expressed as fractions of the diameter.)



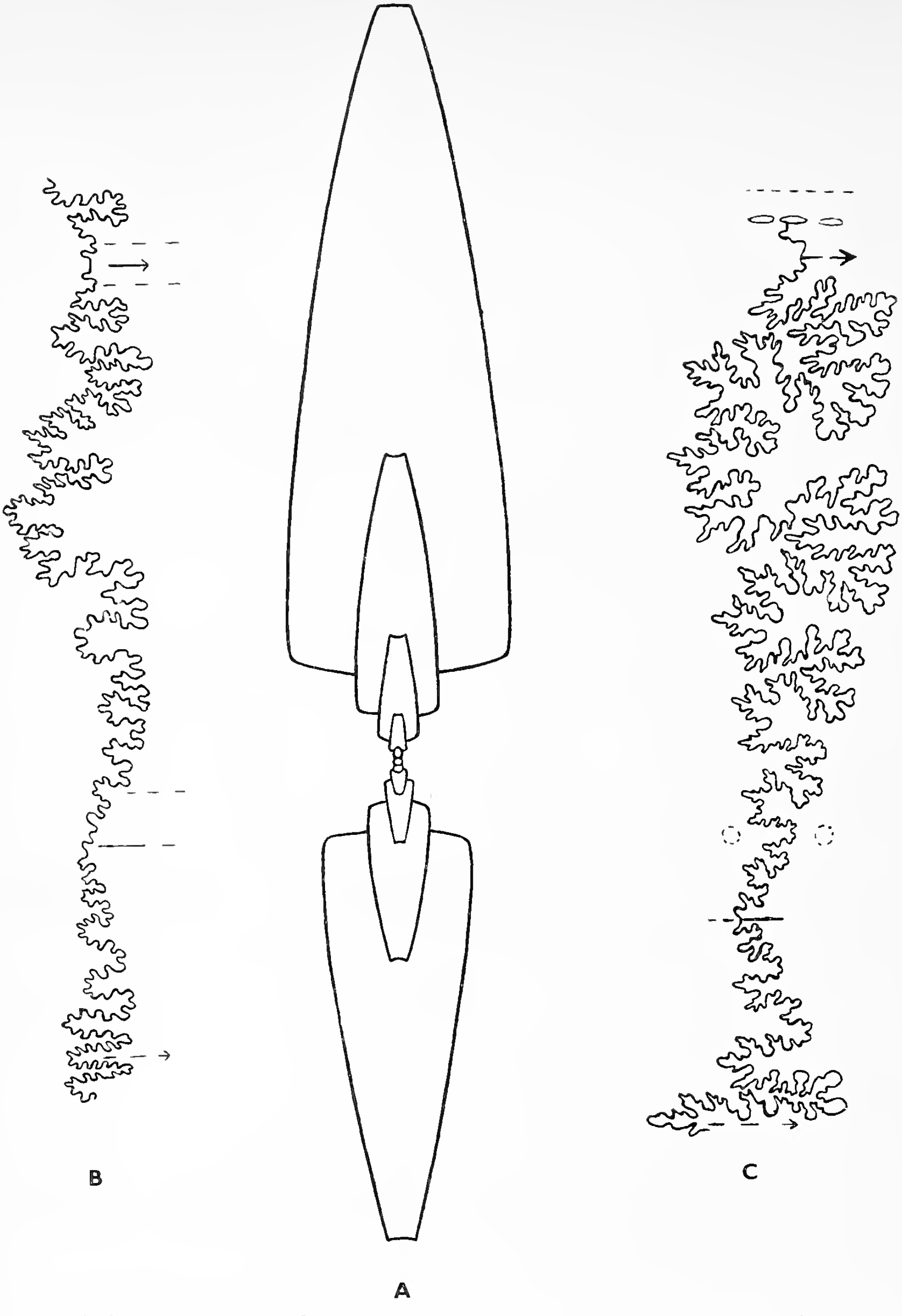
TEXT-FIG. 1. External suture-lines of Placenticeratidae. A, B, C, *Hengestites applanatus* gen. et sp. nov. at 8, 16, and 40 mm. diameter (R. A. Milbourne Coll. 1752). D, E, *Placenticeras meeki* Boehm at 10 and 25 mm. diameter (Upper Cretaceous, Wyoming. After Reeside 1926). F, *Metaplacenticeras californicum* (Anderson) at 50 mm. diameter (Upper Cretaceous, California. After Reeside 1926, reversed). G, *Hypengonoceras warthi* (Kossmat) at about 140 mm. diameter (Lower Cretaceous, S. India. After Kossmat 1895).

Remarks. The above description is based on a large series of specimens drawn from a wide area of south-east England. All the zonally authenticated material was obtained from the *auritus* Subzone of the *inflatum* Zone, corresponding to the main mass of Bed XI of the Gault of Folkestone. This is not one of the best horizons in the English Albian for well-preserved macrofossils and the majority of specimens are crushed or fragmentary. None shows the test or the body-chamber, though large unsutured portions of a smooth and compressed ammonite found in the Upper Albian of Ventnor, Isle of Wight, may prove to be the final stage of *Hengestites.* The holotype is the only complete disk examined; it carries no documentation as to horizon within the Gault but is embedded in a large block of pale-grey marly clay with rusty partings—a type of lithology exclusive to Beds XI and XIII of the Gault. This fact, taken in conjunction with the mode of preservation of the fossil—putty-coloured phosphate with a dark-grey, slightly greenish-tinged surface film—indicates Bed XI as the source of the specimen.

Like *Uhligella derancei* (Casey 1949), *Hengestites applanatus* is only a modern rediscovery and was known to early collectors of the Folkestone Gault under another name. De Rance, who wrote the first systematic account of the Gault at Folkestone (1868) knew the species as a 'grooved variety of *Ammonites splendens*' and on his authority it is recorded as such from Bed XI in Topley's *Geology of the Weald*, published in 1875. The identity of De Rance's ammonite with the present species is confirmed by a specimen in the Geological Survey Museum (G.S.M. 97136), acquired from him in 1868. A similar record from Bed VIII of the Gault refers to immature *Euhoplites* of the group of *E. subcrenatus* Spath (e.g. G.S.M. 97135). The holotype was presented to the Woodwardian (now Sedgwick) Museum by the Reverend Thomas Wiltshire (born 1826, died 1902), who for many years spent holidays fossil-collecting at Folkestone (Woodward 1903). Crushed examples of *H. applanatus* collected by L. F. Spath and S. W. Hester from 6 feet above the base of Bed XI at Folkestone are also in the Geological Survey Museum (G.S.M. RE 4022–3). They were recorded by Spath (1923, p. 76) as *Beudanticeras beudanti* (Brongniart).

There is now little doubt that many of the old records of *Ammonites splendens* J. Sowerby from the Upper Albian of other localities, usually assumed to refer to *Anahoplites planus* (Mantell) or some other smooth Hoplitid, belong in part to *Hengestites* (e.g. the Potterne Rock and the Malmstone of Devizes, recorded by Jukes-Browne 1900, p. 256). This is certainly the case with the Upper Greensand occurrences at Ventnor, Isle of Wight, cited by Norman (1882; 1887), where, as at Folkestone, *Hengestites* is associated with *Mortoniceras inflatum* (J. Sowerby) and *Callihoplites auritus* (J. Sowerby) (Norman Collection, formerly in the Museum of the Ventnor and Bonchurch Literary and Scientific Institution).

The immature specimen illustrated in Pl. 29, figs. 3, 3*a*, is the original of the Wright brothers' (1939) record of *Anahoplites planus* (Mant.), sulcate form, from the Upper Gault of Aston Clinton, Buckinghamshire. This was considered to have originated in Bed IX (*Hysteroceras orbignyi* Subzone) but was not obtained *in situ*. It is a well-preserved fragment with clear but interlocking sutures. Other specimens of the present species in the Wrights' collection comprise two large septate fragments from the Upper Albian of Punfield, Dorset, also cited as a sulcate form of *A. planus* (Wright 1947, p. 188). The horizon of these specimens is now believed to fall within the *auritus* Subzone (C. W. Wright, private communication).



TEXT-FIG. 2. A, B, *Hengestites applanatus* gen. et sp. nov., reconstructed whorl-section, natural size, and complete suture-line at about 90 mm. diameter. The latter is composite, being based on specimens G.S.M. Ca 7256, 7258 and Zn 7101. C, *Anahoplites planus* (Mantell), Upper Gault, Shenley Hill, Beds., complete suture-line at about 60 mm. diameter (after Spath 1925, reversed). Note the asymmetry of the ventral lobe in relation to the siphonal line and to the tubercles on the peripheral margin.

Conditions at Folkestone are no longer favourable for collecting from the higher beds of the Gault, but the species has been obtained in recent years by Mr. R. A. Milbourne from exposures of the *auritus* Subzone in the old Gault workings of the Aylesford Brick and Tile Company at Aylesford, Kent. A pyritic internal mould in his collection shows very clearly the sculptured phase of the young and some of the early stages of sutural development and is figured in Pl. 29, figs. 2, 2*a–b*, and text-fig. 1A–C. A further ten specimens were collected by Geological Survey officers from cuttings made for a new road in Horish Wood, on the north-east side of Maidstone, Kent (G.S.M. Ca 7250, 7256–8, 7881–5; Zn 7101). They are part of a large suite of remanié fossils found in a condensed 'Cambridge Greensand' facies of the *auritus* and *aequatoriale* Subzones. The most complete specimen (Ca 7250) is one-third of a plate-like disk of about 160 mm. diameter, sutured throughout; the whorl is 85 mm. high, the venter scarcely 4 mm. wide; allowing for the missing body-chamber the ammonite must have measured at least 240 mm. diameter. Other fragments belonged to disks of 300 mm. or more. Although dwarfed by the prodigious Placenticeratid of 780 mm. diameter described from the Navarro Group of Texas (Stephenson 1941, p. 432), *Hengestites* was none the less a giant among the ammonoidea of the Gault.

HENGESTITES AND THE SYSTEMATIC POSITION OF THE PLACENTICERATIDAE

The origin and systematic position of the Placenticeratidae are matters of debate. No unequivocal evidence of ancestry is provided by the form of the shell, and the septal sutures, as in most pseudoceratites, have undergone such profound modification that attempts to homologize the component elements with those of normal ammonites are frankly speculative. Douvillé (1890, pp. 288–91) assigned *Placenticeras* and *Stantonoceras* to the Hoplitidae on the basis of supposed similarities of the early sutures to those of *Anahoplites* ('*Hoplites*') *splendens* (J. Sowerby) and *Cleoniceras* ('*Sonneratia*') *quercifolium* (d'Orbigny), an opinion accepted by Grossouvre (1894, p. 123), Pervinquière (1907, p. 197), and others. The same conclusion as to relationship with the Hoplitidae was reached by Smith (1900) from a study of the immature stages of forms now identified as *Metaplacenticeras pacificum* (Smith) and *M. californicum* (Anderson), though he differed from Douvillé in his interpretation of the origin of the elements of the adult suture-line. Hyatt (1903, p. 192), on the other hand, investigated the young stages of *Placenticeras meeki* Boehm (= *P. whitfieldi* Hyatt) and concluded that at no stage in its development is the genus truly comparable with *Hoplites*. Concerning *Metaplacenticeras*, Matsumoto's recent observations on the ontogeny of *M. subtilistriatum* (Jimbo) (Matsumoto 1953) have led him to the belief that this genus was probably derived directly from the Phylloceratidae rather than from the Hoplitidae. This view accords better with the stratigraphical data, since *Metaplacenticeras* is not a Cenomanian ammonite as thought by Smith, but is of Campanian age and thus far removed in time from the Albian-Cenomanian Hoplitidae.

A connexion between the Placenticeratidae and the earlier pseudoceratites, the Engonoceratidae, is an hypothesis favoured at one time by Spath (1930, p. 390) and this is the view taken in the *Treatise on invertebrate paleontology* (Wright 1957, pp. L 109, 390), wherein the Placenticeratidae are shown as the lineal descendants of the Engonoceratidae. This phylogeny was supported by consideration of the Upper Albian genus *Hypengonoceras*, at that time the only Lower Cretaceous Placenticeratid known. With its simple, pincer-like endings to the saddles, *Hypengonoceras* shows great resemblance to the Engonoceratids *Knemiceras* and *Parengonoceras* of Lower and Middle Albian age, though it exhibits the more complete fragmentation of the external saddle characteristic of the Placenticeratidae. Derivation of *Hypengonoceras* from *Parengonoceras* or some allied member of the Engonoceratidae seems probable; nothing is known, however, to bridge the gap between *Hypengonoceras* and the rather diverse forms that comprise the Upper Cretaceous Placenticeratidae.

The phylogenetic scheme is complicated by the introduction of *Hengestites*, for this is a cryptogenetic genus, appearing suddenly in the Upper Albian without evidence of ancestry. Unlike *Hypengonoceras*, its sutural characters are opposed to the idea of descent from the Engonoceratidae, and for reasons given above an origin in the Hoplitinae seems almost equally improbable. Since the boreal developments of the Hoplitidae that tended towards pseudoceratitism (e.g. *Gastroplites* McLearn, *Styracoceras* Hyatt) are also very distinct and there is no apparent link with the Lyelliceratidae, a family which sometimes mimicked the Hoplitid venter (Casey 1957, p. 34), the question of the ancestral source of *Hengestites* must be left open.

The discovery of *Hengestites* makes it difficult to conceive of the Placenticeratidae as a monophyletic group springing from the Engonoceratidae via *Hypengonoceras*. The more or less simultaneous appearance in widely separated geographical provinces of these two ammonites—one on the borders of the Indian Ocean, the other in south-east England—each bearing the hall-marks of the Placenticeratidae yet apparently of dissimilar origins, suggests that the family is polyphyletic. It is probable that both *Hypengonoceras* and *Hengestites* are forerunners rather than direct ancestors of the Upper Cretaceous Placenticeratidae.

The origin of the Engonoceratidae has also never been settled. Wright (1957) includes both the Engonoceratidae and the Placenticeratidae in a broad superfamily Hoplitaceae, though Luppov and Mikhailov (1958) unite them with the Sphenodiscidae in a separate unit, the 'Engonocerataceae'. In view of the uncertainty regarding the stem to which the Engonoceratidae and the Placenticeratidae attach themselves some such grouping seems desirable, though the Sphenodiscidae, of Acanthoceratacean affinities, must be excluded. It seems generally to have been overlooked, however, that the name Placenticerataceae (proposed as Placenticeratida) of Hyatt (1900, p. 584) is available for this group and takes priority over 'Engonocerataceae', put forward by Basse (1952, p. 658).

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CARBONIFEROUS AND PERMIAN FUSULINIDAE FROM SPITSBERGEN

by C. L. FORBES

ABSTRACT. The collections of several expeditions to Spitsbergen have been examined and seventeen species (none new) of Fusulinidae are described from horizons ranging from Middle Carboniferous to Lower Permian. These identifications form the basis of stratigraphical work published elsewhere and here briefly summarized. Previous records of Fusulinidae from Spitsbergen are re-examined.

INTRODUCTION

THIS description of the fusulinids collected by various expeditions to Spitsbergen follows the account of the geology of the area visited by the Cambridge Expedition 1949, as given by Gee, Harland, and McWhae (1952) and by Forbes, Harland, and Hughes (1958). The stratigraphical nomenclature of these authors is summarized in text-fig. 1. It is regretted that No. 13 (1958) of the Trav. Inst. géol. U.R.S.S., with an important series of papers on the fusulinids of the *Schwagerina* horizon, has come to notice too late to receive the consideration it deserves.

All specimens are deposited in the Sedgwick Museum, Cambridge. Locations and horizons are detailed in the Appendix.

Previous work on Fusulinids from Spitsbergen. Goës (1884) identified *Fusulina cylindrica* in material collected by Nathorst and de Geer in 1882 from Tempelfjorden, evidently from the Mid Wordiekammen Limestones. Chernўshev, quoted by Nathorst (1910), pointed out that these fusulinids were not *F. cylindrica.*

Schellwien (1908) described the common fusulinid of the Mid Wordiekammen Limestones as *Fusulina arctica*; he also records doubtfully identifiable *F. anderssoni* presumably also from the Mid Wordiekammen Limestones. His material was from Templet, Gipshuken, and Billefjorden; all these are localities in the area (Gee *et al.*, pl. 1) from which most of the present material has been collected.

Staff and Wedekind (1910) elaborated Schellwien's work. They transferred Schellwien's species to *Schellwienia*, refigured and redescribed *Schellwienia arctica*, and figured *S. anderssoni* for the first time. They also described a new species, *Schubertella transitoria*, making it the type of their new genus, *Schubertella*. They mention *Schellwienia* cf. *verneuili* (v. Möller) and *S.* cf. *exigua* Staff as occurring in Spitsbergen. Horizons and localities are not accurately defined.

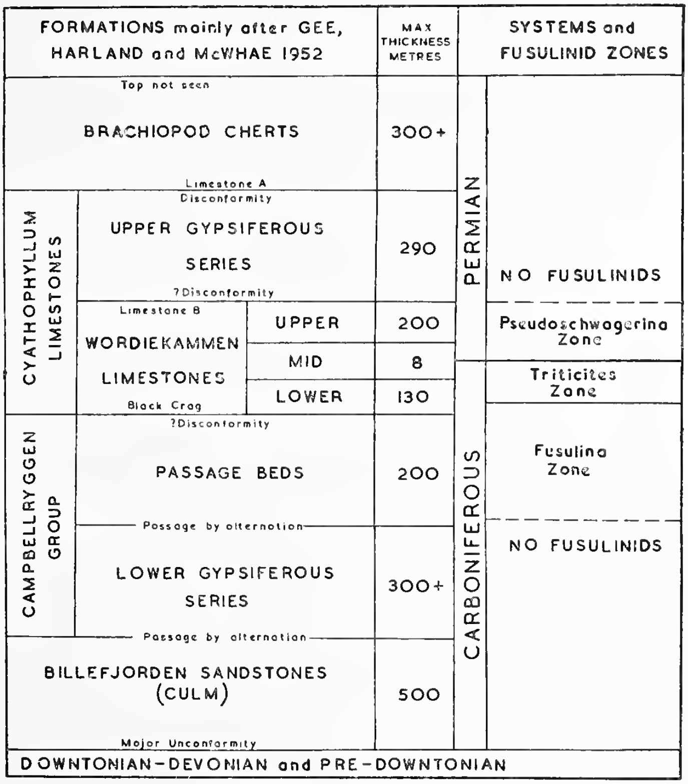
Ozawa (1925*a*) figured and remarked on some '*Fusulinella*-like forms which seem to be congeneric with *Schubertella*', occurring with '*Fusulina*' and '*Staffella*' (i.e. *Ozawainella*) in some Carboniferous limestone from Spitsbergen. This material evidently includes *Fusiella*, *Profusulinella*, or *Fusulinella*, and this was for many years the only record of Moscovian fusulinids from Spitsbergen.

Thompson (1937) redescribed *Schubertella transitoria*, restricting it to the microspheric form of Staff and Wedekind, basing his redescription on material from the Middle Wordiekammen Limestones of Tempelfjorden; he identified and figured *Schwagerina anderssoni* (Schellwien)? and *Schwagerina*? *arctica* (Schellwien) also from this horizon.

[Palaeontology, Vol. 2, Part 2, 1960, pp. 210–25, pl. 30–33.]

Baker, Forbes, and Holland (1952) mention indeterminable fusulinids from Kapp Scania near the entrance to Isfjorden. Forbes, Harland, and Hughes (1958) give faunal lists of which the fusulinid identifications are substantiated and somewhat extended by the descriptions given here, which also supersede the 'very precursory' identifications by H. C. Wang in Gee *et al.*, based on a small part of the material here studied (see Appendix).

Descriptive procedure. The rocks containing the fusulinids here studied are too well cemented for the usual methods of disintegration, so that attention has been focused on those samples with fusulinids sufficiently abundant to give all necessary orientated sections in a reasonably small number of slices.



TEXT-FIG. 1. Summary of Permian and Carboniferous stratigraphy of Central Vestspitsbergen.

Genera are mostly used in the sense of Dunbar (in Cushman 1948), which is in accordance with well-established practice. Specific descriptions and remarks are here given to substantiate my use of the names used; they are based solely on my own specimens; type material has not been re-examined. For economy of space, dimensions have been tabulated (Table 1). The synonymy given for each species comprises only the references actually checked by me; where such references are given by Rauzer *et al.* 1951 they are omitted from both Synonymy and Bibliography.

SYSTEMATIC DESCRIPTIONS

Family FUSULINIDAE Möller emend. Dunbar
Subfamily FUSULININAE Rhumbler emend. Dunbar and Henbest
Genus PSEUDOSTAFFELLA Thompson
Pseudostaffella cf. *antiqua* (Dutkevich)

Plate 30, figs. 3–9

Cf. 1934 *Staffella antiqua* Dutkevich, p. 35, text-figs. 1–3 (trans. Ellis and Messina).
Cf. 1951 *Pseudostaffella antiqua* (Dutkevich); Rauzer *et al.*, p. 97, pl. 5, fig. 6.

Description. Small, globular, or with well-rounded periphery and slightly umbilicate poles. First two whorls coiled at right angles to later whorls. Septa slightly spiralled towards the poles. Chomata rather weak; tunnel angle variable, usually about 27°.

Remarks. *P. antiqua* (Dutkevich) s.s. is slightly smaller in all dimensions and may lack the well-marked endothyroid juvenarium of my material. Of other species few are so nearly spherical; *P. hollingsworthi* (Thompson) is similar but has a larger proloculus and more septa per whorl; *P. needhami* Thompson (type of this genus) is rather smaller in most dimensions but with larger proloculum and more rectangular outline in axial sections. Of Russian species described by Rauzer *et al.* (1951) *P. paracompressa* is very similar, but not quite so globular.

Pseudostaffella sphaeroidea (Möller)

Plate 30, figs. 10–13

1878 *Fusulinella sphaeroidea* (Ehrenberg); Möller, pp. 107–11, pl. 5, figs. 4*a*–*e*, pl. 15, figs. 1*a*–*b*.
1927 *Staffella sphaeroidea* (Möller); Lee, pp. 13–16, pl. 1, fig. 1; pl. 2, figs. 8–11.
1930 *Staffella sphaeroidea* Möller; Lee, Chen, and Chu, pp. 114, 115, pl. 6, fig. 26.
1930 *Staffella parasphaeroidea* Lee and Chen; Lee, Chen, and Chu, pp. 115, 116, pl. 6, figs. 27, 28.
1932 *Staffella sphaeroidea* (Möller); de Terra, p. 157, pl. 15, figs. 21, 22.
1951 *Pseudostaffella sphaeroidea* (Ehrenberg); Rauzer *et al.*, p. 128, pl. 9, figs. 3–5.

Description. Large for this genus, cylindrical, yielding axial sections nearly square. First two whorls more or less oblique to the later whorls. Chomata strong, tunnel angle narrow, about 19°.

Remarks. My material includes only two axial sections, and equatorials seem to differ from Möller's description in having as many as twenty-four (rather than twenty) septa

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EXPLANATION OF PLATE 30

All figures magnified ×25.

Figs. 1–2. *Ozawainella spp.* 1, Black Crag, Lower Wordiekammen Limestones; sample F 30. 2, Passage Beds; sample T 11.

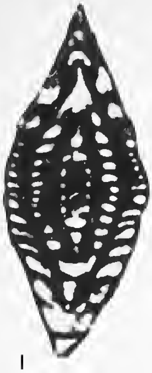
Figs. 3–9. *Pseudostaffella* cf. *antiqua* (Dutkevich). Passage Beds; sample F 51.

Figs. 10–13. *Pseudostaffella sphaeroidea* Möller. Passage Beds; sample T 11.

Figs. 14–15. *Wedekindellina spp.* 14, Probably Black Crag, Lower Wordiekammen Limestones; sample R 64. 15, Black Crag, Lower Wordiekammen Limestones; sample F 30.

Figs. 16–19. *Profusulinella* cf. *pararhomboides* Rauzer *et al.* Passage Beds; sample F 83.

Figs. 20–23. *Fusulinella eopulchra* Rauzer. Passage Beds; sample S 48.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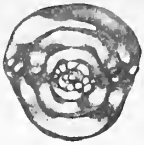
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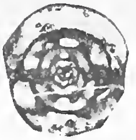
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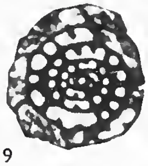
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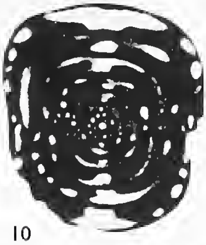
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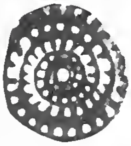
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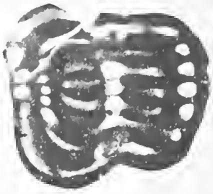
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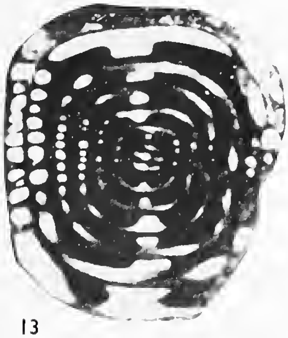
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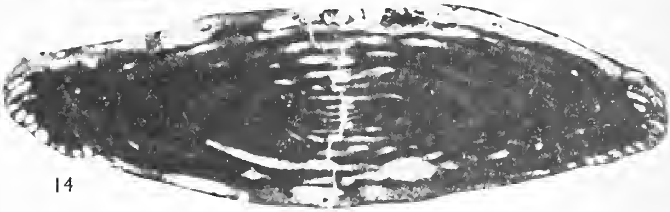
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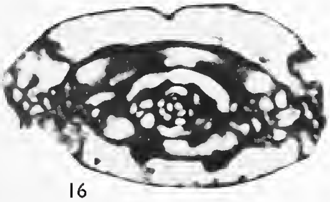
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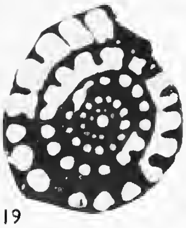
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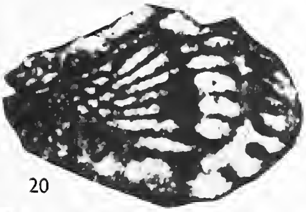
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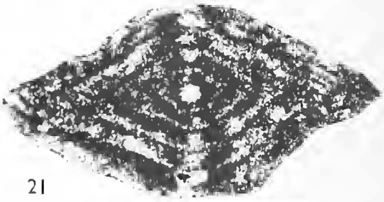
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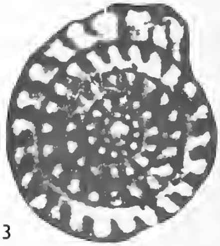
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FORBES, *Fusulinidae from Spitzbergen*, x25.

in the fourth whorl and in being rather smaller (diameters up to 1·53 mm. rather than 1·81 mm.). Lee, Chen, and Chu (1930) distinguish *S. parasphaeroidea* as yielding axial sections subcircular not quadrate, as in Möller's species from which it also differs in being rather larger and in occurring at a slightly higher horizon. I find less than specific difference between these forms; specimens from station T 11 show variation sufficient to cover both. *Fusulinella quadrata* Deprat (1913) is similar to *P. sphaeroidea* and is included by Lee (1927) as a synonym, but to judge from Deprat's figures it differs in having weaker chomata. Other similar large species of *Pseudostaffella* are described by Rauzer *et al.* (1951).

Genus OZAWAINELLA Thompson

Ozawainella spp.

Plate 30, figs. 1, 2

Remarks. Specimens are few, and the absence of any good axial section renders specific identification impossible. It is quite likely that more than one species is present; contrast, for example, the crescentic tunnel in Pl. 30, fig. 1, with the D-section tunnel in Pl. 30, fig. 2. Comparable Russian species from the Middle and Upper Carboniferous are figured and described by Rauzer *et al.* (1951). Some at least of my material might be referred to *Parastaffella* Rauzer (Coogan 1958; Rauzer *et al.* 1951), but this genus would seem to be synonymous, at least in part, with *Ozawainella*.

Genus FUSULINELLA Möller

Fusulinella bocki Möller

Plate 31, figs. 1–3

1878 *Fusulinella bocki* Möller, pp. 104–7; pl. 5, figs. 3*a–g*; pl. 14, figs. 1–4.
1925*b* *Fusulinella bocki* Möller; Ozawa, pp. 17–18, pl. 3, figs. 7, 9, 10.
1927 *Neofusulinella bocki* (Möller); Lee, Chen, and Chu, pp. 121–2, pl. 8, figs. 8–15; pl. 9, figs. 1–9.
1932 *Fusulinella bocki* Möller; de Terra, p. 156, pl. 15, fig. 23.
1951 *Fusulinella bocki* Möller subsp. *timanica* Rauzer *in* Rauzer *et al.*, p. 220, pl. 31, fig. 10, pl. 32, fig. 1.

Description. Stoutly fusiform tapering convexly to bluntly pointed poles. Septa more or less plane for a short distance about the equator, but much convoluted at the poles. Chomata strong, tunnel narrow but expanding gradually, tunnel angle increasing from about 15° in the earlier whorls to 35° or 45° in the fifth and sixth.

Remarks. My material agrees well with Möller's and Lee's descriptions; of the Russian subspecies described by Rauzer *et al.* (1951) it is nearest to subsp. *timanica* but includes rather larger specimens besides more slender ones much resembling *F. bocki* s.s.

Fusulinella eopulchra Rauzer-Chernousova

Plate 30, figs. 20–23

1951 *Fusulinella eopulchra* Rauzer; in Rauzer *et al.*, p. 235, pl. 35, figs. 5–8.

Description. Stout and fusiform with concave flanks sloping from a convex equatorial region to bluntly pointed poles. Septa smooth except at the poles, where they are fluted forming regular chamberlets. Chomata high and narrow, tunnel narrow about 15° tunnel angle throughout.

Remarks. The above description is based on six equatorial or central oblique and two axial sections all from station S 48; other samples have yielded a few oblique sections only. My specimens are generally rather larger than would be strictly conformable with Rauzer's description. Similar species are *F. librovitchi* Dutkevich and *F. cadyi* Thompson, both smaller and with endothyroid juvenaria which are not present in my material. *F. itoi* Ozawa is also small, while *F. devexa* Thompson has more whorls and is more slender. *F. pulchra* Rauzer is closely similar but rather more slender.

Fusulinella usvae Dutkevich

Plate 31, figs. 4–8

1932 *Fusulinella usvae* Dutkevich, p. 15.
?1954 *Pseudofusulinella utahensis* Thompson and Bissell *in* Thompson, p. 34.

Description. Fusiform with moderately pointed poles, axis commonly bent at the proloculum, flanks forming a slightly to markedly concave slope from near the equator to near the poles. In the outermost whorl the spirotheca consists of an outer thin, dark tectum and an inner thick, clear diaphanotheca which is perforate like a keriotheca. To these primary layers which together total about 0·028 mm. there is added in the inner whorls a thick outer tectorium and perhaps an indistinct thin inner tectorium. The keriothecal nature of the diaphanotheca is not well seen in the inner whorls, probably owing to blocking of the pores by secondary calcite, or to recrystallization during fossilization. Chomata high and generally narrow, tunnel narrow and rather sinuous, tunnel angle expanding gradually to about 26°. Secondary deposits present near the axis but not strongly developed.

Remarks. The assignment of this material to *Fusulinella* rather than to *Wearingella*, *Wedekindellina*, or *Fusulina* rests on the probable presence of an inner tectorium, the rather inflated form, the septa not folded except at the poles, and the weakness of secondary axial deposits.

