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THE STRUCTURE, EVOLUTION AND NOMENCLATURE OF THE OSTRACOD HINGE

P. C. SYLVESTER-BRADLEY

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THE STRUCTURE, EVOLUTION AND NOMENCLATURE OF THE OSTRACOD HINGE

BY

PETER C. SYLVESTER-BRADLEY

University of Sheffield

Pp. 1–21; *Pls.* 1–4; 2 *Text-figures*

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THE STRUCTURE, EVOLUTION AND NOMENCLATURE OF THE OSTRACOD HINGE

By P. C. SYLVESTER-BRADLEY

[University of Sheffield]

SYNOPSIS

A revision of Middle Jurassic ostracods from the Fullers' Earth Clay has revealed a series of hinge-types which clearly demonstrate transitional stages between those commonly known as merodont and those known as amphidont. Their study has justified the classification of hinge-types according to the stage reached in a morphogenetic series. The primitive hinge is tripartite in character, and more specialized hinge-types originate by the subdivision of the median element of the basic three. The morphology of the ostracod hinge is discussed, a rational classification is proposed, and in the light of this classification, the terminology of both the hinge as a whole and that of its constituent parts is reviewed. The evolution of the post-Palaeozoic Cytheracea is traced from Palaeozoic ancestors with a similar hinge but different muscle-scar pattern, and a new superfamily, the Quasillitacea, is proposed for these Palaeozoic forms. Two new genera are proposed, *Acanthocythere* (Middle Jurassic) and *Dictyocythere* (Upper Jurassic). The latter is divided into two subgenera, *Dictyocythere* sensu stricto and *Rhysocythere* nov. The distribution of the species of *Dictyocythere* in the Upper Jurassic of England and northwest Germany suggests that the " Purbeck " Beds of the Aylesbury and Swindon districts are earlier than Middle Purbeckian, and that the " Wealden 2 " of the German sequence is probably equivalent to the upper part of the Middle Purbeck Beds of Dorset. The development of the hinge in *Dictyocythere* is shown to be palingenetic.

1. TERMINOLOGY OF THE OSTRACOD HINGE

THE hinge structures of fossil ostracods play an important part in their taxonomic determination, but unfortunately the terms used for their description are ambiguous. Thus the terms " taxodont " and " heterodont " have been used to describe the compound hinge of ostracoda, not always with quite the same meaning. As used by Bold (1946), Kingma (1948), Grekoff (1952) and Malkin (1953),[1] " taxodont " refers to the presence of denticulate elements, and " heterodont " to the development of high, pointed teeth and a hinge-bar. The terms (which have been borrowed from those used to describe the lamellibranch hinge) are not altogether appropriate in their new context, and seem likely to lead to ambiguity. The term " taxodont " as used in lamellibranchs refers to the occurrence of an alternate tooth and socket arrangement, essentially similar in both valves. An exactly similar structure is not known to occur in the Ostracoda, although an alternate tooth and socket arrangement (here termed " interdentate ") is not infrequently found in some or all of the elements

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[1] Malkin (1953) also defines the terms adont, dysodont, desmodont, crasidont and archidont. These terms are not referred to further in this paper, as they do not describe hinge structures here dealt with.

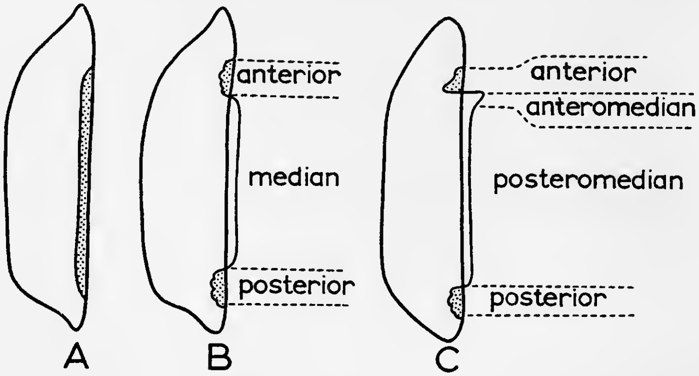
of the compound hinge. This arrangement might well be called " taxodont " and the term has in fact been so used by Kesling (1951) ; this use of the term is not, however, equivalent to that of the earlier definitions, and it would seem advisable to abandon it to prevent further confusion.

Other authors have used different terms descriptive of the same structures ; thus " merodont " = " taxodont ", and " amphidont " = " heterodont " (e.g. Triebel 1950 ; Pokorny, 1952). These terms are not open to the same objections, and are adopted here and fully defined below. Additional terms are also introduced ; some of these are new, some are after Triebel. Technical terms, in standard English, or anglicized from Latin roots, are used to designate structures of the individual elements ; terms derived from the Greek and terminating in " -dont " are used to designate the hinge structure as a whole.

2. DEFINITIONS OF HINGE ELEMENTS

The hinge structure of the ostracod carapace may be *simple* or *compound.*

The *simple hinge* (" adont " of Grekoff, Bold and Kingma) may be thought of as made up of a single *element,* which consists of a groove along the margin into which fits the edge of the other valve (Text-fig. 1, A). The hinge is not further differentiated.



TEXT-FIG. 1.—Diagrams of left valves of three ostracods, dorsal view, to illustrate division of hinge into "elements". (Stippled areas represent sockets).

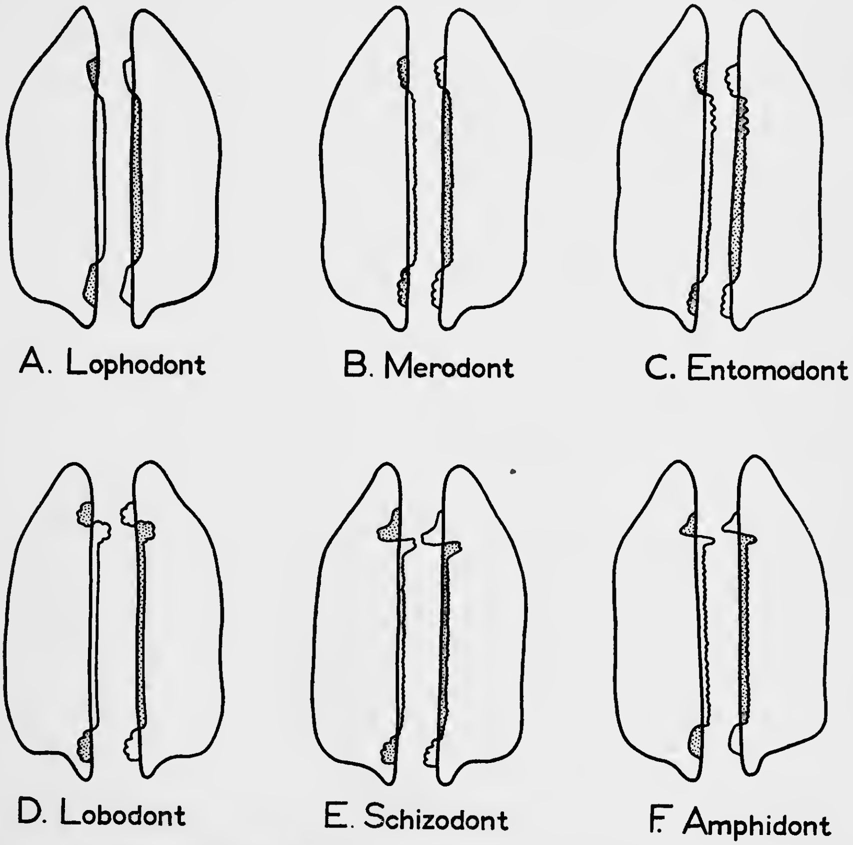
The *compound hinge* is divided into three or four elements in each valve. Primitively there are three elements, anterior, median and posterior (Text-fig. 1, B). Usually these elements alternate so that if (as is usual in the right valve) the anterior and posterior are ridges, the median element separating them will be a groove ; or if (as is usual in the left valve) the terminal elements are grooves or sockets, the median will be a ridge. Though genera are known which are exceptions to this (in *Haplocytheridea,* for example, all three elements of the left valve are grooves, those of the right being ridges), the distinction between the constituent elements remains clear, the terminal elements being more coarsely dentate than the median.

It will be shown below that the more primitive compound hinge with three elements evolves, by subdivision of the median element, into a more advanced type in which there are four elements—anterior, anteromedian, posteromedian and posterior. The division into two parts of the median element is at first not pronounced—the anterior part being merely more coarsely dentate than the posterior (Text-fig. 2, C), but later developed forms have a more clear-cut distinction, the anteromedian becoming rather similar in proportions to the anterior element, the posteromedian usually being much the longest element of the four (Text-fig. 1, C). Rarely the anterior element also becomes differentiated, with denticles of two sizes (e.g. *Amphicythere* and *Dictyocythere*; see p. 14).

These hinge elements themselves display a great deal of variation, and the following definitions are of terms used in their description:

A. *Ridge and groove.*

1. A hinge element may consist of a smooth *ridge* fitting into a corresponding *groove* in the opposite valve, e.g. the median element of *Camptocythere* (Text-fig. 2, A).



TEXT-FIG. 2. Diagrams illustrating the six main types of dentition developed in the ostracod hinge. Each pair of valves in dorsal view. (Stippled areas represent sockets).

2. A *dentate* element consists of a ridge divided into projections (*denticles*) which fit into a socketed groove termed *loculate*.
3. The median element may be furnished with finer denticles, when it is termed *denticulate*, the groove *locellate* (Text-fig. 2, B).
4. A ridge may be divided into separate teeth between which lie alternating sockets for the reception of projections from the complementary groove. Such a ridge is termed *interdentate*, the groove *interloculate*.
5. The median element of the left valve (which is usually a ridge or a bar) often lies under an elongated, sub-triangular, excavated area termed the *accommodation groove*. This, it would seem, serves to receive the projecting dorsal edge of the right valve when the carapace is open.

B. *Bar.*

6. The median element may consist of a ridge which is raised up from the shell margin behind it ; this is differentiated as a *hinge-bar*.

C. *Boss and pit.*

7. An element may be raised up as a hemispherical *boss*, which may show division into two or more lobes, when it is referred to as *bi-*, *tri-*, or *multilobate* ; a lobate boss fits into a *loculate pit* in the complementary valve (Text-fig. 2, D).

D. *Tooth and socket.*

8. An element may consist of a single tooth, projecting from a platform which itself projects more or less beyond the hinge margin, when it is referred to as *stirpate* (e.g. the anterior element in *Trachyleberis*) (Text-fig. 2, F).
9. The tooth may be a simple, more or less *conical* projection ;
10. or it may have more or less parallel sides, when it is called *pessular* ;
11. or it may be split into two lobes, when it may be called *bifid* (Text-fig. 2, E) ;
12. or it may be *crescentic*, half-surrounding a socket ;
13. or it may be a slightly elongated and slightly curved projection, when it is termed *reniform* (as in the posterior element of many amphidont hinges (Text-fig. 2, F). A reniform tooth may be smooth (*Hemicythere* or *Trachyleberis*) or lobate (*Bradleya*) or dentate (some species of *Cythereis*).

3. CLASSIFICATION OF HINGE TYPES

Using the above definitions of the elements of the compound hinge as a basis, it is possible to classify hinges developed in the Cytheracea in the six main groups outlined below. This classification does not take into consideration hinge-types developed in other superfamilies of the Podocopa. For example, whereas the Quasillitacea (here defined) have hinges very like the Cytheracea (though apparently confined to the more primitive lophodont and merodont types), the Bairdiacea have a more complicated compound hinge not always homologous with that in the Cytheracea—compare, for example, *Bairdoppilata* (Coryell, Sample & Jennings, 1935) with *Macrocypris* (Sylvester-Bradley, 1948*c*) and *Triebelina* (lophodont ; Triebel, 1948). The Cypridacea, on the other hand, have mostly simple hinges with a single element, though a few are lophodont (e.g. *Cypridea* ; Sylvester-Bradley, 1949).

1. ***Lophodont:*** e.g. *Bythocythere*, *Camptocythere*, in which the hinge elements are divided into three in each valve, all consisting of ridges and grooves (Text-fig. 2, A). The most usual arrangement is as follows :

	Left valve	Right valve
Anterior element	Groove	Ridge.
Median element	Ridge	Groove.
Posterior element	Groove	Ridge.

2. ***Merodont:*** (= " taxodont " of some authors) e.g. *Cythere*, in which anterior and posterior elements are dentate or loculate, the median element either smooth or denticulate, but not subdivided (Text-fig. 2, B). The most usual arrangement is as follows :

	Left valve	Right valve
Anterior element	Loculate groove	Dentate ridge.
Median element	Denticulate ridge	Locellate groove.
Posterior element	Loculate groove	Dentate ridge.