The genus *Pseudofusulinella* Thompson (1951) includes forms from the *Pseudoschwagerina* zone which are similar to my material, especially in having a perforate spirotheca. It seems to me, however, that *Pseudofusulinella* should not be separated from *Fusulinella*. Thompson remarks on the similarity between the two genera and bases his separation on the presence of axial deposits in *Pseudofusulinella* and on the nature of the spirotheca. But pores have been described in the spirotheca of *Fusulinella* (Dunbar and Skinner, 1937, interpreting earlier work), and the presence of axial deposits is not in itself of generic importance.

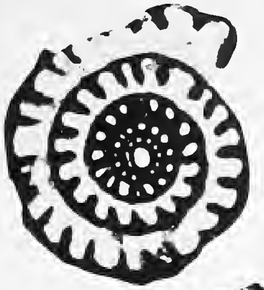
EXPLANATION OF PLATE 31

All figures magnified ×25.

Figs. 1–3. *Fusulinella bocki* Möller. Passage Beds; sample B 372.

Figs. 4–8. *Fusulinella usvae* Dutkevich. 4–5, Upper Wordiekammen Limestones; sample S 91. 6–8 Lower Wordiekammen Limestones; sample 201.

PLATE 31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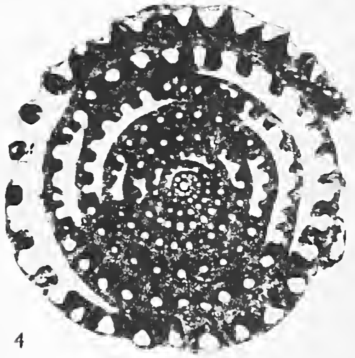
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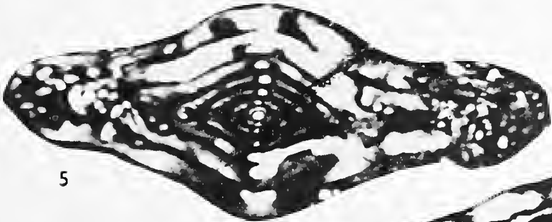
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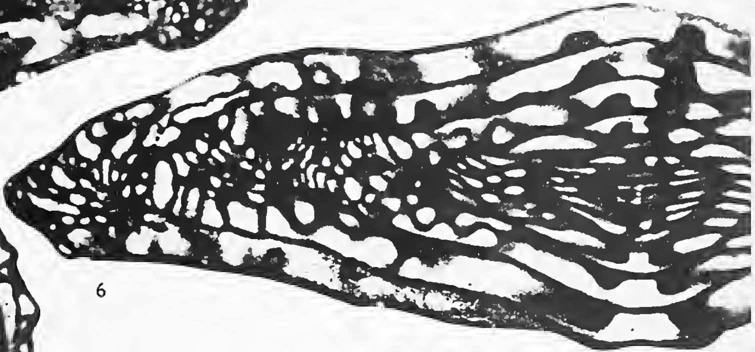
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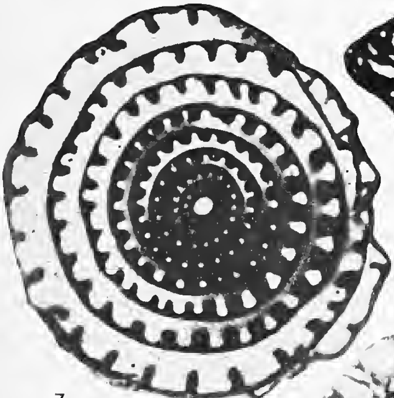
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FORBES, *Fusulinidae from Spitzbergen*, x25.

Similar species of *Fusulinella* are discussed under *F. eopulchra*. *Wearingella bailkeyi* Thompson, Verville, and Bissell, 1950, has a very similar gross appearance but is stated to lack an inner tectorium. *Pseudofusulinella utahensis* is closely similar but rather stouter in proportion to its length.

Genus PROFUSULINELLA Rauzer *et al.*

Remarks. Dunbar *in* Cushman (1948) considered *Profusulinella* to be a junior subjective synonym of *Fusiella* Lee and Chen, both genera being based on small fusulinids with similar wall structure and from similar horizons. Thompson (1948) cites the smaller size, more elongate form, and presence of axial fillings as distinguishing *Fusiella* from *Profusulinella*, and he is here followed in conformity with current Russian practice for the species considered; but if the numerous Russian and American species now known do form a continuous series, all should evidently be placed in *Fusiella*.

Profusulinella cf. *pararhomboides* Rauzer *et al.*

Plate 30, figs. 16–19

Cf. 1951 *Profusulinella pararhomboides* Rauzer and Belyaev *in* Rauzer *et al.*, p. 172, pl. 17, fig. 3.
Cf. 1948 *Profusulinella pararhomboides* Rauzer and Belyaev; Thompson, p. 39, pl. 6, fig. 2.

Description. Fusiform, tapering evenly to bluntly pointed poles, or barrel-shaped with broadly rounded poles. First two whorls usually oblique to axis of later whorls. Septa plane for most of their length, with irregular folding at the extreme poles. Chomata moderately strong, tunnel angle variable, 10°–15°, expanding to 30° or 40° in the fourth whorl or up to 66° in the fifth.

Remarks. My material differs from *P. pararhomboides* in having a greater tendency to rounded ends and smaller prolocula; the spirotheca is also rather thicker.

Genus WEDEKINDELLINA Dunbar and Henbest

Wedekindellina spp.

Plate 30, figs. 14, 15

Remarks. Sections are few and poor, and no axial sections have been obtained. Pl. 30, fig. 15 closely resembles *W. euthysepta* (Henbest), the type species of the genus figured by Thompson (1948), and *W. dutkevichi* Rauzer and Belyaev figured by Rauzer *et al.* (1936; 1951) is also a possible identification.

Genus SCHUBERTELLA Staff and Wedekind

1910 *Schubertella* Staff and Wedekind, p. 121, pl. 4, figs. 7, 8.
1937 *Schubertella* Thompson, p. 120 (including *Eoschubertelle* Thompson, p. 123).

Remarks. My specimens are too few or, in some cases, too poorly preserved to say here what species are present. Material from the Mid Wordiekammen Limestones comprises only the two individuals in Sample 140 identified by Wang as *S. transitoria* Staff and Wedekind. These oblique sections agree fairly well with the original description by Staff and Wedekind (1910), but are rather larger in all dimensions than the larger of their two figured specimens. Thompson (1937) redescribed *S. transitoria* on the basis of material evidently from the Mid Wordiekammen Limestones and he may well be right in suspecting that the magnification of Staff and Wedekind's figures is less than they say. He is more likely to be wrong in suggesting that the figures (which are drawings) are composite, since the authors state that by good luck they found their two well-orientated sections in one slice.

S. transitoria was described by Staff and Wedekind from an unspecified horizon or locality in Spitsbergen. Thompson's material is not from accurately located horizons or localities and the originals should therefore be re-examined before Thompson's 'topotypes' are accepted as such and before his restriction of the species to 'forms with small prolocula' is accepted.

Genus EOFUSULINA Rauzer, *in* Rauzer *et al.*, 1951

Eofusulina cf. *triangula* (Rauzer and Belyaev)

Plate 32, figs. 1, 2

Cf. 1951 *Eofusulina triangula* (Rauzer and Belyaev); Rauzer *et al.*, p. 269, pl. 43, figs. 1, 2.
Cf. 1958 *Eofusulina triangula* (Rauzer and Belyaev); Coogan, p. 307, text-figs. 2, 6.

Description. Slender and biconical with pointed or slightly rounded poles, axis often bent at the proloculum. Septa deeply and regularly folded forming chamberlets over the whole length. Chomata weak or quite absent. Tunnel wide, tunnel angle increasing from 51° to 71°.

Remarks. Specimens are few but attain a larger size, with larger prolocula and more septa per whorl than is given in the published descriptions. The spirotheca is thin but the fine structure is not seen.

Subfamily SCHWAGERININAE Dunbar and Henbest

Genus TRITICITES Girty

Triticites arcticus (Schellwien)

Plate 32, figs. 10–17

1908 *Fusulina arctica* Schellwien, pp. 173–4, pl. 16, figs. 3–9.
1910 *Schellwienia arctica* (Schellwien); Staff and Wedekind, pp. 115–18, pl. 4, figs. 4–6.
1938 *Triticites arcticus* Schellwien; Rauzer, pp. 115–17, pl. 4, figs. 5, 6.

Description. Moderately slender, the flanks curving evenly convex from equator to slightly rounded poles. Septa deeply folded, generally irregular but sometimes in part regular. Septal pores present but not often seen. Tunnel angle irregular, increasing from

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EXPLANATION OF PLATE 32

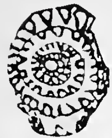
All figures magnified × 10.

Figs. 1–2. *Eofusulina* cf. *triangula* (Rauzer and Belyaev). Passage Beds; sample T 11.

Figs. 3–5. *Quasifusulina longissima* (Möller) s.l. Passage Beds; sample B 372.

Figs. 6–9. *Triticites* cf. *osagensis* Newell, Lower Wordiekammen Limestones. 6–7, Sample S 88 (location not known). 8–9, Sample LM 12.

Figs. 10–17. *Triticites arcticus* (Schellwien). Mid Wordiekammen Limestones. 10–11, Sample LM 5. 12–13, Sample S 29. 14, Sample S 50. 15–17, Sample S 90, pieces 1, 2.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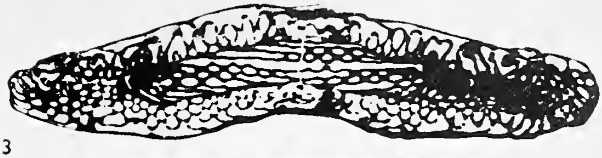
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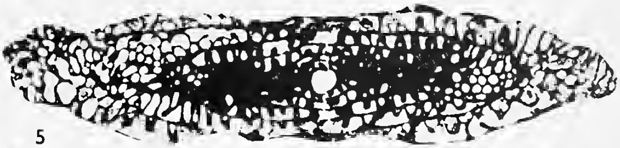
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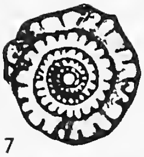
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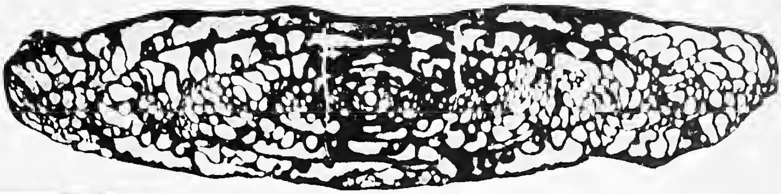
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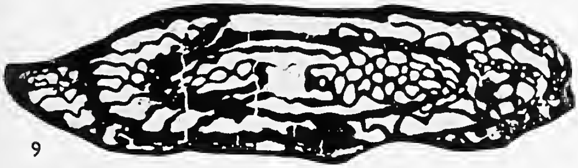
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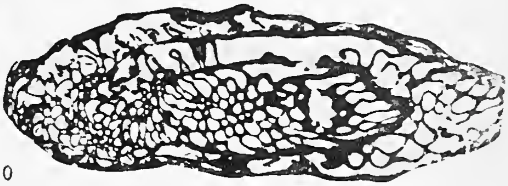
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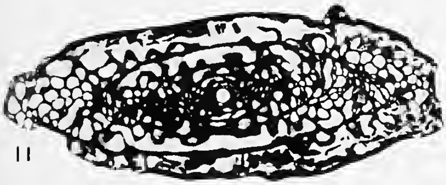
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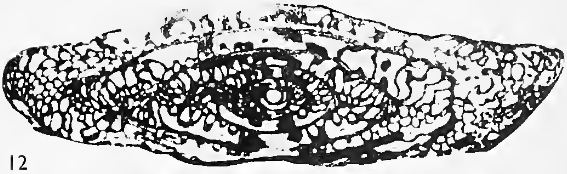
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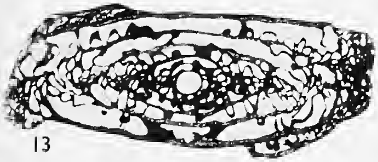
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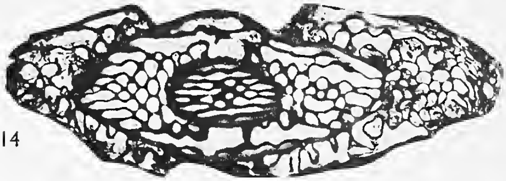
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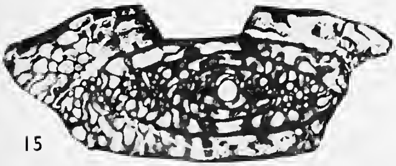
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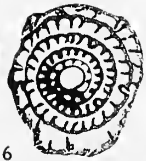
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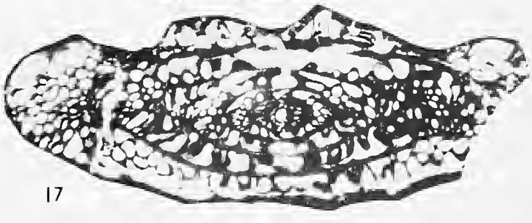
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FORBES, *Fusulinidae from Spitzbergen*, x10.

about 30° in the inner whorls to as much as 50° or 73° in the fifth or sixth whorl. Chomata present in at least the first three whorls. Secondary axial deposits weak or absent.

Remarks. The above description is based on specimens from S 90 pieces 1, 2, which have been investigated in rather more detail than other samples. It seems that the Schwagerinids in these samples are best considered as belonging to one single, highly variable, advanced species, *Triticites arcticus.* No *Schwagerina* species is clearly separable though small specimens may resemble *Schwagerina anderssoni.* This is the conclusion also reached by Schellwien (1908, p. 193) who distinguishes *S. anderssoni* as having more septa in the fourth whorl and more regular septal folding; *S. anderssoni* is described below, and the close similarity of size and axial ratio is seen in Table 1.

The relationship and possible synonymy of *T. arcticus* with '*Fusulina*' *alpina* Schellwien needs further investigation; Staff and Wedekind (1910, p. 118) separate these species on very slight grounds.

Triticites cf. *osagensis* Newell

Plate 32, figs. 6–9

Cf. 1934 *Triticites osagensis* Newell, pp. 423–4, pl. 52, figs. 4*a–f*, pl. 52, fig. 4.
1950 *Triticites* (*Triticites*) *ohioensis* Rozovskaya [*non* Thompson], pp. 22–23, pl. 4, figs. 12–22.

Description. Elongate fusiform, large individuals being especially slender, with bluntly rounded poles. Septa irregularly fluted over the whole length, forming chamberlets and perforated by numerous septal pores, especially near the poles. Chomata weak, and almost obsolete by the outer whorl. Tunnel angle about 20° in the inner whorls expanding widely especially in the outer whorl to about 90° or as much as 105° in one specimen.

Remarks. T. ohioensis of Rozovskaya differs from Thompson's species in having a rather larger proloculum, rather stouter form, seemingly coarser alveolar structure in the inner whorls, and more strongly folded septa. (See Dunbar and Henbest 1942, for an extended account of Thompson's species.)

Of other American species *T. osagensis* Newell agrees quite well with my material and the Russian, but is more slender and has a minute proloculum.

Of other Russian species described by Rozovskaya *T.* (*Rauserites*) *variabilis* is nearest my material but, at least in well-grown specimens, it has a stouter form.

The rapid expansion of the tunnel in the last whorl, which is characteristic of this group of *Triticites*, is very well seen in my material.

This species differs from *T. arcticus* (see above) in having generally a smaller proloculum, a more slender form, very irregular septal fluting, and very numerous large septal pores.

Genus SCHWAGERINA Möller 1877

Type species *Borelis princeps* Ehrenberg

1936 *Schwagerina* Dunbar and Skinner, p. 85.
1948 *Schwagerina* Dunbar *in* Cushman, p. 157.

Remarks. Usage of the name *Schwagerina* is confused. Dunbar *in* Cushman (1948) and

Thompson (1948) use it in slightly different senses; Dunbar keeps *Pseudofusulina* Dunbar and Skinner in synonymy, but Thompson separates it. The usage of recent Russian authors (e.g. Rauzer and Belyaev 1938; Rauzer and Shcherbovich 1949; Rozovskaya 1952) would include the species described below, in *Pseudofusulina*, understanding *Schwagerina* in a sense roughly equivalent to *Paraschwagerina* Dunbar and Skinner. Opinion 213 of the International Commission on Zoological Nomenclature (1954) has, it is to be hoped, stabilized *Schwagerina* in Dunbar and Skinner's sense, as here used.

Schwagerina princeps (Ehrenberg) Dunbar and Skinner

Plate 33, figs. 8–11

1908 *Fusulina krotowi* Schellwien, pp. 190–2, pl. 20, figs. 1–10.
1932 *Schwagerina princeps* (Ehrenberg); de Terra, pp. 155–6, pl. 15, figs. 27–28.
1936 *Schwagerina princeps* (Ehrenberg); Dunbar and Skinner, pp. 86–87, pl. 10, figs. 1–11.

Description. Stout and fusiform, the flanks forming convex slopes to the pointed poles. Chomata weak or nearly absent especially in the outer whorls; tunnel narrow and wandering slightly in an irregular manner with tunnel angle expanding slightly to about 27°.

Remarks. My specimens are few from each sample, but the axial sections are plainly of this species. Comparison with Dunbar and Skinner's redescription of the types shows that my specimens are generally about one whorl larger, rather more elongate, and perhaps with more septa per whorl in the outer whorls. They agree better with Schellwien's *F. krotowi*, which Dunbar and Skinner cite as a synonym of *S. princeps*. See Rauzer and Belyaev (1938) for several species which may be synonyms.

Schwagerina anderssoni (Schellwien)

Plate 33, figs. 1–4; cf. Plate 33, figs. 5–7

1908 *Fusulina anderssoni* Schwellwien, pp. 192–3 (no figures).
1910 *Schellwienia anderssoni* (Schellwien); Staff and Wedekind, pp. 119–20, pl. 3, figs. 1–5.
1927 *Schellwienia anderssoni* (Schellwien); Lee, pp. 57–59, pl. 7, figs. 11–13.
1934 *Pseudofusulina anderssoni* (Schellwien); Chen, pp. 60–62, pl. 4, fig. 20, pl. 5, fig. 15.
1936 *Pseudofusulina anderssoni* (Schellwien); Rauzer *et al.*, pp. 195–7, pl. 4, figs. 1, 2.
1937 *Schwagerina anderssoni* (Schellwien); Thompson, pl. 20, fig. 11.

Description. Fusiform with straight or convex lateral slopes and bluntly pointed poles.

EXPLANATION OF PLATE 33

All figures magnified ×10.

Figs. 1–4. *Schwagerina anderssoni* (Schellwien). Mid Wordiekammen Limestones; sample 140.

Figs. 5–7. *Schwagerina* cf. *anderssoni* (Schellwien). Mid Wordiekammen Limestones; sample S 90, piece 3.

Figs. 8–11. *Schwagerina princeps* (Ehrenberg) Dunbar and Skinner. Upper Wordiekammen Limestones. 8–9, Sample S 91. 10–11, Sample S 10.

Figs. 12–15. *Schwagerina* cf. *emaciata* (Beede). Upper Wordiekammen Limestones. 12–14, Sample 210–14. 15, Sample S 10.

Figs. 16–18. *Schwagerina schwageriniformis* (Rauzer *et al*). Upper Wordiekammen Limestones. 16–17, Sample S 30. 18, Sample S 92.

Figs. 19–20. ?*Parafusulina lutugini* (Schellwien). Upper Wordiekammen Limestones; sample S 32.


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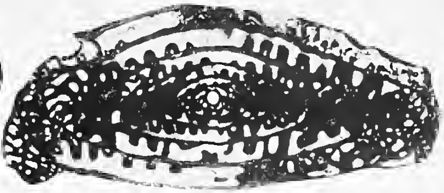
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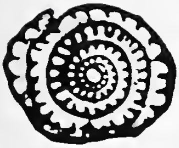
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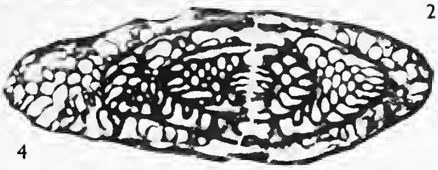
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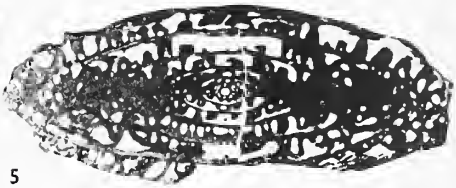
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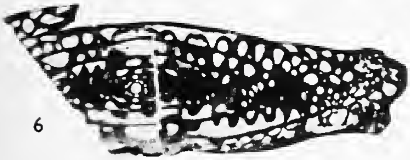
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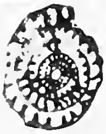
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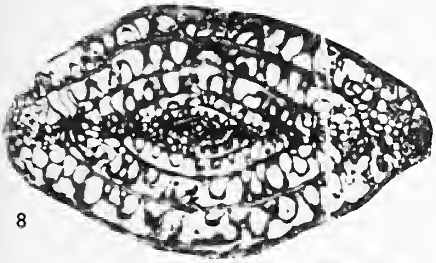
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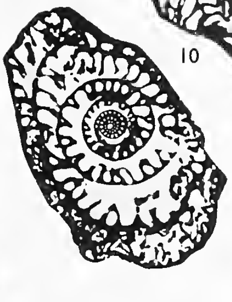
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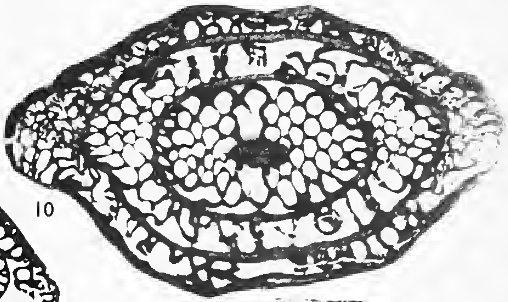
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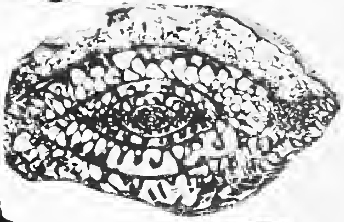
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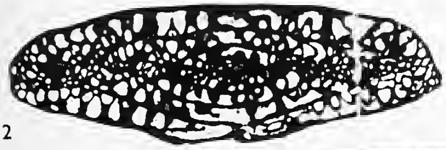
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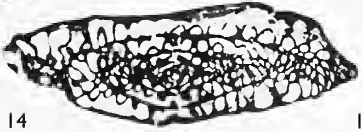
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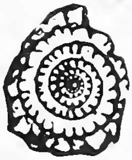
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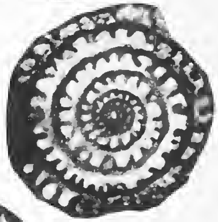
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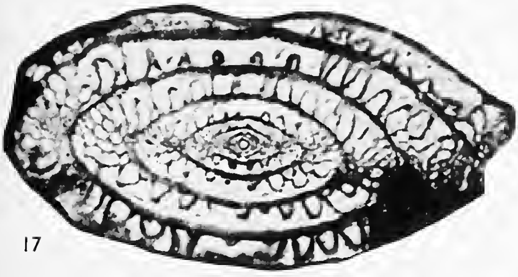
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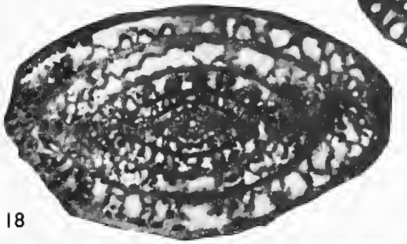
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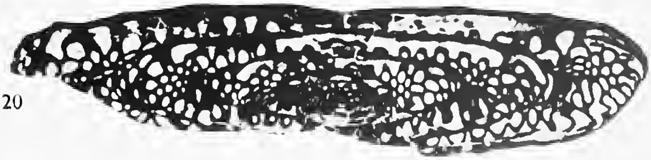
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FORBES, *Fusulinidae from Spitzbergen*, x10.

Septal folds typically high, narrow, and regular with incipient cuniculi. Septal pores not seen. Tunnel angle increasing throughout to an average maximum about 54° in the last whorl. Chomata present, axial deposits well developed.

Remarks. The above description is based on material from sample 140 which comprised one piece of rock only. Samples 130, 139 nominally from the same place yield only *Triticites arcticus*, which differs in having septal folding less regular and less intense, tunnel generally expanding more in the last whorl, slightly larger proloculum, axial deposits quite or nearly absent, and septal pores present. The few *Triticites sp.* present in sample 140 seem to differ from *T. arcticus* in being more slender, with thinner spirotheca and septal folding quite irregular, features which also give a clear differentiation from *Schwagerina anderssoni.*

S. cf. *anderssoni* from sample S 90, piece 3, is in most respects identical with *S. anderssoni* as here described but is rather smaller and more slender; see Table 1.

Schwagerina cf. *emaciata* (Beede)

Plate 33, figs. 12–15

Cf. 1927 *Fusulina emaciata* Beede; Dunbar and Condra, p. 116, pl. 10, figs. 1–3.
Cf. 1937 *Schwagerina emaciata* Beede; Dunbar and Skinner, p. 633, pl. 56, figs. 1–12.

Description. Small and moderately stout with lateral slopes usually straight but sometimes convex; poles rounded or bluntly pointed. Septal folding moderately deep and regular; septal pores not seen. Tunnel angle 30°–57°, average 42°, expanding slowly throughout growth to this value. Chomata present but generally in first four whorls only. Secondary axial deposits generally absent, and never well developed.

Remarks. The dimensions in Table 1 are based on Sample 210–4, specimens in other samples being few but similar. This species is distinguished from others occurring in Spitsbergen by a combination of small size, rather slender habit, and absence of secondary axial deposits. It differs from *S. emaciata* s.s. in being slightly smaller and with a somewhat wider tunnel angle; *S. emaciata* v. *jarillaensis* Needham 1937 is closely similar but has less strongly fluted septa. *S. patens* Dunbar and Newell 1946, *S. providens* Thompson and Hazzard 1946, *S. vervillei* Thompson 1954 are all similar but rather larger, though still small compared to most members of this genus.

Schwagerina schwageriniformis (Rauzer *et al.*)

Plate 33, figs. 16–18

1936 *Pseudofusulina schwageriniformis* Rauzer *et al.*, pp. 198–200, 224, pl. 4, figs. 3–6, pl. 5, fig. 1.

Description. Stout and fusiform with more or less rounded poles and convex rounded flanks. Tunnel angle 23°–44°, average 33°. Axial deposits absent. Chomata absent or nearly so.

Remarks. My individuals are generally smaller than the types, but the largest agree very well.

Genus PARAFUSULINA Dunbar and Skinner
? *Parafusulina lutugini* (Schellwien)

Plate 33, figs. 19–20

?1908 *Fusulina lutugini*, Schellwien, pp. 177–8, pl. 17, figs. 2, 3, 7, 8, 12–14.
?1908 *Fusulina verneuli* (Möller), Schellwien, *partim* (i.e. slender specimens).
?1935 *Pseudofusulina lutugini* (Schellwien); Rauzer, pp. 142–5, pl. 1, figs. 1–5.
?1939 *Parafusulina lutugini* Likharev, p. 40, pl. 3, figs. 6, 7.

Description. Cylindrical with rounded poles. Septal folds rather low but regular. Cuniculi not clearly seen. Tunnel angle 41°, 42° in two axial sections. Chomata present, at least in the earlier whorls. Axial deposits absent or weak.

Remarks. My material comprises few individuals, and I have not seen clearly the generically characteristic cuniculi formed by deep septal folding. The subcylindrical form and minute proloculum are characteristic, but both specific and generic identification must remain doubtful for the present.

Dunbar (1946) quotes Rauzer as having found cuniculi absent in this species, but Likharev must presumably have observed them since he places the species in *Parafusulina*. The matter evidently requires closer investigation.

Parafusulina alaskensis Dunbar 1946 is similar and may be a synonym, if *P. lutugini* is rightly placed in *Parafusulina*. *P. kattaensis* (Schwager) and *P. subtensa* Chernȳshev are similar but have larger prolocula (Dunbar 1946). '*Schellwienia*' *granumavenae* Roemer is a *Schwagerina* species very similar to *P. lutugini*, and considered by Ozawa 1927 to be a senior synonym of it.

Genus QUASIFUSULINA Chen
Quasifusulina longissima (Möller) s.l.

Plate 32, figs. 3–5

1878 *Fusulina longissima* Möller, pp. 59–64, pl. 1, fig. 4; pl. 2, figs. 1*a–c*; pl. 7, figs. 1*a–d*.
1908 *Fusulina longissima* Möller; Schellwien, pp. 163–5, pl. 13, figs. 14–20.
1927 *Schellwienia longissima* Möller; Lee, pp. 111–18; pl. 19, figs. 11–14; pl. 20–21, pl. 22, figs. 1–5.
1934 *Quasifusulina longissima* (Möller); Chen, pp. 92–93, pl. 5, figs. 6–9.

Description. Fusiform, nearly cylindrical. Septal folds forming regular chamberlets. Tunnel angle 18° expanding to about 40° in the outer whorls. Chomata present, not well seen. Secondary axial deposits well developed.

Remarks. The fine structure of the spirotheca is indistinctly seen, but seems to have the pores described by Chen, and by Dunbar *in* Cushman 1948; it is rather thick for this species. The gross appearance of the shell agrees well with Schellwien's description and figures; my specimens are more slender than most of those figured by Chen. The material is too scanty for varietal identification to be attempted here.

Acknowledgements. The work on which this paper is based has been done at the Sedgwick Museum, Cambridge, and I am indebted to my former Supervisor, Mr. A. G. Brighton, for his interest and encouragement at all stages. Mr. W. B. Harland took me as a member on the Cambridge Spitsbergen Expedition 1949, and has since allowed me full access to notes and specimens of several expeditions.

Dr. G. L. Wilde of the Humble Oil and Refining Co. and Dr. N. D. Newell have greatly assisted by discussing various fusulinid problems. I am indebted to the Master and Fellows of Clare College, Cambridge, for a grant and later for a Minor Research Studentship while I have been studying Spitsbergen fossils. All photographs are by Mr. A. Barlow of the Sedgwick Museum.

TABLE 1

All dimensions are in millimetres. The 'Axial Ratio' quoted is the ratio Length: Diameter.