The elements in some merodont genera (e.g. the terminal elements of *Pleurocythere*) are interdentate and interloculate rather than dentate and loculate. Many species of Middle Jurassic age have a merodont hinge with smooth median element (e.g. *Schuleridea*), and this condition may well be the more primitive.

3. ***Entomodont:*** e.g. *Lophocythere*, *Progonocythere* and *Xenocythere* (Triebel, 1949, 1951), in which the median element becomes subdivided, the anterior part remaining dentate, the posterior smooth or denticulate (Text-fig. 2, C). A common arrangement is as follows :

	Left valve	Right valve
Anterior element	Loculate groove	Dentate ridge.
Anteromedian element	Short dentate ridge	Short, wide loculate groove.
Posteromedian element	Long denticulate ridge	Long, narrow locellate groove.
Posterior element	Loculate groove	Dentate ridge.

The genus *Macrodentina* has a hinge transitional between entomodont and lobodont (see p. 14).

4. ***Lobodont:*** e.g. *Acanthocythere* gen. nov., in which the anterior element and the anteromedian elements are lobed bosses (see Pl. 1, figs. 3, 4, 8, 9 ; Text-fig. 2, D).

	Left valve	Right valve
Anterior element	Loculate pit	Lobate boss.
Anteromedian element	Lobate boss	Loculate pit.
Posteromedian element	Smooth or denticulate bar	Smooth or locellate groove.
Posterior element	Loculate groove	Dentate ridge.

The genus *Amphicythere* has a dentition transitional between lobodont and amphidont. The anterior element is lobate, but the antero-median element is almost entire (see p. 14).

5. ***Schizodont:*** e.g. *Schizocythere, Palmenella, Paijenborchella* (Triebel, 1950), in which teeth of the anterior and anteromedian elements are bifid (Text-fig. 2, E).

	Left valve	Right valve
Anterior element	Biloculate socket	Bifid, stirpate tooth.
Anteromedian element	Bifid tooth	Biloculate socket.
Posteromedian element	Denticulate bar	Locellate groove.
Posterior element	Loculate socket	Lobate, reniform tooth.

6. ***Amphidont:*** (= " heterodont " of some authors ; Triebel uses the term amphidont in a wider sense than that proposed here—to include dentitions of both schizodont and lobodont types) e.g. *Dictyocythere, Trachyleberis,* in which the median element is further differentiated into a single anterior tooth and a posterior bar or ridge. A common arrangement (Text-fig. 2, F) is as follows :

	Left valve	Right valve
Anterior element	Socket	Stirpate tooth.
Anteromedian element	Conical or pessular tooth	Socket.
Posteromedian element	Smooth or denticulate bar	Smooth or locellate groove.
Posterior element	Loculate socket	Lobate, reniform tooth.

Young moults of amphidont species usually have merodont or entomodont hinges (see p. 19). The ontogeny is therefore recapitulatory .

This classification is not comprehensive. The hinge structures listed form a useful morphogenetic series, but complications are developed in some genera which are not covered—for example, the differentiations of the median element found in some genera of the Cytherideinae (e.g. *Cytheridea, Cyprideis*), and the development of crescentic teeth in the terminal elements in *Loxoconcha* and other genera.

4. THE EVOLUTION OF THE HINGE AND ITS BEARING ON THE CLASSIFICATION OF THE PODOCOPA

Well-defined compound hinge-structures are particularly characteristic of the superfamily Cytheracea, which in post-Palaeozoic times provided a far greater number of species of marine ostracods than all the remaining superfamilies taken together. The series of hinge-types classified above is a morphogenetic series and not phylogenetic. Genera have passed through the various stages at different times during their racial history. The most advanced stage reached by Middle Jurassic times is the lobodont, but the amphidont hinge appears before the close of the Upper Jurassic (e.g. *Dictyocythere*, see p. 14). It is not unlikely that earlier genera with an amphidont hinge remain to be discovered. In Recent and Tertiary ostracods, merodont and amphidont hinge-structures predominate but entomodont hinges also occur (e.g. *Leptocythere*) ; in Middle Jurassic times the Cytheracea have hinges which are predominantly either merodont (usually with a smooth median element) or entomodont; lobodont hinges are rare. Elsewhere (Sylvester-Bradley, 1948*b*) attention has been drawn to the series leading from the Middle Jurassic *Oligocythereis* (entomodont) through the Cretaceous *Cythereis* to the Tertiary and Recent *Trachyleberis* (amphidont). This series is thought to be broadly phylogenetic, and the three genera in question are placed in the same subfamily, the Trachyleberidinae. Several other undescribed genera from the Middle Jurassic have reached various stages in similar series. It seems unlikely that any of these forms are directly related to the Trachyleberidinae; they probably represent other lineages undergoing parallel evolution. The acquisition of the amphidont hinge is considered to be a well-marked trend. If this view is correct, the diagnosis of the subfamily Progonocytherinae (Sylvester-Bradley, 1948*a* : 189) for Cytheracea with entomodont hinge, needs drastic revision, and it is now suggested that *Lophocythere*, *Progonocythere* and *Oligocythereis* should not be grouped together in one subfamily, although they all have entomodont hinges.

Before attempting to assess which of the hinge-types described can truly be taken as primitive, it is necessary to refer to older faunas and seek possible Palaeozoic ancestors of the Cytheracea.

The genus *Monoceratina* is the longest lived of the Cytheracea according to present ideas. The type species is Carboniferous in age, and Recent species have been recorded (Stephenson, 1946; Bold, 1946). However, the hinge structure is rather obscure; the shape differs much from the majority of the Cytheracea; the muscle-scar patterns differ sufficiently in different species to warrant query as to whether there has not been a mistake in the identification of some of the post-Palaeozoic material, and it is not in any case easy to postulate that *Monoceratina* exhibits an ancestral type of hinge-structure.

Perhaps the Palaeozoic family that most invites comparison with the Cytheracea is the Middle Devonian Ropolenellidae first described by Coryell & Malkin (1936), especially the two genera *Ropolenellus* and *Euglyphella*. By the courtesy of Mr. Raymond R. Hibbard, who presented me with several samples rich in ostracods, which he collected from the Middle Devonian of New York State, I am able to describe the more intimate details of the shell of some species of *Euglyphella*. Some of the earlier authors who dealt with the Ropolenellidae have oriented the ostracods so that the higher end is posterior. The investigation of the hinge reveals that they are closely analogous, if not homologous, with those found in the Cytheracea; the higher end is therefore here regarded as anterior in conformity with the known orientation of the Cytheracea. Consequently the terms " left " and " right " used here have the reverse meaning to those used in description by some previous authors.

The shape of these two genera of the Ropolenellidae, in marked contrast to many other described species of Palaeozoic ostracods, is similar to many genera of the Cytheracea (Pl. 2, figs. 5–7). A broadly rounded anterior tapers to a narrow, rounded or triangular posterior. Either or both ends may be spinose. The hinge-line is straight, delimited by well-marked anterior and posterior cardinal angles and is shorter than the length of the shell. The ventral border is straight or slightly concave.

The genus *Euglyphella* was proposed by Warthin (1934) with *Strepula sigmoidalis* Jones as type species. Several other species have since been assigned to the genus.

It possesses a striking ornament of carinae not unlike those developed in many post-Palaeozoic Cytheracea (e.g. *Lophocythere*, from the Bathonian; see Sylvester-Bradley, 1948*a*). The hinge in *Euglyphella* is divided into three elements as follows:

	Left valve	Right valve
Anterior	Rather long, deeply overhung, loculate groove	Projecting ridge, forming a continuation of the selvage.
Median	Bar, lying below a long, narrow accommodation groove	Long groove.
Posterior	Short, curved loculate groove	Short, curved projecting ridge.

The hinge margin of this genus is in fact almost exactly similar to that of many post-Palaeozoic Cytheracea. The loculate nature of the terminal elements in the left valve cannot be made out in more than a few specimens, and I have not detected any specimen showing a corresponding dentation on the terminal elements of the right valve, but this may well be due to indifferent preservation.

The free margin is also similar to that seen in many Cytheracea. There is a wide duplicature, no vestibule, but a pronounced selvage. The muscle-scar pattern, however, is quite unlike anything known in the post-Palaeozoic Cytheracea; a central, circular muscle-scar pit bears a cluster of small oval scars in the form of slight tubercles, which are in close juxtaposition.

Another genus referred by Coryell & Malkin (1936) to the Ropolenellidae is *Bufina* (Pl. 2, figs. 3, 4). Species of this genus differ somewhat in shape from *Euglyphella* and *Ropolenellus* in that the dorsal margin of the left valve is markedly curved. The characteristic ornament of the genus is unlike that of any post-Palaeozoic ostracod known to the author, though Henningsmoen (1953) has pointed out that it is shared by other Palaeozoic genera such as *Ponderodictya* (see below). The details of hinge, duplicature and muscle-scar, however, are as described for *Euglyphella*, and though Coryell & Malkin were clearly correct in concluding that the genera are related, Henningsmoen is probably right in removing *Bufina* to the Quasillitinae.

The Ropolenellidae are apparently only known from Middle Devonian strata, in which they are often fairly common. They seem to represent a successful though short-lived line of evolution which in many respects anticipated the much later Cytheracea.

Another family well represented in the Middle Devonian of North America is the Quasillitidae. An examination of *Quasillites* (Pl. 2, figs. 1, 2) shows that it has a hinge-structure very similar to that of the Ropolenellidae and the two families should almost certainly be grouped together. Henningsmoen (1953) regarded them as subfamilies of one family; it is here suggested that they are related families in the same superfamily, the Quasillitacea (see p. 11). Near to *Quasillites* is the Carboniferous genus *Graphiadactylus*.

It may also be mentioned that the genus *Ponderodictya* (described by Coryell & Malkin from the Middle Devonian and placed by them in the Cytherellidae; see figs. in Triebel, 1954) bears a hinge comparable to that of the Ropolenellidae, differing mainly in that the anterior element is longer in proportion (as long, in fact, as the median element). The ornament is not unlike that developed in *Bufina*. The genus has been placed in the Healdiidae as a member of the Platycopa (Henningsmoen, 1953; Triebel, 1954), but the hinge makes this assignment a little doubtful. *Ponderodictya* may perhaps be a member of the Quasillitacea, and as such one of the Podocopa. It is clear that in Devonian times the Healdiidae, Quasillitidae and Bairdiidae possessed characters in common which suggest that all three families had been derived from a common ancestor of not much greater antiquity than the Devonian. Subsequently the three families diverged in morphology so that they have been placed far apart in classification.

From the foregoing brief survey it will be seen that several families of Palaeozoic ostracods possessed features in common with the later Cytheracea. It seems probable that the first members of the Cytheracea were derived from one or more of the Quasillitacea towards the close of Palaeozoic time. Somewhat similar views have been advanced by Kellett (1943). Thus the superfamilies Quasillitacea and Cytheracea form part of the suborder Podocopa, and are distinguished by the muscle-scar pattern, which in the Quasillitacea is *aggregate* (i.e. consisting of a group of individual scars crowded in close juxtaposition; Pl. 2, figs. 3, 4, 6), and in the Cytheracea *discrete* (i.e. consisting of a series of individual scars separated from each other).

The primitive hinge was therefore lophodont. Whether the elements were primitively dentate or smooth cannot be certainly stated, for the apparently smooth elements in much Palaeozoic material may well be due to a loss of finer structure on recrystallization. The fact that loculate grooves have been detected in the terminal elements of both *Euglyphella* and *Quasillites* shows that at least the terminal elements were dentate in these genera by Devonian times. Some Palaeozoic specimens show a well-developed accommodation groove, so that structure cannot be taken as an advanced feature. It seems to be the inevitable consequence of any considerable difference in size between the two valves.

5. SYSTEMATIC DESCRIPTIONS

Suborder PODOCOPA

Superfamily QUASILLITACEA (Coryell & Malkin).

(First introduced here as a superfamily)

TYPE GENUS. *Quasillites* Coryell & Malkin. (Middle Devonian.)

DIAGNOSIS. Podocopa with a primitively tripartite hinge and an aggregate muscle-scar pattern.

FAMILIES INCLUDED. Quasillitidae (including Graphiadactyllidae) and Ropolenellidae. Other families no doubt remain to be described.