		Pseudostaffella cf. *antiqua*	*Pseudostaffella sphaeroidea*	*Fusulinella bocki*	*Fusulinella eopulchra*	*Fusulinella usvae*	*Profusulinella pararhombiodes*	*Eofusulina triangula*	*Quasifusulina longissima*
Sections	Axial	11	2	3	1	3	3	2	2
measured	Other	6	11	5	8	7	7	4	4
Proloc.	Range	0·03–0·05	0·05–0·09	0·06–0·15	0·12–0·20	0·06–0·19	0·05–0·10	0·20–0·30	0·28–0·44
diam.	Av.	0·04	0·07	0·11	0·15	0·13	0·07	0·25	0·37
Length	Range	0·44–0·76	1·10–1·20	3·30–4·10	2·03–2·76	2·86–6·02	0·84–1·88	2·92–8·20	5·40–8·10
	Av.	0·57		3·83		4·65			
Diameter	Range	0·56–0·84	0·68–1·53	1·29–2·31	0·90–1·55	1·17–1·97	0·50–1·00	0·60–1·80	1·40–1·61
	Av.	0·66	1·08	1·67	1·16	1·70			
Axial	Range	0·68–1·00	0·90–0·95	1·80–2·00	1·97	2·64–3·06	1·70–1·90	4·90–4·95	3·84–5·10
ratio	Av.	0·86	0·93						
No. of whorls		4–5½	5–8½	4–5½	4–6	6–8½	4–5½	2–4½	4–5½
Spirotheca max. thickness		0·15–0·30	0·02–0·04	0·05–0·09	0·02 (apx.)	0·03–0·06	0·01–0·03	0·02–0·03	0·03

		Triticites arcticus	*Triticites* cf. *osagensis*	*Schwagerina princeps*	*Schwagerina anderssoni*	*Schwagerina* cf. *anderssoni*	*Schwagerina schwageriniformis*	*Schwagerina* cf. *emaciata*	?*Parafusulina lutugini*
Sections	Axial	12	9	8	12	17	11	7	2
measured	Other	10	10	7	10	10	7	5	5
Proloc.	Range	0·15–0·32	0·18–0·28	0·07–0·17	0·16–0·24	0·12–0·21	0·13–0·23	0·07–0·12	0·12–0·22
diam.	Av.	0·25	0·24	0·09	0·20	0·17	0·18	0·09	0·14
Length	Range	3·42–8·80	3·0–10·24	3·46–5·90	3·42–7·22	2·90–6·92	4·94–7·40	2·74–5·28	6·66–9·28
	Av.	5·90	7·10	4·59	5·52	4·95	6·58	4·20	7·94
Diameter	Range	1·14–2·71	0·91–2·67	1·72–3·48	1·50–2·54	1·01–2·10	2·34–3·54	1·23–1·97	1·75–2·22
	Av.	2·03	2·50	2·39	1·97	1·45	2·95	1·57	1·97
Axial	Range	2·71–3·27	3·30–4·30	1·54–2·12	2·28–3·45	2·76–4·16	1·93–2·77	2·45–3·20	3·40–4·18
ratio	Av.	2·90	3·77	1·79	2·75	3·35	2·52	2·69	3·69
No. of whorls		4–6	3–6	6–8	5–6½	4½–6½	4½–7	5–6½	5–8
Spirotheca max. thickness		0·06–0·10	0·05–0·08	0·07–0·12	0·06–0·10	0·05–0·07	0·08–0·13	0·07–0·09	0·06–0·09

APPENDIX

List of samples and faunas

(*a*) Samples collected in 1938, including the material identified by Wang *in* Gee *et al.*, table 3.

75–79, 81, 100. Gee *et al.*, table 3 column c, and pl. 2, Section H 740 ft. above base of Black Crag; Upper Wordiekammen Limestones. *Schwagerina schwageriniformis*, including specimens ident. Wang as *Triticites secalicus*, misprinted as *Triticites secularis.*

139. Gee *et al.*, table 3 column 1, and pl. 2, Section H 400 ft. above base of Black Crag; Mid Wordiekammen Limestones. See also sample 140. *Triticites arcticus*, including specimens ident. Wang as *Schwagerina anders*[*s*]*oni.*

140. Location and horizon nominally the same as samples 139 above. *Schwagerina anderssoni*, including specimens ident. Wang as *Schwagerina arctica*, and as *Schwagerina anders*[*s*]*oni. Schubertella sp.*, ident. Wang as *Schubertella transitoria.*

184. Gee *et al.*, table 3 'Watsondalen I', Mid Wordiekammen Limestones. *Triticites arcticus*?, including specimens ident. Wang as *Schwagerina anders*[*s*]*oni*. Insufficient for certain identification.

201. Gee *et al.*, table 3 column 1, and pl. 2, Section I Campbellryggen south-west spur 110 ft. above base of Black Crag; Lower Wordiekammen Limestones. *Fusulinella usvae*, ident. Wang (but not sectioned by him) as *Schwagerina* cf. *arctica.*

210–14. Gee *et al.*, table 3 Tyrellfjellet, north spur, Middle, 560 ft. above base of Black Crag; Upper Wordiekammen Limestones. *Schubertella sp.* Not seen by Wang. *Schwagerina* cf. *emaciata*, including specimens ident. Wang as *Schwagerina anders*[*s*]*oni*, and as *Schwagerina arctica.*

215. Gee *et al.*, table 3 Tyrellfjellet, north spur, Lower, 370 ft. above base of Black Crag; ?Upper Wordiekammen Limestones. ?*Triticites arcticus*, ill-preserved material including specimens ident. Wang as *Schwagerina arctica.*

286 Gee *et al.*, table 3 and pl. 2, Section D, Campbellryggen north-east spur. Lower 740 ft. above base of Black Crag; Upper Wordiekammen Limestones. ?*Schwagerina princeps* and *Schwagerina sp.*, ill-preserved material including specimens ident. Wang as *Schwagerina arctica.*

(*b*) Samples collected after 1938 and not seen by Wang. Place names and locations refer to Gee *et al.*, pl. 1, unless otherwise stated.

B 372. To the north of mid-Chydeniusbreen above Raudryggen, about 20 miles north-east of the area shown by Gee *et al.*, pl. 1. Passage Beds. *Fusulinella bocki*, *Wedekindellina sp*?, *Quasifusulina longissima*, s. 1.

F 30. Highest exposed bed of massive limestone, just below rubbly limestone; east spur of Ferrierfjellet, Black Crag, Lower Wordiekammen Limestones. *Ozawainella sp.*, *Wedekindellina sp.*

F 36. Near base of 45 ft. massive grey crag-forming limestone, i.e., about 20 ft. above highest gypsum; north side of Urmstonfjellet; lat. 78° 37·5′ N., long. 17° 10′ E. Passage Beds. *Pseudostaffella sphaeroidea*, *Ozawainella sp.*

F 51. Lower part of 11 ft. grey limestone with base 33 ft. above unconformity at base of Carboniferous; spur of Minkinfjellet; lat. 78° 38′ N., long. 17° 22′ E. Passage Beds. *Pseudostaffella* cf. *antiqua.*

F 83. 4 ft. carious limestone with base 186 ft. above top of bed containing F 51. Passage Beds. *Profusulinella* cf. *pararhomboides.*

F 85. Near base of 10 ft. dark limestones, with base 15 ft. above F 83. Passage Beds. ?*Ozawainella sp.*, *Fusulinella eopulchra*, *Profusulinella pararhomboides*, *Pseudostaffella sphaeroidea.*

LM 5. Black bituminous limestone; stream section below Burn Murdochbreen; Mid Wordiekammen Limestones. *Triticites arcticus.*

LM 12. Black bituminous limestone, about 40 ft. stratigraphic thickness below LM 5. Lower Wordiekammen Limestones. *Schubertella sp.*, *Triticites* cf. *osagensis.*

R 64. Massive grey limestone; about 1½ km. south of fault outcrop on shore between Anservika and Phantomodden. ?Black Crag. ?*Pseudostaffella sphaeroidea*, *Ozawainella sp.*, *Fusulinella eopulchra*? *Wedekindellina sp.*

S 10. Black limestone with shale partings. Gee *et al.*, pl. 3. Section N, 410 ft. above base of Black Crag, Upper Wordiekammen Limestones. *Schwagerina princeps*, *Schwagerina* cf. *emaciata*, *Schubertella sp.*

S 29. 10 ft. Black fusuline limestone above scree. Gee *et al.*, pl. 2, Section J, 420 ft. above base of Black Crag. Mid Wordiekammen Limestones. *Triticites arcticus.*

S 30. Pale grey-brown siliceous limestone at asterisk 200 ft., above S 29. Upper Wordiekammen Limestone. *Schubertella sp.*, *Schwagerina schwageriniformis.*

S 32. Pale-grey limestone with fusulinids partly silicified, asterisk 130 ft. above S 30. Upper Wordiekammen Limestones. ?*Parafusulina lutugini.*

S 41. Black fusulinid limestone 20 ft. thick base about 620 ft. above base of Black Crag; near summit of Wordiekammen; lat. 78° 41·5′ N., long. 16° 41·5′ E. Mid Wordiekammen Limestones. *Triticites arcticus.*

S 43. Grey limestone 30 ft. thick to summit of hill above S 41. Upper Wordiekammen Limestones. *Schwagerina princeps*, *Schwagerina anderssoni*, *Schwagerina* cf. *emaciata*?

S 48. 5 ft. black limestone, base at 600 ft. below base of Black Crag south-east flank of De Geerfjellet; lat. 78° 41·5′ N., long. 16° 50′ E. Passage Beds. *Fusulinella eopulchra.*

S 50. Black limestone at summit of De Geerfjellet, 360 ft. above base of Black Crag, point marked 1022. Mid Wordiekammen Limestones. *Triticites arcticus.*

S 66. 10 ft. grey porcellanous limestone, base 400 ft. above base of Black Crag. Gee *et al.*, pl. 3 and text-fig. 3, Section L. Lower Wordiekammen Limestones. *Triticites* cf. *osagensis*, *Schubertella sp.*

S 67. 5 ft. black limestone base 57 ft. above S 68. Mid Wordiekammen Limestones. *Triticites arcticus.*

S 85. 70 ft. massive grey bedded limestone, lower part of Limestone B, Upper Wordiekammen Limestones; lat. 78° 31·5′ N., long. 16° 30·5′ E. ?*Schwagerina princeps.*

S 90. 26 ft. black carbonaceous fusulina limestone, base 363 ft. above base of Black Crag, 9th bed up in Singleton's Campbellryggen North Section, Gee *et al.*, p. 328. Mid Wordiekammen Limestones. The sample comprises several pieces of which three have been examined: Pieces 1 and 2. *Triticites arcticus.* Abundant. Piece 3. *Schwagerina* cf. *anderssoni*, *Fusulinella usvae.*

S 91. 30 ft. limestone including 3 ft. flinty bed at the top, base 459 ft. above base of Black Crag. 11th bed up in Singleton's section, see S 90. Upper Wordiekammen Limestones. *Schwagerina princeps*, *Fusulinella usvae.*

S 92. 9 ft. limestone below main cliff, base about 600 ft. above base of Black Crag, included in thick fossiliferous limestone cliff (Limestone B) of Singleton's section, see S 90. Upper Wordiekammen Limestones. *Schwagerina schwageriniformis.*

T 11. 10 ft. limestone, top 400 ft. below base of Black Crag; lat. 78° 44·2′ N., long. 17° 5′ E. Passage Beds. *Pseudostaffella sphaeroidea*, *Ozawainella sp.*, *Eofusulina* cf. *triangula*, *Fusulinella eopulchra*?

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A NEW VARIETY OF *ORTHORETIOLITES HAMI* WHITTINGTON

by D. SKEVINGTON

ABSTRACT. A variety of *Orthoretiolites hami* Whittington is recorded from two levels in the Viola limestone of Oklahoma. The varietal distinction is based on the more robust nature of the clathria and the presence of a structureless periderm. Early growth stages recovered illustrate the initial development of the species *O. hami* whilst adult stages are represented in several rhabdosomes. It is concluded that, in spite of its mode of development, the genus *Orthoretiolites* could be most conveniently placed in the family Retiolitidae.

INTRODUCTION

NUMEROUS specimens of a variety of *O. hami* were recovered from fragments of Ordovician Viola limestone collected by Dr. P. K. Sutherland from a horizon 50 feet above the base in the Criner Hills at Rock Crossing, 6 miles south-west of Ardmore, Oklahoma. These include growth stages both earlier and later than those which Whittington obtained of his species, *O. hami*; though differing in certain structural features, to be described later, the actual mode of development of the two forms is identical. The purpose of this note is to clarify one or two points, concerning early development, which Whittington had, of necessity, to leave undecided; to justify the creation of a variety of the species *O. hami*; and to comment on the affinities of the genus *Orthoretiolites*.

The fragments of limestone were left to decalcify in strong HCl for about three weeks; they were then washed and transferred to HF for from four to five hours, by which time the limestone was usually completely broken down and the graptolites set free; the specimens ranged from immature siculae to seemingly adult rhabdosomes. The early growth stages were cleared in a solution of concentrated nitric acid and potassium chlorate, dehydrated in alcohol, and mounted in euparal. No attempt was made to clear the larger specimens, which were also mounted in euparal.

The author is indebted to Professor O. M. B. Bulman for his supervision throughout the preparation of this paper. Thanks are due also to Dr. P. K. Sutherland who collected the material. The originals of all figured specimens are in the Sedgwick Museum, Cambridge, and numbered A24581–600.

Orthoretiolites hami Whittington var. *robustus* nov.

Plates 34 and 35

1934 *Lasiograptus* (*Thysanograptus*) *eucharis* Ruedemann and Decker (non Hall), pp. 324–6, pl. 43, figs. 18–20.
1945 (?) *Lasiograptus* (*Thysanograptus*) *eucharis* Decker and Coleman, *Bull. Amer. Ass. Petrol. Geol.* **29**, p. 457, pl. 1, fig. 1.
1947 *Lasiograptus* (*Thysanograptus*) *eucharis* Ruedemann, pl. 82, figs. 23–26.
1950 (non) *Lasiograptus* (*Thysanograptus*) *eucharis* Decker. *Bull. Amer. Ass. Petrol. Geol.* **34**, pp. 1904, 1908–9, pl. 1, fig. 19.

Diagnosis. Rhabdosome 1 mm. in width at first thecal pair (excluding apertural spines), increasing to 2·2 mm. at fifth pair, thereafter increase slight. Greatest length preserved

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7·7 mm. Sicula and proximal parts of th1^1, th1^2, and th2^1 provided with complete periderm, remainder of rhabdosome represented by clathria with covering of structureless periderm (presumably cortical tissue alone). Virgula straight, central, and confined to obverse wall; reverse wall has zigzag 'virgula'. Paired lateral spines developed infrequently on true virgula. Development non-septate diplograptid, thecae alternating and of orthograptid type with straight ventral walls and provided with long, single, apertural spines. Thecae numbering 15 in 10 mm. at proximal end; probably about 12 in 10 mm. distally.

Description. In a comparison of Whittington's holotype (Specimen MCZ 511—see Whittington 1954, p. 615, fig. 4) with the specimens collected from the 50-foot level in the limestone, two differences are at once apparent: (*a*) the stouter clathrial lists and more pronounced lateral spines of the latter; and (*b*) the presence, in some of the latter, of a periderm throughout the rhabdosome of the larger growth stages and adult specimens.

Every specimen of *Orthoretiolites* collected from the 50-foot horizon possesses lists which are much stouter than those of Whittington's species. The fact that this feature is shown by even the earliest growth stages which possess lists indicates that it is not developed only with the onset of maturity. The lateral spines are similarly more strongly developed. Furthermore, their arrangement shows a marked tendency towards regularity; thus, a pair of such spines—one obverse and one reverse—is present on the sicula, about one-third of the distance down from the base of the nema (Pl. 34, fig. 3). Both spines are directed outwards approximately normal to the axis of the rhabdosome. The obverse spine is unrelated to the skeletal framework, but the reverse spine, on the other hand, is linked with the rods of the clathria. In specimen A24592 (Pl. 34, fig. 3) it passes through the mid-point of the dorsal list of th2^2, whilst in specimen A24594 (Pl. 35, fig. 2) it cuts across the junction of the dorsal lists of th2^1 and th2^2 and the parietal list between th2^1 and th3^1. Thus, in its initial part, between the sicula and the clathrial lists, the reverse spine functions as an additional, transverse list, strengthening the clathria. A similar pair of spines may be present at the level of the fourth or fifth thecal pairs (Pl. 35, fig. 2). These spines are again obverse and reverse and both originate at the same level on the virgula proper; in consequence, the reverse spine, in its early part, again acts as a transverse list, in this case linking the obverse and reverse walls of the clathria in the mid-line.

In *Orthoretiolites hami*, continuous periderm is present only in the sicula and the proximal parts of th1^1, th1^2, and th2^1, though Whittington (1954) states that shreds of this material are occasionally found in more distal thecae, in the angles between the lists of the clathria. On the other hand, with a single exception (Pl. 34, fig. 2), all the adult and later growth stage specimens from the 50-foot level—together with examples from a horizon 3 feet above the base at the same locality—show a damaged, though apparently once continuous, periderm throughout (Pl. 34, fig. 3; Pl. 35, figs. 1–4). This periderm is quite structureless and presumably represents only cortical tissue. Several growth stages, younger than Whittington's holotype, show this periderm, which again is therefore not a feature acquired only at a late stage in development.

In spite of the features noted above, the mode of development, the extent of fusellar tissue, and the arrangement of the clathrial lists correspond in the specimens from the two levels. The differences which exist are a matter only of degree and do not merit the erection of a new species. They represent, at the most, a variety of *O. hami*—an ancestral form in which the reduction of the skeleton had not progressed so far as in the typical *O. hami*—for which the name *robustus* is proposed.

Additional material, collected 3 feet above the base of the limestone, possesses features identical with those of specimens from the 50-foot horizon and it can be concluded that this material also belongs to the new variety of Whittington's species (Pl. 35, figs. 3, 4).

Development. The prosicula is typically subcylindrical in shape. At its proximal end it merges into the base of the nema and shortly below this point it attains a width which is retained, with little increase, to its distal margin. In the original of text-fig. 1*b* the prosicula is 0·31 mm. in length and 0·10 mm. in width at the margin; in text-fig. 2*b* the respective dimensions are 0·31 mm. and 0·11 mm. In one specimen, text-fig. 1*e*, there is, however, a slight contraction towards the apertural margin, the maximum width being at a level about two-thirds of the way down the prosicula. In the original of text-fig. 1*a* the prosicula is missing and the 'bifurcating virgula' is attached directly to the metasicula. The longitudinal rods are four or five in number and extend the length of the prosicula; the intervening, short, secondary rods, growing up from the margin, total eight or more.

The slight increase in diameter of the prosicula towards its distal margin is followed by a much more definite increase in the proximal part of the metasicula. The growth lines in this initial part of the metasicula are closely spaced and meet, on both the virgellar and anti-virgellar sides, along a zigzag suture. On the anti-virgellar side, as noted by Whittington, the margins of the chitinous growth bands are straight, but on the virgellar side they bend downwards to a progressively increasing degree as the origin of the virgella is approached, becoming asymptotic to the long axis of the sicula as they pass into the virgella (text-figs, 1*c*, *d*, *e*). This latter originates usually between 0·20 and 0·30 mm. below the prosicular margin, but in one specimen this distance is only 0·15 mm. (text-fig. 1*d*). At about the level of the virgella origin there is typically a marked increase in the width of the metasicula; the diameter thus attained remains more or less constant to the aperture.

Variation in the shape of the sicula was a feature commented upon by Whittington and can be verified by a consideration of the accompanying text-figures, the originals of which were preserved in full relief. Despite the variety of shapes possible, however, there is a form typical of the species having a subcylindrical prosicula and showing expansion of the proximal part of the metasicula down to the level of the virgella origin, where a swelling occurs giving an increase in diameter which is more or less retained to the aperture.

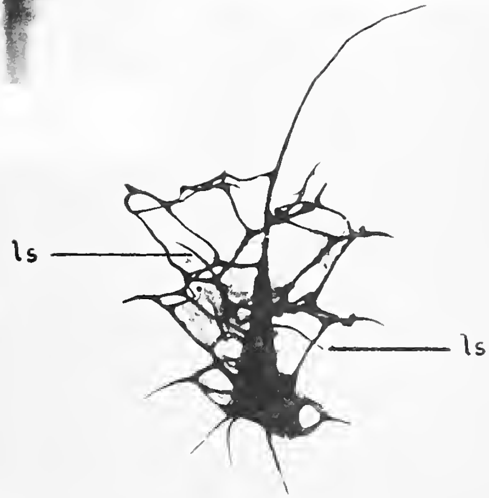
In the earliest growth stages of the metasicula, before the appearance of the virgella proper, the position of that feature on the growing edge is marked by a blunt tubercle. In later stages, however, the virgella forms a prominent part of the metasicula and in the fully developed sicula it projects as a spine below the aperture, only slightly less than the length of the metasicula itself; thus, in the original of text-fig. 1*f*, the metasicula measures 0·55 mm. and the virgella extends a further 0·42 mm. beyond the level of the aperture.

EXPLANATION OF PLATE 34

Figs. 1–3. *Orthoretiolites hami* Whittington var. *robustus* nov. Viola limestone, 50 feet above the base, at Rock Crossing, 6 miles south-west of Ardmore, Criner Hills, Oklahoma. 1, Reverse view, $th1^1$ incomplete, flange representing proximal part of $th1^2$, ×86. A24590. 2, Obverse view, growth stage with four thecae complete, total absence of structureless periderm, ×20. A24591, 3, Reverse view, growth stage with six thecae complete, note patches of periderm. *ls*—lateral spine. ×20. A24592.

1

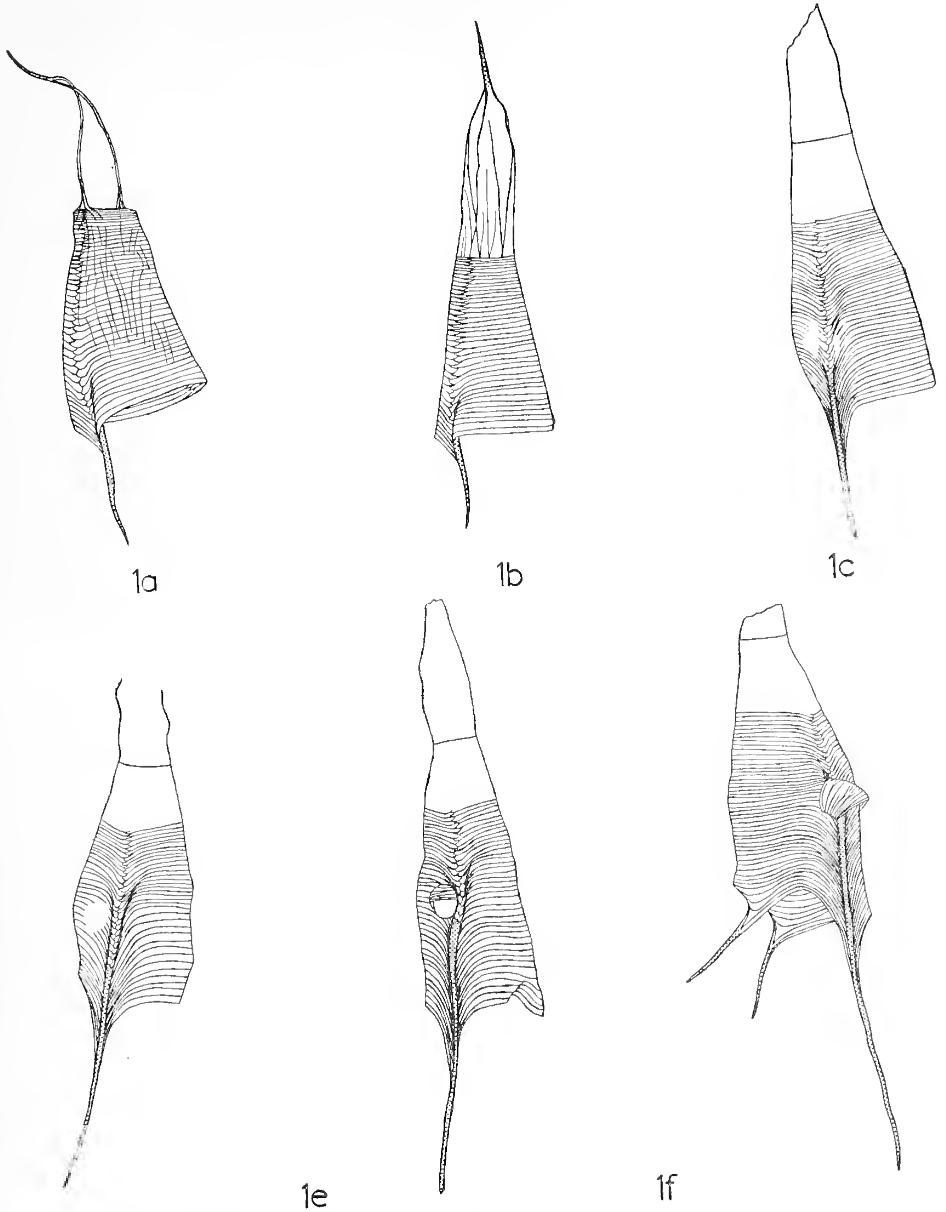
2



3

SKEVINGTON, *Orthoretiolites*.

On the anti-virgellar side of the metasicular aperture are two diverging spines directed outwards and downwards and making an angle of 45° with the axis of the sicula. In fully mature siculae the spines may attain a length of 0·25 mm. The two spines are



TEXT-FIG. 1. *Orthoretiolites hami* Whittington var. *robustus* nov. Stages of growth up to the appearance of the initial bud, ×35. *a*, Malformed immature sicula A24581. *b*, Prosicula complete, beginning of metasicula and appearance of virgella. A24582. *c*, Appearance of resorption foramen; specimen slightly damaged. A24583. *d*, Foramen complete, virgella prominent. A24584. *e*, Initial bud, development of apertural spines on sicula. A24585. *f*, Initial bud, sicula complete. A24586.

separated by a section of the apertural margin along which growth has been checked, resulting in an embayment which may extend proximally for as much as 0·11 mm. above the general level of the aperture. In addition, the apertural margin of the sicula commonly exhibits a noticeable thickening.

The foramen, marking the point at which the initial bud—the proximal part of th1^1—originates, is produced by the resorption of periderm (text-figs. 1*c*, *d*). It is situated just distally to the virgellar origin, and to the left of that feature. The foramen is formed at or about the stage when the apertural spines are beginning to develop; it lies below the mid-point of the metasicula and typically three-fifths of the distance from the prosicular aperture. The initial bud originates as a hood at the top of the foramen (text-fig. 1*e*). In the very early stages of formation growth is directed outwards from the sicula and downwards towards the sicular aperture; by the time the bud has grown to the level of the lower rim of the foramen the sicular is normally fully developed. The direction of growth of the bud soon changes so that the right-hand edge crosses the virgella to the obverse side of the sicula; the left-hand edge of the bud grows towards the virgella, and may pass on to it, but does not cross it.

At approximately the stage of growth represented by the original of text-fig. 2*a*, growth is checked along the left-hand, or reverse, growing edge of the initial bud—thus producing an embayment which becomes the upper rim of the foramen of th1^2. This latter, therefore, takes the form of a primary notch, as distinct from the resorption foramen of th1^1. Further growth of th1^2 is by the addition of periderm to the outer margin of the foramen, producing a flap or flange (text-fig. 2*b*), and this is contemporaneous with the continued development of th1^1. In its earliest stage, therefore, th1^2 is elongated parallel to the axis of the sicula, and at the same time its outer margin is extended round the reverse wall of the sicula, and generally towards the anti-virgellar side. When complete, the margin of the foramen is oval in shape. Text-fig. 2*b* shows an early stage in the development of the flange, and the growth lines of this feature indicate that the direction of growth is downwards (towards the metasicular aperture), across (towards the anti-virgellar side of the sicula), and outwards so as to form a sheath-like structure about the sicula. The right-hand, or obverse, wall of the initial bud is unaffected by flange development and continues to grow downwards until the level of the metasicular aperture is reached.

In the original of text-fig. 3 the flange has extended across the metasicula, half-way to the anti-virgellar side, and downwards, partly obscuring the foramen of th1^2. The flange is in contact with the sicula along its upper edge, and with the outer margin of the foramen; the inner margin of this latter is coincident with the virgella. The growing edge of the flange is affected by folding, but it is probable that this is mostly a preservational

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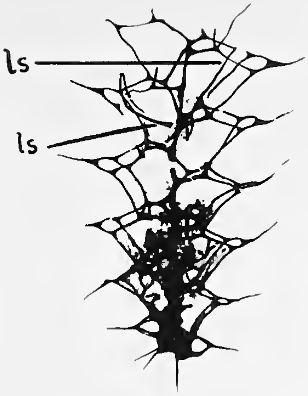
EXPLANATION OF PLATE 35

Figs. 1–4. *Orthoretiolites hami* Whittington var. *robustus* nov. 1, 2, Viola limestone, 50 feet above the base, at Rock Crossing, 6 miles south-west of Ardmore, Criner Hills, Oklahoma. 1, Obverse view, adult rhabdosome extending to seventh thecal pair, structureless periderm strongly in evidence. × 10. A24593. 2*a*, Reverse view, damaged adult rhabdosome, note pair of lateral spines (*ls*) developed at fifth thecal pair. × 10, A24594. 2*b*, Obverse view of same. 3, 4, Viola limestone, 3 feet above the base, at Rock Crossing. 3, Part of surface of fragment of Viola limestone. Obverse view with fourteen thecae visible; darker patches within the thecae represent the structureless periderm. × 15. A24599. 4, Ditto. Several specimens crushed together, periderm clearly developed. × 15. A24600.

1



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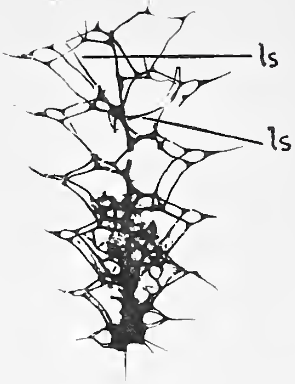

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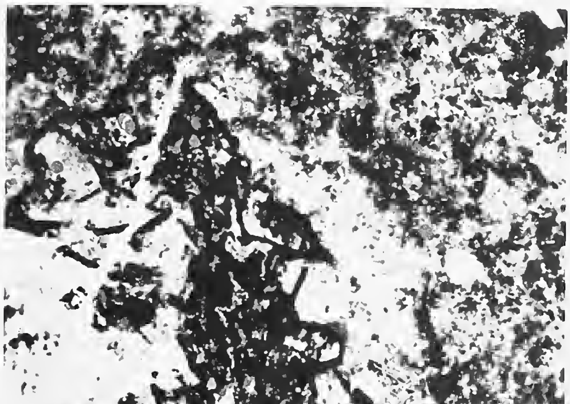
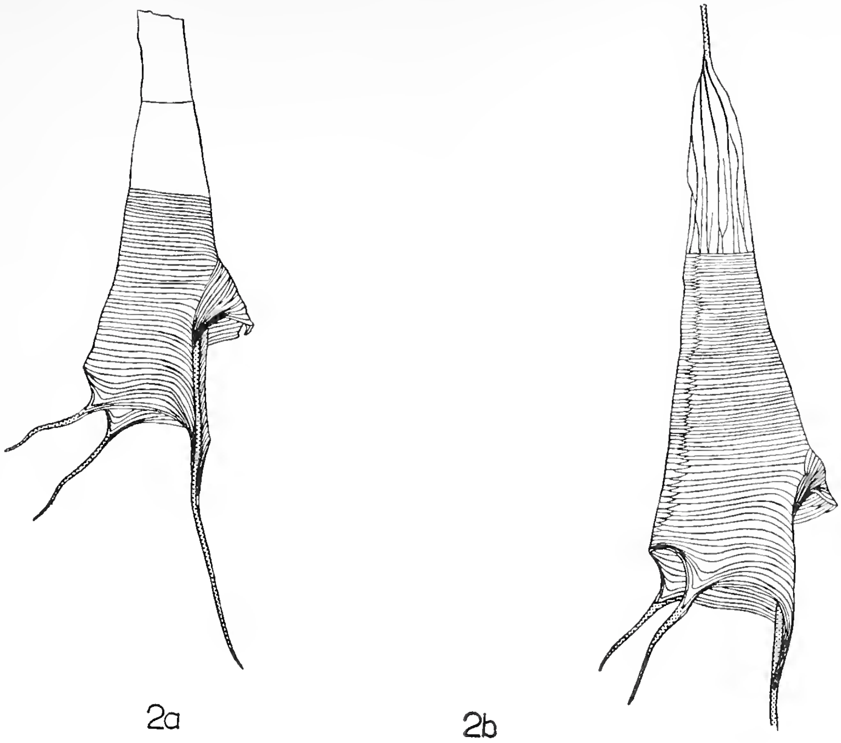
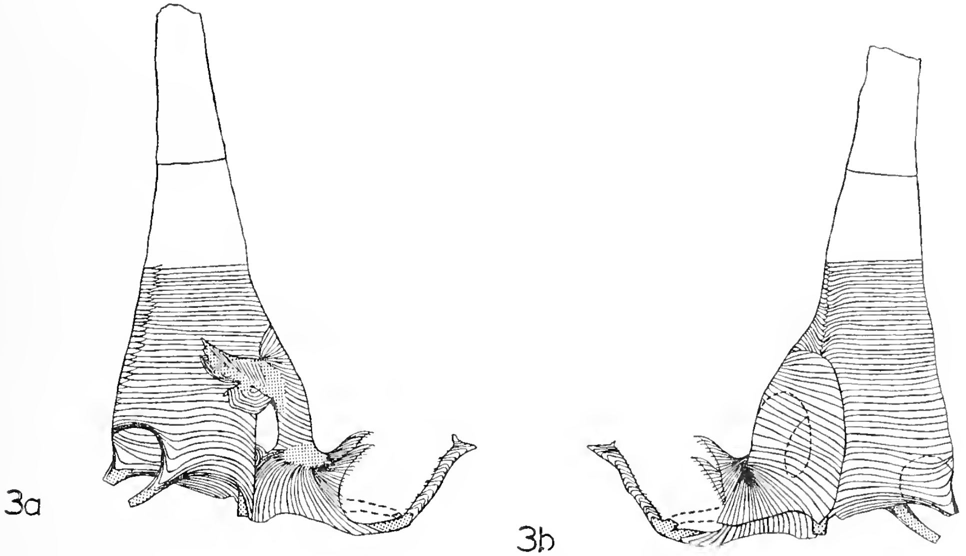


SKEVINGTON, *Orthoretiolites.*





TEXT-FIGS. 2, 3. *Orthoretiolites hami* Whittington var. *robustus* nov. Initial development of th1^2, ×35. 2*a*. Reverse view, appearance of the foramen of h1^2 in the reverse wall of the initial bud. A24587. 2*b*. Reverse view, appearance of the flange. A24588. 3*a*. Reverse view, th1^1 incomplete, flange representing proximal part of th1^2. A24589. 3*b*. Obverse view of same.

feature. The growth lines on the flange are quite indistinct, except in one part where the flange lies above the virgella; elsewhere, only vaguely defined striations are evident, very closely set, but parallel to the directions in which one would have expected the growth lines to trend.

Down to approximately the level of the lower rim of the foramen of th1^2, th1^1 grows as a hood which is interrupted only on its reverse side by the formation of that foramen. Below this level, however, striking developments occur (text-fig. 3; Pl. 34, fig. 1). At the level of the metasicular aperture the obverse side of th1^1 recrosses the virgella and the growth of this theca as a whole is then directed outwards normal to the sicula axis. At a short distance from the sicula the growth of thl^1 becomes concentrated along its obverse and reverse edges, both dorsally and ventrally. The dorsal obverse and reverse edges become respectively the obverse and reverse parietal lists of thl^1; in their subsequent growth these lists diverge and are directed upwards and away from the sicula. The obverse and reverse ventral lists develop from the respective ventral edges and their direction of growth is such that they extend outwards, away from the sicula, and also towards each other, so that eventually they meet and fuse. The single ventral list so produced continues to grow, but in a different direction: upwards and outwards, away from the sicula. When this single list has reached the level of the base of the foramen of th1^2, a second change in growth direction is begun, and it is at this point that the single ventral list becomes the apertural spine of th1^1. The method of formation of the lists is best illustrated by reference to text-fig. 3, which shows the detailed courses of the growth lines.

It is highly probable that, at the stage represented by the original of text-fig. 3, the lateral walls of the free part of th1^1, between the parietal and ventral lists, were present, being formed of a periderm so thin as to defy preservation. This is suggested by the course of the growth lines of the parietal lists which project beyond the intervening preserved periderm and are directed towards the ventral lists and their fused representative (text-fig. 3). This may be true also of the dorsal and ventral walls of the free part of th1^1, but there is no similar evidence to support this contention.

Specimen A24595—which is too poorly preserved to be figured—is a slightly later stage than the original of Pl. 34, fig. 1, and it shows the beginnings of the two pleural lists necessary to complete th1^1. These lists originate at the base of the apertural spine and they grow towards the terminal points of the respective parietal lists, which have turned slightly out and down to meet the pleural lists. These two lists—obverse and reverse—are essentially backward projections of the apertural spine, with which they are in alignment.

In the latest early growth stage recovered—Pl. 34, fig. 1—apart from the damaged specimen A24595, the flange has extended down to the level of the base of the foramen of th1^2 and across almost to the anti-virgellar side of the sicula. The growth is still, in general, across the sicula, but now there is an upward tendency as distinct from the earlier downward one. The detailed form of the upper edge of the flange is uncertain, but there appears to be incipient development of a spine which is directed upwards and across the sicula—this will become the reverse parietal list of th1^2. The blunt tubercle on the anti-virgellar side of the sicula is the initial part of the obverse pleural list of th1^2.

Growth lines on the flange are discernible only in the vicinity of its growing edge, and the remaining part is either composed of a structureless film or is missing altogether, presumably having been too thin to be preserved and thus paralleling the case of the distal lateral walls of th1^1, as noted above. Several of the adult specimens show the flange incompletely developed—just as the distal part of th1^1 shows no trace of fusellar material; yet, in both features, the early growth stages provide evidence that fusellar tissue was present. Thus, it may have existed during the life of the graptolite colony, but was too delicate to be preserved.

THE VALIDITY OF WHITTINGTON'S PARIETAL LIST

Holm defined the parietal list as the outer line of contact with the theca immediately above or below; that is, it would represent the trace of the interthecal septum on the lateral wall of the rhabdosome, if such a septum were present.

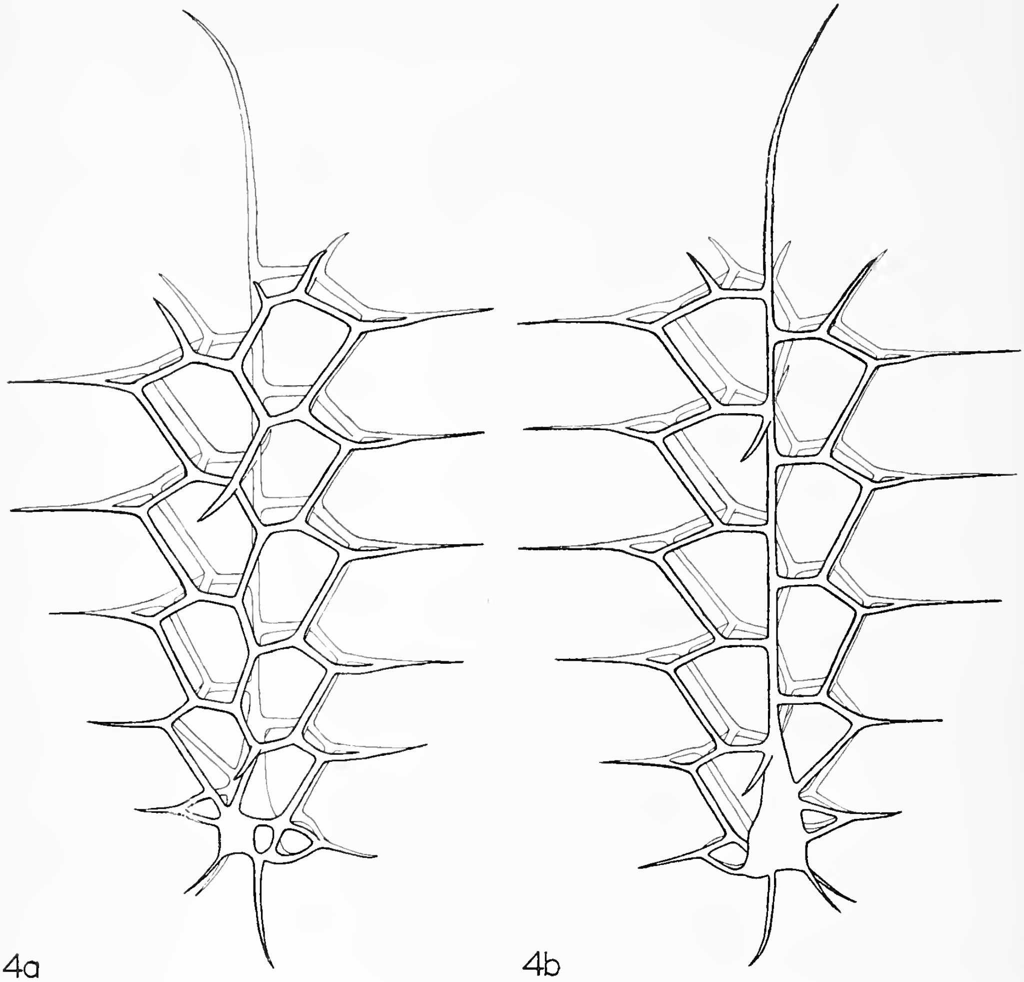
The list which Whittington defines as parietal is, in *Orthoretiolites*, inclined at a remarkably high angle to the ventral list with which it is in contact. It might be expected that the interthecal septum, if present, would lie approximately parallel to the free ventral wall of which it is the internal continuation—especially as Whittington claims the thecae to be of 'orthograptid type with straight ventral wall' (1954, p. 614). Bearing this in mind, two possibilities exist regarding the mutual relationship of the thecae in *Orthoretiolites*. If it is assumed that the interthecal septa were present but not preserved, nor their margins indicated by lists on the walls of the rhabdosome, then adjacent thecae overlapped to an unknown extent, and the parietal list of Whittington is, in reality, a connecting rod (Bouček and Münch 1952). On the other hand, if Whittington's parietal list is correctly identified, it may very well correspond to that small section of the parietal list which, in Holm's diagram of a retiolitid (reproduced in Elles and Wood 1908, p. 337, fig. 220*f*), is separated from the main part of the list by a geniculate bend. Admittedly, the orientation of the lists in the two cases is different, but Holm's diagram is of a retiolitid with completely overlapping thecae. If this should be the correct interpretation then, in *Orthoretiolites*, the thecae overlap for approximately one-quarter of their length.

AFFINITIES OF THE GENUS

The incorporation of the virgula into one of the lateral walls of the rhabdosome (text-fig. 4) gives *Orthoretiolites* a superficial resemblance to certain retiolitids, in particular *Paraplectograptus* Bouček and Münch 1948 and *Retiolites* Barrande 1850. In addition, Whittington has noted the features which distinguish his genus from two other retiolitid genera: *Plegmatograptus* Elles and Wood 1908 and *Archiretiolites* Eisenack 1935. A detailed comparison of *Paraplectograptus* and *Retiolites* with *Orthoretiolites* likewise reveals important differences. *Paraplectograptus* lacks both dorsal and parietal lists and possesses instead diagonal lists; whereas, in this genus, the zigzag 'virgula' is formed of diagonal lists, in *Orthoretiolites* it is the dorsal lists which are responsible for that feature (text-fig. 4). Neither lateral nor apertural spines have been recorded, and the corona takes the place of the chitinized sicula; the shape and course of the thecae in *Paraplectograptus* are unknown and a comparison cannot, therefore, be attempted.

In *Retiolites* the thecae are completely overlapping and, in consequence, ventral lists cannot be present. On the other hand, *Orthoretiolites* has nothing to compare with the aboral (or interior) list of *Retiolites*. Furthermore, the deficient chitinization of the sicula of the latter serves also to distinguish it from Whittington's genus.

The discovery of adult rhabdosomes further justifies the erection of the genus *Orthoretiolites* Whittington, which cannot be associated with any genus at present included in the family Retiolitidae. It is provisionally placed in the sub-family Archiretiolitinae, although a superficial resemblance to such genera as *Paraplectograptus* and *Retiolites* suggests that it may be a parallel development to later retiolitids. Whittington preferred to regard the genus as a diplograptid; certainly the development is of diplograptid type, but so also is that of *Archiretiolites*, *Plegmatograptus* and ?*Retiograptus* Hall 1859, all of which are at present grouped in the sub-family Archiretiolitinae of the family Retiolitidae.



TEXT-FIG. 4. *Orthoretiolites hami* Whittington var. *robustus* nov. Diagrammatical reconstruction of the clathria, ×20. Dimensions are based on measurements of specimens A24593 and A24594 but, apart from the width of the lists, this reconstruction may be regarded as typical of the genus. *a*, Reverse side, *b*, Obverse side.

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AN OPPOSITE-LEAVED CONIFER FROM THE JURASSIC OF ISRAEL

by W. G. CHALONER and J. LORCH

Abstract. *Cupressinocladus ramonensis* sp. nov., a species of Jurassic conifer based on compressions of leafy shoots, is described, and the genus *Cupressinocladus* Seward emended. The material is from the Makhtesh Ramon (Wadi Raman) in southern Israel. The leaves are small, closely appressed, and are decussate in arrangement, suggesting comparison with the living Cupressaceae. Faunal evidence shows that *C. ramanensis* sp. nov. is not younger than Middle Jurassic and that it is probably of Lower Jurassic age. No well-founded record of the Cupressaceae has been previously known earlier than the Cretaceous.

The conifer described in this paper, *Cupressinocladus ramonensis* sp. nov., occurs in the form of compressions of small leafy shoots in a Jurassic black shale from the Makhtesh Ramon (Wadi Raman) in southern Israel. The material was collected from an exploratory tunnel dug in the Makhtesh with a view to exploiting the 'flint clay' (Würzburger 1958) in which the shale band occurred. A number of species of conifers were represented by fragments of leafy shoots and cones exposed on the bedding planes. One of us (J. L.) is preparing an account of these for publication elsewhere. The shoots dealt with here are of interest in having decussate leaves, and in being in their general character similar to those of living Cupressaceae. The age of the material, which is not younger than Middle Jurassic, is considered in more detail below.

A few fragments of *C. ramonensis* sp. nov. were seen exposed on the bedding planes of the rock, but much more material was obtained by bulk maceration of the matrix. Some breakdown of the shale was effected simply by soaking in water and subsequent drying, repeated a number of times. More complete breakdown was obtained by soaking pieces of shale in concentrated nitric acid for several days, washing off the acid, and soaking in dilute ammonia solution. Sieving of the residue produced several shoots comprising a few internodes which had cohered throughout the treatment. Others had separated into pairs or even single leaves. Some of these shoot fragments have been figured as opaque objects (Pl. 36, figs. 4 and 5) while others were further macerated in Schulze's solution (nitric acid and potassium chlorate), washed in distilled water, and mounted in glycerine jelly (Pl. 36, fig. 3). Individual leaves could be separated from shoots macerated in this way, and the upper and lower cuticles pulled apart and examined individually (Pl. 36, fig. 2).

The conifer shoots described here are assigned to the form-genus *Cupressinocladus* Seward. An emended diagnosis of the genus is given here, and the reasons for doing this are considered in the discussion below.

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[Palaeontology, Vol. 2, Part 2, 1960, pp. 236–42, pl. 36.]

SYSTEMATIC DESCRIPTION

CUPRESSINOCLADUS Seward 1919 emend.

Cupressinocladus Seward 1919, pp. 303–4.

Emended diagnosis. Conifer twigs with decussate leaf arrangement. Leaves small, decurrent, the free part not exceeding the length of the decurrent part.

Type species. *C. salicornoides* (Unger) Seward 1919, p. 307. Although Seward does not specifically cite this as the type species, it is the first species for which he uses the generic name *Cupressinocladus*, and it has accordingly been acknowledged by Andrews (1955) as the type species. Unger's figure (reproduced in Seward) leaves open the possibility that the leaves in this species were borne in groups of more than two—possibly in fours. Further, the cuticle of Unger's material is not known. However, we have had access to the holotype of Seward's own species, *C. valdensis* (see p. 240 below). This emendation of *Cupressinocladus* is meant rather as a more precise statement of what was intended by Seward than as a reinterpretation based on the type species.

Cupressinocladus ramonensis sp. nov.

Plate 36, figs. 1–8

Diagnosis. Branchlets without dorsiventral differentiation. Leaves decussate, regularly spaced. Leaf base decurrent, rectangular, in contact with the opposite leaf base. Distal part of the leaf free, one-quarter of the length of the decurrent part in larger shoots, but in smaller shoots, up to the full length of the decurrent part; triangular, concavo-convex. Junction of the small adaxial leaf surface with the remainder of the leaf marked with a narrow scarious margin. Stomata of the adaxial surface forming a few rows confined to the marginal zones, leaving the central part of this surface free of stomata. Abaxial surface with stomata rather widely separated in eight to fifteen regularly spaced longitudinal rows. Stomata monocyclic, or incompletely amphicyclic, with four to six (typically five) subsidiary cells, the walls of which are about as thick as the walls of the remaining epidermal cells. Majority of epidermal cells bearing a single cuticular papilla; each subsidiary cell bearing a broad rounded papilla extending over the stomatal aperture. Guard cells not seen, presumably lying originally below the level of the subsidiary cells and overlapped by them.

Syntypes. Specimens number V 36332 and V 36334, British Museum (Natural History); Plate 36, figs. 3 and 4.

Occurrence. From the plant bed in the 'Marly Cuesta' of the Lower Jurassic (Nevo 1954) from the exploratory tunnel of the Israel Mining Company at lat. 30° 37′ 15″ N., long. 34° 54′ 50″ E. (Survey of Israel Grid ref. 1417500350); Makhtesh Ramon, Israel.

Description. Only short leaf-bearing branchlets 2–4 mm. wide have been found. The free part of the leaf is about equal in length to the decurrent part in some leaves (cf. Pl. 36, fig. 4) but may be only a quarter that length in others (cf. Pl. 36, fig. 3). The free part of the leaf is concavo-convex (Pl. 36, figs. 1, 3), more or less appressed to the branch, with a pointed tip of which the margins subtend an angle of about 60°. The small adaxial surface has stomata confined to two to three lateral rows which converge towards the apex, leaving a central zone of about one-half the total width free of stomata (Pl. 36, fig. 2). Apart from the stomata and subsidiary cells the epidermis is composed of rectangular cells each bearing a papilla with its apex turned so as to lie at the distal end of the cell. Towards the edge of the leaf the epidermal cells become narrower and more heavily cutinized, merging into a scarious margin consisting of one layer of cells elongated perpendicular to the edge of the leaf. The abaxial surface is in contact at its margin with the corresponding margin of the opposite leaf (Pl. 36, fig. 3). The stomata, in eight to fifteen longitudinal rows, are rather sparse in the proximal part of the leaf. Higher up the leaf they are rather uniformly arranged in longitudinal rows which are separated by four to six rows of normal epidermal cells. Two to four epidermal cells lie between the subsidiary cells of neighbouring stomata of the same row. Only very few stomata within a row are ever seen with their subsidiary cells in contact. The stomatal apparatus, including the four to six subsidiary cells, is 45–50 μ across. The subsidiary cells are all of similar shape, with radial and tangential walls about as thick as, or slightly thinner than, those of typical epidermal cells. Some of the epidermal cells in contact with the subsidiary cells have one or two of their walls continuous with the radial walls of the subsidiary cells, and the stomata may therefore be regarded as being incompletely amphicyclic (Pl. 36, figs. 6–8). The inner tangential wall of each subsidiary cell bears a broad hemispherical papilla. The development of this papilla is such that in the flattened cuticle the papillae sometimes seem to fill the whole stomatal aperture (Pl. 36, fig. 7). The almost circular shape of the stomata and the absence of the guard cells make it difficult to determine the orientation of the stomatal apertures. The general impression given is that the orientation is more or less random.

SOURCE AND AGE OF MATERIAL

The plant bed containing *Cupressinocladus ramonensis* is exposed in an exploratory tunnel in the Makhtesh Ramon (see p. 236 above for the exact location). A map showing the position of the Makhtesh is given in Hudson 1958, p. 417. Shaw (1947, pp. 20–21) gives the complete Jurassic sequence in the Makhtesh. In his account the bed containing the plant remains is that shown as the 18-metre layer extending from 40·2–58·2 metres

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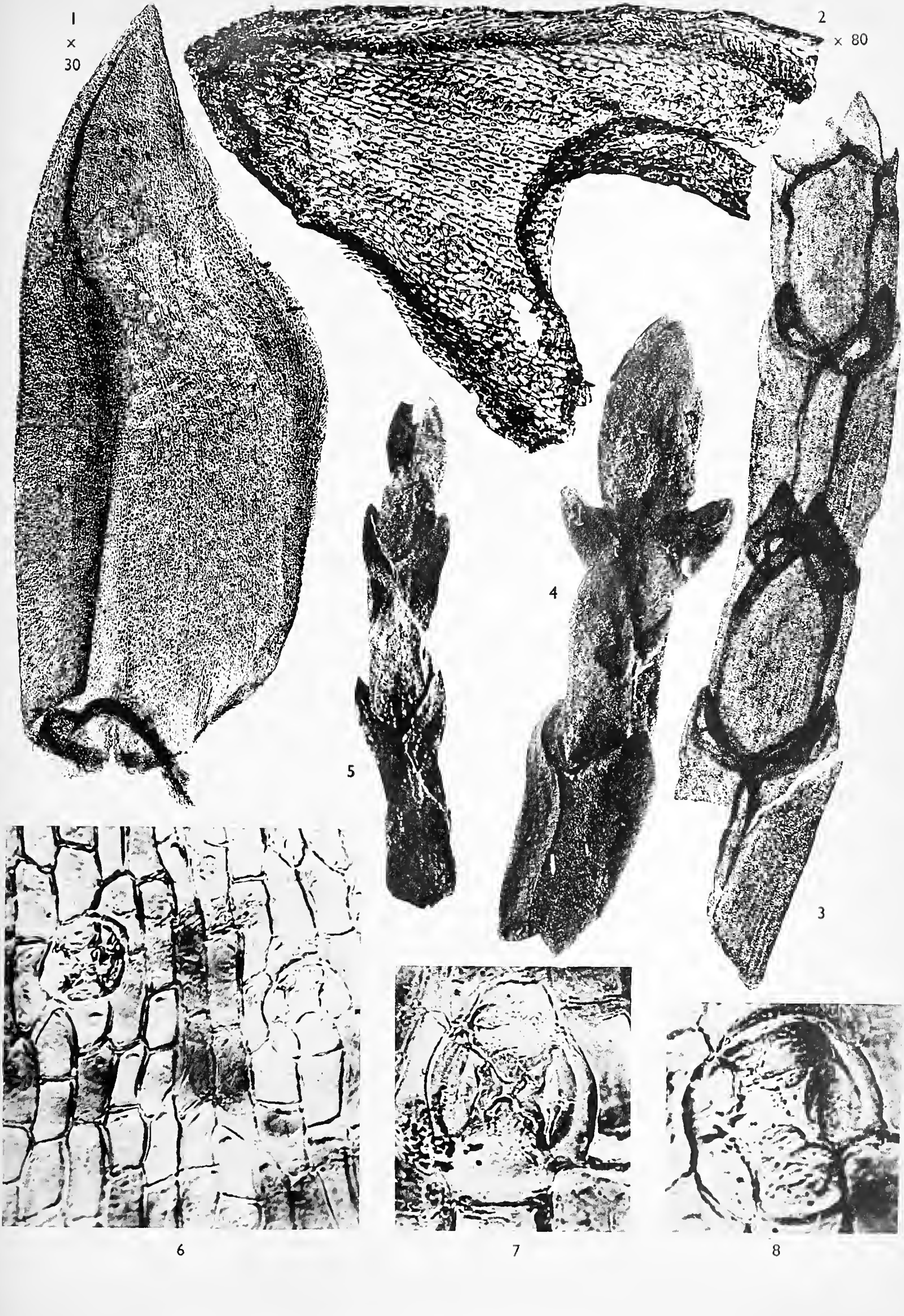
EXPLANATION OF PLATE 36

Figs. 4 and 5 have been photographed by reflected light and the remainder by transmitted light.

Figs. 1–8. *Cupressinocladus ramonensis* sp. nov. from the Jurassic of Makhtesh Ramon, Israel. 1, Cuticle of a whole leaf, × 30. In the upper part the cuticles of both adaxial and abaxial surfaces are superimposed, and at the left side the abaxial cuticle is folded over. Several longitudinal rows of stomata are recognizable over most of the length of the leaf. The scarious margin can be seen along much of the right-hand edge (V.36333). 2, Cuticle of the adaxial (upper) leaf surface, showing central band of papillate cells free of stomata, and the several marginal stomatal rows, × 80 (V.36331). 3, Cuticle preparation of a whole leafy shoot showing the decussate decurrent leaves, × 10 (V.36334). 4, 5, Leafy shoots, after removal from the matrix, showing decussate leaf arrangement and variation in leaf shape, × 10. 6, Part of the cuticle of the abaxial leaf surface from the decurrent part of the leaf, showing rectangular epidermal cell outlines, low rounded papillae, and two stomata, × 300 (V.36336). 7, 8, Two stomata from the vicinity of the last preparation; the guard cells are missing, only the subsidiary cells indicating the positions of the stomata. Papillae overarch the stomatal aperture, almost obliterating it in fig. 7; × 600 (V.36336).

(The numbers in brackets are slide numbers in the Palaeontology collection of the British Museum, Natural History, London.)



CHALONER and LORCH, *Cupressinocladus ramanensis* sp. nov.

from the base of the 458 metres assigned to the Jurassic. Nevo (1954) places the bed (which is included in his 'Marly Cuesta') even closer to the base of the Jurassic, within the 'Lower Marine Jurassic (Lias)'.

Palaeontological evidence for the dating of the plant bed is as follows. Shaw (1947) records '*Terebratula subsella* and *Rhynchonella moravica*' from 350 metres above the plant bed horizon. According to Dr. R. G. S. Hudson (verbal communication Oct. 1958) this latter species, when recorded from this area, can be regarded as representing *Somalirhynchia jordanica* (Noetling), and in association with *T. subsella* this indicates an Oxfordian (s.l.) age. This means that the plant bed is certainly older than Upper Jurassic. Mr. Lehrman (Geological Institute of Israel, verbal communication Dec. 1958) states that 32 metres below the plant bed there is a limestone band containing *Myophoria* sp., indicating an Upper Triassic age; and that 20 metres above the plant bed the occurrence of *Nerinella* indicates a Lower Jurassic age. This would mean that the plant bed is not younger than Lower Jurassic, nor older than Upper Triassic.

DISCUSSION

Generic assignment. The genus *Cupressinocladus* was made by Seward (1919, p. 303) for 'vegetative shoots agreeing in habit of branching and in the predominance of a decussate arrangement of appressed leaves with recent Cupressineae such as *Cupressus*, *Thuya*, *Libocedrus*, and similar types. When cones are present which throw any light on generic affinity some other term should be adopted.' Seward leaves open the rather critical question of just what constitutes predominance in this context. In the past there has been some confusion as to whether some small-leaved *Cupressus*-like leafy shoots had a truly spiral or decussate leaf arrangement. Kendall (1949) has pointed out that several of Sternberg's *Thuites* species had in fact spirally arranged leaves of the *Brachyphyllum* type. We have given an emended diagnosis of *Cupressinocladus* to restrict it to forms showing an exclusively opposite leaf arrangement. Seward gave no formal diagnosis, but the type species that he uses (*C. salicornoides*) and his own species (*C. valdensis*) are in accord with this emendation. Defined in this way, *Cupressinocladus* becomes a form genus comparable with the spiral-leaved genera *Brachyphyllum* and *Pagiophyllum*, but having decussate, *Cupressus*-like leaves. *Cupressinocladus* may consequently include forms other than Cupressaceae; decussate leaves are not restricted to this one family in the conifers, but occur also in the Podocarpaceae and Taxodiaceae. Within this latter family, the leaf arrangement of *Metasequoia* combined with the leaf shape of *Sequoiadendron* would give the essential characters of *Cupressinocladus*. However, when cuticle characters are also available, as with our material, more certain evidence of affinity is available.

Several genera, having priority in date of publication over *Cupressinocladus*, have been based on leafy conifer shoots with minute decussate (or supposedly decussate) leaves. A few are based on fertile material, but the cuticle characters of the majority are unknown. Of these genera, the two following warrant close comparison with *Cupressinocladus*:

1, *Frenelopsis* Schenck 1869. This genus was based on *Thuites hoheneggeri* Ettingshausen (1852), from the Lower Cretaceous of Austria; this consisted of leafy conifer shoots with very reduced, whorled leaves. According to Seward (1919, p. 343) the leaves were borne sometimes in twos, sometimes in whorls of four, although Schenck (1869) in his diagnosis mentions only pairs of decussate leaves. Zeiller's (1882) re-examination of this species makes it clear that the leaves were borne in fours, and that the leaves of each whorl are partially fused along their margins. Florin (1955) considers that on their vegetative structure alone (wood attributed to this genus, and its cuticle) *Frenelopsis* is of Cupressaceous affinity. While this gives *Frenelopsis* a claim to being one of the earliest known Cupressaceae, the arrangement of its leaves in fours is a clear distinction from the Israeli material described here.

2, *Widdringtonites* Endlicher 1847. Endlicher founded this genus on a number of previously described specimens, including *Thuites gramineus* Sternberg and *Juniperites baccifera* Unger 1843. The inclusion of the latter species is particularly significant as Unger's material of *J. baccifera* was fertile. Unger describes the 'fruit' as being of about the same size as those of *Juniperites communis*. Endlicher describes the leaves of *Widdringtonites* as spiral in arrangement, although Unger's figures of *Juniperites baccifera* (loc. cit., pl. 21, figs. 1–3) suggest a decussate arrangement, and Berry's fertile material of *Widdringtonites* from Alabama (Berry 1912) is also clearly decussate. Regardless of leaf arrangement, *Widdringtonites* is based on material with well-characterized cones, and should accordingly be reserved for specimens with the same type of fructification, or for specimens with cuticle characters giving strong evidence of affinity with such material.

Saporta (1894) described and figured some apparently decussate shoots from the Upper Jurassic of Portugal under the name *Widdringtonites*. Some of Saporta's figures superficially resemble the Israeli material described here. Teixeira (1948) has since reassigned this material of Saporta's (which the latter author had placed in *Palaeocyparis*, *Brachyphyllum*, *Thuites*, and *Widdringtonites*) to a single species, *Cyparissidium micromerum*. The type of this genus (*Cyparissidium gracile* Heer) has a spiral arrangement of the leaves and cone scales, and Teixeira also describes cones with spirally arranged scales in his Portuguese material. From this work of Teixeira it is evident that the decussate leaf arrangement suggested by some of Saporta's figures may be misleading and that further comparison between our Israeli material and the Portuguese based solely on Saporta's figures would be unwise.

Comparison with Cupressinocladus valdensis *Seward*. *Cupressinocladus valdensis* Seward is based on a single specimen of a leafy conifer shoot from the British Wealden (Seward 1895, p. 209, pl. 20, fig. 6). This is still the only specimen of the species known to us. Originally described as *Thuites valdensis* Seward 1895, the species was transferred to *Cupressinocladus* by Seward (1919) when he erected that genus. Examination of the holotype (British Museum, Natural History No. V 2139) shows that the leaves are small, appressed, have strongly decurrent bases, and are undoubtedly decussate in arrangement. In its general superficial appearance it is quite similar to some specimens of the Israeli *Cupressinocladus ramonensis*.

The carbonaceous matter of Seward's holotype was fractured by shrinkage into minute fragments. Such a leaf fragment was removed from the base of the specimen, and a cuticle preparation was made. This suffieed to show that its cuticle is distinct from that of *C. ramonensis*. Beyond this, we make no attempt to redescribe Seward's species here, nor to give a full account of its cuticle characters.

Our cuticle preparation of *C. valdensis* Seward consisted of a fragment about 1 mm. square, apparently from the decurrant base of a leaf; only a single cuticle was present and this was regarded as being that of the abaxial leaf surface. The cuticle was very much thicker and more opaque than that of the Israeli species, after similar maceration. We regard this as an original feature, and not an effect of different states of preservation. Forty stomata were counted on the fragment, arranged in rather clearly defined rows much as in *C. ramonensis*. At the contact between their subsidiary cells and the surrounding epidermal cells, a ridge of cuticle is developed, giving a dark rim encircling each of the stomata. The epidermal cells between the stomatal rows are rounded-rectangular, generally rather elongated in the longitudinal direction and lack papillae. The cuticle of *C. valdensis* therefore differs from that of *C. ramonensis* in its much greater thickness, the lack of papillae on the epidermal cells, and the markedly sunken stomata within an encircling cuticular ridge.