REMARKS. Distinguished from Cytheracea by muscle-scar pattern; from Cypridacea and Bairdiacea by hinge and muscle-scar pattern; from Healdiidae (Platycopa) by hinge.

DISTRIBUTION. So far known only from the Palaeozoic. Mesozoic Platycopa with an aggregate muscle-scar pattern are, however, known (*Ogmoconcha*, Lower Lias) and it may be expected that the Podocopa underwent a parallel development; Mesozoic Quasillitacea may yet be discovered.

Superfamily CYTHERACEA

Family uncertain

Genus ***ACANTHOCYTHERE*** nov.

TYPE SPECIES. *Cythere sphaerulata* Jones & Sherborn, 1888: 253, pl. 1, fig. 6.

DERIVATION OF NAME. ἄκανθα, a thorn or prickle + genus *Cythere*. Gender: feminine.

DIAGNOSIS. Cytheracea with lobodont hinge, surface more or less spiny, carapace plump, eye tubercles shiny, rather prominent.

OCCURRENCE. The two species of the genus here described are so far known only from the Upper Fullers' Earth Clay (Bathonian) of the Bath district.

Acanthocythere sphaerulata (Jones & Sherborn)

(Plate 1, figs. 1–4)

1888. *Cythere sphaerulata* Jones & Sherborn, p. 253, pl. 1, fig. 6.

DIAGNOSIS. Carapace oblong, tumid, ornamented with closely-set blunt spines arranged in a faint reticulate pattern.

HOLOTYPE. Geol. Dept. Brit. Mus. (N.H.) no. I.1835. A complete carapace.

TYPE LOCALITY. "Yellow Fullers-earth Clay, Midford" (Jones & Sherborn, 1888: 254).

OTHER FIGURED SPECIMENS. Geol. Dept. Brit. Mus. (N.H.) nos. In.42433–34.

DESCRIPTION. Both valves with sub-parallel dorsal and ventral margins, no taper, anterior and posterior ends evenly rounded. Sexual dimorphism rather pronounced, the presumed males longer than females.

	Dimensions (mm.)			Proportions		
	L	H	W	L	H	W
Carapace ♂ (I.1835; holotype)	0·51	0·31	0·32	1·65	1	1·03
Left valve ♂ (In.42434)	0·67	0·37	0·26	1·81	1	0·70
Right valve ♂ (In.42433)	0·69	0·38	0·22	1·82	1	0·58

The whole surface (with the exception of the eye tubercles) covered with very fine spines set close together and forming a reticulate pattern which is clearer in worn specimens than in those more perfectly preserved.

Normal pore canals large, sparse, about 20 to the valve in the female. Radial pore canals simple, sparse, straight, about 8 to the anterior end. Duplicature fairly wide at anterior end (Pl. 1, fig. 3), with flange-groove well developed in left valve. Muscle-scar not seen. Hinge lobodont, in detail as follows:

Hinge element	Left valve	Right valve
Anterior	Circular pit, presumably loculate	4-lobate boss.
Anteromedian	4-lobate boss	Oval pit, presumably loculate.
Posteromedian	Smooth bar lying below accommodation groove which is rather wide in the female, but narrow, and developed only in posterior half in male	Narrow groove lying below rather prominent dorsal margin which forms a ridge complementary to the accommodation groove.
Posterior	Loculate groove	Prominent, slightly curved 5 to 7 dentate ridge, set at a slight angle to the median element.

The state of preservation is not sufficiently perfect to make it quite certain that the posteromedian element is not denticulate.

MATERIAL. Fourteen specimens (in addition to the holotype) from the same horizon and locality as *A. spiniscutulata.*

Acanthocythere spiniscutulata n. sp.

(Plate 1, figs. 5–9)

DERIVATION OF NAME. Latin *spina*, spine + *scutulatus*, diamond-shaped.

DIAGNOSIS. Carapace tapering, with prominent cardinal angles; ornament of subtriangular or diamond-shaped spinose ridges.

HOLOTYPE. Geol. Dept. Brit. Mus. (N.H.) no. In.42435. A left valve.

TYPE LOCALITY. Upper Fullers'-Earth Clay (in top foot of economic "Fullers Earth"), Fosse Way Fullers'-Earth Mine, near Bath. Nat. Grid. ref 31/727613. Author's field ref. no. 47 *FW* 9.

PARATYPES. Same locality and horizon. In.42436–37.

DESCRIPTION. Carapace tapering, in side view, towards posterior. Ornament of subtriangular or diamond-shaped rather coarsely spinose ridges. Sexual dimorphism not observed.

	Dimensions (mm.)			Proportions		
	L	H	W	L	H	W
Carapace (In.42437)	0·57	0·40	0·35	1·43	1	0·88
Left valve (In.42435; holotype)	0·57	0·37	0·22	1·54	1	0·59
Right valve (In.42436)	0·56	0·32	0·19	1·75	1	0·59

Details of hinge, duplicature and pore canals as in *A. sphaerulata.*

MATERIAL. Nine specimens from the type-locality and horizon.

Genus ***DICTYOCYTHERE*** nov.

TYPE SPECIES. *Cythere retirugata* Jones, 1885: 350, pl. 9, figs. 21–24.

DERIVATION OF NAME. δίκτυον, a net + genus *Cythere.* Gender: feminine.

DIAGNOSIS. More or less trapezoidal Cytheracea, usually reticulate, with amphidont hinge, the anterior element undifferentiated (subgenus *Dictyocythere*) or differentiated into denticles of two sizes (subgenus *Rhysocythere*), the posterior element dentate. No accommodation groove. Eye tubercles not developed.

OCCURRENCE. This genus includes several species from the Purbeck Beds of Buckinghamshire and Swindon, the Middle Purbeck Beds of Dorset and the so-called Wealden Beds of N.W. Germany. *D. transiens* is abundant in the Upper Portland Beds of the Aylesbury district.

REMARKS. Species of this genus were placed by Martin (1940) in his genus *Macrodentina*. However, the type-species of *Macrodentina* (*M. lineata*) is Upper Oxfordian; Triebel (1954) has shown that two homeomorphs were confused by earlier authors under the name *M. lineata*, one of which (the true *M. lineata*) has an advanced type of entomodont hinge, verging on the lobodont. The Kimmeridgian genus *Amphicythere*, described by Triebel in the same paper, has an interesting hinge transitional between lobodont and amphidont. In it the anterior element of the hinge has denticles differentiated into two series. This rather rare variation is also found in *Macrodentina* and in some species of *Dictyocythere*, which suggests that the three genera may be related.[1] The hinge of *Dictyocythere* resembles that of *Amphicythere* but has moved nearer to the typical amphidont type, showing its primitive nature only in those species possessing a differentiated anterior element (subgenus *Rhysocythere*). The details of the hinge of *Amphicythere semisulcata*, derived from Triebel's (1954) description, are tabulated below for comparison with those of *Dictyocythere*.

	Left valve	Right valve
Anterior part of anterior element	Loculate groove	Low tridentate ridge.
Posterior part of anterior element	Loculate pit	Trilobate boss.
Anteromedian element	Faintly bilobate boss	Deep pit.
Posteromedian element	Smooth ridge	Shallow groove.
Posterior element	Loculate groove	Slightly curved, 7-dentate ridge.

SUBGENERA. The fact that two hinge-types exist in the group of species here regarded as forming *Dictyocythere* might be regarded as evidence that they should be split up into two distinct genera. In other characters, however, *D. rugulata* seems to be so close to *D. retirugata* that I prefer to separate the groups as subgenera only, as follows:

(i) *Subgenus* **Dictyocythere** *sensu stricto* (*with undifferentiated anterior element to hinge*):

D. retirugata (Jones).
D. mediostricta n. sp.
D. decorata (Anderson).

(ii) *Subgenus* **Rhysocythere** (*with differentiated anterior element*):

D. rugulata (Jones).
D. transiens (Jones).

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[1] However, fairly prominent eye tubercles are developed in *Amphicythere*, but not in the other two genera.

STRATIGRAPHICAL VALUE. The distinction, made below, between species of the genus found in the Purbeck Beds of Buckinghamshire and in the Swindon Series on the one hand (*D.* (*R.*) *rugulata, D. retirugata*), and in the Middle Purbeck Beds of the Dorset coast on the other (*D. mediostricta*), lends further support to the supposition that the Swindon Series (and the Aylesbury " Purbeck " Beds) were earlier than the Middle Purbeck Beds of the Dorset coast (see Arkell & Sylvester-Bradley, 1941). It appears that no species of *Dictyocythere* or of *Cypridea* is identical in the two regions[1]. It is *D. mediostricta* that is found in the so-called Wealden of N.W. Germany, not *D. retirugata,* as recorded by Martin. The abundance of *D. transiens* in undoubted Portland Beds at Aylesbury (below horizons yielding *Titanites*) shows that the genus was certainly in existence before the close of Portlandian time, and it still seems possible that Blake (1885) may have been right when he suggested that the so-called Purbeck Beds of Swindon and Aylesbury were deposited at the same time as the Portland Beds further south. *D.* (*R.*) *rugulata* and *D. retirugata* have been both recorded from the Swindon Sands and Stone (Sylvester-Bradley, 1941 : 358), which has always been regarded as Portlandian.

Subgenus ***DICTYOCYTHERE*** sensu stricto

DIAGNOSIS. *Dictyocythere* with undifferentiated anterior element to hinge.

Dictyocythere (Dictyocythere) retirugata (Jones)

(Plate 3, figs. 7–10 ; Pl. 4, figs. 3, 4, 11, 16, 17)

1885. *Cythere retirugata* Jones, p. 350, pl. 9, figs. 21–24 (including var. *textilis*).
[not *Macrodentina retirugata* (Jones) Martin, 1940.]
1941. *Cythere retirugata* Jones var. *textilis* Jones : Anderson, p. 374 (part), pl. 18, fig. 3, ? fig. 2.

DIAGNOSIS. Surface reticulate. Shape trapezoidal. Median constriction absent or slight. Sexual dimorphism pronounced.

LECTOTYPE (here designated). Geol. Dept. Brit. Mus. (N.H.) no. In.48601. Figured Jones, 1885, pl. 9, fig. 23. (Jones' no. 253, 11.) A right valve ♂[2].

TYPE LOCALITY. " Last Portland bed ", Hartwell, Bucks.

DESCRIPTION. Surface evenly reticulate except immediately above muscle scar. Shape trapezoidal, with pronounced cardinal angles. Sexual dimorphism pronounced, the presumed males proportionately longer than the females.

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[1] Wolburg (1950) suggests that *Ulwellia papulata* Anderson from the Swindon Series may be synonymous with *Cypridea sowerbyi* Martin from N.W. Germany, but specimens of the latter species that Dr. Wolburg kindly sent me show that this is not the case. On the other hand the specimen figured by Anderson (1941, pl. 18, fig. 2) from the Middle Purbeck of Poxwell, Dorset, does appear to have been correctly identified as *Cythere retirugata.*

[2] Lectotype of " *Cythere retirugata* var. *textilis* Jones " (here designated) : Geol. Dept. Brit. Mus. (N.H.) no. In. 48602, figured Jones, 1885, pl. 9, fig. 24. A right valve ♀. (Jones' no. 166, 1). " Shaly beds, Barnard's Pit, Hartwell ".

	Dimensions (mm.)			Proportions		
	L	H	W	L	H	W
Left valve ♂ (In.48609)	0·92	0·47	0·25	1·97	1	0·53
Right valve ♂ (In.48608)	0·97	0·49	0·29	1·98	1	0·59
Left valve ♀ (In.48610)	0·80	0·51	0·28	1·58	1	0·55
Right valve ♀ (In.48611)	0·84	0·51	0·24	1·66	1	0·47

Normal pore canals large ; radial pore canals sparse, straight. Muscle-scar pattern of usual Cytheracea type, with four scars in vertical superposition, and a single scar in front. Hinge amphidont (see Pl. 4. figs. 3, 4, 11, 16, 17) details as follows :

Hinge element	Left valve	Right valve
Anterior	Pit	Smooth protuberant boss with a slight anterior swelling, perhaps representing the relict of anterior denticulation.
Anteromedian	Smooth protuberant boss	Pit.
Posteromedian	Smooth, slightly projecting bar. No accommodation groove	Smooth groove.
Posterior	Loculate groove	Curved, dentate ridge.

REMARKS. Jones (1885) and Anderson (1941) regarded this species as composed of a number of varieties based on differences in the strength and complexity of the reticulate ornament. Two of these varieties are here raised to specific rank, since the different ornament is correlated with slight differences in shape and with (in one case) a difference in the hinge. Moreover there are no transitional forms, and though they occur together in the same bed at Swindon, they have a different distribution at other horizons and in other localities. I have been unable, however, to maintain a distinction between the typical *D. retirugata* and the forms referred by Jones and Anderson to var. *textilis*.