The affinity of Cupressinocladus ramonensis *sp. nov.* Only vegetative material of *C. ramonensis* is known at present, so that its attribution to a family of living conifers must be qualified to this extent. The only family of living conifers having opposite scale-like leaves with decurrent bases (as in *C. ramonensis*) is the Cupressaceae, and, so far as we know, no leafy shoots of this type ever occurred in any other family. The same general type of leaf arrangement and shape occurs in the Cupressaceae in the genera *Widdringtonia*, *Thuja*, *Thujopsis*, *Libocedrus*, *Cupressus*, and *Chamaecyparis*. Stomata occur in more or less clearly defined rows on both leaf surfaces in these genera as in *Cupressinocladus ramonensis*; however, our fossil differs from all of them in having the stomata on the lower (abaxial) leaf surface arranged in a series of longitudinal rows extending across the whole width of the leaf, instead of being restricted to two marginal stomatal bands (cf. Florin 1931). In their structure the stomata themselves are similar to those of several living Cupressaceae (*Thuja*, *Cupressus*) in being monocyclic or incompletely amphicyclic, with four to six subsidiary cells which are papillate. However, in our fossil the papillae overarch the stomatal aperture more than in those living Cupressaceae (e.g. *Libocedrus*) which have similar, distinct proximal papillae on the subsidiary cells. Papillate epidermal cells (similar to those of *C. ramonensis*) are widespread in the Cupressaceae. On the basis of this comparison it can be said that while *Cupressinocladus ramonensis* agrees with the Cupressaceae more closely than with any other family of conifers, it does not agree with any one living genus in all the features considered.

Hitherto there has been no bona fide record of the Cupressaceae earlier than the Cretaceous (cf. Arnold 1948). Florin (1958) in his recent work on Mesozoic taxads and conifers states (p. 383) that 'there are no indisputable members of the . . . Cupressaceae in northern Lower and Middle Jurassic floras'. The fossil described here appears to extend the record of this family back to at least the Middle Jurassic.

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UPPER MESOZOIC MICROPLANKTON FROM AUSTRALIA AND NEW GUINEA

by ISABEL C. COOKSON and A. EISENACK

ABSTRACT. Thirty-one species of microplankton from Upper Jurassic deposits in north-western Australia are identified, six new genera are proposed and the following new species described: *Gonyaulax eumorpha*, *G. clathrata*, *G. bulloidea*, *Scriniodinium playfordi*, *S. dictyotum*, *S. ceratophorum*, *S. apatelum*, *Belodinium dysculum*, *Canningia reticulata*, *Hystrichosphaeridium pachydermum*, *H. torynum*, *H. capitatum*, *Cyclonephelium areolatum*, *C. densebarbatum*, *Cannosphaeropsis apiculata*, *Leiosphaeridia similis*, *Chlamydophorella wallala*, *Dictyopyxis areolata*, *Diplotesta glaessneri*, *Kalyptea diceras*, *K. monoceras*, *Komewuia glabra*, *Palaeostomocystis cylindrica*, *P. sinuosa*.

IN a previous paper (Cookson and Eisenack 1958) several microplankton species were described from the lower portion of the Jarlemai Siltstone at Broome in north-western Western Australia. The sample from which they were recovered came from between 1,405 and 1,427 ft. in the Broome No. 3 Artesian Bore and the age at this level is considered to be Oxfordian to Lower Kimeridgian (McWhae *et al.* 1958, p. 89).

The present paper is mainly concerned with the classification and distribution of a number of new forms recently isolated from upper portions of the Jarlemai Siltstone obtained from bores at Broome and other localities in the Canning Basin, Western Australia. The age of this part of the Siltstone is still uncertain but at present is taken as Lower Tithonian (McWhae *et al.* 1958, p. 89). In addition a few forms which are common to both uppermost Jurassic and lowermost Cretaceous sediments in Western Australia, Eastern Australia, and New Guinea are included.

Extraction methods were the same as those described in Deflandre and Cookson (1955).

Acknowledgements. We wish to express our indebtedness to Dr. Ross McWhae of West Australian Petroleum Pty. Ltd.; to Mr. B. E. Balme of the University of Western Australia; and to Mr. J. N. Montgomery of Australasian Petroleum Co. Ltd., for rock samples and information regarding their stratigraphical position and age. One of us (I. C. C.) has received considerable financial assistance from the Commonwealth Scientific and Industrial Research Organization.

LOCATION AND AGE OF SEDIMENTS

Most of the Western Australian samples were supplied by West Australian Petroleum Pty. Ltd. (to be referred to hereafter as 'Wapet'), those from Papua by Island Exploration Co. Ltd. (to be referred to hereafter as 'I.E.C.').

Western Australia, Canning Basin

1. Broome No. 3 Artesian Bore. Jarlemai Siltstone (lower portion) between 1,405 and 1,427 ft.; Oxfordian to Lower Kimeridgian (Teichert 1940; McWhae *et al.*, 1958, p. 89). Jarlemai Siltstone (upper portion 1,200 and 1,211 ft., and 1,001 and 1,042 ft.; probably Tithonian (McWhae *et al.* 1958, p. 89).

2. Broome No. 1 Bore. Jarlemai Siltstone (upper portion) at 963 and 977 ft.; probably Tithonian (Authors).

[Palaeontology, Vol. 2, Part 2, 1960, pp. 243–61, pl. 37–39.]

3. Wallal Core hole about 200 miles south-south-west of Broome. Alexander Formation between 560 and 575 ft.; Oxfordian to Lower Kimeridgian (J. R. H. McWhae pers. comm.). Jarlemai Siltstone at 350 ft. and between 305 and 320 ft.; probably Tithonian (Authors).

4. Roebuck Bay, 30 miles south-east of Broome, Wapet's No. 1 Well, core 11, between 972 and 982 ft.; base of Alexander Formation, Oxfordian to Lower Kimeridgian according to Wapet, probably Tithonian (Authors).

Western Australia, Exmouth Gulf area of Carnarvon Basin

1. Cape Range. Dingo Claystone (upper portion). Wapet's Well No. 1 between 3,825 and 3,840 ft. and Well No. 2 between 3,970 and 3,991 ft.; Oxfordian or Lower Kimeridgian (McWhae *et al.* 1958, p. 91).

2. Rough Range. Muderong Shale. Wapet's Well No. 8 between 3,863 and 3,883 ft.; Aptian (McWhae *et al.* 1958, p. 112).

Western Australia, south-west portion of Carnarvon Basin

Birdrong Formation (Grierson Member). Wapet's Meadow Station Bore No. 9; Upper Neocomian or Lower Aptian (McWhae *et al.* 1958, p. 111).

South Australia

South Australia Northern Territory Oil Search Ltd. ('Santos'), Oodnadatta Bore between 1,052 and 1,061 ft.; Lower Cretaceous, Aptian or older (Authors). Lake Phillipson Bore about 12 miles east of eastern margin of lake (Brown 1905, p. 6) at 87 ft. 10 in.; Lower Cretaceous, Aptian, or older (Authors).

Northern Queensland

1. Longreach Drill Co.'s Balmoral Well No. 1 on Padua property at 1,000 ft.; probably Aptian (Authors).

2. Roma Formation. Well on Batavia Downs Station, Cape York Peninsular, between 45 and 49 ft.; Aptian.

New Guinea

1. Omati River District, Western Papua. I.E.C.'s Well No. 1, sample 21 (Cookson and Eisenack 1958, fig. 2); late Upper Jurassic as determined by I.E.C.

2. Komewu, Papua. I.E.C.'s Well No. 1, core 15; probably late Upper Jurassic (Authors); Well No. 2, core 10; Neocomian (on faunal evidence, J. N. Montgomery, pers. comm.).

SYSTEMATIC DESCRIPTIONS

DINOFLAGELLATES

Family GONYAULACIDAE

Genus GONYAULAX Diesing 1866

Gonyaulax serrata Cookson and Eisenack

Gonyaulax serrata Cookson and Eisenack 1958, p. 34, pl. 3, fig. 2.

Occurrence. Upper Jurassic to? Neocomian: Omati, Papua, I.E.C.'s Well No. 1, samples 19, 20, 25 (Cookson and Eisenack 1958, fig. 2). Upper Jurassic probably Tithonian: Broome, W.A., No. 1 Bore at 977 ft. Neocomian, Komewu, Papua, I.E.C.'s Well No. 2, core 10.

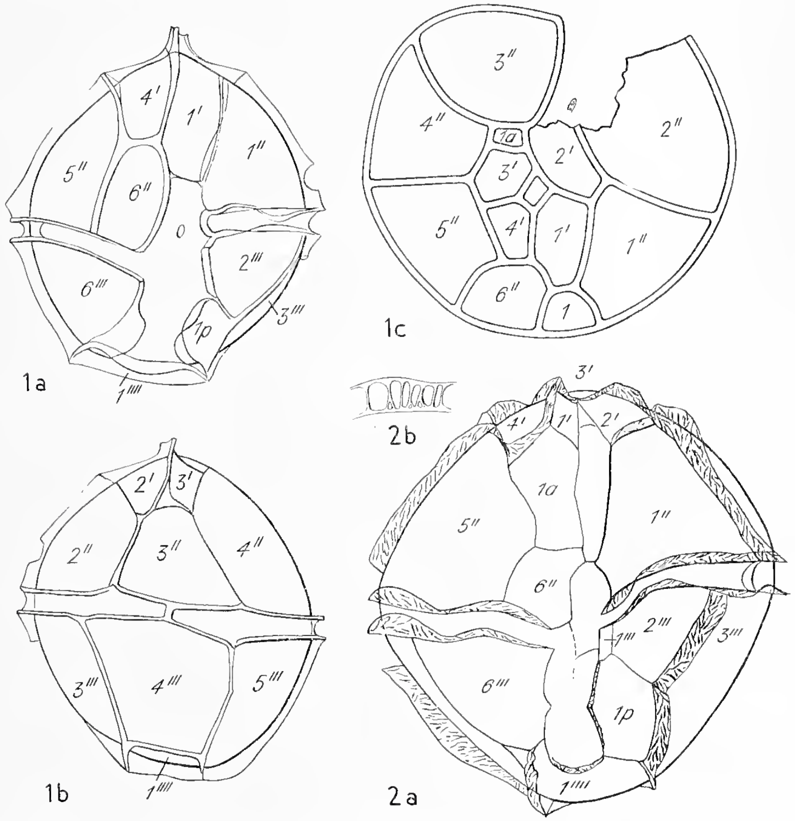
Comments. The occurrence of *G. serrata* at Broome and Komewu, here recorded, suggests that the range in age of this species is from Tithonian to Neocomian.

Gonyaulax cf. *ambigua* Deflandre

Plate 37, fig. 4; text-fig. 1

Gonyaulax ambigua Deflandre 1939, p. 144, pl. 1, fig. 2.
Occurrence. Probably Tithonian: Jarlemai Siltstone (upper portion), W.A., Wapet's Wallal Core hole at 350 ft.

Comments. Shells having the main features of *G. ambigua* are fairly numerous in the Wallal deposit; they differ, however, from the description of the French examples, given by Deflandre, in the presence of plate 1p on the hypotheca. A funnel-shaped 'horn' is formed by the ledges of the four apical plates. Formula: $4'$, (1a), $6''$, $5'''$, 1p, $1''''$. Sometimes 1a is present (text-fig. 1*c*), $1'$ is long and narrow, $6''$ small; longitudinal furrow short, $1'''$ absent (text-fig. 1*a*).



TEXT-FIGS. 1, 2. 1, *Gonyaulax* cf. *ambigua* Defl.; *a*, ventral surface of specimen shown on Pl. 37, fig. 4; *b*, dorsal surface of same specimen; *c*, apical view of another specimen; ×*c*. 500. 2, *Gonyaulax clathrata* sp. nov.; *a*, ventral surface of specimen shown on Pl. 37, fig. 5; ×*c*. 500; *b*, portion of a ledge (schematic).

G. ambigua was first described from Kimeridgian shales of Orbagnoux, France; since then it has been recorded from Kimeridge in England (Downie 1957) and from the Dingo Claystone (upper portion), Western Australia (Cookson and Eisenack 1958).

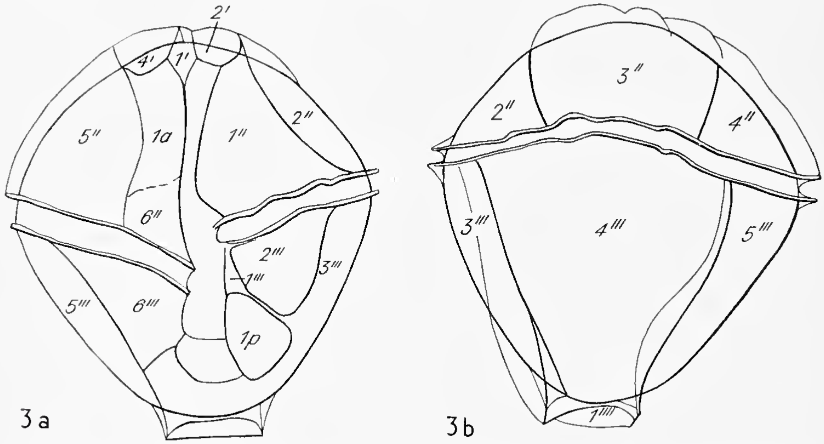
A certain identification of the Wallal specimens with *G. ambigua* will only be possible when better material of this species from the type locality is described.

Gonyaulax eumorpha sp. nov.

Plate 37, figs. 1–3; text-fig. 3; holotype fig. 1, Nat. Mus. Vic. P17767

Occurrence. Oxfordian to Lower Kimeridgian: Alexander Formation, W.A., Wapet's Wallal Core hole between 560 and 575 ft.; Jarlemai Siltstone (lower portion), W.A., Broome No. 3 Bore between 1,405 and 1,427 ft. Probably Tithonian, Jarlemai Siltstone (upper portion), W.A., Broome No. 1 Bore at 977 ft.

Description. Shell rather large, ovoidal, flattened dorso-ventrally; epitheca broadly rounded, hypotheca narrowing somewhat towards the antapex. The girdle, which is equatorial, helicoid and broad, and the plates are bordered by thin, rather high ledges which may be perforated. The formula is $4'$, $6''$, $5'''$, 1p, $1''''$, but it seems that $6''$ is very small and a long intercalary plate, the transverse boundary of which is indistinct, is developed on the ventral surface (text-fig. 3*a*). Three of the four apical plates are always evident on the ventral surface (text-fig. 3*a*). Dimensions: holo type—112 μ long, 110 μ broad. Paratype (Pl. 37, fig. 3) 98 μ long, 93 μ broad. Range—length 86–112 μ, breadth 86–110 μ.



TEXT-FIG. 3. *Gonyaulax eumorpha* sp. nov.; *a*, ventral surface of specimen shown on Pl. 37, fig. 3; in this example plate $1'''$ is faintly indicated; *b*, dorsal surface of same specimen; × *c*. 500.

Comments. G. eumorpha and *G.* cf. *ambigua* have the general shape and tabulation of the members of the genus *Gonyaulax*, however plate $1'''$ seems to be missing. In spite of this fact we see no necessity for the creation of a new genus, since in some species of *Gonyaulax* (*G. polyedra* Stein) plate $1'''$ is very considerably reduced.

Gonyaulax clathrata sp. nov.

Plate 37, fig. 5; text-fig. 2; holotype Nat. Mus. Vic. P17775

Occurrence. Probably Tithonian, Jarlemai Siltstone (upper portion), Broome No. 3 Bore between 1,200 and 1,211 ft., and 1,001 and 1,042 ft.; Roebuck Bay, W.A., Wapet's No. 1 Bore between 972 and 982 ft.

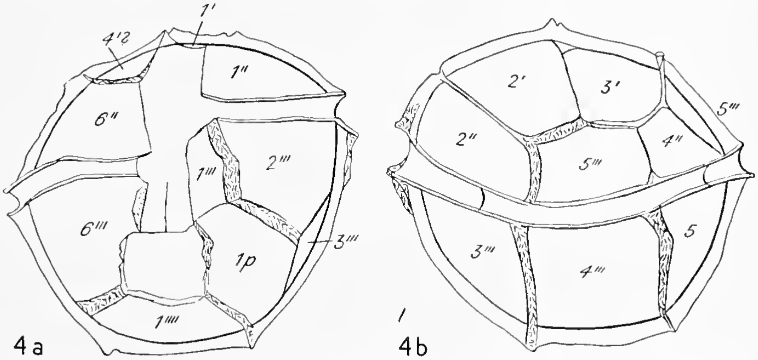
Description. Shell spherical to somewhat polygonal, approximately isodiametric. The transverse furrow is helicoid and divides the shell nearly equally. The plates and furrows are bordered by rather high ledges with radially arranged rectangular perforations which give them a palisade-like appearance. A large pylome is developed on the dorsal side (plate 3″). The formula is 4′, 1a, 6″, 6‴, 1p, 1⁗. Plates 1a and 1 of the longitudinal furrow are long and narrow, plates 6″ and 1‴ are small, especially the latter (text-fig. 2*a*). Dimensions: holotype—100 × 100 μ. Range in diameter—70–100 μ.

Gonyaulax bulloidea sp. nov.

Plate 37, fig. 11; text-fig. 4; holotype Nat. Mus. Vic. P17788

Occurrence. Probably Tithonian: Jarlemai Siltstone (upper portion), Broome No. 1 Bore at 977 ft.

Description. Shell spherical, rather thick-walled, epitheca and hypotheca nearly equal, separated by a rather broad, helicoid girdle. Longitudinal furrow broadened towards the antapex. Plates mostly squarish or broadly trapezoid; plates 2′ and 3′ especially large, plate 1‴ rather large, nearly rectangular. Formula 4′, 6″, 6‴, 1p, 1⁗. The girdle, longitudinal furrow, and plates are bordered by low but well-developed ledges; both plates and ledges are ±granular, a feature which, when taken in conjunction with the spherical shape and squarish plates, gives the shell a very characteristic appearance. The apex is marked by a small pointed projection. In all the examples observed, plate 3″, which in many species of *Gonyaulax* becomes detached to form the pylome, has always been in position. On the other hand, in some specimens the apical plates have been missing (? Ekdysis). Dimensions: holotype—78 μ long, 83 μ broad. Range—60–88 μ × 57–83 μ.



TEXT-FIG. 4. *Gonyaulax bulloidea* sp. nov., *a.* ventral surface of specimen shown on Pl. 37, fig. 11; *b.* dorsal surface of same specimen; × *c.* 500.

Family DEFLANDREIDAE
Genus SCRINIODINIUM Klement 1957
Scriniodinium luridum (Deflandre)

Plate 37, fig. 10

Gymnodinium luridum Deflandre 1938, p. 166, pl. 5, fig. 4–6.
Scriniodinium luridum (Deflandre); Klement 1957, p. 410.
Gymnodinium luridum Deflandre; Cookson and Eisenack 1958, p. 24, pl. 1, figs. 3, 4.
Scriniodinium luridum (Deflandre); Ibid., p. 79.

Occurrence. Oxfordian to Lower Kimeridgian: Alexander Formation, Wapet's Wallal Core hole between 560 and 575 ft.; Jarlemai Siltstone (lower portion), Broome No. 3 Bore between 1,405–27 ft. Probably Tithonian: Jarlemai Siltstone (upper portion), W.A., Broome No. 1 Bore at 977 ft., Broome No. 3 Bore between 1,200 and 1,211 ft., and 1,001–42 ft.; Roebuck Bay, W.A., Wapet's No. 1 Well, core 11, between 972 and 982 ft.

Scriniodinium playfordi sp. nov.

Plate 37, fig. 6; holotype Nat. Mus. Vic. P17233

Gymnodinium crystallinum Deflandre *in* Cookson and Eisenack 1958, p. 24, pl. 1, fig. 2.
Scriniodinium crystallinum (Deflandre); ibid., p. 79.

Occurrence. Oxfordian to Lower Kimeridgian: Dingo Claystone (upper part), W.A., Wapet's Cape Range Well No. 1 between 3,825 and 3,890 ft. and Well No. 2 between 3,970 and 3,991 ft.; Alexander Formation, W.A., Wapet's Wallal Core hole between 560 and 575 ft. Probably Tithonian: Wallal Core hole at 350 ft.; Roebuck Bay, W.A., Wapet's No. 1 Well between 972 and 982 ft.

Description. Shell flat, somewhat arched, oval in outline, divided equally by a deep circular girdle; the hypotheca is rounded; the epitheca terminates in a rather short, stout horn the apex of which is truncate and carries a small median projection. The capsule fills the cavity of the shell and projects into the base of the apical horn, its wall is thin and ornamented either entirely or at the periphery only by a small-meshed reticulum of variable width. The shell-membrane is rather wide, smooth, and hyaline. A large pylome is developed. Dimensions: holotype—166 μ long, 147 μ broad. Range—108–166 $\mu \times$ 90–147 μ. The species is named after Mr. P. E. Playford of West Australian Petroleum Pty. Ltd.

Scriniodinium dictyotum sp. nov.

Plate 37, figs. 8, 9; holotype fig. 9, Nat. Mus. Vic. P17768

Occurrence. Oxfordian to Lower Kimeridgian: Alexander Formation, W.A., Wallal Core hole between 560 and 575 ft. Probably Tithonian: Jarlemai Siltstone (upper portion) Wallal Core hole at 350 ft. and between 305 and 320 ft., and Broome No. 3 Bore between 1,001 and 1,042 ft.; Roebuck Bay, W.A., Wapet's No. 1 Well between 972 and 982 ft.

Description. Shell flat, oval, divided by a ± distinct and relatively broad girdle into an epitheca and hypotheca of approximately equal size; epitheca prolonged into a broadly based, short, blunt apical projection. Capsule oval with a short apical prominence. The wall of the capsule bears numerous thin perpendicular ledges which form a small-meshed supporting reticulum for the thin outer membrane. The meshes of the reticulum

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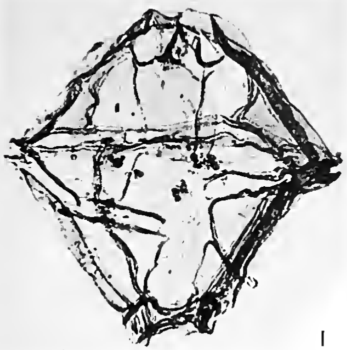
EXPLANATION OF PLATE 37

Figs. 1, 2. *Gonyaulax eumorpha* sp. nov. Broome No. 1 Bore, 977 ft. 1, ×400. 2, ×*c.* 500.
Fig. 3. *Gonyaulax eumorpha* dorsal surface. Wallal Core hole, 560-75 ft., ×*c.* 500.
Fig. 4. *Gonyaulax* cf. *ambigua* Defl. Wallal Core hole, 350 ft., ×*c.* 400.
Fig. 5. *Gonyaulax clathrata* sp. nov. Broome No. 3 Bore, 1001–42 ft., ×*c.* 400.
Fig. 6. *Scriniodinium playfordi* sp. nov. Cape Range, W.A., Well 2, 3970–91 ft., ×400.
Fig. 7. *Scriniodinium ceratophorum* sp. nov. Broome No. 3 Bore 1405–27 ft., ×*c.* 400.
Figs. 8, 9. *Scriniodinium dictyotum* sp. nov. 8, Wallal Core hole, 560–75 ft., ×400. 9, Wallal Core hole, 350 ft., ×400.
Fig. 10. *Scriniodinium luridum* (Defl.). Broome No. 1 Bore, 977 ft., ×400.
Fig. 11. *Gonyaulax bulloidea* sp. nov. Broome No. 1 Bore, 977 ft., ×*c.* 400.
Figs. 12, 13. *Scriniodinium apatelum* sp. nov. Wallal Core hole, 560–75 ft., ×*c.* 680.
Fig. 14. *Belodinium dysculum* sp. nov. Broome No. 1 Bore at 977 ft., ×*c.* 400.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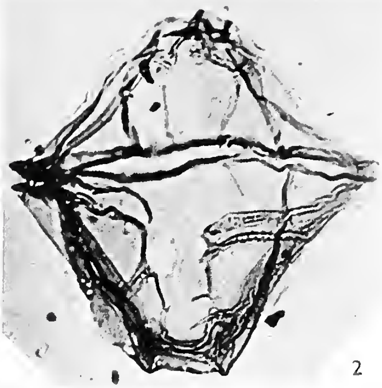
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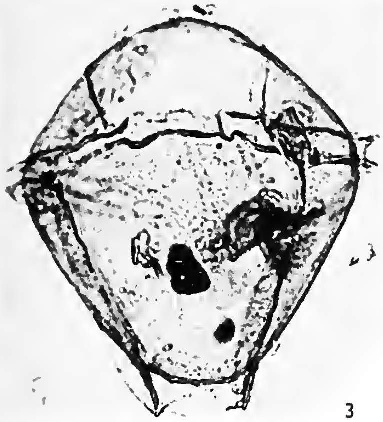
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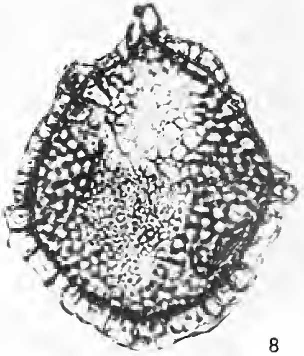
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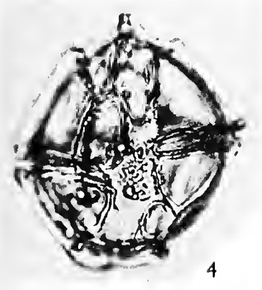
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COOKSON and EISENACK

vary considerably in size and are usually widest towards the periphery. The pylome is broadly hoof-shaped and reaches the girdle. Dimensions: holotype—109 μ long, 95 μ broad, capsule 95×83 μ. Paratype (Pl. 37, fig. 8) 115 μ long, 100 μ broad, capsule 95 μ×83 μ. Range—109–135 μ×92 μ–112 μ.

Scriniodinium ceratophorum sp. nov.

Plate 37, fig. 7; holotype Nat. Mus. Vic. P17769

Occurrence. Oxfordian to Lower Kimeridgian: Jarlemai Siltstone (lower portion), W.A., Broome No. 3 Bore between 1,405 and 1,427 ft.

Description. Shell flat, consisting of a larger triangular epitheca and a smaller rounded hypotheca which are separated by an apparently broad girdle with thin borders. Shell-membrane thin, either smooth or, as in the type, finely granular, prolonged into a well-developed apical horn having a truncate apex with a small median projection. The capsule has a small apical prominence and almost fills the shell. A large pylome is developed in the vicinity of the girdle. Dimensions: holotype—125 μ long, 94 μ broad, capsule 97×96 μ, horn 24 μ. Another example 110 μ long, 71 μ broad, capsule 70×67 μ, horn 33 μ.

Scriniodinium apatelum sp. nov.

Plate 37, figs. 12, 13; holotype fig. 12, Nat. Mus. Vic. P17770

Occurrence. Oxfordian to Lower Kimeridgian: Alexander Formation, W.A., Wapet's Wallal Core hole between 560 and 578 ft.; Jarlemai Siltstone, W.A., Broome No. 3 Bore between 1,405 and 1,427 ft. Probably Tithonian: Jarlemai Siltstone, Wallal Core hole at 350 ft. between 305 and 320 ft., and Broome No. 3 Bore between 1,001 and 1,042 ft.; Roebuck Bay, W.A., Wapet's No. 1 Well between 972 and 982 ft.

Description. Shell flat, the main portion ovoidal to somewhat rhomboidal; epitheca with a small, thin-walled, cylindrical and truncate horn; hypotheca narrowing distally towards a square opening with a smooth or serrated edge and sometimes with a short spine-like projection at each angle. The girdle is circular, occasionally well marked but usually only indicated by narrow ledges on the two sides. Membrane of shell thin, smooth, perforate or serrate at the sides. The capsule, which fills the shell laterally and follows its outline in the middle region, terminates in a short apical prominence. A relatively large, hoof-shaped pylome extends from just beneath the apex to the level of the girdle. Dimensions: holotype—120 μ long, 58 μ broad, capsule 80 μ long and 58 μ broad. Paratype (Pl. 37, fig. 11) 95 μ long, 57 μ broad, capsule 62 μ long, 51 μ broad. Range—70–145 μ×42–72 μ.

Comments. S. apatelum has some of the features of *Gonyaulax jurassica* Defl. and *G. eisenacki* Defl., but none of the specimens have shown any sign of tabulation.

FAMILY INCERTA

Genus BELODINIUM gen. nov.

Description. Shell elongate, unequally divided by a circular girdle; main body marked into fields by delicate ledges; epitheca with a hollow membranous horn, hypotheca with a flattened membranous expansion. Type species *Belodinium dysculum* sp. nov.

Belodinium dysculum sp. nov.

Plate 37, fig. 14; Plate 39, fig. 10; holotype fig. 14, Nat. Mus. Vic. P1771

Occurrence. Probably Tithonian: Broome No. 1 Bore at 977 ft.; Broome No. 3 Bore between 1,200–1,211 ft., and between 1,001–1,042 ft.; Roebuck Bay, W.A., Wapet's No. 1 Well between 972 and 982 ft.

Description. Shell elongate, 2·5–4 times longer than broad, divided unequally by a conspicuous girdle into a longer epitheca and shorter hypotheca. The surface of the main body or capsule is divided by delicate, relatively high, sometimes undulate ledges into five to six nearly rectangular or trapezoid fields in the epitheca and into an unascertained number of ± isodiametric fields in the hypotheca; the ledges are supported by small spinules arranged in rows which arise from the surface of the capsule. The membrane which forms the ledges extends apically as a short, hollow, bluntly pointed horn and antapically as a hollow, rounded expansion which, in one example, appears to open terminally. A circle of rather strong spine-like processes is developed at the apical and antapical ends of the capsule. The shell apparently opens by the complete detachment of the apical part including the extreme anterior portion of the capsule. Dimensions: type—97 μ long, 42 μ broad, capsule $60 \times 32\,\mu$. Range—length 76–108 μ, breadth 24–42 μ, capsule 48–57 $\mu \times$ 20–32 μ.

Comments. The shells of *Belodinium dysculum* are so delicate and transparent that the interpretation given above is to be regarded as both provisional and incomplete. *B. dysculum* is a readily distinguishable form and not uncommon in the Broome No. 3 Bore between 1,001 and 1,042 ft.

Genus BROOMEA Cookson and Eisenack 1958
Broomea simplex Cookson and Eisenack

Broomea simplex Cookson and Eisenack 1958, p. 42, pl. 6, fig. 9.

Occurrence. Late Upper Jurassic: Omati, Papua, I.E.C.'s Well No. 1, Sample 24 (Cookson and Eisenack 1958, fig. 2). Probably Tithonian: Jarlemai Siltstone (upper portion), W.A., Broome No. 1 Bore at 963 and 977 ft., and Bore No. 3 between 1,200 and 1,211 ft., and 1,001 and 1,042 ft.

Comments. Previously *Broomea simplex* was known only from one of the uppermost samples in the Upper Jurassic section of the Omati bore, Papua. Its appearance in approximately the same stratigraphical position in Western Australia is therefore of interest.

Genus DINGODINIUM Cookson and Eisenack 1958
Dingodinium jurassicum Cookson and Eisenack

Dingodinium jurassicum Cookson and Eisenack 1958, p. 39, pl. 1, fig. 10.

Occurrence. Oxfordian to Lower Kimeridgian: Alexander Formation, W.A., Wapet's Dingo Claystone (upper part), W.A. (Cookson and Eisenack 1958, p. 39); Jarlemai Siltstone (lower part) Broome No. 3 Bore between 1,405 and 1,427 ft. Probably Tithonian: Jarlemai Siltstone (upper part) Wallal Core hole at 350 ft.; Broome No. 3 Bore between 1,200 and 1,211 ft., and 1,001 and 1,042 ft.; Broome No. 1 Bore at 977 ft.