OCCURRENCE. This species is abundant in the Cythere Marl of the Swindon Series at Swindon, and occurs also at higher and lower horizons. It is found at several horizons and localities in the Purbeck Beds of Buckinghamshire.

Dictyocythere (Dictyocythere) mediostricta n.sp.

(Plate 3, figs. 2–6)

1940. *Macrodentina retirugata* (Jones) : Martin, p. 330, pl. 5, figs. 74–78.

DERIVATION OF NAME. Latin *medius*, middle—*strictus*, drawn tight.

DIAGNOSIS. Large, reticulate, trapezoidal *Dictyocythere*, with a slight constriction in the mid-dorsal region.

HOLOTYPE. Geol. Dept. Brit. Mus. (N.H.) no. In.48607. A male carapace (Pl. 3, figs. 3–6).

TYPE LOCALITY. Upper part of the *Cypridea fasciculata* subzone of the Middle Purbeck Beds (shale 24 ft. above the Cinder Bed ; author's field ref. no. *WT* 33), Worbarrow Tout, Dorset (Nat. Grid ref. 30/869796).

PARATYPE (same locality and horizon). In.48606. A female carapace (Pl. 3, fig. 2).

DESCRIPTION. Strongly reticulate and trapezoidal, superficially much resembling *D. retirugata*, but larger, and with a constriction about the middle of the back. Sexual dimorphism marked, the females usually shorter than the specimen figured :

	Dimensions (mm.)			Proportions
	L	H	W	L H W
Carapace ♂ (In.48607 ; holotype) . .	1·12	0·63	0·56	1·79 : 1 : 0·89
Carapace ♀ (In.48606) . . .	1·02	0·67	0·52	1·54 : 1 : 0·78

Internal details not well displayed, owing to recrystallization of material. Hinge distinctly amphidont, however, with anteromedian boss of left valve strongly protuberant.

MATERIAL AND OCCURRENCE. This is a very abundant ostracod in the upper part of the Middle Purbeck Beds of the Dorset coast, where it is associated with species of *Cypridea*, but alternates in dominance with that genus in successive beds. Hundreds of specimens have been isolated from several horizons at Worbarrow Tout, and the species has also been found at other Dorset localities. Specimens from N.W. Germany (sent by the kindness of Dr. J. Wolburg) from Lingen (Boring No. 29 at 1195 m.) are slightly smaller, but have an almost identical ornament to that of the Dorset specimens. Wolburg (1950) classifies this horizon as " Wealden 2 ", and correlates it with the British Upper Purbeck. The type-locality in Dorset is in the upper part of the *C. fasciculata* subzone at the top of the Middle Purbeck.

Dictyocythere (Dictyocythere) decorata (Anderson)

(Plate 3, fig. 1)

1941. *Cythere retirugata* Jones var. *decorata* Anderson, p. 374, pl. 18, fig. 4.

DIAGNOSIS. Reticulate *Dictyocythere* with a " second order " reticulation within the main cells.

HOLOTYPE. Geol. Surv. Mus. no. 70339. Figured Anderson, 1941, pl. 18, fig. 4. A right valve.

TYPE LOCALITY. Cythere Marl, Swindon Series, Swindon. Author's field ref. no. *TGA 7*.

REMARKS. This is a rare species known only by three specimens from the Swindon Series (Sylvester-Bradley, 1941). The hinge appears to be exactly as in *D. retirugata*, but the shape is a little different, and the ornament more complex (see Pl. 3, fig. 1) ; the " second-order " reticulation noticed by Anderson is not confined, as suggested and figured by him, to the centre of the valve.

	Dimensions (mm.)			Proportions
	L	H	W	L H W
Left valve (In.48618)	0·94	0·57	0·36	1·65 : 1 : 0·63

Subgenus ***RHYSOCYTHERE*** nov.

TYPE-SPECIES. *Cythere retirugata* var. *rugulata* Jones, 1885.

DERIVATION OF NAME. ῥυσός, wrinkled + genus *Cythere*. Gender: feminine.

DIAGNOSIS. *Dictyocythere* with anterior element of hinge differentiated so that, in the right valve, an anterior group of denticles lies in front of the usual boss.

Dictyocythere (Rhysocythere) rugulata (Jones)

(Plate 4, figs. 1, 2, 5–10, 12–15)

1885. *Cythere retirugata* var. *rugulata* Jones, p. 350, pl. 9, figs. 17–20.
1941. *Cythere retirugata* Jones var. *rugulata* Jones: Anderson, p. 373, pl. 18, fig. 1.

DIAGNOSIS. Shape trapezoidal. Surface smooth over anterodorsal region, strongly ridged along venter and anterior margin.

LECTOTYPE (here designated). Geol. Dept. Brit. Mus. (N.H.) no. In.48600. A carapace, ♀, not left valve, as stated by Jones. Figured Jones, 1885, pl. 9, fig. 17. (Jones' No. 256, 2.)

TYPE LOCALITY. Hartwell, Buckinghamshire.

DESCRIPTION. Shape trapezoidal, dorsal and ventral margins being subparallel. Moderate sexual dimorphism, males somewhat longer than females and much rarer.

	Dimensions (mm.)			Proportions		
	L	H	W	L	H	W
Carapace ♂ (In. 48616)	0·98	0·56	0·49	1·76	1	0·88
Left valve ♂ (In.48615)	0·97	0·57	0·28	1·70	1	0·49
Left valve ♀ (In.48604)	0·84	0·55	0·29	1·54	1	0·54
Right valve ♀ (In.48605)	0·86	0·55	0·29	1·59	1	0·54
Left valve, juv. (In.48614)	0·68	0·45	0·24	1·50	1	0·53
Right valve, juv. (In.48613)	0·67	0·41	0·20	1·61	1	0·48

Valves almost smooth over the anterodorsal region of the carapace, but minutely punctate over a small region just below and behind the centre of the carapace (Pl. 4, fig. 6). Venter and anterior border strongly ridged (Pl. 4, figs. 12–14). Normal pore canals large and obvious in translucent specimens (Pl. 4, fig. 6) though they have often been misinterpreted as pits or bosses. Radial pore canals few, straight, sparse. Anterior duplicature fairly wide, with slight vestibule. Muscle-scar pattern (Pl. 4, fig. 5) consisting of four scars in vertical superposition, with one oval scar in front of them. Hinge of adult is amphidont, the anterior element clearly differentiated into an anterior group of about four small denticles in front and to a well-marked boss behind (Pl. 4, figs. 1, 2 and 10):

Adult	Left valve	Right valve
Anterior element	Deep pit, with an anterior loculate groove leading out from it	Protuberant boss lying at the posterior end of a dentate ridge, the denticles decreasing in size towards the anterior.
Anteromedian element	Rounded boss	Deep pit.
Posteromedian element	Smooth bar	Shallow groove.
Posterior element	Loculate groove	Dentate ridge.

The hinge of juvenile moults (Pl. 4, figs. 7–9) is particularly interesting, as it is transitional between merodont and entomodont, with a subdivided, nearly smooth, median element, but dentate terminal elements. The hinge of this species is therefore palingenetic, and it seems that all investigations of the ontogeny of hinge development so far published show that recapitulation takes place.

Juvenile	Left valve	Right valve
Anterior element	Loculate groove	Dentate ridge.
Median element	Smooth bar, the anterior end swollen and protruding further than posterior	Groove, the anterior end more deeply excavated than posterior.
Posterior element	Loculate groove	Dentate ridge.

Dictyocythere (Rhysocythere) transiens (Jones)

(Plate 3, figs. 11–13)

1885. *Cythere transiens* Jones, p. 349, pl. 9, figs. 13–16.

Diagnosis. Small reticulate *Dictyocythere*, tapering strongly to posterior in side view; with *Rhysocythere* hinge

Lectotype (here designated). Geol. Dept. Brit. Mus. (N.H.) no. In.48603. A left valve. Figured Jones, 1885, pl. 9, fig. 16. (Jones' No. 364, 2.)

Type locality. " Lower Purbeck, Swindon " (but see below).

Description. Fairly coarsely reticulate, tapering strongly to posterior in side view, sexual dimorphism not observed.

	Dimensions (mm.)			Proportions		
	L	H	W	L	H	W
Carapace (In.48617)	0·60	0·37	0·31	1·61 :	1 :	0·82

Hinge appears to be exactly as in *D.* (*R.*) *rugulata*.

Occurrence. Although the type locality is at Swindon, only a few specimens have been found there by the author in the " Swindon Series ", and these may have been derived from the Portlandian " Swindon Sands and Stone " below. The species is abundant at a certain horizon of the " Bugle Pit ", Hartwell, within the Creamy Limestones of undoubted Portlandian age (author's field ref. no. *BP* 18; this is from Bed 6 of Arkell, 1947 : 126). The species is characteristic, in fact, of the Upper Portlandian, and only with some doubt can its range be said to include the Lower Purbeck, despite Jones' contention. The horizon " Lower Purbeck" appears to be an inference by Jones, and was not indicated by Blake, who collected the specimens (see Jones, 1885 : 328).

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PLATE 1

Acanthocythere sphaerulata (Jones & Sherborn)

Figs. 1, 4. Left valve male (external and internal lateral views). In.42434 (0·67 mm. long).

Figs. 2, 3. Right valve male (external and internal lateral views). In.42433 (0·69 mm. long).

Acanthocythere spiniscutulata n. sp.

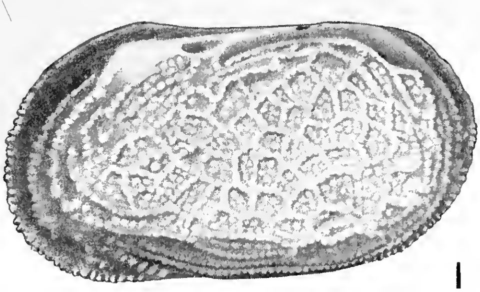
Figs. 5, 8. Left valve (external and internal lateral views), holotype. In.42435 (0·57 mm. long).

Figs. 6, 9. Right valve (external and internal lateral views), paratype. In.42436 (0·56 mm. long).

Fig. 7. Carapace (dorsal view), paratype. In.42437 (0·57 mm. long).

All figures approx. × 90 (exact lengths given above), from pencil drawings by Miss D. Robinson based on camera lucida sketches by the author.

All specimens from the economic Fullers' Earth (Upper Fullers' Earth Clay, Bathonian, Middle Jurassic) from the Fosse Way mine, nr. Bath, collected by the author, now in the British Museum (Nat. Hist.).



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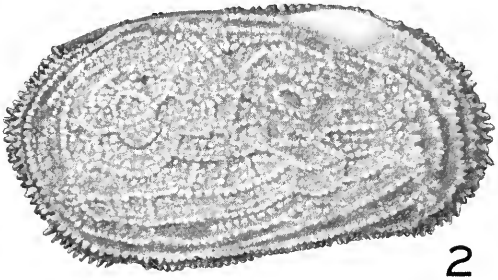

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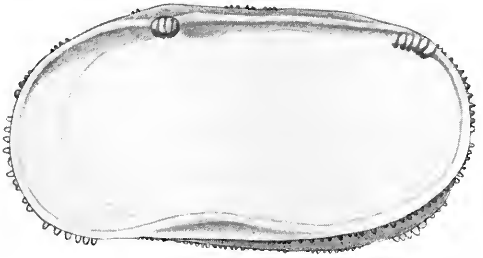

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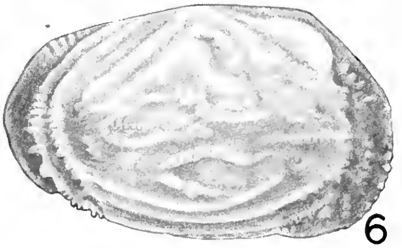

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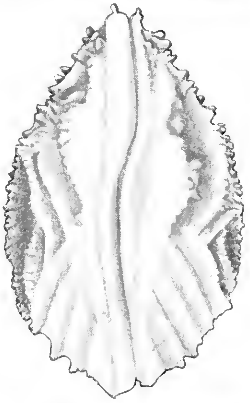

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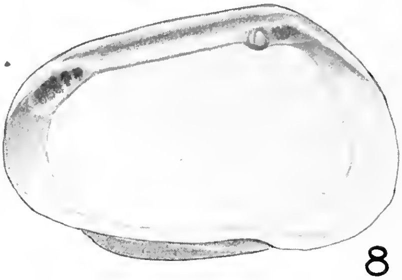

8

9

ACANTHOCYTHERE GEN. NOV. (MIDDLE JURASSIC)

PLATE 2

Quasillites sp.

Fig. 1. Right valve, external lateral view. The irregularly shaped blank space below the centre is obscured by matrix. In.48624 (1·16 mm. long).
Fig. 2. Left valve, internal lateral view. In.48623 (1·09 mm. long).

Bufina sp.

Fig. 3. Left valve, external lateral view. In.48622 (0·89 mm. long).
Fig. 4. Right valve, external lateral view. In.48621 (0·93 mm. long).

Euglyphella sp.

Figs. 5, 6. Right valve, external lateral and internal lateral views. In.48619 (0·99 mm. long).
Fig. 7. Left valve, internal lateral view. In.48620 (1·13 mm. long).

Figs. 1, 2, approx. × 70; 3–7, × 65. Exact lengths given above. All are pencil drawings by Miss D. Robinson based on camera lucida sketches by the author.

All specimens from the Pleurodictyum Bed (Ludlowville, Hamilton Group, Middle Devonian) of Bay View, Erie County, New York, U.S.A., collected by Raymond R. Hibbard, now in the British Museum (Nat. Hist.).

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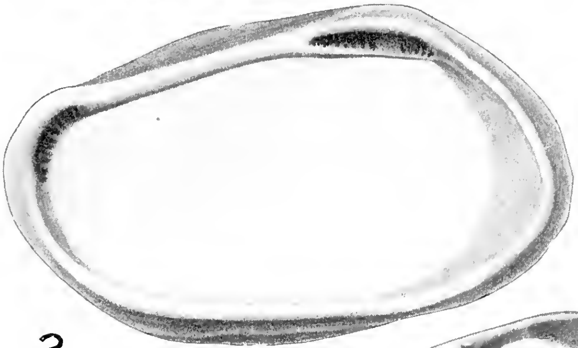

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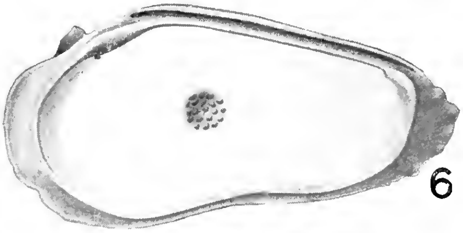

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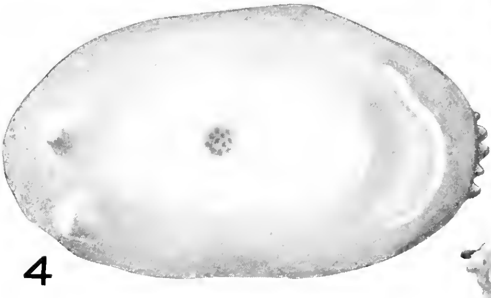

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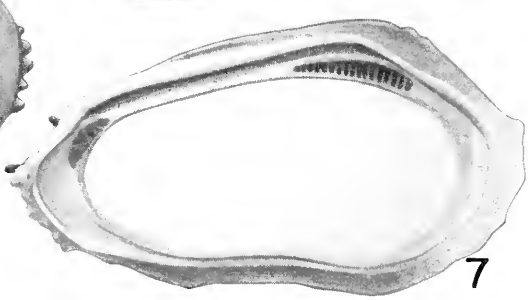


7

MIDDLE DEVONIAN QUASILLITACEA

PLATE 3

Dictyocythere (*Dictyocythere*) *decorata* (Anderson)

Fig. 1. Left valve, external lateral view. In.48618 (0·94 mm. long). Cythere Marl, Swindon Series, Swindon (? Purbeckian).

Dictyocythere (*Dictyocythere*) *mediostricta* n. sp.

Fig. 2. Carapace ♀, left lateral view. In.48606 (1·02 mm. long).
Figs. 3–6. Carapace ♂, right lateral, left lateral, dorsal and ventral views, holotype. In. 48607 (1·12 mm. long). Middle Purbeck Beds, Worbarrow Tout, Dorset.

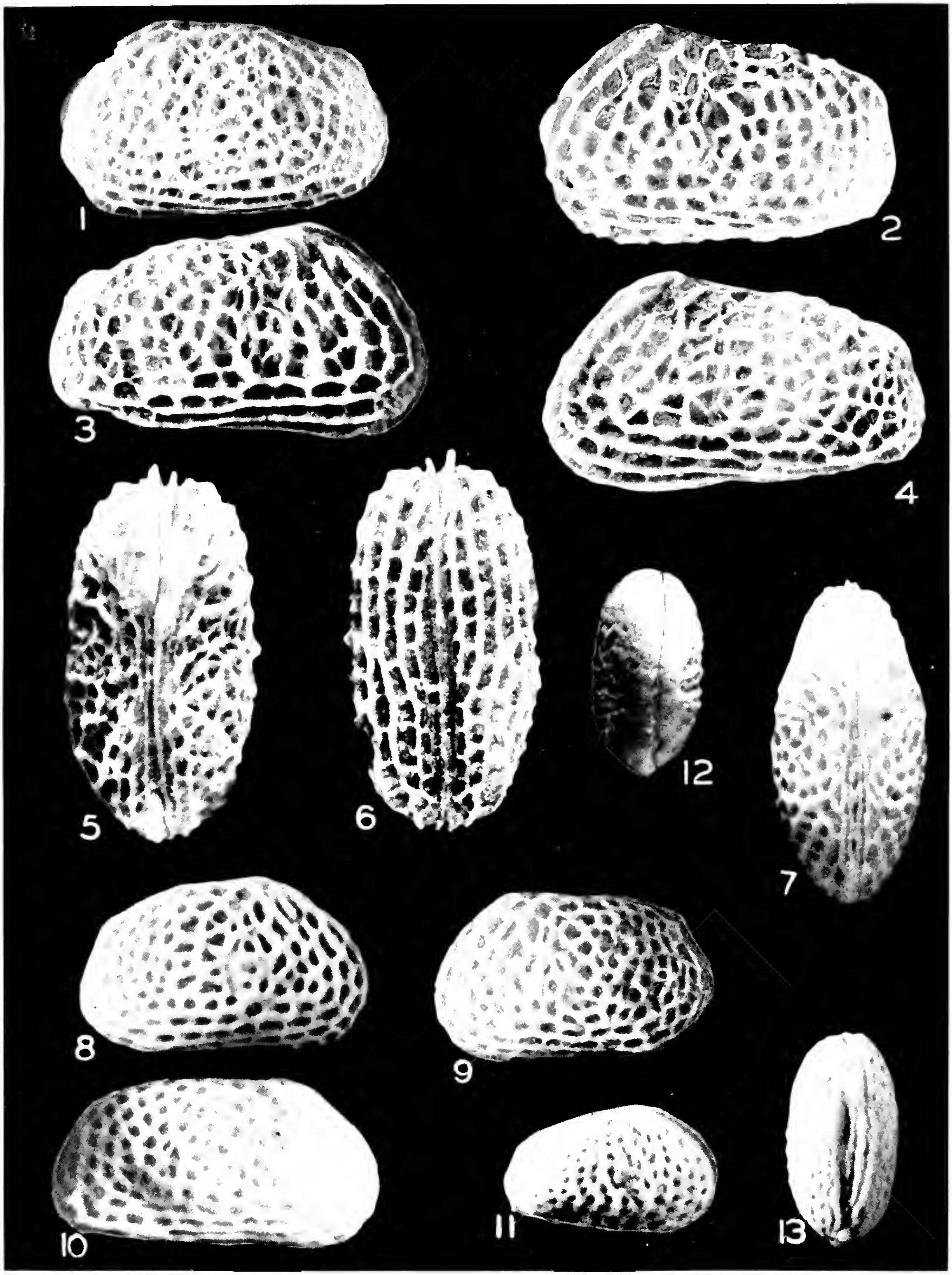
Dictyocythere (*Dictyocythere*) *retirugata* (Jones)

Fig. 7. Carapace ♂, ventral view. Specimen accidentally destroyed.
Fig. 8. Right valve ♀, external lateral view. In.48611 (0·84 mm. long).
Fig. 9. Left valve ♀, external lateral view. In.48610 (0·80 mm. long).
Fig. 10. Right valve ♂, external lateral view. In.48608 (0·97 mm. long).
All from Cythere Marl, Swindon Series, Swindon (? Purbeckian).

Dictyocythere (*Rhysocythere*) *transiens* (Jones)

Figs. 11–13. Carapace (right), lateral, dorsal and ventral views. In.48617 (0·60 mm. long). Upper Portland Beds, Bugle Pit, Hartwell.

All figures from photographs by the author, × 60 approx. The specimens whitened with magnesium oxide before being photographed.



DICTYOCYTHERE GEN. NOV. (UPPER JURASSIC)

PLATE 4

Dictyocythere (Rhysocythere) rugulata (Jones)

FIGS. 1, 2. Left and right valves ♀, dorsal views. In.48604 (0·84 mm. long), In.48605 (0·86 mm. long).

Dictyocythere (Dictyocythere) retirugata (Jones)

FIGS. 3, 4. Left and right valves ♀, dorsal views. In.48610 (0·80 mm. long), In.48611 (0·84 mm. long).

Dictyocythere (Rhysocythere) rugulata (Jones)

FIG. 5. Internal view of centre of right valve to show muscle-scar pattern. In.48612 (× 200).

FIG. 6. Left valve ♀ photographed under water by reflected light to show normal pore canals and minute punctation behind and below central region. In.48604 (0·84 mm. long).

FIGS. 7, 8. Dorsal views of left and right valves of juvenile moults showing entomodont hinge. In.48614 (0·68 mm. long), In.48613 (0·67 mm. long).

FIGS. 9, 10. Anterior hinge elements of juvenile and adult right valves in dorsal view. In. 48613, In.48605 (× 200).

Dictyocythere (Dictyocythere) retirugata (Jones)

FIG. 11. Anterior element of right valve in dorsal view. In.48611 (× 200).

Dictyocythere (Rhysocythere) rugulata (Jones)

FIG. 12. External lateral view of left valve of ♂. In.48615 (0·97 mm. long).

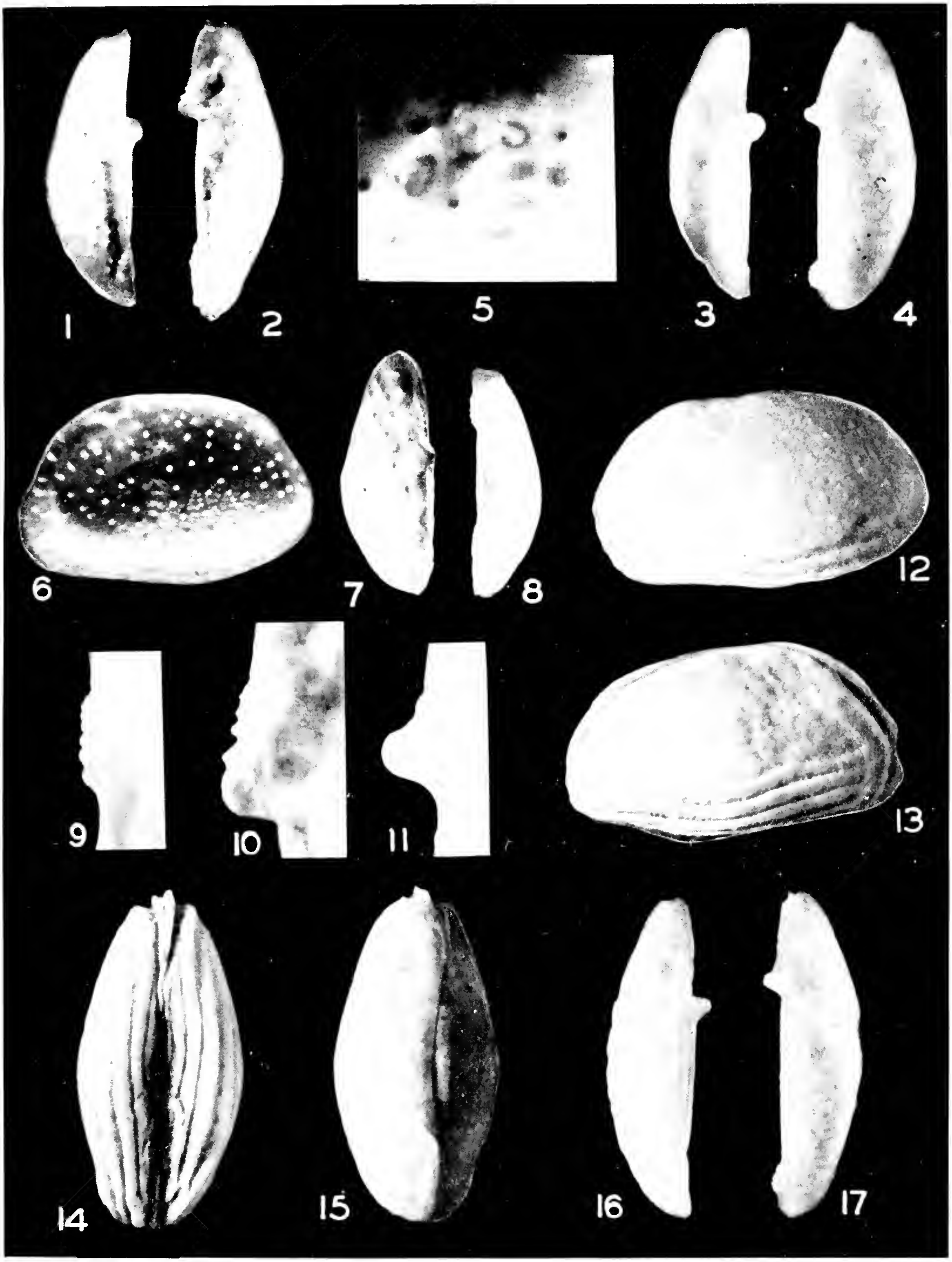
FIGS. 13–15. ♂ carapace in right lateral, ventral and dorsal views. In.48616 (0·98 mm. long).