Comments. D. jurassicum appears to be restricted to deposits of Upper Jurassic age and to be replaced in the Lower Cretaceous by the closely related but distinct species

D. cerviculum Cookson and Eisenack. The occurrence of *D. jurassicum* in the upper portion of the Jarlemai Siltstone is therefore suggestive of an Upper Jurassic age.

Genus CANNINGIA gen. nov.

Description. Shell flattened, roughly five-sided to almost circular with a slight apical prominence and a broadly indented base. The basal projections (corresponding to antapical horns) are either equal or unequal and frequently differ slightly in shape. An equatorial girdle is either absent or faintly indicated both on the surface or by re-entrant angles at the sides. The shell opens by a proximal break which results in the complete detachment of the apical region. Type species *Canningia reticulata* sp. nov.

Canningia reticulata sp. nov.

Plate 38, figs. 1, 2; holotype fig. 1, Nat. Mus. Vic. P17778

Occurrence. Probably Tithonian: Jarlemai Siltstone (upper portion), W.A., Broome No. 1 Bore at 977 and 963 ft.

Description. Shell with straight or rounded sides; apical projection not prominent, basal indentation clearly marked; a 'girdle' is usually present slightly above the equator. Shell-membrane densely and irregularly reticulate, the reticulum low, small-meshed and thick-walled. Dimensions: holotype—100 μ long and 86 μ broad. Paratype (Pl. 38, fig. 2) *c.* 95 μ long and 98 μ broad. Range—94–108 $\mu \times$ 74–98 μ.

Canningia colliveri sp. nov.

Plate 38, figs. 3, 4; holotype fig. 4, Nat. Mus. Vic. P17779

Occurrence. Aptian: Longreach Drill Co., Balmoral No. 1 Well at 1,000 ft.; Roma Formation, North Queensland, Well on Batavia Downs Station between 45 and 49 ft.; Muderong Shale, W.A., Wapet's Rough Range No. 8 Well between 3,863 and 3,883 ft.

Description. Shell somewhat longer than broad, widest at the equator; apex $\pm$ prominent, antapical projections short and blunt or only slightly indicated. Girdle if present only faintly showing at the sides. Wall thin, granular or closely to sparsely spinulate. Dimensions: holotype—107 μ long, 100 μ broad. Paratype (Pl. 38, fig. 3) 106 μ long, 90 μ broad. The species is named after Mr. F. S. Colliver of the University of Queensland.

HYSTRICHOSPHERES

Family HYSTRICHOSPHAERIDAE

Genus HYSTRICHOSPHAERIDIUM Deflandre 1936

Hystrichosphaeridium pachydermum sp. nov.

Plate 38, fig. 5; text-fig. 5; holotype Nat. Mus. Vic. P17772

Occurrence. Oxfordian to Lower Kimeridgian: Alexander Formation, W.A., Wapet's Wallal Core hole between 560 and 575 ft. Probably Tithonian: Jarlemai Siltstone (upper portion), W.A., Wallal Core hole at 350 ft. and between 305 and 320 ft.; Broome No. 1 Bore at 963 ft.

Description. Shell spherical, thick-walled (*c.* 3–6 μ) with closely to sparsely arranged short, solid appendages of varying shape some being simple with $\pm$ capitate ends others flattened and equally or unequally bifurcate (text-fig. 5). Dimensions: holotype—

diameter 105 μ, diameter of shell 95 μ. Range—diameter 74–138 μ, diameter of shell 70–109 μ. Appendages 4–10 μ long.

Hystrichosphaeridium torynum sp. nov.

Plate 38, figs. 6, 15; holotype fig. 15, Nat. Mus. Vic. P17773

Occurrence. Probably Tithonian: Jarlemai Siltstone (upper portion), W.A., Broome No. 1 Bore at 963 and 977 ft.; Broome No. 3 Bore between 1,001 and 1,042 ft. Neocomian: Komewu, Papua, I.E.C.'s No. 2 Well, core 10.

Description. Shell cylindrical with rounded ends and numerous short and apparently solid appendages of variable shape and size which are arranged in ± well-defined whorls around the circumference. The appendages are either narrow and simple with capitate ends or flattened and terminally branched. The opening of the shell appears to have been terminal (Pl. 38, fig. 6). Dimensions: holotype—shell 68 μ long, 33 μ broad; overall 81–56 μ. Appendages *c.* 10 μ long. Range of shell 64–78 μ × 32–38 μ.

Hystrichosphaeridium capitatum sp. nov.

Plate 39, fig. 5; holotype Nat. Mus. Vic. P17774

Occurrence. Oxfordian to Kimeridgian: Alexander Formation, W.A., Wallal Core hole between 560 and 578 ft.; Jarlemai Siltstone (lower portion), W.A., Broome No. 3 Bore between 1,405 and 1,427 ft.

Description. Shell cylindrical with rounded ends, densely covered with short, solid appendages with capitate or somewhat bifurcate ends and opening by the complete detachment of one end of the shell. Dimensions: holotype—shell 64 μ long, 42 μ broad, overall 72 × 50 μ. Range of shell 64–66 μ × 28–44 μ.

Comments. H. capitatum seems distinct from all described species of *Hystrichosphaeridium* with elongate shells; the appendages show some similarity to those of *Hystrichosphaeridium* (*Hystrichosphaera*) *intermedia*? O. Wetzel 1933, but in the absence of a specific description and a satisfactory illustration a close comparison with this species is not possible.

EXPLANATION OF PLATE 38

Figs. 1, 2. *Canningia reticulata* sp. nov. Broome No. 1 Bore, W.A., at 977 ft., × *c.* 400.

Figs. 3, 4. *Canningia colliveri* sp. nov. 3, Muderong Shale, W.A., Wapet's Rough Range Well No. 8, 3863–83 ft., × 400. 4, Longreach Drill Co's Balmoral Well No. 1, Queensland, at 1,000 ft., × 400.

Fig. 5. *Hystrichosphaeridium pachydermum* sp. nov. Wallal Core hole, W.A., 560–75 ft., × *c.* 500.

Figs. 6, 15. *Hystrichosphaeridium torynum* sp.nov. Broome No. 1 Bore, W.A., at 977 ft. 6, × *c.* 430. 15, × *c.* 570.

Figs. 7, 8. *Cyclonephelium areolatum* sp. nov. Broome No. 1 Bore, W.A., at 977 ft. 7, × *c.* 400. 8. × *c.* 400.

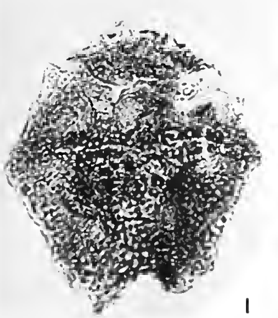
Figs. 9, 10. *Cyclonephelium densebarbatum* sp. nov. 9, Wallal Core hole, W.A., at 305 ft., × *c.* 400. 10, Broome No. 1 Bore, W.A., at 963 ft., × *c.* 400.

Figs. 11, 12. Incertae sedis, Form A. 11, Komewu, New Guinea, No. 2 well core 10, × *c.* 400. 12, Broome No. 1 Bore at 977 ft., × *c.* 400.

Fig. 13. *Chlamydophorella wallala* sp. nov. Wallal Core hole, W.A., 560–75 ft., × *c.* 500.

Fig. 14. *Leiosphaeridia similis* sp. nov. Wapet's Roebuck Bay Well No. 1, 972–82 ft., × *c.* 400.

Figs. 16, 17. *Palaeostomocystis sinuosa* sp. nov. Broome No. 1 Bore at 977 ft., × *c.* 400.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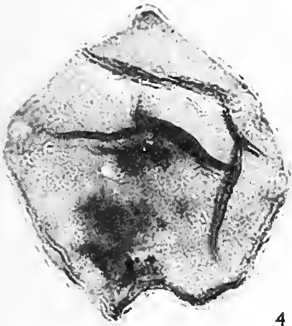
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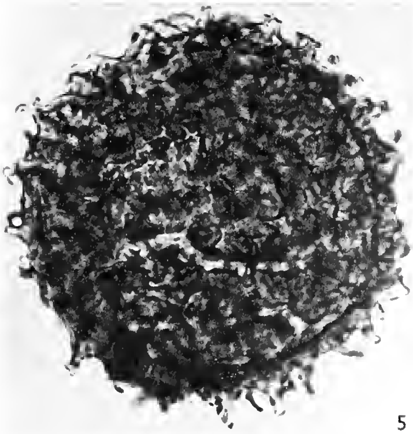
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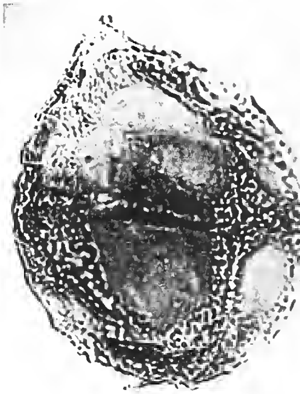
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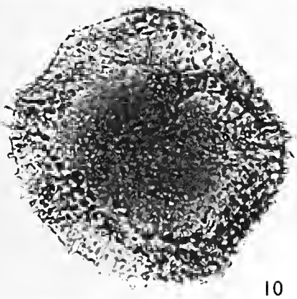
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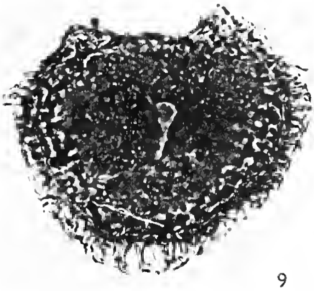
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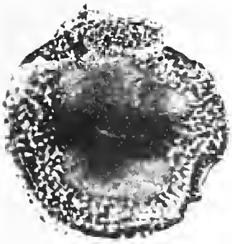
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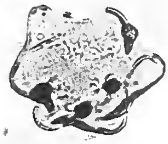
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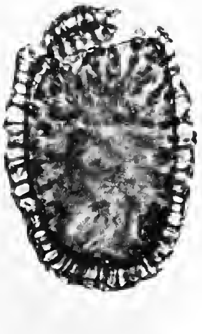
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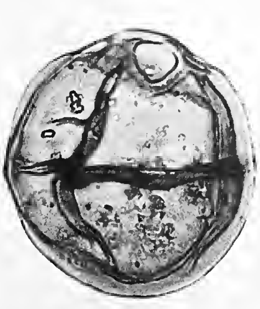
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Genus CYCLONEPHELIUM Deflandre and Cookson 1955

Cyclonephelium areolatum sp. nov.

Plate 38, figs. 7, 8; holotype fig. 8, Nat. Mus. Vic. P177791

Occurrence. Probably Tithonian; Broome No. 1 Bore at 963 and 977 ft.

Description. Shell flat, circular or slightly oval in outline with a peripheral sculptured zone (*c.* 15–20 μ broad) on both sides, in the form of a thin, finely vermiculate or areolate membrane; the unsculptured portion of the shell is generally smooth. A transverse 'girdle' is usually present. A pylome is formed by the detachment of the apical region. Dimensions holotype—70 μ long, 62 μ broad. Range—57–90 μ × 62–74 μ.

Cyclonephelium densebarbatum sp. nov.

Plate 38, figs. 9, 10; holotype fig. 10, Nat. Mus. Vic. P17776

Occurrence. Oxfordian to Lower Kimeridgian: Alexander Formation, W.A., Wapet's Wallal Core hole between 560 and 575 ft. Probably Tithonian: Jarlemai Siltstone (upper portion), W.A., Broome No. 1 Bore at 963 ft. and 977 ft.; Wapet's Wallal Core hole between 305 and 320 ft., Broome No. 3 Bore between 1,200 and 1,211 ft., and 1,001 and 1,042 ft.; Roebuck Bay, W.A., Wapet's No. 1 Well, core 11 between 972 and 982 ft.

Description. Shell flat, circular to slightly polygonal with a broad (*c.* 16–24 μ) peripheral zone ornamented on both sides with short, densely arranged, rod-shaped bristles ranging from *c.* 2–12 μ in length, with simple, usually capitate or sometimes bifurcate ends, and inner areas without bristles but with granular surfaces. A transverse 'girdle' is sometimes evident; a large terminal pylome results from the complete detachment of the apical region. Dimensions: holotype—shell 95 μ long, 92 μ broad, overall 100 × 98 μ. Range—overall diameter 86–114 μ.

Comments. When the genus *Cyclonephelium* was created the number of examples of the genotype *C. compactum* Defl. and Cookson was insufficient for the exact orientation of the shell. Since then more specimens of this species have been seen and from them and particularly from the new species *C. areolatum* and *densebarbatum* it is clear that the shells of *Cyclonephelium* are bilaterally and not radially symmetrical as was originally thought. A bilateral construction is supported by the frequent presence of a transverse 'girdle', an apical pylome and the sometimes stronger development of the ornament at the apex. It follows therefore that the ornamented and unornamented portions of the shell of *Cyclonephelium* are neither 'equatorial' nor 'polar', respectively, as given in the generic description.

C. densebarbatum differs from *C. distinctum* Defl. and Cookson, the species of *Cyclonephelium*, to which it is most closely similar, in the stouter nature of the shell and the much denser arrangement of the bristles. The examples from the Wallal deposit on the whole have longer bristles, especially at the antapical region (Pl. 38, fig. 9), than those from the Broome and Roebuck Bay deposits.

Genus CANNOSPHAEROPSIS O. Wetzel 1933

Cannosphaeropsis mirabilis Cookson and Eisenack

Cannosphaeropsis mirabilis; Cookson and Eisenack 1958, p. 48, pl. 8, fig. 3.

Occurrence. Upper Jurassic to ?Neocomian: Omati, Papua, I.E.C.'s Well No. 1, samples 19, 20, 25, 26, 29 (Cookson and Eisenack 1958, fig. 2). Probably Tithonian: Broome No. 1 Bore at 963 and 977 ft. Neocomian: Komewu, Papua, I.E.C.'s Well No. 2, core 10.

Comment. From the above occurrences it seems likely that *C. mirabilis* ranged from late Upper Jurassic to Neocomian. The age of the Omati core samples 19 and 20 is still in doubt. The occurrence of *C. mirabilis* in Broome No. 1 Bore provides the first record of this species outside New Guinea.

Cannosphaeropsis apiculata sp. nov.

Plate 39, fig. 15; holotype Nat. Mus. Vic. P17789

Occurrence. Probably Tithonian: Broome No. 1 Bore between 1,001 and 1,042 ft. Neocomian: Komewu Papua, I.E.C.'s Well No. 2, core 10.

Description. Shell small, spherical with a simple network composed of about eight to twelve solid and sometimes flattened supporting processes which branch distally and thin connecting threads which bear small spinules. Dimensions: holotype—shell 40 μ, overall 86 μ; other specimens shell 30–40 μ, overall 55–76 μ.

Family LEIOSPHAERIDAE

Genus LEIOSPHAERIDIA Eisenack 1958

Leiosphaeridia similis sp. nov.

Plate 38, fig. 14; holotype Nat. Mus. Vic. P17777

Occurrence. Probably Tithonian: Jarlemai Siltstone (upper portion), W.A., Broome No. 3 Bore between 1,200 and 1,211 ft., and 1,001 and 1,042 ft.; Broome No. 1 Bore at 977 ft.; Roebuck Bay, W.A., Wapet's No. 1 Well, core 11, between 972 and 982 ft. Late Upper Jurassic: Omati, Papua, I.E.C.'s No. 1 Well, sample 21 (Cookson and Eisenack 1958, fig. 2).

Description. Shell relatively large, spheroidal but generally folded, with a circular pylome; the shell-membrane, which is thin and faintly granular, is somewhat thicker around the pylome. Dimensions: diameter of shell 70–100 μ, diameter of pylome 13–22 μ.

Comments. A form which appears close to, if not identical, with *Leiosphaeridia similis* has been recorded, without description, from the Kimeridge Clay of England by Downie (1957, fig. c 3) under the name *?Leiosphaera hyalina* Defl. However, since Deflandre's

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EXPLANATION OF PLATE 39

Fig. 1. *Kalyptea diceras* sp. nov. Broome No. 1 Bore at 977 ft., ×400.

Figs. 2, 3. *Kalyptea monoceras* sp. nov. Komewu, Papua, No. 1 Well, core 15. 2, ×500. 3, ×400.

Figs. 4–6. *Diplotesta glaessneri* sp. nov. 4, Broome No. 3 Bore, W.A., 1001–42 ft., ×*c.* 500. 5, Lake Phillipson Bore, S.A., 87 ft., ×500. 6, showing longitudinal striations, Broome No. 3 Bore, 1001–42 ft., ×680.

Figs. 7, 8. *Komewuia glabra* sp. nov. Broome No. 3 Bore, W.A., 1001–42 ft. 7, ×300. 8, showing 'lid' of pylome, ×*c* 300.

Fig. 9. *Hystrichosphaeridium capitatum* sp. nov. Broome No. 3 Bore, 405–27 ft., ×*c.* 500.

Fig. 10. *Belodinium dysculum* sp. nov. Broome No. 3 Bore, 1001–42 ft., ×470.

Fig. 11. *Chlamydophorella wallala* sp. nov. Wallal Core hole 560–575 ft., ×480.

Figs. 12–14. *Dictyopyxis areolata* sp. nov. Broome No. 3 Bore, 1405–27 ft., ×*c.* 400.

Fig. 15. *Cannosphaeropsis apiculata* sp. nov. Komewu, Papua, No. 2 Well, core 10, ×*c.* 400.

Fig. 16. *Palaeostomocystis cylindrica* sp. nov. Broome No. 1 Bore, 977 ft., ×*c.* 530.


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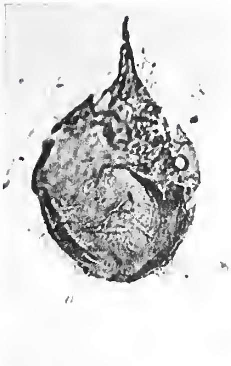
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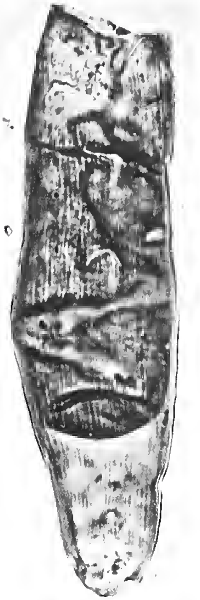
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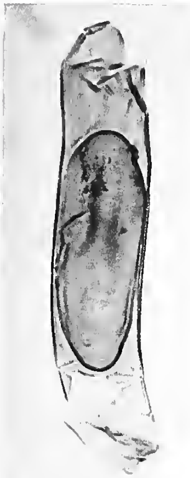
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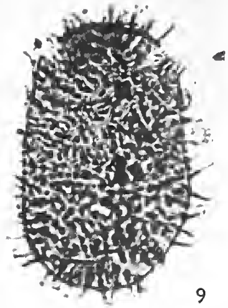
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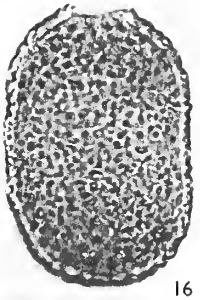
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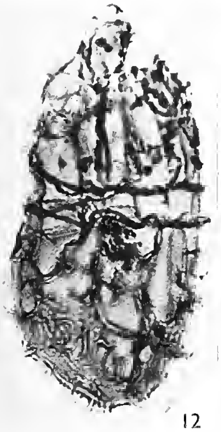
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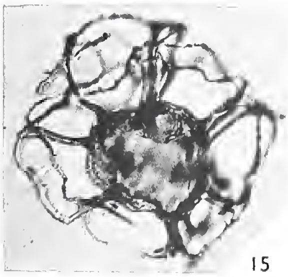
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description, based on material from the French Kimeridgian, gives no indication that a pylome is present, identification of the Australian form, of which a clearly defined pylome is a constant feature, with this species does not seem justifiable. *Leiosphaeridia similis* is distinct from *L. voigti* Eisenack 1958 from the Ordovician *Dictyonema* Shale of Esthonia in its smaller size and the less pronounced annular thickening around the pylome.

INCERTAE SEDIS

Genus CHLAMYDOPHORELLA Cookson and Eisenack 1958

Chlamydophorella wallala sp. nov.

Plate 38, fig. 13; Plate 39, fig. 11; holotype, fig. 13, Nat. Mus. Vic. P17780

Occurrence. Oxfordian to Lower Kimeridgian: Alexander Formation, W.A., Wapet's Wallal Core hole between 560 and 575 ft. Probably Tithonian: Jarlemai Siltstone (upper part), Wallal Core hole at 350 ft.

Description. Shell approximately cylindrical in outline with rounded ends, covered with numerous short bifurcate processes which support a delicate external membrane; on one surface the processes tend to be linearly arranged especially in the equatorial region. An apical process is not developed; the shell opens by the detachment of the wall of one end. Dimensions: holotype—shell 57 μ long, 40 μ broad; overall 67 μ–50 μ. Paratype (Pl. 39, fig. 11) 52 $\mu \times$ 38 μ, overall 57 $\mu \times$ 43 μ. Overall range—57–81 $\mu \times$ 38–62 μ. Processes *c.* 3–8 μ.

Comments. C. wallala is distinct from the type species, *C. nyei* Cookson and Eisenack, in its elongate form and in the absence of an apical projection.

Genus DICTYOPYXIS gen. nov.

Description. Shell elongate with rounded ends and a reticulate wall; a division into epitheca and hypotheca and the presence of a 'girdle' may be suggested by the more regular shape and arrangement of the meshes at or near the equator. The shell opens by the detachment of one of the ends. Type species *Dictyopyxis areolata* sp. nov.

Dictyopyxis areolata sp. nov.

Plate 39, figs. 12–14; holotype fig. 12, Nat. Mus. Vic. P17781

Occurrence. Oxfordian to Lower Kimeridgian: Jarlemai Siltstone (lower portion), W.A., Broome No. 3 Bore between 1,405 and 1,427 ft.; Alexander Formation, W.A., Wapet's Wallal Core hole between 560 and 575 ft.

Description. Shell ellipsoidal to nearly cylindrical. Reticulum irregular, thin-walled with four- to six-sided meshes of varying size. In the equatorial region the meshes tend to be more regularly arranged and square to rectangular in shape giving the impression of a 'girdle'. A longitudinal row of elongate meshes is sometimes evident but the significance of this arrangement is not clear. Dimensions: holotype—*c.* 100 μ long, 66 μ broad. Range—86–124 $\mu \times$ 54–66 μ.

Comments. D. areolata superficially resembles *Palaeoperidinium reticulatum* Valensi (1953, p. 28) from French Bajocian and Bathonian flints but shows no indication of the two superimposed reticula which characterize this species.

Genus DIPLOTESTA gen nov.

Description. Shell cylindrical or elongate-ellipsoidal, straight or curved, with rounded or bluntly pointed apices and partially filled with an elongate oval capsule. Membrane of shell smooth or finely and longitudinally striate; wall of capsule smooth. Type species *Diplotesta glaessneri* sp. nov.

Diplotesta glaessneri sp. nov.

Plate 39, figs. 4–6; holotype fig. 4, Nat. Mus. Vic. P17782

Occurrence. Upper Jurassic (Oxfordian to Lower Kimeridgian); Alexander Formation, W.A., Wapet's Wallal Core hole between 560 and 575 ft.; Jarlemai Siltstone (lower portion), W.A., Broome No. 3 Bore between 1,405 and 1,427 ft. Probably Tithonian: Jarlemai Siltstone (upper portion), Wallal Core hole between 305 and 320 ft.; Broome No. 3 Bore between 1,200 and 1,211 ft. and between 1,001 and 1,042 ft.; Broome No. 1 Bore at 977 ft.; Roebuck Bay, W.A., Wapet's Well No. 1 between 972 and 982 ft. Lower Cretaceous (Aptian or older): Lake Phillipson Bore, S.A., at 87 ft. 10 in.; Santos Ltd., Oodnadatta Bore between 1,052 and 1,061 ft.; Wapet's Meadow Station Bore No. 9, W.A.

Description. Shell cylindrical, straight or curved, distal end bluntly pointed, proximal end not diminishing in size and apparently rounded. In all of the many examples observed the proximal end of the shell has been open and the edge clean-cut; in a number of them, including the type, and the example shown in Pl. 39, fig. 5, the proximal wall has separated off as a 'lid', seemingly along a preformed line of weakness, and is to be seen still attached at one side.

The capsule has a thin, smooth wall and extends laterally to or almost to the shell membrane, the latter is either smooth or longitudinally striate (Pl. 39, fig. 6). The capsule opens by means of a V-shaped apical split to one side of the middle line. Dimensions: holotype—length (without lid) 100μ, breadth 24μ, capsule 58μ long, 24μ broad. Paratype (Pl. 39, fig. 5) $80\mu \times 38\mu$, capsule $62\mu \times 38\mu$. Range—length (without lid) 80–128μ, breadth 24–38μ. Capsule 53–84μ long, 24–38μ broad. The specific name is after Dr. M. F. Glaessner, University of Adelaide.

Comments. Although the Upper Jurassic and Lower Cretaceous representatives of *Diplotesta* have been included in one species slight differences between them exist. In the Upper Jurassic forms the shell is usually straight and the wall frequently longitudinally striate, whereas in the Lower Cretaceous examples observed the shells have all been curved and have unpatterned walls, moreover the latter are somewhat broader and shorter.

Genus KALYPTEA gen. nov.

Description. Shell spherical, oval to ellipsoidal, narrowing to an apical horn of variable length and either with or without an antapical horn; shell-membrane thin, smooth or finely granular. The shell, itself, is surrounded by a diaphanous veil-like external membrane. Type species *Kalyptea diceras* sp. nov.

Kalyptea diceras sp. nov.

Plate 39, fig. 1; holotype Nat. Mus. Vic. P17783

Occurrence. Probably Tithonian: Jarlemai Siltstone (upper portion), W.A., Broome No. 1 Bore at 977 ft. and Broome No. 3 Bore between 1,001 and 1,042 ft.

Description. Shell ellipsoidal with apical and antapical horns of unequal length. The apical horn is relatively long, straight or curved, and consists of a short hollow basal region and a longer and more slender solid apex. The antapical horn is considerably shorter but like the apical horn ends in a solid tip. The membrane of the shell is thin and finely granular; the external membrane in the type specimen is clearly attached to the tip of the apical horn. Dimensions: holotype—shell 152 μ long, 47 μ broad; apical horn 48 μ long, antapical horn about 15 μ. Another example 168 μ × 33 μ.

Comments. K. diceras is similar in general features to a specimen from the high Dogger described, in an unpublished thesis submitted to the University of Tübingen, by Mr. G. Alberti, the only apparent difference being the more circular shell outline of the latter. In the Australian specimens the amount of the outer membrane present seems to be dependent upon the state of preservation.

Kalyptea monoceras sp. nov.

Plate 39, figs. 2, 3; holotype fig. 2, Nat. Mus. Vic. P17784

Occurrence. Probably Tithonian: Jarlemai Siltstone (upper portion), Broome No. 1 Bore at 963 ft.; Broome No. 3 Bore between 1,200 and 1,211 ft., and 1,001 and 1,042 ft. Late Upper Jurassic: Komewu, Papua, I.E.C.'s No. 1 Well, core 15.

Description. Shell oval to almost circular in outline narrowing distally towards a short, slender horn, the terminal half of which is solid. Shell-membrane thin and finely granular. Outer 'veil' typically strongly developed but sometimes only slightly preserved. Dimensions: holotype—75 μ long, 43 μ broad, overall length 80 μ, breadth 100 μ. Paratype (Pl. 39, fig. 4) 88 μ long, 52 μ broad, overall *c.* 100 μ × 100 μ.

Comments. It seems possible that the specimen referred to as *Pareodinia aphelis* by Cookson and Eisenack (1958, pl. 12, fig. 4) might be an imperfect example of *K. monoceras*.

Genus KOMEWUIA gen. nov.

Description. Shell ±flattened, rounded-rhombic in outline with relatively short apical and antapical horns and without tabulation, girdle, or furrows. A pylome is developed. Type species *Komewuia glabra* sp. nov.

Komewuia glabra sp. nov.

Plate 39, figs. 7, 8; holotype fig. 8, Nat. Mus. Vic. P17785

Occurrence. Late Upper Jurassic: Komewu, Papua, I.E.C.'s No. 1 Well, core 15. Probably Tithonian: Jarlemai Siltstone (upper portion), W.A., Broome No. 3 Bore between 1,200 and 1,211 ft., and 1,001 and 1,042 ft.; Roebuck Bay, W.A., Wapet's No. 1 Well, core 11 between 972 and 982 ft.

Description. Shell flattened, rounded-rhombic in outline, longer than broad with rather strong, bluntly pointed apical and antapical horns of unequal length, the apical horn being the longer, and sometimes a relatively large pylome just below the apical horn. Shell-membrane faintly granular, smooth in optical section. Dimensions: holotype—132 μ long, 102 μ broad; lid of pylome 50 μ × 40 μ. Range 80–157 μ × 66–104 μ.

Genus NANNOCERATOPSIS Deflandre 1938

Nannoceratopsis pellucida Deflandre

Nannoceratopsis pellucida Deflandre 1938, p. 183, pl. 8, fig. 10.

Occurrence. Oxfordian to Lower Kimeridgian: Alexander Formation, W.A., Wapet's Wallal Core hole between 560 and 575 ft.; Dingo Claystone (upper portion), W.A. (Cookson and Eisenack 1958, p. 52); Jarlemai Siltstone (lower portion), W.A., Broome No. 3 Bore between 1,405 and 1,427 ft.; Omati, Papua, I.E.C.'s Well No. 1, samples 31, 35. Probably Tithonian: Jarlemai Siltstone (upper portion), Wallal Core hole at 350 ft. and between 305 and 320 ft. Late Upper Jurassic: Komewu, Papua, I.E.C.'s Well No. 1, core 15.

Comments. The occurrence of *N. pellucida* in the upper portion of the Jarlemai Siltstone supports the Upper Jurassic (probably Tithonian) age suggested for this portion of the Siltstone. The Australian and New Guinea shells referred to *N. pellucida* have varied somewhat in the degree of ornamentation, some have been almost smooth, others densely and finely granular, while a few have been finely reticulate. These variations seem to us too inconstant for a subdivision of *N. pellucida* on this character.

Genus PALAEOSTOMOCYSTIS Deflandre 1935

Palaeostomocystis cylindrica sp. nov.

Plate 38, fig. 16; holotype Nat. Mus. Vic. P17786

Occurrence. Oxfordian to Lower Kimeridgian: Alexander Formation, W.A., Wallal Core hole between 560 and 575 ft. Probably Tithonian: Jarlemai Siltstone (upper portion), W.A., Broome No. 3 Bore between 1,200 and 1,211 ft., and 1,001 and 1,042 ft., Broome No. 1 Bore at 963 and 977 ft.; Wallal Core hole at 350 ft., and between 305 and 320 ft.; Roebuck Bay, W.A., Wapet's No. 1 Well between 972 and 982 ft. Neocomian: Komewu, Papua, I.E.C.'s Well No. 2, core 10.

Description. Shell cylindrical with rounded ends and a terminal, slightly sunken opening. Wall about 4 μ thick, finely granular, ornamented with a low, small-meshed, thick-walled reticulum. Dimensions: holotype—71 μ long, 48 μ broad, opening *c.* 14 μ. Range—76–86 μ × 38–56 μ, opening 10–20 μ.

Palaeostomocystis sinuosa sp. nov.

Plate 38, figs. 16, 17; holotype fig. 16, Nat. Mus. Vic. P17787

Occurrence. Probably Tithonian: Broome No. 1 Bore at 977 ft.; Broome No. 3 Bore between 1,011 and 1,042 ft.