Dictyocythere (Dictyocythere) retirugata (Jones).

FIGS. 16, 17. Dorsal views of left and right valves ♂. In.48609 (0·92 mm. long), In.48608 (0·97 mm. long).

Figs. 1, 2, 6–10, 12–15 from so-called Purbeck Beds of Bugle Pit, Hartwell. Figs. 3, 4, 5, 11, 16, 17 from Cythere Marl, Swindon Series, Swindon (? Purbeckian).

All figures from photographs by the author. Figs. 1–4, 6–8, 12–17 × 55 approx. Specimens in Figs. 12–14 whitened with magnesium oxide before being photographed.



DICTYOCYTHERE GEN. NOV. (UPPER JURASSIC)

EOCENE MOLLUSCA FROM NIGERIA: A REVISION

F. E. EAMES

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 3 No. 2
LONDON: 1957

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EOCENE MOLLUSCA FROM NIGERIA: A REVISION

BY

FRANK E. EAMES

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By F. E. EAMES

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SYNOPSIS

The molluscan fauna described by R. B. Newton (1922) from the Eocene of Bende Ameki (Nigeria) is revised. Fifteen new gastropod species and eight new lamellibranch species are described; ten new genera and seven new subgenera of gastropoda and four new genera and six new subgenera of lamellibranchia are proposed, one of the lamellibranch genera belonging to a new family. The Eocene age of the fauna is confirmed, but it is believed to be of Upper Eocene (Bartonian), rather than Middle Eocene (Upper Lutetian), age.

I. INTRODUCTION AND GENERAL REVIEW

During the course of exploration in Nigeria by the joint Shell and British Petroleum organization it has frequently been necessary to consult R. B. Newton's work on Eocene Mollusca from Nigeria (1922). Certain problems concerning the age of the beds arose, and these led the writer to investigate the fauna more fully. A detailed study of the material described by Newton, which is in the collections of the British Museum (Natural History), was undertaken, with the result that, while the conclusions agreed fairly closely with Newton's opinion as to the age, it became apparent that many of the generic determinations required revision, and that not only was only one European species present, but also that all forms compared by Newton with European ones were specifically, and in some cases even generically, distinct. A full description of many of the forms is given in Part II of this paper.

On the basis of the fauna he described, Newton concluded that the beds were of Upper Lutetian age, although he recognized that the Bartonian facies was very apparent. The result of the present revision has been to show that only two lamellibranchia—*Plicatula polymorpha* Bellardi and *Raetomya schweinfurthi* (Mayer-Eymar)—occur outside Nigeria, in the Upper Mokattam Beds of Egypt; the *Plicatula* has been found also in the Priabonian of Italy, and the *Raetomya* in the Eocene of Senegal and the Cameroons. Of the gastropod genera, *Strepsidura* (sensu lato) ranges from Eocene to Oligocene, and *Exechostoma* and the subgenus *Buccinorbis* range from Maestrichtian to Eocene; not one of the gastropod species has yet been found elsewhere. The cephalopod genus *Belosepia* is restricted to the Eocene. Although the bryozoan genus *Cupuladria*, hitherto believed to range only from Miocene to Recent, has been found in the beds by palaeontologists of the Shell Oil Company, the Eocene age indicated by the mollusca is also confirmed by the fish remains recorded, which include the genus *Cylindracanthus*. The coral *Turbinolia*, which is also of fairly common occurrence in the beds, is known only from Eocene and Oligocene deposits.

Although two of the lamellibranch species have been recorded from the Upper Mokattam Beds of Egypt, these beds have also yielded *Nummulites beaumonti* and *Orbitolites complanatus*; these latter fossils suggest a rather earlier age than Bartonian (to which stage the Upper Mokattam Beds have been assigned), and appear to suggest that the Upper Mokattam is not entirely of Bartonian age.

In Angola, Dartevelle & Roger have recently clearly shown that the beds (Quimbriz Beds) in which *Platyodon klinghardti* (mistakenly referred to *Raetomya schweinfurthi* by Caster) and *Macrocallista palmerae* (to which the Nigerian form here named *Sinodiopsis coxi* was erroneously referred) are really of Miocene age. Any similarity of the Angola fauna to that of the Nigerian Bende Ameki Beds is evidently purely superficial, no species being in common. Dartevelle & Roger refer to *Raetomya* as a mactrid, but Newton has clearly shown that it is a myid; indeed, Dartevelle & Roger had some doubts about referring the species *klinghardti* to the American genus *Platyodon*, and it may well be that it also is a *Raetomya*.

As a result of the revision of the molluscan fauna from Bende Ameki, the writer believes that the evidence and the general relationships of the fauna, while confirming Newton's opinion as to the Eocene age, suggest that an Upper Eocene (Bartonian) rather than a Middle Eocene (Upper Lutetian) age, is indicated.

II. SYSTEMATIC DESCRIPTIONS

GASTROPODA

Family Potamididae

Genus *EXECHOSTOMA* Cossmann, 1889

Exechostoma cossmanni Newton

1922. *Exechostoma cossmanni* Newton, p. 45, pl. 5, figs. 8–9.

Remarks. Specimen G.42177 (Newton's fig. 9) is now selected as lectotype.

Genus *TEREBRALIA* Swainson, 1840

Terebralia nigeriensis sp. nov.

1922. *Terebralia* sp.A. Newton, p. 46, pl. 4, fig. 10.

Material. The holotype (G.42174).

Description. Apical whorls missing and aperture broken. Of medium size, turriculate-conic, spire angle 19°. Whorls (of which four or five are preserved) almost flat-sided, their height very slightly more than half their width; sutures deeply impressed, distinctly undulatory. Ornament consisting of moderately coarse and fairly widely-spaced ribs crossed by strong spiral threads; ribs somewhat irregularly spaced, sometimes only slightly narrower than, but sometimes (especially on the later whorls) only half the width of, their intervals, gently opisthocline adapically, their forward-directed face slightly concave, more strongly so abapically, where they tend to be slightly swollen. On the whorls preserved there are 11 strong spiral threads with intervals of about the same width. There is no noticeable development of varices. Abapical portion of last whorl poorly preserved, without ribs, but with about nine incised spiral grooves separated by intervals of approximately half their width. Columella moderately concave and callous; other apertural characters not determinable.

Dimensions. Height (incomplete) 49·7 mm. Diameter of last whorl 21·0 mm.

Remarks. The above characters are sufficient for specific determination.

Terebralia amekiensis sp. nov.

1922. *Terebralia* sp.B. Newton, p. 48, pl. 4, fig. 11.

MATERIAL. The holotype (G.42175).

DESCRIPTION. Apical whorls missing and aperture broken, about five whorls preserved. Of small-medium size, turriculate-conic, spire angle 17°–18°. Whorls flat-sided, their height about two-fifths of their width; sutures linear and moderately deep, gently undulatory. Ornament consisting of relatively fine and closely-spaced ribs crossed by strong spiral threads; ribs of about the same width as their intervals, their forward-directed face sometimes gently concave, vertical or slightly opisthocline abapically. On the whorls preserved there are eight to ten fairly strong spiral threads with intervals of about the same width; no noticeable development of varices. Base broken, without ribs, but carrying strong spiral threads with intervals of about the same width.

DIMENSIONS. Height (incomplete) 38·4 mm. Diameter of last whorl 15·3 mm.

REMARKS. The above characters are sufficient to define the species.

Family TURRITELLIDAE

Genus ***TURRITELLA*** Lamarck, 1799

Turritella amekiensis sp. nov.

(Pl. 5, figs. 1, 2)

1922. *Turritella* cf. *sulcifera* Deshayes: Newton, p. 50, pl. 5, fig. 7.

MATERIAL. Numerous specimens, including the holotype (G. 42215, Newton's fig. 7).

DESCRIPTION. Of medium size, turriculate-conic, spire angle 15°, last whorl about one-eighth of the total height. Protoconch not preserved, evidently small. Whorls distinctly convex, their greatest convexity slightly below the middle, upper slope less convex than the lower. Sutures linear. Height of whorls about seven-twelfths of their width. The earliest whorls seen carry four spiral threads, the number increasing to about 18 on the last spire whorl, on which a few very fine additional threads are present in some of the intervals. Base of last whorl with threads of a similar type. Columella gently concave; columellar lip narrow, especially abapically. Aperture evidently rounded-subquadrate. No siphonal fasciole. Growth lines concave forwards, distinctly prosocline adapically, very slightly prosocline abapically, the maximum concavity at about three-fifths the height of the whorl.

DIMENSIONS. Height 27·4 mm., width 7·5 mm.

REMARKS. The Nigerian form is consistently smaller than *T. sulcifera* Deshayes of the Paris Basin Lutetian; its whorls do not tend to be concave above, and the details of the spiral ornament are different.

Subgenus ***COELOCONICA*** nov.

Type species. *Turritella mauryana* Newton.

Subgeneric characters. Of moderate size to fairly large, distinctly coeloconoid. Protoconch not preserved, evidently small. Early whorls subcylindrical to slightly convex, with three sharp spiral threads the uppermost of which is fairly close to the suture ; traces of a fourth thread at the lower suture ; all four threads with sharp, closely-spaced, vertically diposed crenulations where crossed by growth lines ; rest of surface with microscopic spirals. With growth the third thread from the adapical suture gradually develops into a very prominent, sharp flange. Base of last whorl with a second prominent, but feebler, keel and two obscure threads below, as well as microscopic spirals. Aperture rounded-subquadrate, as in *Turritella*. Growth-lines with a deep U-shaped sinus the apex of which is slightly above the second keel ; markedly prosocline at the adapical suture, orthocline at the abapical suture, their lower end immediately below the upper.

Remarks. The high, gently coeloconoid spire, the details of ornament (including development of the strong flange), and the form of the growth-lines differentiate this from other described groups of *Turritella*.

Turritella (Coeloconica) mauryana Newton

1922. *Turritella mauryana* Newton, p. 48, pl. 5, figs. 4–6.

Material. Several specimens, including the lectotype (G. 42209, Newton's fig. 4) here selected.

Family Architectonicidae

Genus ***ARCHITECTONICA*** (Bolten MS.) Röding, 1798

Subgenus ***NIPTERAXIS*** Cossmann, 1915

Architectonica (Nipteraxis) bendeica sp. nov.

(Pl. 5, figs. 3*a–c*)

1922. *Solariaxis* cf. *canaliculata* (Lamarck): Newton, p. 54.

Material. The holotype (G.42373) and a few other specimens.