Description. Shell small, rather flat, outline squarish and ± deeply embayed with four to seven rounded prominences; a clearly marked circular opening occupies the greater part of one of the 'bays'. The shell-membrane is thin and finely granular, sometimes more pronouncedly so over the ends of the prominences. Dimensions: holotype—48 μ × 48 μ, opening 16 μ. Range—38–54 μ, opening 12–24 μ.

Comments. Palaeostomocystis cylindrica and *P. sinuosa* have been placed in the genus *Palaeostomocystis* because the opening in the shells of both species appears to be a constant morphological feature.

Gen. et sp. indet. Form A

Plate 38, figs. 11, 12; Nat. Mus. Vic. P17790

Occurrence. Probably Tithonian: Broome No. 1 Bore at 977 ft.; Broome No. 3 Bore between 1,200 and 1,211, 1,001 and 1,042 ft. Neocomian: Komewu, Papua, I.E.C.'s Well No. 2, core 10.

Description. Shell hollow, always compressed and frequently damaged, usually longer than broad with one side convex, the other straight or slightly concave; the ends of the shell are generally broken but one appears to have been straight, the other rounded. A narrow girdle-like zone due to the uneven thickening of the wall sometimes encircles the middle part of the shell in much the same way as in *Fromea amphora* Cookson and Eisenack 1958. Dimensions: 43–86 μ long, 40–67 μ broad.

Comments. The interest of Form A lies in its occurrence in deposits that appear to be situated close to the Cretaceo–Jurassic boundary.

MICROPLANKTON ASSEMBLAGES

A. *Oxfordian to Lower Kimeridgian*

1. Jarlemai Siltstone (lower portion), Broome No. 3 Bore between 1,405 and 1,427 ft. In addition to the species already listed (Cookson and Eisenack 1958, p. 62) the following have been observed: Dinoflagellata: *Gonyaulax eumorpha, Scriniodinium apatelum, S. ceratophorum.* Hystrichosphaeridea: *Hystrichosphaeridium capitatum.* Incertae sedis: *Dictyopyxis areolata, Diplotesta glaessneri.*

2. Alexander Formation, Wapet's Wallal Core hole between 560 and 575 ft. The microplankton includes: Dinoflagellata: *Gonyaulax eumorpha, Scriniodinium apatelum, S. dictyodermum, S. luridum, Dingodinium jurassicum, Wetzeliella irregularis* Cookson and Eisenack. Hystrichosphaeridea: *Hystrichosphaeridium pachydermum, H. capitatum, Cannosphaeropsis aculeata* (Defl.). *Cyclonephelium densebarbatum, Leiofusa jurassica* Cookson and Eisenack, *Pyxidiella pandora* Cookson and Eisenack. Incertae sedis: *Chlamydophorella wallala, Nannoceratopsis pellucida, Palaeostomocystis cylindrica, Wanaea clathrata* Cookson and Eisenack, *Pareodinia aphelia* Cookson and Eisenack, *Dictyopyxis areolata.*

B. *Probably Tithonian*

1. Jarlemai Siltstone (upper portion)

(*a*) Broome No. 3 Bore, 1,001 and 1,211 ft. Dinoflagellata: *Gonyaulax clathrata, Scriniodinium luridum, S. apatelum, S. dictyodermum, Dingodinium jurassicum, Broomea simplex, Belodinium dysculum.* Hystrichosphaeridea: *Cyclonephelium densebarbatum, Cannosphaeropsis apiculata, Leiosphaeridia similis.* Incertae sedis: *Diplotesta glaessneri, Kalyptea diceras, K. monoceras, Komewuia glabra, Palaeostomocystis cylindrica, P. sinuosa.*

(*b*) Wallal Core hole at 350 ft. Dinoflagellata: *Gonyaulax* cf. *ambigua, Scriniodinium dictyodermum, S. apatelum, S. playfordi, Dingodinium jurassicum.* Hystrichosphaeridea: *Hystrichosphaeridium pachydermum.* Incertae sedis: *Nannoceratopsis pellucida, Palaeostomocystis cylindrica, Chlamydophorella wallala.*

(*c*) Wallal Core hole between 305 and 320 ft. Dinoflagellata: *Scriniodinium luridum, S. dictyodermum, S. apatelum.* Hystrichosphaeridea: *Hystrichosphaeridium pachydermum, Cyclonephelium densebarbatum.* Incertae sedis: *Diplotesta glaessneri, Nannoceratopsis pellucida, Palaeostomocystis cylindrica.*

(*d*) Broome No. 1 Bore between 963 and 977 ft. Dinoflagellata: *Gonyaulax eumorpha, G. serrata, G. bulloidea, Scriniodinium luridum, Wetzeliella irregularis, Belodinium dysculum, Canningia reticulata, Broomea simplex.* Hystrichosphaeridea: *Hystrichosphaeridium pachydermum, H. torynum, Cyclonephelium areolatum, C. densebarbatum, Cannosphaeropsis mirabilis.* Incertae sedis: *Diplotesta glaessneri, Kalyptea diceras, Palaeostomocystis cylindrica, P. sinuosa.*

2. Roebuck Bay, Well No. 1 between 972 and 982 ft. Dinoflagellata: *Scriniodinium playfordi, S. apatelum, S. dictyodermum, S. clathratum, Belodinium dysculum.* Hystrichosphaeridea: *Cyclonephelium densebarbatum, Leiosphaeridia similis.* Incertae sedis: *Komewuia glabra, Palaeostomocystis cylindrica.*

STRATIGRAPHICAL CONCLUSIONS

This study of the microplankton obtained from the upper portion of the Jarlemai Siltstone has shown that:

1. Although the total microplankton population of different localities varies, sometimes considerably, there are a sufficient number of species in common to permit of an approximate correlation between them (see Table).

2. The microplankton content of the upper portion of the Jarlemai Siltstone is distinct from that of the lower portion both in the presence of species not occurring at the lower level (Broome No. 3 Bore between 1,405 and 1,427 ft.) and the apparent absence of such Oxfordian and Lower Kimeridgian types as: *Scriniodinium crystallinum* (Defl.), *Gonyaulax jurassica* Defl., and *Wanaea digitata* Cookson and Eisenack.

TABLE

Distribution of some of the microplankton occurring in the Upper Jurassic of the Canning Basin, Western Australia

	Oxfordian to Lower Kimeridgian		*Probably Tithonian*						
Species	Broome B. 3 1405–27 ft.	Wallal C.h. 560–75 ft.	Broome B. 1 963 ft.	Broome B. 1 977 ft.	Broome B. 3 1001–20 ft.	Broome B. 3 1200–11 ft.	Wallal C.h. 350 ft.	Wallal C.h. 305–20 ft.	Roebuck Bay 972–82 ft.
Gonyaulax eumorpha	+	+	−	+	−	−	−	−	−
Gonyaulax clathrata	−	−	−	−	+	+	−	−	+
Scriniodinium luridum	+	+	+	+	+	+	−	+	+
Scriniodinium dictyodernum	−	+	−	−	+	−	+	+	+
Scriniodinium apatelum	+	+	−	+	+	−	+	+	+
Dingodinium jurassicum	+	+	−	−	+	+	+	−	−
Nannoceratopsis pellucida	+	+	−	−	−	−	+	+	−
Diplotesta glaessneri	+	+	−	−	+	+	−	+	+
Leiosphaeridia similis	−	−	−	+	+	+	−	−	+
Komewuia glabra	−	−	−	−	+	+	−	−	+
Palaeostomocystis cylindrica	−	+	+	+	+	+	+	+	+
Cyclonephelium densebarbatum	−	+	+	+	+	+	−	+	+
Kalyptea monoceras	−	−	+	−	+	+	−	−	−

3. The age of the upper portion of the Jarlemai Siltstone in containing such Upper Jurassic types as *Scriniodinium luridum* (Defl.), *Dingodinium jurassicum* Cookson and Eisenack, and *Nannoceratopsis pellucida* Defl. is almost certainly Upper Jurassic and not Lower Cretaceous as at one time was suspected.

4. The deposit from the Roebuck Bay No. 1 Well between 972 and 982 ft. for which a Kimeridgian–Oxfordian age has been tentatively suggested by Wapet geologists, probably approximates to the age of the Broome No. 3 sample between 1,001 and 1,042 ft., i.e. probably Tithonian.

5. The microplankton content of the Wallal deposit between 560 and 575 ft. agrees well with that of the upper portion of the Dingo Claystone, W. A. (Oxfordian to Lower Kimeridgian). It seems probable, therefore, that the age of the sediments at this level is similarly Oxfordian to Lower Kimeridgian.

6. Seven of the species present in the upper portion of the Jarlemai Siltstone also occur in Upper Jurassic and/or Neocomian deposits in Papua, New Guinea, namely *Gonyaulax serrata*, *Hystrichosphaeridium torynum*, *Cannosphaeropsis apiculata*, *C. mirabilis*, *Komewuia glabra*, *Leiosphaeridia similis*, and *Palaeostomocystis cylindrica*.

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THE PRESERVATION OF MOULDS OF THE INTESTINE IN FOSSIL *NUCULANA* (LAMELLIBRANCHIA) FROM THE LIAS OF ENGLAND

by L. R. COX

ABSTRACT. The paper describes specimens of *Nuculana* from the Lower Lias in which clear moulds of the coiled intestine are preserved. The Nuculacea are deposit feeders in which the stomach and intestine become filled with compacted sediment from which nutriment is derived. In the present instance the shells remained closed and unfilled by sediment after death, while impregnation of the intestinal moulds with ferruginous matter and their hardening seems to have taken place very rapidly. The rather complicated coiling of the intestines resembles that now characteristic of *Nucula* rather than of *Nuculana*, and seems to be a primitive feature. Longitudinal grooves on the moulds, corresponding to ridges on the interior of the actual intestine, are clearly preserved, and resemble those seen on the faecal pellets of modern *Nucula*. The species to which the specimens belong is described as *Nuculana* (*Dacryomya*) *gaveyi* sp. nov.

INTRODUCTION

MORE than a century ago G. E. Gavey (1853, p. 34), when listing the fossils he had collected from the railway tunnel (marked Campden Tunnel on modern maps) and cuttings between Chipping Campden and Mickleton, Gloucestershire, recorded the discovery of a series of specimens which he described as '*Nucula*; with cast of the intestinal canal present in most of the specimens'. The specimens came from shales belonging to the Zone of *Prodactylioceras davoei*, that is, from the top of the Lower Lias, as understood by British stratigraphers. Gavey acknowledged help from P. B. Brodie, H. E. Strickland, and T. Wright in the identification of his fossils, but it is uncertain if they saw these particular specimens. Remarkable as it was, the discovery attracted no attention, possibly because the recognition of casts of the intestinal canal was assumed to be an amateur's mistake. Even in so comprehensive a work as that of Abel (1935), which brings together much information on the evidence of the fossil record on the life processes of extinct animals, there is no reference to any comparable occurrence.

In 1956 the Rev. J. Crompton, O.B.E., then of Winterbourne Zelston, near Blandford, Dorset, presented to the British Museum (Natural History) a series of fossils from the Gavey Collection which had come into the possession of Mrs. Crompton, a granddaughter of their collector. It was while looking through this material that Messrs. C. P. Palmer and D. L. F. Sealy, of the Palaeontological Department of the Museum, discovered and called my attention to a series of small shells, recorded as coming from Mickleton Tunnel, which had been broken to disclose the presence of worm-like coils inside them. The presence of longitudinal grooves on the coils showed that these were not worm casts and at once recalled Moore's (1931) illustrations of faecal pellets of *Nucula* and other genera. Further investigation has confirmed the fact that Gavey, long before any detailed work on the feeding and digestive processes and organs of the Nuculacea had been carried out, or faecal pellets described, had interpreted the nature of the coils

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quite correctly. The specimens containing the fossil intestines belong to a species of *Nuculana* which, although quite well known, has had no valid name, so that it is here described as *Nuculana* (*Dacryomya*) *gaveyi* sp. nov. Specimens of this species from the same bed, with the shell complete, were acquired from Gavey long ago by the British Museum (Natural History) and the Geological Survey, and with them, in the collection of each Museum, was found a single broken specimen in which the intestine is just visible. Evidently, however, Gavey had not parted with the best specimens illustrating his remarkable find.

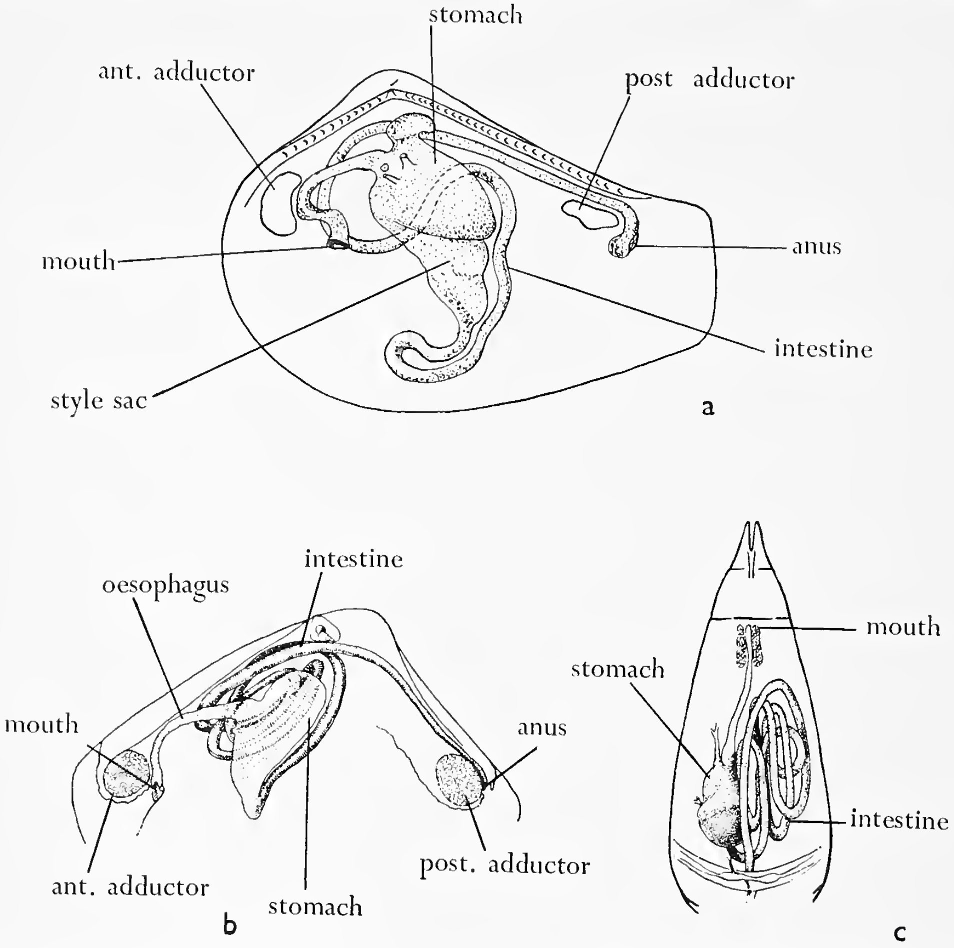
FEEDING HABITS AND DIGESTIVE SYSTEM OF THE NUCULACEA

The most important papers on the general anatomy of the Nuculacea are those of Pelseneer (1891), Drew (1897), Stempell (1898), and Heath (1937). Yonge (1939) has given a valuable account of the mode of life and the mechanisms of respiration, feeding, and excretion in several genera belonging to the superfamily. Caspers (1940) has described experiments on the feeding habits of *Nucula*, but his observations have been considered of little value by Owen (1956) in an interesting paper on the stomach and digestive processes in the Nuculidae.

The Nuculacea live on a sea bottom of mud or muddy sand, burrowing into it until the shell is just or almost covered by the sediment, and feeding while so buried. According to Yonge's observations, *Nucula* buries itself with its antero-dorsal margin nearly horizontal and its short posterior end pointing obliquely downwards, its exhalant current (the animal has no siphons) reaching the surface of the substratum by a small pit formed by expulsion of water from the shell. Forms such as *Nuculana* and *Yoldia*, in which the shell is elongated posteriorly and often rostrate, and in which the animal has inhalant and exhalant siphons, usually burrow with their long axis vertical or steeply inclined, the tips of their siphons, and sometimes also the posterior end of the shell, just protruding above the surface of the substratum.

The mouth is situated near the anterior adductor muscle, on its posterior or postero-ventral side. Extending backwards from it on each side are large, paired, flap-like structures, the labial palps, here developed as palp-lamellae, and, attached to the postero-dorsal corner of each outer lamella, is a feeler-like process, known as a palp proboscis, which is capable of extending far beyond the shell margins, and has at its proximal end a small receptacle known as the palp pouch. The Nuculacea are essentially deposit feeders, material suspended in the inhalant current contributing very little to their food. During feeding the palp proboscides are extended between the opened shell valves and grope about (within the sediment in the case of *Nucula* and over its surface in the case of *Nuculana*) for food. The material collected at the tip of each proboscis passes along a ciliated groove in the latter to its proximal end, and thence by way of the palp pouch to the palp lamellae. It is then conveyed between these, still by ciliary action, to the mouth, a certain amount being sorted out in the process and carried to the edges of the lamellae, where it is rejected. The material that finds its way from the mouth through the rather short oesophagus to the stomach includes sand grains and more finely divided mineral matter, together with living organisms and organic detritus. In freshly caught animals the stomach is invariably distended.

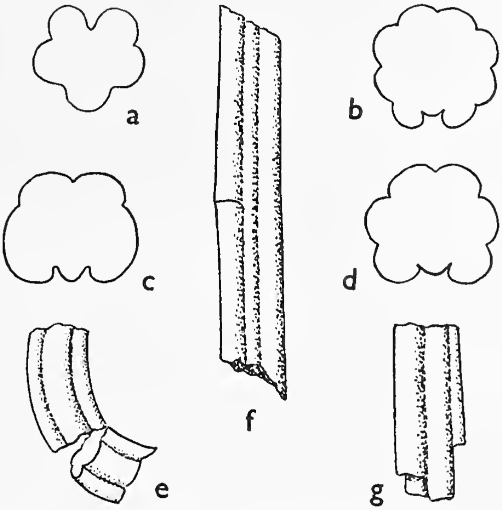
The stomach consists of a globular dorsal region and, below, of a large, tapering, funnel-shaped ventral region, termed the style sac, although a crystalline style is absent. The intestine emerges from the ventral end of the style sac. Digestion takes place by means of secreted enzymes, which are thoroughly mixed with the food-bearing matter by the rotating action of cilia of the style sac. The soluble products of digestion are absorbed by the epithelium of the stomach and intestine. The compacted faecal mass is allowed to enter the latter periodically by relaxation of a sphincter muscle. In the Nuculidae the intestine, illustrations of which are here reproduced (text-fig. 1*b*, *c*), is long and rather complicated. After leaving the style sac it bends in a dorsal direction past the posterior side of the stomach, and then takes an anterior course; it next describes a series of coils before merging into the relatively straight rectum, which leads to the anus on the posterior side of the posterior adductor. About mid-way along the intestine in most species, and in two or more places in some, there is a sharp backward bend so that



TEXT-FIG. 1. Alimentary canal in modern Nuculacea. *a*, *Nuculana sulculata* (Gould), ×10 (after Stempell, slightly modified). *b*, *Acila fultoni* (Smith), ×1·8 (after Heath). *c*, *Nucula taeniolata* Dall, ×6 (after Heath).

the direction of coiling is reversed. The coils lie more to the right-hand side of the sagittal plane of the animal, while the stomach lies more to the left-hand side (text-fig. 1*c*). In *Nucula nucleus* (Linné) there are about four coils, but in *N. cancellata* Jeffreys, as figured by Heath (1937, pl. 1, fig. 2), there are about nine, with three sharp reversals of the direction of coiling. Heath found that in *Nucula* the coiling is most complicated in species living at the greatest depths, and thought that this might be because the amount of nutritive material in the sediment decreases with depth, so that a greater length of intestine is necessary for its absorption.

In living Nuculanidae and Malletiidae the intestine is less complicated and varied than in the Nuculidae. In *Nuculana sulculata* (Gould) (text-fig. 1*a*), from the coast of Chile, it bends back and up, remaining close to the posterior side of the stomach, and then bends forward, passing the stomach on the right-hand side, until it almost reaches the anterior adductor, and finally bends round again, occupying a dorsal position until it terminates, behind the posterior adductor, at the anus. In *Nuculana minuta* (Müller), from Norway, as figured by Yonge (1939, p. 96, fig. 14) its general course is almost exactly the same.



TEXT-FIG. 2. Faecal pellets of *Nucula* seen in cross-section or in side view. *a*, *N. tenuis* (Montagu), ×100. *b*, *N. sulcata* Bronn, ×100. *c*, *N. nitida* G. B. Sowerby, ×100. *d*, *N. nucleus* (Linné), ×100, *e*, *f*, *g*, *N. nucleus* (Linné), ×40. (After H. B. Moore.)

The intestine in the Nuculacea has thickened longitudinal ridges bearing long cilia. The faeces are voided as rods of compact mud which break up into faecal pellets up to about 1 mm. in length and bear longitudinal grooves which are impressions of the intestinal ridges. Moore (1931), some of whose illustrations are reproduced as text-fig. 2, has recorded that in British species of *Nucula* the number of ridges ranges from five to nine. Galliher (1931) has figured faecal pellets of *Acila castrensis* (Hinds). So far as I know, the faecal pellets of *Nuculana* have not yet been illustrated. Moore states that the diameter of the faecal pellets of a *Nucula* with a shell 1 cm. long is 0·15 mm. Schenck

(1936, p. 12) records that the diameter of faecal pellets from shells of *Acila castrensis* (Hinds) 14·5 mm. long may be as much as 0·8 mm. In Heath's (1937) figures of *Acila* the diameter of the intestine is represented as being 0·7–0·8 mm. in shells about 30 mm. long. Its diameter in a specimen of *Nuculana sulculata* (Gould) figured by Stempell (1898, pl. 24, fig. 24), whose illustration is here reproduced (Text-fig. 1*a*) appears to have been about 0·2 mm. for a shell only 6 mm. long, and in a specimen of *Yoldia thraciaeformis* (Storer) 37 mm. long the corresponding diameter, according to Heath's illustration (1937, pl. 9, fig. 78), was as much as 1·0 mm. Moore states that faecal pellets of *Nucula* are still well enough preserved for specific identification after fifty years on the sea-floor, but Galliher and Schenck found them to be much less permanent.

From these facts it may be seen that there is a remote possibility of the preservation fossil of the compacted mass of mainly argillaceous material that occupies the intestine and much of the stomach in the Nuculacea, when the actual organic tissues have decayed away, although usually it would become obscured by or mixed with the very similar sediment which would fill the shell after the death of the animal. The possibility of the occasional preservation of faecal pellets in sedimentary formations would appear to be much less remote. Dr. R. Casey has called my attention to a paper by Stoyanow (1949) in which (p. 63, pl. 8, figs. 5, 7, 8) three supposed faecal pellets, found near a specimen of that author's species *Acila* (*Truncacila*) *schencki*, are described from the Lower Cretaceous of Arizona. The objects in question, however, are about 2 mm. in diameter and the shell only 14 mm. long, so that considerable doubt remains as to their identity, as comparison with the measurements cited above will show. I know of no other published record of fossil faecal pellets.

DESCRIPTION OF THE FOSSIL SPECIMENS FROM MICKLETON TUNNEL

The material consists of about twelve shells broken open by Gavey to show the coiled intestine inside and seven more completely dissected coils. In addition there are a number of complete bivalve specimens from the same locality and horizon, together with part of a small ironstone nodule containing a cluster of specimens, one broken to show the coiled intestine inside. In this nodule (Pl. 40, fig. 3), presumably one of several from which Gavey obtained his specimens, the shells lie in all directions. There is no question of their being preserved in the original position of growth. They are hollow except for a varying amount of ferruginous matter which has been deposited inside them and serves to cement the fossil intestines in the positions which they occupy. Presumably, as the result of some disturbance, the molluscs, while still living, were swept together on the sea-floor with their valves closed for protection, and very soon afterwards were

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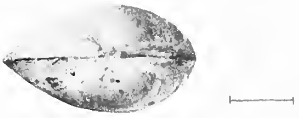
EXPLANATION OF PLATE 40

Figs. 1–6. *Nuculana* (*Dacryomya*) *gaveyi* sp. nov., from the uppermost Lower Lias of Mickleton Tunnel, Glos. 1, Interior of a right valve (Brit. Mus., LL. 8232), with coils of intestine partly embedded in ferruginous matter; ×9. 2, Interior of a right valve (LL. 8231), showing coils of intestine. The chondrophore is visible, but the hinge-teeth are hidden by a piece of shell broken away from the other valve: ×10. 3, Fragment of ironstone nodule containing several specimens, one broken to show coiled intestine inside (L. 6556); ×4. 4*a*, *b*, Holotype (LL. 8226), ×3. 5, Interior of a left valve (LL. 8233), with hinge-line broken away. The intestine ends near the top left-hand corner of the figure, very close to the position of the anus in modern *Nuculana*; ×9. 6, Interior of fragment of a left valve (LL. 8238), showing coils of intestine; ×14.

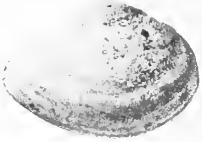
1 × 9

2 × 10

3 × 4



4b × 3



4a × 3

5 × 9

6 × 14

COX, *Nuculana* (*Dacryomya*) *gaveyi* sp. nov.

subjected to the action of iron-bearing waters; concretions were formed with clusters of the shells as nuclei, and at the same time the intestinal moulds became impregnated with ferruginous matter and hardened. Within most of the shells the coils, some of which are now cemented to the right valve and some to the left, have been displaced to some extent from the positions which they occupied during life, but in one specimen (Pl. 40, fig. 5) the last, straight part of the intestine can be clearly seen to run just below the postero-dorsal margin and terminate near what must have been the position of the posterior adductor muscle. This same feature is visible, although less clearly, in at least two other specimens. In one or two cases the intestine originates in a globular or pyriform mass which appears to be the internal mould of the stomach or part of it.

A most interesting fact is that these intestines, with their somewhat complicated series of coils, more closely resemble those of modern species of *Nucula* than of *Nuculana*. The number of coils is about three, and a crossing over and reversal of direction of the intestine is seen near the middle of its length (Pl. 40, fig. 6), as in Recent *Nucula*. Of great interest is the presence of a series of longitudinal grooves exactly like those on the faecal pellets of modern *Nucula*. The number of grooves appears to be seven; the deepest and broadest lies on the concave side of the coil, and the remainder are almost equal in depth and spacing. The diameter of the intestinal moulds ranges from about 0·2 mm. to 0·45 mm. This measurement agrees quite well with the intestinal diameter in Recent species of *Nucula* and *Nuculana* of comparable size.

DESCRIPTION OF THE SPECIES IN WHICH THE FOSSIL INTESTINES ARE PRESERVED

Family NUCULANIDAE
Genus NUCULANA Link 1807
Subgenus DACRYOMYA Agassiz 1840
Nuculana (*Dacryomya*) *gaveyi* sp. nov.

Plate 40

1833 *Nucula inflata* Sow.; Zieten, *Versteinerungen Württembergs*, p. 77, pl. 57, figs. 4*a–c* (*non* J. de C. Sowerby 1827).
1837 *Nucula acuminata* v. Buch; Goldfuss, *Petrefacta Germaniae*, 2, p. 155, pl. 125, figs. 7*a–c* (*non* Zieten *ex* v. Buch MS. 1833).
1853 ?*Nucula inflata* Zieten; Oppel, *Württemb. naturwiss. Jahreshefte*, 10, p. 122, pl. 4, fig. 24.
1855 *Arca* (*Nucula*) *minor* Simpson, *Fossils of Yorkshire Lias*, p. 115 (*non Arca minor* v. Hagenow 1842).
1856 *Nucula acuminata* Quenstedt, *Der Jura*, p. 187, pl. 23, fig. 14.
1869 *Leda acuminata* (v. Buch); Dumortier, *Études paléontologiques. Lias-moyen*, p. 259, pl. 30, fig. 3.
1871 *Leda zieteni* Brauns, *Der untere Jura im nordwestlichen Deutschland*, p. 373 (*non Leda zietenii* d'Orbigny 1850).
1876 *Leda minor* (Simpson); Tate, *in* Tate and Blake, *Yorkshire Lias*, p. 383, pl. 11, fig. 9.
1876 *Leda zieteni* Brauns; Tate, op. cit., p. 383.
1883 *Nucula inflata* Zieten; Langenhan, *Versteinerungen des Lias am Grossen Seeberge bei Gotha*, pl. 3, figs. 33*a*, *b*.
1918 *Leda minor* (Simpson); Richardson, *Trans. Woolhope Nat. Fld. Cl.* (for 1916), p. 150, pl. 155, fig. 1.
1935 *Leda zieteni* Brauns; Kuhn, *Neues Jb. Miner.*, Beil.-Bd. 73, p. 475, pl. 18, figs. 8*a*, *b*.

Holotype. Brit. Mus. (Palaeont. Dept.) no. LL. 8226, from the uppermost Lower Lias (*Prodactylioceras davoei* Zone) of Mickleton Tunnel, near Chipping Campden, Gloucestershire.

Description. Of medium size for the genus, longitudinally pyriform, not greatly elongated, gibbose, with submedian, moderately prominent, incurved, opisthogyrous umbones; posterior extremity narrow, subrostrate. Antero-dorsal outline convex, merging in an even curve with the strongly convex anterior margin, which is continued by the evenly and rather strongly convex ventral margin. Escutcheon cordiform, unimpressed, not limited by distinct umbonal ridges; postero-dorsal margin visible in side-view of shell except where the umbonal region projects to a moderate extent above it. Hinge with about ten teeth on each side of a projecting, spoon-like chondrophore. Pallial line without sinus. Shell with nacreous inner layer.

Measurements of holotype. Length 8·3 mm., height 6·0 mm., inflation 4·6 mm.

Remarks. I have described *Nuculana gaveyi* as a new species instead of publishing the name as a *nomen novum* for either of the homonyms (*minor* Simpson and *zieteni* Brauns) cited in the synonymy, as no type specimen would have been available if the latter course had been adopted. It is probable that several specimens in the Whitby Museum identified as *Leda minor* are Simpson's unfigured syntypes, but they are not so labelled. The holotype of *N. gaveyi* and a number of topotypes in the collections of the British Museum (Natural History) and the Geological Survey had been identified as *Nuculana minor*, and, after comparing them with specimens of Simpson's species from Yorkshire I agree that they are conspecific with them. Moreover, comparison of the Gloucestershire specimens of *N. gaveyi* with the above-cited illustrations of Zieten, Goldfuss, Quenstedt, and Kuhn of the species from Germany to which Brauns assigned the name *Leda zieteni* has revealed no differences of specific importance. Tate recorded both *Leda minor* and *L. zieteni* from the Yorkshire Lias, supposing the former to occur in slightly higher zones than the latter, but he hinted that they might prove to be the same species.

I have commented previously (Cox 1940, pp. 27, 28) on the presence of nacre in Jurassic Nuculanidae (in modern species of the family the shell is porcellanous), and also on the frequent absence of a pallial sinus (one is present in the modern representatives). Brauns also mentioned the entire pallial line when describing *L. zieteni.* The feature is clearly seen in specimens of *Nuculana gaveyi* from Mickleton Tunnel in the British Museum (Natural History) (reg. no. L. 17905).

Occurrence. Lower and Middle Lias (*oxynotum-margaritatus* Zones) of Yorkshire, Lincolnshire, Northamptonshire, Oxfordshire, Warwickshire, Gloucestershire, Somerset, and Raasay (Inner Hebrides). It is probable that records of '*Leda minor*' from the Upper Lias of Gloucestershire refer to *Nuculana rostralis* (Lamarck) or to *N. claviformis* (J. de C. Sowerby). Specimens in the Geological Survey Museum said to come from the *semicostatum* Zone of Scunthorpe, Lincs., are from a much lower zone than any others seen. Brauns records that in north-west Germany the species occurs in the *davoei* and *margaritatus* zones.