Description. Moderately small, low-conic to slightly cyrtoconoid, apical angle 140°–145°. Protoconch smooth, anastrophic ; 3–4 flattened, very slightly convex spire whorls with deep, sunken sutures. Ornament consisting of five crenulated spiral threads, the uppermost one the most prominent and with the strongest crenulations, the others subequal. Last whorl sharply rounded at the periphery where there is a sixth and broader cordon, and with a fine subsidiary thread in each interval ; on large specimens a second order of intercalaries may appear. Base gently convex, with seven crenulated or beaded spiral threads, the outer three finer and moderately widely spaced, the inner three coarser and with coarser beading, the innermost one well within the umbilicus ; blunt, accentuated growth lines join the crenulations. Umbilicus deep, wide and completely visible, occupying about two-fifths of the diameter of the base. Growth lines gently prosocline, slightly sinuous, becoming orthocline at the upper suture. Aperture rounded kite-shaped, peristome discontinuous ; columella thin, slightly excavated, with two small furrows corresponding to the two innermost spiral threads on the base, the upper furrow more distinct.

Dimensions. Holotype : height 5·7 mm., width 12·0 mm.

A topotype (G.42374) has a width of 13·8 mm.

Remarks. Compared with *A. canaliculata* (Lamarck), this form lacks the sharp peripheral keel, and the details of the ornament are quite distinct.

Subgenus ***STELLAXIS*** Dall, 1892

Architectonica (Stellaxis) bicingulata (Newton)

(Pl. 5, fig. 4)

1922. *Stellaxis bicingulata* Newton, p. 52, pl. 5, figs. 10–11.

Material. Numerous specimens, including the lectotype (G. 42355, Newton's fig. 10) here selected.

Supplementary description. Of medium size, solarioid, spire slightly cyrtoconoid ; spire angle decreasing during growth from about 125° to about a right angle or slightly less ; last whorl forming slightly more than one-third of the height. Protoconch smooth and loosely coiled, anastrophic. About five spire whorls, which are gently convex, the main surface separated from a narrow but distinct, smooth, abapical sutural cord by a spiral groove ; main surface smooth in the earlier stages, later developing extremely vague, irregular spiral threads. Sutures linear. Growth lines almost straight, prosocline. Marginal keel on last whorl with a few very faint threads, occasionally appearing to be slightly bifid. Base gently convex medially, flatter marginally where there is one smooth spiral cord close to the peripheral keel. Umbilicus very deep, wide and completely visible, occupying about a third of the diameter of the base, margined by blunt teeth which are sometimes made to appear vaguely bifid by the accentuated growth-lines, its inner wall vertical and with a spiral thread at about two-thirds of its height ; a fine spiral groove limits the teeth externally in young forms, but is often obsolete or absent in adults. Aperture kite-shaped, with a small indentation level with the row of umbilical teeth, and a still fainter one by the umbilical thread above.

Subgenus ***SOLARIAXIS*** Dall, 1892

Architectonica (Solariaxis) amekiensis sp. nov.

(P. 5, figs. 5*a–c*)

1922. *Solariaxis* cf. *spectabilis* (J. de C. Sowerby): Newton, p. 53, pl. 5, figs. 12–13.

Material. A few specimens, including the holotype (G.42361, Newton's fig. 12).

Description. Of medium size, moderately low, gently cyrtoconoid, spire angle decreasing during growth from about 130° to about 105° (excluding the peripheral downturning of the last whorl). Protoconch not well preserved, anastrophic. About five flattened spire whorls with deep sutures, slightly imbricate. Ornament consisting of seven rather finely crenulated, not very coarse spiral threads, the fourth and sixth (from the adapical suture) finer than the others, the second, third and fifth coarser, the first even a little coarser than these. Last whorl bluntly angular at the periphery, its upper four primary threads rather wide-spaced, with a faint double intercalary, a fine single intercalary, and a stronger double intercalary in the upper, median and lower intervals, respectively; the five lower primary threads more closely-spaced, the upper interval with a fine intercalary, the peripheral thread double. Base flattened, only very slightly convex, with seven crenulated or beaded spiral threads increasing in strength towards the umbilicus, the wall of the latter with two finer, widely-spaced threads; growth lines serrate but not thickened. Umbilicus deep, wide and completely visible, occupying about a third of the diameter of the base. Growth lines distinctly prosocline, fairly straight, but becoming orthocline at the adapical suture. Aperture oval, kite-shaped; peristome discontinuous. Columella thin, gently concave, with four slight furrows corresponding to the two umbilical threads and the two innermost spiral threads on the base.

DIMENSIONS. Holotype: height 13·4 mm., width 22·8 mm.

REMARKS. Compared with that of *A.* (*Solariaxis*) *spectabilis* (J. de C. Sowerby) the spiral ornament is coarser and differently disposed.

Family SCALIDAE

Genus *ACRILLA* H. Adams, 1860

Acrilla nigeriensis sp. nov.

(Pl. 5, fig. 6)

1922. *Acrilla* cf. *affinis* (Deshayes): Newton, p. 50, pl. 3, figs. 10–12.

MATERIAL. The holotype (G.42285, Newton's fig. 10), and a few other specimens.

DESCRIPTION. Specimens incomplete, apical whorls missing and aperture broken. The largest specimen (the holotype) has about eight whorls preserved, spire angle 11°; they are rather loosely coiled, with deep, linear sutures, and are very strongly convex, with a tendency to angularity at about three-quarters or more of their height. Ornament consisting of fine, sharp, prominent axial ribs with subdued spiral threads in the intervals. The ribs are considerably narrower than their interspaces, occasionally slightly varicose, straight or gently concave forward, gently prosocline, and more strongly bent forward at the adapical suture. There are some 30–35 vague, irregular spirals on the last-preserved whorl of the holotype. A topotype (G. 42286) shows a basal disk limited by a fairly sharp carina; the ribs continue over the disk, but are much flattened, and there are some 20 spirals similar to those on the spire whorls. Aperture oval, a little higher than wide; columellar lip slightly concave, more callous abapically, where a small auricle is developed.

Remarks. This species was compared by Newton with *A. affinis* (Deshayes) of the Paris Basin Eocene, but is distinctly more aciculate, the spire angle being smaller. The whorls are distinctly more convex, and the sutures more deeply sunk, the shell being more loosely coiled.

Family Calyptraeidae

Genus *CALYPTRAEA* Lamarck, 1799

Calyptraea newtoni sp. nov.

(Pl. 5, figs. 7*a*, *b*)

1922. *Calyptraea crepidularis* Lamarck: Newton (pars), p. 59.

Material. The holotype (G.42438) and one topotype (G.42439).

Description. Of moderate size, calyptraeiform, irregularly conic. Protoconch small, smooth, dextral, *Nerita*-like, obliquely set. Surface ornamented, at least in the later stages, with oblique threads bearing papillae, the threads becoming more nearly parallel to the apertural margin as they approach it. Aperture subcircular, with margin lying in one plane, septum with very concave edge.

Dimensions. Height 4·7 mm., width 12·8–13·5 mm.

Remarks. *C. crepidularis* Lamarck, of the Paris Basin Eocene, with which Newton identified this form, is much flatter, is subrectangular in outline, has a markedly eccentric apical region, and does not possess oblique threads bearing papillae.

Genus *TURBOCALYPTRAEA* nov.

Type species. *T. scabrosa* sp. nov.

Generic characters. Of medium size to moderately small, calyptraeiform, tending to turbinate, apex markedly eccentric. Whorls strongly convex, with several spirally disposed rows of short, hollow, forward-directed spines together with obliquely disposed threads. Aperture as in *Calyptraea*, subcircular to suboval. A distinct, sunken, gently concave septum, the margin of which is noticeably concave in its upper part and gently convex in its lower part, occupies nearly half the aperture. A small, deep umbilicus is developed in the upper part of the septum.

Remarks. The form, ornament, character of the septum, and presence of an umbilicus together characterize this new genus.

Turbocalyptraea scabrosa sp. nov.

(Pl. 5, figs. 8, 9*a*, *b*)

1922. *Calyptraea crepidularis* Lamarck: Newton (pars), p. 59, pl. 4, figs. 18–19.

Material. A few specimens, including the holotype (G.42437, Newton's fig. 19).

Description. As above.

Remarks. *C. crepidularis* Lamarck, from the Eocene of the Paris Basin, with which Newton identified this species as well as the last, differs markedly in its almost flat form and subrectangular outline, its very small spire, its lack of coarse ornament, and in the characters of the septum.

Genus *CREPIDULA* Lamarck, 1799

Subgenus *CONCAVIMARGO* nov.

Type species. *Crepidula falconeri* Newton.

Subgeneric characters. Like *Crepidula*, but teleoconch whorls not in contact; surface smooth; body cavity deep; aperture oval; septum rather deeply sunk and with a cavity extending underneath the inner lip; edge of septum distinctly concave.

Crepidula (Concavimargo) falconeri Newton

1922. *Crepidula falconeri* Newton, p. 58, pl. 2, figs. 13, 13*a*.

Material. Several specimens, including the lectotype (G.42411, Newton's fig. 13) here designated.

Family Xenophoridae

Genus *XENOPHORA* Fischer von Waldheim, 1807

Xenophora nigeriensis (Newton)

(Pl. 6, figs. 1*a–c*)

1922. *Tugurium nigeriense* Newton, p. 51, pl. 4, figs. 20–21.

Material. Numerous specimens, including the lectotype (G.42291, Newton's fig. 21) here designated.

Remarks. The presence of numerous agglutinated objects covering most of the whorl surface indicates that the species is better regarded as a *Xenophora*; an umbilicus as small as the one it possesses may occur in this genus.

Family Strombidae

Genus *TIBIA* (Bolten MS.) Röding, 1798

Tibia bidigitata (Newton)

1922. *Rostellaria bidigitata* Newton, p. 12, pl. 4, figs. 8–9.

Material. Several specimens, including the lectotype (G.41643, Newton's fig. 8) here designated.

Genus *CYRTULOTIBIA* nov.

Type species. *Rostellaria unidigitata* Newton.

Generic characters. Form somewhat like that of a *Tibia* with a very short, inclined siphonal canal; often developing a strong shoulder on the last whorl and thus recalling *Cyrtulus*. Protoconch conic, of two or three smooth, moderately convex whorls. Spire like that of *Tibia*, conic, of five or six gently convex whorls; early stages with fine axial riblets, which are orthocline above and opisthocline below (i.e., concave forwards), crossed by increasingly broad spiral threads; coarse, swollen varices developed occasionally. On later spire whorls the axial riblets become obsolete and are represented by accentuated growth lines only. Last whorl slightly to very strongly shouldered, the more strongly shouldered specimens with a narrow callous band (an extension of the callus of the posterior sinus) extending back some one and a half to two whorls along the sutural region. Last whorl smooth except for spiral threads on the base, rather conic, base very slightly excavated, neck oblique. Rostrum short, curved to the right. Aperture oval, with a narrow, slit-like posterior sinus curving back on to the suture; columellar lip callous, developing a prominent, raised knob of callus limiting the inner side of the posterior sinus; a broad notch to the right of the rostrum is delimited on the right by a short spine. Outer lip rather thick, not varicose, internally smooth, with no additional spines, gently parasigmoidal, distinctly opisthocline as a whole.

Remarks. The general form, short inclined rostrum, single abapical labial spine, the contour of outer lip, broad abapical notch, and extremely strong adapical parietal callus (extending back along the suture for two or three whorls) readily distinguish this genus from *Tibia*.

Cyrtulotibia unidigitata (Newton)

1922. *Rostellaria unidigitata* Newton, p. 14, pl. 4, figs. 3–7.

MATERIAL. Many specimens, including the lectotype (G.41688, Newton's fig. 3) here selected.

Genus ***SEMITEREBELLUM*** Cossmann, 1889

Subgenus ***AFRICOTEREBELLUM*** nov.

TYPE SPECIES. *Semiterebellum elongatum* Newton.

SUBGENERIC CHARACTERS. Form much like that of *Terebellum*, but more narrowly fusiform. Protoconch consisting of some three to four smooth, moderately convex whorls, less acute than the shell as a whole. About six spire whorls, at first gently convex, becoming flatter with growth. Ornament in the earlier stages consisting of a sharp, fine adapical thread finely crenulated by growth lines, with a narrow, shallowly excavated band below it, the abapical half of the remaining portion of the whorls with four to six fine, incised spiral lines; ornament obsolete on later whorls. Last whorl with numerous irregular spiral threads (finer and with broader intervals abapically) on the base, which is only vaguely concave; neck short, gently swollen. Rostrum extremely short, its end barely projecting more than the outer lip abapically. Aperture oval-subtriangular, narrower adapically, with a broad, shallow notch to the right of the rostrum. Columellar callus thin, especially medially, with a low, oblique ridge adapically, forming the upper edge of the short posterior sinus which extends only slightly above and back along the suture. Outer lip opisthocline as a whole, forming a strongly projecting, rounded lobe to the right of the abapical channel, thin, not varicose, internally smooth.