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A LOWER CRETACEOUS GASTROPOD WITH FOSSILIZED INTESTINES

by RAYMOND CASEY

ABSTRACT. *Margarites* (*Atira*) *mirabilis* sp. nov. is a small trochid gastropod of Lower Cretaceous (Albian) age and is found in the Lower Greensand (Folkestone Beds) of Kent and Surrey. A unique feature in the description of this fossil gastropod is an account of the digestive tract, based on discovery of a specimen in which the contents of the gut have been phosphatized, thus reproducing as a mould the form and internal structures of the organ. The presence of the intestinal groove with bordering typhlosoles, minor longitudinal folds of the intestine, and an anal sphincter are all clearly demonstrable. Similarities with the gut of Recent Trochidae suggest that ecology and feeding habits of the family have remained unchanged. From the arcuate course of the rectum it is inferred that the left hypobranchial gland, missing in living species of *Margarites*, if ever present, was probably lost already in Lower Cretaceous times.

FROM time to time attention is drawn to the freak preservation of internal organs or other portions of the soft anatomy of animals known in the fossil state normally by shells, bones, or other hard parts or by traces only. A prime example is the Tremadocian annelid described by Whittard (1953) which has retained the form of the gut, the jaw apparatus, and minute details of the surface of the skin. Among mollusca, Roger (1944) has illustrated and described a dibranchiate cephalopod from the Upper Cretaceous of Syria in which indications of the stomach, intestines, and other organs can be made out. More recently, Cox (1959) has confirmed observations made by Gavey (1853) on the preservation of moulds of the intestines in nuculid lamellibranchs from the Lias of Gloucestershire.

The occurrence of remains of the gut in a fossil species of *Margarites*, described herein, is believed to be a unique record in the Gastropoda. The specimen was collected by the author in 1945 from a phosphatic concretion in the Lower Greensand (Folkestone Beds) of Sandling Junction, near Hythe, Kent, and was presented to the Geological Survey Museum, London, in 1946. The discovery is all the more remarkable in view of the rarity and generally poor condition of fossils in the Folkestone Beds.

I am indebted to Mr. I. C. J. Galbraith of the Zoology Department of the British Museum (Natural History) for supplying specimens of a living species of *Margarites* for dissection, and to Mr. M. Pulsford for photographic assistance. The paper is published by permission of the Director of the Geological Survey and Museum.

SYSTEMATIC DESCRIPTION

Family TROCHIDAE

Genus MARGARITES Gray 1847

Subgenus ATIRA Stewart 1927

Margarites (*Atira*) *mirabilis* sp. nov.

Plate 41, figs. 1–3, 5–8; text-fig. 1A, B.

Trochus sp., Wright and Wright 1942, p. 86.

Holotype. Geological Survey Museum No. 97302, Lower Greensand, Folkestone Beds (*tardefurcata* Zone, *Farnhamia* horizon), Coxbridge pit, Farnham, Surrey.

[Palaeontology, Vol. 2, Part 2, 1960, pp. 270–6, pl. 41.]

Description. Shell small, nacreous internally, helicoidal, trochiform, consisting of five or six moderately convex whorls separated by simple sutures; apical angle about 85°. Body-whorl large, three-quarters the total height. Base very gently convex, with a funnel-shaped, rapidly expanding umbilicus, angular at the rim. Aperture elliptical, holostomous, having a small sinus corresponding to the umbilical rim. Peristome disconnected, the outer and inner lips being joined only by a film of nacreous material. Outer lip thin, inclined at about 60° to the suture. Inner lip in the same plane as the outer lip, smooth, not reflected. Spire and body-whorl with numerous fine spiral ridges which are traversed obliquely by the growth-lines, giving a subdued trellis-like pattern to the surface. Ornament intensified just below the suture, where the ridges are delicately nodulated. Base finely striated concentrically. Umbilical walls and rim with weak spiral ridges and vertical riblets, minutely beaded at their points of intersection.

Measurements of holotype. Total height 10 mm., height of body-whorl 7·5 mm., diameter of base 10 mm., width of umbilicus 4·9 mm.

Remarks. This gastropod is a characteristic fossil of the Folkestone Beds (Lower Albian) of Kent and Surrey and occurs principally in the *jacobi* Subzone of the *nodosocostatum* Zone and the basal part of the *tardefurcata* Zone. Preservation is generally poor. The holotype, a perfect shell, was isolated by hardening the fossil and its sandy matrix with nitrous cellulose and then applying amyl acetate as a solvent to small areas at a time, removing the sand-grains when loosened, and rehardening the shell as each portion was cleaned.

The shell has the general aspect of Recent *Margarites* but possesses the angular umbilical border diagnostic of the subgenus *Atira*. This border is not coarsely crenulated as in *Garramites*, nor ridged as in *Solariella*. The present species differs from the type-species of *Atira*, *Margarites* (*A.*) *ornatissimus* (Gabb) of the Upper Cretaceous of California (Stewart 1927, pl. 24, fig. 1), chiefly in its less angular whorl-profile; and the same character distinguishes it from species of *Margarites* described from the Cretaceous of Japan by Nagao (1939) and from Texas by Stanton (1947). *Margarites* (*A.*) *inornatus* (Gabb), also from the Californian Upper Cretaceous, resembles the Lower Greensand form in its rounded whorls but has a much lower, smaller spire. '*Turbo*' *moniliferus* J. de C. Sowerby of the Upper Greensand (Upper Albian) of Blackdown, Devon, is superficially similar to *M.* (*A.*) *mirabilis*, though it is a taller species with grosser ornament, a canaliculated suture, and subcircular aperture.

THE ECOLOGY AND THE ALIMENTARY SYSTEM OF THE TROCHIDAE

The Trochidae, of which family *Margarites* is regarded as the most primitive member (Thiele 1929), are everywhere characteristic of the intertidal fauna of rocky shores and find an ideal environment on the hard surfaces of coral reefs. Retention of the aspidobranch ctenidium probably debars them from life on a soft substratum with much suspended sediment in the water (Yonge 1947, p. 473). They are microphagous and live mostly under stones and seaweed, browsing on diatoms, algae, and algal debris (Graham 1955), which, together with mineral and other detritus, is rasped into the mouth by the action of the radular teeth. *Margarites helicinus* (Fabricius), the type species of the genus, is a common boreal form of the laminarian and lower littoral zones which attains its southwards range on the northern shores of the British Isles (Cooke 1895, p. 365). Spawn-masses of *Margarites*, each with a hundred or more eggs, have been collected with the adults from the under surfaces of stones at Cullercoats, Northumberland (Fretter 1955, p. 162).

Following the work of Robert (1900) and Randles (1904) the gross morphology of the alimentary system of the Trochidae is well known. The mouth leads to a buccal cavity or crop, which in turn is connected by a thick-walled oesophagus with a stomachal cavity. The last-named is the principal dilation of the digestive tract and is furnished at its posterior end with a coiled caecum. Owing to the torsion of the visceral mass undergone by the Gastropoda, the digestive tube doubles back from the stomach to the anterior end of the animal, via a long, more or less cylindrical intestine, thrown into coils. Like the stomach, this part of the gut is lined with ciliated epithelium, and it bears an intestinal groove, bordered on either side by a prominent fold (typhlosole), which runs along the gut to the anus. The origin of this groove and accompanying typhlosoles in the stomach is well illustrated by Graham (1949). The rectal continuation of the intestine may be of uniform calibre throughout its length or it may be distended as depicted in Pl. 41, fig. 4, and it is often provided with an anal constriction or sphincter. It ascends to the roof of the mantle-cavity to discharge on the right (exhalent) side of the cavity.

In correlation with the opening of the anus into the mantle-cavity (essentially a respiratory chamber) there is elaborate intestinal mechanism for consolidation of the faeces into compact pellets too heavy to be drawn in by the inhalent current (Yonge 1947). In vegetarian animals faecal matter is always bulky and it is probable, as postulated by Graham (1932) in the case of *Patella*, that the long coiled intestine of herbivorous feeders like the Trochidae is concerned chiefly, if not exclusively, with the formation of firm faeces. Indigestible and undigested matter is compacted together into a string, cemented by secretions from the secretory cells of the digestive gland, and driven along the gut by ciliary action. In *Patella* Graham has noted that the cilia on the double folds of the mid-gut beat into the groove between, along which a current runs to the anus. The faeces are voided as rod-shaped masses which break into lengths four or five times the diameter (Moore 1932). Moorhouse (1932), speaking of *Trochus niloticus* from

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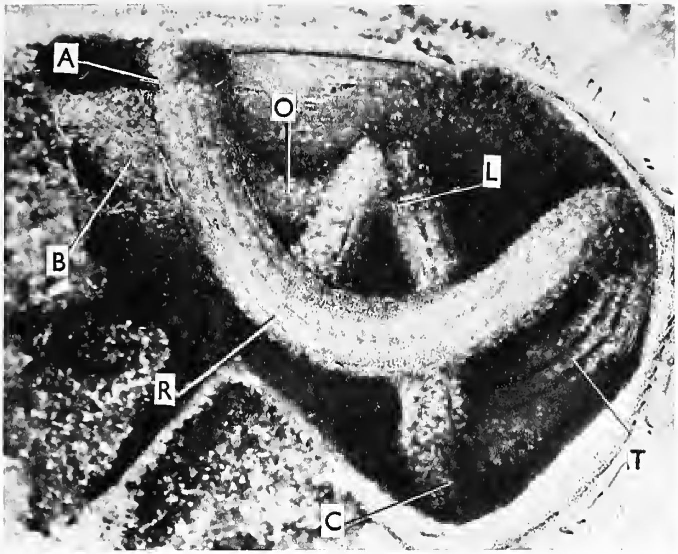
EXPLANATION OF PLATE 41

Figs. 1–3, 5–8. *Margarites* (*Atira*) *mirabilis* sp. nov. 1, Specimen with body-whorl broken open and exposing a mould of the gut. The specimen is seen in oblique lateral aspect with the spire pointing upwards and the base tilted slightly into the field of view. The terminal half of the body-whorl, on the observer's left, is filled with detritus and the aperture lies buried in the matrix. Lower Greensand (Folkestone Beds) (*nodosocostatum* Zone, *jacobi* Subzone), Sandling Junction sandpit, near Hythe, Kent (Geological Survey Museum No. Zm 490; author's coll.), ×6. 2, Pencil sketch of same specimen to clarify relationship of internal organs to shell morphology. 3, Portion of same specimen enlarged ×24, showing anal sphincter (A), rectum (R), with impressions of longitudinal folds on the dorsal surface, and, on the ventral surface, a mould of the intestinal groove and pair of typhlosoles (T); a loop of the intestine (L) protrudes from below the right side of the rectum and its descending limb may be followed to a convolution indicated at C; the buccal cavity and part of the oesophagus may be represented by the structures lettered B and O respectively. 5, 6, 7. Three views of holotype to show aperture (5), side (6), and base (7). Lower Greensand (Folkestone Beds) (*tardefurcata* Zone, *Farnhamia* horizon), Coxbridge pit, Farnham, Surrey (Geological Survey Museum No. 97302; author's coll.), ×4. 8, Portion of same specimen enlarged ×6 to show details of ornament.

Fig. 4. Gut of *Trochus turbinatus* (Born.), seen from above and with the rectum (R) laid over to the right. The anterior part of the buccal cavity (B) and the posterior part of the stomach (S) are omitted, and the stomach is opened to show the intestinal groove and bordering typhlosoles (T). Other parts are lettered as in fig. 3. Redrawn from Robert 1900, ×about 5.



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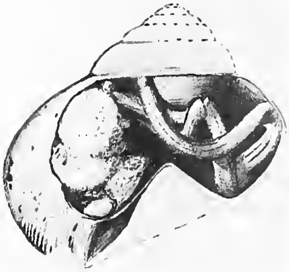

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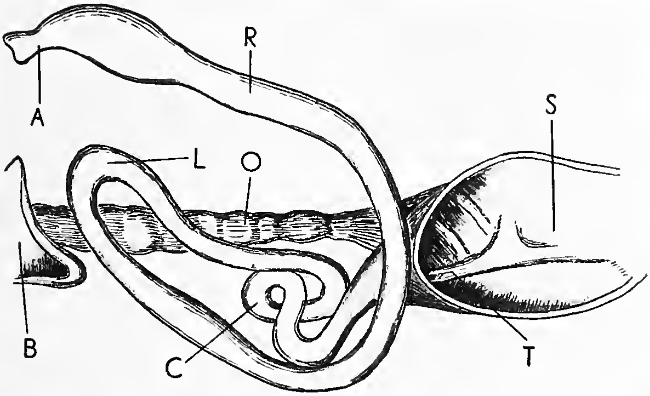

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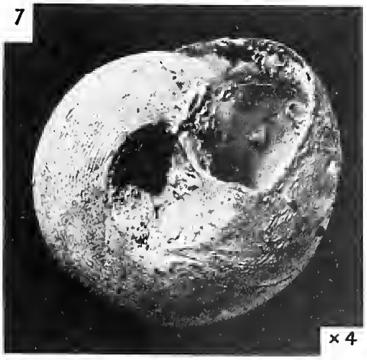

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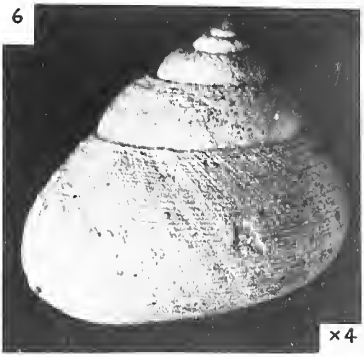


6 ×4

CASEY, *Fossil and Recent Trochidae.*

the Great Barrier Reef, says: 'Feeding appears to proceed at every opportunity, so that the amount of faecal matter deposited is very great.' Rao (1939) dissected scores of specimens of this species and found that the stomach and intestines were always full, even though the oesophagus was empty. Individuals starved for a few hours under laboratory conditions were found on dissection to contain very little food material in the stomach, although the intestinal loops were nearly always full.

Clark (1958), in a study of the mantle-cavities of some Trochidae and Turbinidae, has observed that there is an association between the course of the rectum across the roof of the mantle-cavity and the development of the hypobranchial glands (organs which secrete mucus to bind the fine sediment carried in with the respiratory current). In species with a straight rectum the right gland is small, while in species where the rectum takes an arcuate course the right gland is variously developed. The greater the arc of the rectum, the larger is the right hypobranchial gland, since it appears always to occupy the whole of the space available between the right side of the rectum and the point where the roof and floor of the mantle-cavity meet. Fretter (1955) showed that in *Margarites helicinus* the left hypobranchial gland is entirely lacking, while the right is well developed. Dissections of *Margarites groenlandicus* carried out by the author confirmed the extreme condition of disparity of development of these glands and also the strongly arcuate shape of the rectum in this genus (text-fig. 1D).

FOSSILIZATION OF THE GUT IN *MARGARITES* (*ATIRA*) *MIRABILIS*

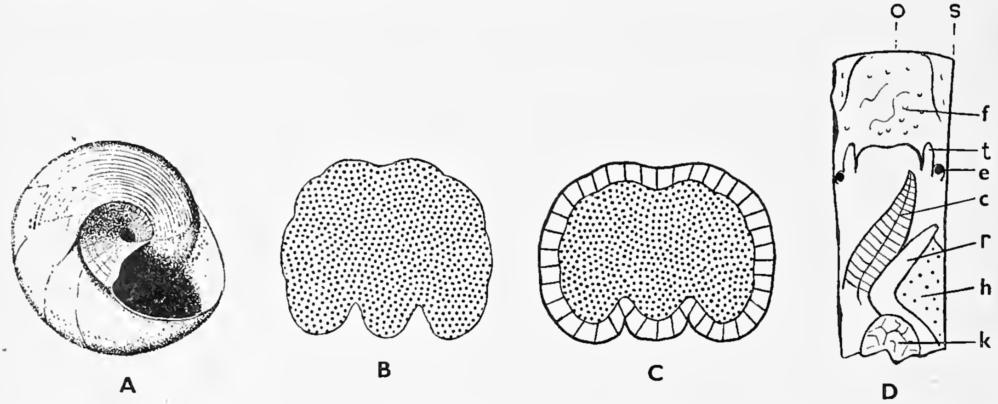
The specimen which forms the nucleus of this paper was obtained from a phosphatic concretion in the Folkestone Beds of Sandling Junction sandpit, near Hythe, Kent (horizon 3 of Casey 1939). This horizon falls within the *jacobi* Subzone of the *nodosocostatum* Zone, here taken as the basal zone of the Albian. Above and below the bed in question are unfossiliferous sands exhibiting well-marked current-bedding. Concretions from this bed are one of the few sources of abundant fossils in the Folkestone Beds and within their sandy and pebbly matrix contain a varied fauna of mollusca, bryozoa, echinodermata, and brachiopoda. They appear to represent aggregations of organic debris that accumulated in hollows on the sea-floor and were cemented by syngenetic formation of calcium-phosphate, the shell-substance of mollusca and other carbonate being converted to collophane. Ammonites and gastropods are usually hollow, and the preservation and mode of occurrence of the fossils suggest that the shells were buried rapidly more or less where they died.

Margarites (*Atira*) *mirabilis* is the commonest gastropod in this bed and it is not unusual to find a dozen or more specimens in the space of a few cubic inches. The body-whorl of a hollow specimen was accidentally punctured, revealing inside the cavity, about half a turn back from the aperture, a minute worm-like structure of problematical origin. Enlargement of the 'window' resulted in exposure of the structure illustrated in Pl. 41, figs. 1–3, which is now interpreted as a mould of the intestines of the animal.

From data discussed in the preceding section it is apparent that retention of food and faecal matter in the alimentary tract after death is normal in the Trochidae. Moreover, it seems likely that this singular example of fossilization was made possible in the first place through the habit of these gastropods of consolidating the contents of the intestines. Material in the gut must have been firm enough to have stayed intact after decomposition of the surrounding tissues and to have remained in that condition long enough to become involved in the process of phosphatization. In this manner the form of the gut and its internal features have been preserved as a mould in much the same way as the internal moulds of hollow shells are formed by compaction of infilling sediment. Contents of the digestive tract being of much finer grain than detrital sediment, minute structural detail of the gut is faithfully reproduced.

When comparing the fossil specimen with the gut of *Trochus* (Pl. 41, fig. 4) it must be borne in mind that in the fossil we see the organ as it is disposed when the animal is retracted in its shell, while in the living form it is shown spread out.

Reference to Pl. 41, fig. 3 will identify the anus, with well-marked sphincter-muscle (A), lying adjacent to the suture of the whorl and directed to the anatomically right side of the animal. The cylindrical rectum (R), about 0·4 mm. in diameter, takes a strongly arcuate course convex to the left (corresponding to its course over the roof of the mantle-cavity) and then plunges down through the space that was once occupied by the visceral mass. Here, inside the bend, on the ventral side of the rectum may be seen very clearly the mould of the intestinal groove and its bordering typhlosoles (T). A loop of the intestine (L), homologous with that indicated in the figure of *Trochus*, lies underneath the rectum; its contents have been fractured, presumably owing to the sharp folding consequent to retraction of the animal at death. It is not possible to follow the posterior prolongation of the intestine beyond the obscure convolution indicated at C. Passing below both rectum and intestinal loop is another length of digestive tract that might conceivably be part of the buccal cavity (B) and the oesophagus (O). In addition to the typhlosoles, there were about eight minor longitudinal folds on the lateral and dorsal areas of the rectum and intestine; these are reproduced as shallow, parallel grooves on the mould, and between these grooves the surface is broken into microscopic, closely spaced undulations, the whole resembling in texture a peeled banana. Anteriorly, these structures end at the mass of detrital and mineral matter that fills the apertural half of



TEXT-FIG. 1. A, B, *Margarites* (*Atira*) *mirabilis* sp. nov. Base of holotype (A) showing details of aperture and umbilicus, ×3; and (B) cross-section of mould of the rectum of specimen figured in Pl. 41, figs. 1–3, × about 70. C, D, *Margarites groenlandicus* (Chemnitz) var. *umbilicalis* (Posselt), Angonagssalik, East Greenland (British Museum, Natural History, No. 1939. 7. 25. 456), cross-section of rectum (C), × about 50; and (D) view of animal in retracted position, the shell and part of the mantle removed, ×5. s = whorl-suture of shell, o = operculum, f = foot, t = cephalic tentacle, e = eye, c = ctenidium, r = rectum, h = right hypobranchial gland, k = kidney.

the whorl. It is possible that a mould of the stomach is preserved out of sight in the depths of the body-whorl.

Moore, in a series of papers, has shown that the faecal pellets of a variety of invertebrates have characteristic shapes and structures. His studies of the Trochidae have special bearing on the present work in that they demonstrate striking similarities between the fossil mould of the rectum of *Margarites* (*A.*) *mirabilis* and the faecal pellets of Recent members of the family. Moore (1932) found that in *Gibbula umbilicalis* (Da Costa) and *G. cineraria* (Linné) animals with shells of diameter 15 mm. formed pellets with an average diameter of 0·6 mm.; in *Cantharus clelandi* (Wood) an animal with a shell of 10 mm. produced pellets of 0·4 mm. diameter, which are precisely the sizes of the shell and the rectal diameter of *Margarites* (*A.*) *mirabilis*. Pellets from the two species of *Gibbula* mentioned above are roughly circular in section but on the ventral side are two deep V-shaped longitudinal grooves with an upstanding ridge between them. These are obviously moulded by the intestinal groove and the typhlosoles. The ventro-lateral lips bordering the ventral grooves are smooth, but the rest of the dorsal and lateral regions of the surface are cut by furrows into longitudinal panels. These panels are thrown into tightly packed lateral undulations of varying degrees of regularity and coarseness. Pellets taken from the littoral zone were found to have the undulations coarse and irregular; those from depths of 5 to 20 fathoms were more regular and finer in texture. The mould of the rectum of *Margarites* (*A.*) *mirabilis* (text-fig. 1B) agrees closely in cross-section with that of faecal pellets of *Gibbula umbilicalis* illustrated by Moore, but in the finely sculptured undulations of the panels it compares better with pellets of *Cantharus clelandi*. A cross-section of the rectum of *Margarites groenlandicus* (Chemnitz) is also figured in text-fig. 1 for comparative purposes.

The known ecology of the Trochidae, and of *Margarites* in particular, is consistent with our knowledge of the environment of deposition of the Folkestone Beds, namely near-shore, shallow-water conditions, and absence of very fine detritus. From the long coiled intestine of *Margarites* (*A.*) *mirabilis* it may be inferred that this species, like its living relatives, was a microphagous and herbivorous animal, and from the other details of its alimentary anatomy it would appear that its constitution closely resembles that of the family as living today. If the relationship noted by Clark between the course of the rectum and the development of the hypobranchial glands is valid throughout the family, we are permitted to infer also that the left hypobranchial gland, missing in Recent *Margarites*, was either never present or had been lost already by Lower Cretaceous times.

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THE PALAEONTOLOGICAL ASSOCIATION

Extracts from the Annual Report of the Council for 1958

MEMBERSHIP. On 31 December 1958 there were 607 members.

FINANCE. The Accounts and Balance Sheet for 1958 are given below. New donations to the Foundation Fund were received from British Petroleum Co. and Burmah Oil Co., and previous donations from other oil companies were renewed for another year. The Council wishes to thank the managements of the companies concerned for their continued support and generosity. £676 has been transferred from the Foundation Fund to maintain a balance of £159 in the General Account. The subscription income for 1958 was unusually high, since 214 new members also paid for 1957, but in future years it will largely relate to the current year. The sum of £500 has been invested in 5 per cent. Defence Bonds, and further investments are contemplated.

'PALAEONTOLOGY'. Volume 1, parts 2 and 3, were published during the year. These contained 16 papers with 34 plates, and 1 note.

MEETINGS. Six meetings were arranged during 1958, all of which were successful and well attended. The Association is grateful to the Director of the Geological Survey and Museum, the Council of the Geological Society of London, Prof. P. Allen (Reading), Prof. O. M. B. Bulman (Cambridge), Prof. B. C. King (Bedford College), and Prof. D. Williams (Imperial College) for generously granting facilities for meetings; and to the Local Secretaries for their efficient services.

a. A Joint Meeting with the Palaeontographical Society on the 'Nomenclature of Parataxa' was held at 2.0 p.m. on 22 January in the Lecture Room, Geological Survey Museum, London. Four resolutions adopted at the meeting were included in the Agenda Paper for the Colloquium on Zoological Nomenclature held before the XVth International Congress of Zoology in London in July (Bull. Zool. Nomencl. 15 B, 687–8). The Joint Secretaries were Mr. R. V. Melville and Dr. Gwyn Thomas.

b. The first Annual General Meeting was held in the Rooms of the Geological Society of London, on 12 March. The Annual Report of the Council for 1957 was adopted, and the Council for 1958 elected. Professor O. M. B. Bulman delivered the first Annual Address on 'The Sequence of Graptolite Faunas'.

c. A Demonstration Meeting was held in the department of Geology, The University, Reading, on 10 May. There were sixteen exhibitors. Dr. F. Hodson was Local Secretary.

d. A Special Lecture by Prof. T. N. George on 'Evolution and the Palaeontological Record' was delivered on 21 July in Imperial College, London, in connexion with the XVth International Congress of Zoology.

e. A Demonstration Meeting was held in Bedford College, London, on 18 October. There were eleven exhibits, including one by the Editor on the preparation and assembly of photographs for collotype plates. Dr. C. H. Holland was Local Secretary,

f. A Discussion Meeting was held in the Sedgwick Museum, Cambridge, on 12/13 December. The subject was 'Micropalaeontology'. Nearly 100 persons attended. Sixteen papers were read during two sessions, and there were twenty-four exhibits. A dinner was held in Queens' College on 12 December. Mr. N. F. Hughes was Local Secretary.

EXHIBITION. In conjunction with the Geological Survey and Museum, the Association prepared an exhibition on 'Palaeontology and Evolution' to coincide with the International Congress of Zoology meeting in London in July. It has remained on view in the Geological Museum since 9 July. The Council wishes to thank those members of the Association and the Geological Survey and Museum who assisted in preparing the exhibition and also Messrs. Ilford Ltd., for photographic work. An explanatory leaflet was prepared by Professor T. N. George, a part of the cost of which was defrayed by a grant from the Congress authorities.

INTERNATIONAL PALAEONTOLOGICAL UNION. The Association assisted in arranging the I.P.U. meetings on 16 and 17 July, at the time of the International Congress of Zoology, during which a new Constitution was adopted and the Union's future programme and financial policy discussed. Two day-excursions were also arranged for foreign palaeontologists attending the Colloquium and Congress; Dr. W. S. McKerrow led an excursion to the Oxford area on 19 July, and Dr. R. Casey one to the Wrotham and Sevenoaks area on 20 July.

CONSTITUTION. In order to strengthen the Association's claim for recognition as a charity by the Inland Revenue authorities, a special general meeting was convened before the meeting at Reading on 10 May at which it was resolved that Rule 1 of the Constitution be amended to read as follows:

> 'This Association shall be known as "The Palaeontological Association", and its objects shall be to promote research in palaeontology and its allied sciences by holding public meetings and other meetings for the reading of original papers and the delivery of lectures, and to extend knowledge of the science by demonstration and publication, and by such other means as the Council may from time to time determine.'

OFFICERS AND COUNCIL. The following were elected for 1958 at the Annual General Meeting on 12 March: *President*: Dr. R. G. S. Hudson. *Vice-Presidents*: Mr. N. F. Hughes, Dr. L. R. Cox. *Treasurer*: Dr. W. S. McKerrow. *Editor*: Dr. W. H. C. Ramsbottom. *Secretary*: Dr. Gwyn Thomas. *Other members of Council*: Dr. F. W. Anderson, Dr. T. Barnard, Prof. O. M. B. Bulman, Mr. M. A. Calver, Dr. F. E. Eames, Prof. T. N. George, Mr. T. F. Grimsdale, Dr. F. Hodson, Dr. C. H. Holland, Dr. Dorothy H. Raynor, Prof. H. F. T. Rhodes, Mr. P. C. Sylvester-Bradley, Dr. J. T. Temple, Prof. Alan Wood.

COMMITTEES. The Executive Committee, 1958, consisted of the Officers of the Association together with Dr. T. Barnard, Mr. M. A. Calver, and Dr. F. Hodson. The Publications Sub-Committee, 1958, was composed of the Editor (Chairman), Mr. M. A. Calver (Secretary), the President, Dr. L. R. Cox, and Mr. T. F. Grimsdale.

ACCOUNTS FOR YEAR ENDING 31 DECEMBER 1958

General Account

Income	£	*s.*	*d.*	*Expenditure*	£	*s.*	*d.*
Balance from 1957	56	18	6	*Palaeontology*, Volume 1: Parts 1–3 and provision for part 4	2,400	6	5
Subscriptions	1,741	6	3	Sundry printing	30	19	11
Sale of separate parts	39	13	11	Officers' expenses	73	19	2
Interest	39	1	7	Exhibition costs	4	16	10
Packing, postage	12	13	3	Geological Society (A.G.M.)	1	16	0
Palaeontology and Evolution booklet	22	10	0	Fees and stamp duty	5	2	0
Sale of reprints	124	16	6	*Palaeontology and Evolution* booklet	36	10	0
	2,037	0	0		2,553	10	4
Transfer from Foundation Fund	676	1	0	Excess of general income over expenditure (after transfer from Foundation Fund of £676 1*s.* 0*d.*	159	10	8
	£2,713	1	0		£2,713	1	0

Foundation Fund

Income	£	*s.*	*d.*	*Expenditure*	£	*s.*	*d.*
Balance from 1957	726	1	0	Transfer to General Account	676	1	0
Donations:							
Apex (Trinidad) Oilfields, Attock Oil Co., British Petroleum Co., Burmah Oil Co., Iraq Petroleum Co., Shell Petroleum Co., Ultramar Co.	950	0	0	Balance	1,000	0	0
	£1,676	1	0		£1,676	1	0

Balance Sheet

Liabilities	£	*s.*	*d.*	*Assets*	£	*s.*	*d.*	£	*s.*	*d.*
Excess of general income over expenditure	159	10	8	5% Defence Bonds				500	0	0
Balance of Foundation Fund	1,000	0	0	Barclays Bank Ltd.						
				Deposit Account	1,250	15	10			
				Current Account	158	14	10			
					1,409	10	8			
				Less provision for Part 4	750	0	0	659	10	8
	£1,159	10	8					£1,159	10	8

Auditors: H. G. Reading, W. J. Wadsworth

THE SILURIAN TRILOBITE *DALMANITES MYOPS* (KÖNIG)

by W. T. DEAN

FOR some years the name *Dalmanites vulgaris* (Salter) has figured prominently in lists of trilobites from rocks of middle and upper Silurian age, particularly in the Welsh Borders and parts of Wales. *Dalmanites vulgaris* was proposed originally by Salter (1864, p. 51) as a variety of *D. caudatus* (Brünnich), the type species of *Dalmanites* which has been reviewed by Delo (1935). It has not, however, been generally appreciated that *D. vulgaris* is identical with the trilobite described earlier by König (1825, p. 3, pl. 4, fig. 53) as *Asaphus myops*, and, in fact, König's holotype was employed by Salter (1864, pl. 3, fig. 13) as one of the syntypes of *D. vulgaris*. The König Collection, housed in the British Museum (Natural History), contains fossils belonging to several different phyla and is to be redescribed at a future date. In the meantime it is proposed here to select as lectotype of *D. vulgaris* the syntype, from Dudley, figured by Salter (1864, pl. 3, fig. 13) and mentioned above. This specimen, Brit. Mus. In.54865, is the holotype of *D. myops* (König), of which *D. vulgaris* thus becomes an objective synonym.

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