REMARKS. This subgenus differs from *Semiterebellum* (sensu stricto) in being more lanceolate, in the less projecting rostrum, in the posterior sinus which does not ascend partly up the spire, and in the more opisthocline outer lip which is more lobate below.

Semiterebellum (Africoterebellum) elongatum Newton

(Pl. 5, figs. 10*a*, *b*)

1922. *Semiterebellum elongatum* Newton, p. 17, pl. 2, figs. 14–15.

MATERIAL. Numerous specimens, including the lectotype (G.41762, Newton's fig. 15) here selected.

Genus ***AMEKICHILUS*** nov.

TYPE SPECIES.—*Semiterebellum suturocostatum* Newton.

GENERIC CHARACTERS. Of small-medium to medium size, having the general form of *Ectinochilus*. Protoconch helicoid-trochoid, consisting of about four smooth, moderately convex whorls. Spire gently cyrtoconoid; last whorl slightly more than half the height of the shell. Whorls only slightly convex, sutures distinct; five to six spire whorls. An incised line separates a narrow juxtasutural band which is always crenulated or beaded in the early stages; later, the band is either smooth or beaded, and may be vaguely bifid. Last whorl oval, base declivous; neck short, not swollen. Rostrum short, scarcely projecting, inclined gently to the right, with a broad, very shallow notch to its right, the notch limited externally by a short, sharp spine. Aperture oval, rather small, with a long, narrow, callous posterior sinus which curves over and slightly down on to the suture of the last whorl, extending only a short distance back. On those specimens which have a heavily beaded juxtasutural thread, the upper part of the posterior sinus extends back right up the spire as a gently convex callous band occupying the lower half of the whorls. Columella gently concave, smooth, with thick callus developing an even thicker ridge along the upper side of the posterior sinus. Outer lip thin, varicose, internally smooth, but with a slight internal thickening, externally strongly varicose, especially at the posterior sinus, nearly straight and orthocline, slightly convex adapically. Ornament consisting of a few incised spiral lines with minute pits, widely spaced posteriorly, often obsolete on the middle of the last whorl, changing to more closely spaced spiral threads on the base.

REMARKS. This form is shorter and more oval than *Semiterebellum*, and has a less projecting rostrum, a distinct juxtasutural band, and an abapical labial spine; the posterior sinus does not ascend above the suture of the last whorl. Its closest relatives seem to be the *Ectinochilus* and *Dientomochilus* group of shells, but there are no obvious varices and the posterior sinus curves over at the suture of the last whorl. The posterior sinus in *Africoterebellum* is similar, but in that genus the form of the shell, ornament and labial spine are quite different.

Amekichilus suturocostatum (Newton)

1922. *Semiterebellum suturocostatum* Newton, p. 15, pl. 4, figs. 14–17.

MATERIAL. Many specimens, including the lectotype (G.41757, Newton's fig. 14) here selected.

Family AMPHIPERATIDAE

Genus ***EOVOLVA*** Schilder, 1932

Eovolva nigeriensis (Newton)

(Pl. 6, figs. 2, 3)

1922. *Amphiperas nigeriensis* Newton, p. 18, pl. 3, figs. 14–15.
1932. *Eovolva nigeriensis* (Newton): Schilder, p. 212.

MATERIAL. Several specimens, including the lectotype (G.41786, Newton's fig. 14) here selected.

REMARKS. This is the monotype of *Eovolva*.

Genus ***SPHAEROCYPRAEA*** Schilder, 1927

Sphaerocypraea sudanensis (Schilder)

(Pl. 6, figs. 4*a*, *b*)

1922. *Cypraea* cf. *bowerbanki* J. de C. Sowerby: Newton, p. 18, pl. 3, fig. 13.
1929. *Sphaerocypraea bowerbankii* (J. de C. Sowerby): Schilder, p. 305.
1932. *Eocypraea* (*Sphaerocypraea*) *bowerbanki* (J. de C. Sowerby) var. *sudanensis* Schilder, p. 218.

MATERIAL. A few specimens, including the lectotype (G.41780, Newton's fig. 13) here selected.

Remarks. In spite of its general similarity to *S. bowerbanki*, Schilder (1929) suspected that the Nigerian form was probably specifically distinct. The details of the fossula cannot be compared as they are not seen in available British specimens, but the outer lip of the Nigerian form is somewhat broader and is distinctly more callous and margined, and the shell was evidently a little more globose. It seems advisable to regard the Bende Ameki specimens as constituting a distinct species for which Schilder's name must be adopted, in spite of its unsuitability.

Family NATICIDAE

Genus ***NEVERITA*** Risso, 1826

Neverita amekiensis sp. nov.

(Pl. 6, figs. 5*a*, *b*)

1922. *Neverita* cf. *calvimontana* (Deshayes): Newton, p. 55, pl. 5, figs. 16–17.

MATERIAL. The holotype (G. 42383).

Description. Of small-medium size, having the form of *Polinices* rather than *Neverita*, a little less flattened than is usual in the latter genus. Protoconch conic, very low, of about two smooth, gently convex whorls. Last whorl forming about four-fifths of the height of the shell. Spire consisting of about two and a quarter almost flat, smooth whorls with fine linear sutures. Last whorl very large, rather flattened adapically, its flank moderately sharply rounded ; base declivous. Aperture semilunar, not much produced to the right. Columella straight, its callus very heavy, a solid, gently convex plug almost, but not quite, filling the umbilicus.

Remarks. In *N. calvimontana* (Deshayes), from the Eocene of the Paris Basin, the umbilical callus is less extensive and solid, the whorls are more distinctly convex, and the sutures are not quite linear.

Genus ***SINUM*** (Bolten MS.) Röding, 1798

Sinum africanum Newton

(Pl. 6, figs. 6*a–c*)

1922. *Sinum africanum* Newton, p. 57, pl. 4, figs. 12–13.

Material. Several specimens, including the lectotype (G.42406, Newton's fig. 12) here selected.

Sinum nigeriense sp. nov.

(Pl. 6, figs. 7*a*, *b*)

1922. *Sinum* cf. *clathratum* (Gmelin): Newton, p. 56, pl. 2, figs. 16–17.

Material. Several specimens, including the holotype (G.42390, Newton's fig. 16).

Description. Of small-medium size, not very thin-shelled, not very auriform, outline more like that of *Polinices*. Protoconch conic, very low, of two smooth, slightly convex whorls with a small nucleus. One and a quarter almost flat spire whorls with 13–15 wavy, fine spiral threads the course of which is slightly deflected at each growth line ; up to three microscopic spirals developed in the intervals on the penultimate whorl. Last whorl very large, occupying most of the height of the shell, adapical portion rather extensive and flattened, flanks rounded, base declivous ; ornament as on the spire whorls, but primary threads more numerous (approximately 40 in number). Aperture rounded-subquadrate, somewhat produced abapically and to the right. Umbilical callus narrow, but distinct, leaving a very small umbilical opening. Outer lip markedly prosocline and gently convex.

Remarks. *S. clathratum* is more auriform and compressed, has a lower spire and a more ample aperture, and does not have the adapically flattened whorls which in the new species produce a rather conic appearance.

Family Cymatiidae

Genus ***VARICOHILDA*** nov.

Type Species. *Hilda turriculata* Newton.

Generic characters. Of small-medium size, having the general form of *Hilda*.

Protoconch not well preserved, evidently smooth and naticoid. Last whorl constituting about half the height of the shell. Spire consisting of four to five whorls which are about half as high as wide and carry a quite sharp median angulation ; ornament consisting of narrow, rather widely-spaced, straight, orthocline or slightly opisthocline axial ribs crossed by fairly prominent spiral threads which are a little broader than their intervals ; no varices on spire whorls. Last whorl ornamented like the spire whorls, with the addition of fine intercalary spiral threads near the shoulder and a very strong varix 240° back from the outer lip ; base excavated abapically, the ribs becoming fainter but the spiral ornament persisting ; neck short, swollen, inclined to the left. Aperture narrow and parallel-sided, rather like that of *Anachis*, a fairly broad, oblique adapical part limited by a spiral parietal fold ; a fairly short, narrow siphonal canal, slightly inclined to the left, has a deep lateral notch at the end. Siphonal fasciole swollen. Outer lip almost orthocline, with a very strong varix slightly behind its sharp edge, internally thickened and with long lirae. Columellar lip straight and vertical, with three strong, spiral columellar folds, forming angular junctions with the parietal lip and with the siphonal canal ; callus well-developed, spreading a little over the base, distinctly limited, becoming slightly detached by the siphonal fasciole, with numerous knobs and transverse wrinkles between its outer margin and the columellar and parietal folds.

Remarks. Although generally resembling *Hilda*, this genus differs in having a slightly shorter spire, angular whorls, a strong varix in addition to the labral varix on the last whorl, a narrower and more parallel-sided aperture, the canal inclined to the left, and three strong columellar folds in addition to wrinkles and knobs on the inner lip.

Varicohilda turriculata (Newton)

(Pl. 7, figs. 1*a–c*)

1922. *Hilda turriculata* Newton, p. 29, pl. 4, figs. 24–25.

Material. Many specimens, including the lectotype (G.41971, Newton's fig. 24) here selected.

Family Muricidae

Genus ***HEXAPLEX*** Perry, 1811

Subgenus ***PAZIELLA*** Jousseaume, 1880

Hexaplex (Paziella) bendeica sp. nov.

1922. *Poirieria* cf. *calcitrapa* (Lamarck) : Newton, p. 31, pl. 3, figs. 22–23.

Material. The holotype (G.41983, Newton's fig. 22).

Description. Of small-medium size, fusiform, ribs aligned in seven irregular axial series, each rib being, on the last three whorls, slightly behind that on the whorl above. Protoconch not preserved. Last whorl forming about half the height of the shell. Spire conic, consisting of five to six whorls which are distinctly angulated medially, irregularly flattened and shelving above, subcylindrical or even slightly inturned below, with linear, wavy sutures. Adapical shelf with two or three very vague spirals near the middle ; one spiral thread on the angulation, and one close to the abapical suture, the latter on later whorls with a faint spiral just above it. Ribs nodular and subspinose at the shoulder on early whorls, a little narrower than their intervals, becoming considerably narrower than the intervals with growth and also developing short upturned spines at the shoulder, the spines being channelled on the forward-facing side. Last whorl inflated, base well excavated, neck moderately long ; siphonal fasciole bulging, carrying widely-spaced scales. Three primary threads and vague intercalaries on the flank of the last whorl. Aperture oval, with no distinct adapical channel, with a moderately long, narrow, gently curved siphonal canal which is gently inclined to the left. Columella gently excavated, smooth, twisted, and with a vague fold at the beginning of the canal. Columellar lip callous, not widely spread, becoming detached abapically, leaving a small false umbilicus between it and the siphonal fasciole. Outer lip thin, with a varix close behind it, gently parasigmoidal and definitely prosocline adapically, with a deep lateral notch at the spine on the shoulder, internally thickened, dentate below the notch. Growth lines serrate on forward-facing side of varices.

REMARKS. *H.* (*P.*) *calcitrapa* has a much more inflated last whorl and a lower spire. *Poirieria* has five, not seven, axial rows of varices.

Genus ***PTERYNOTUS*** Swainson, 1833

Pterynotus newtoni sp. nov.

1922. *Pteropurpura* cf. *tricarinata* (Lamarck) : Newton, p. 30, pl. 4, figs. 26–27.

MATERIAL. The holotype (G.41982, Newton's figs. 26–27).

DESCRIPTION. Of medium size, fusiform, markedly triangular when viewed from above on account of three rows of lamellar, non-spinose varices, each varix being slightly behind the corresponding one on the preceding whorl. Protoconch (nucleus missing) apparently rather tectiform, of about three smooth, gently convex whorls. Last whorl forming slightly more than half the height of the shell. Spire conic, consisting of nearly five convex whorls with linear, undulatory sutures. Early whorls carry two ribs, later whorls only one, between the varices ; ribs nodular and crossed by muricate spiral threads, three orders of which are present on the last whorl ; serrate, rather widely-spaced growth threads are also present. Last whorl inflated ; base well excavated, neck long and straight except for the protuberant, tubular siphonal fasciole. Aperture oval, with an abapical channel and a long, narrow siphonal canal which is slightly longer than the height of the aperture, inclined to the left but vaguely curved towards the right, and then curved well back at the tip. Columella gently concave, twisted at the start of the canal. Inner lip callous, a little wider adapically, rather detached medially, well detached abapically, smooth except for a spiral ridge limiting the adapical channel. Outer lip with a broad, leaf-like, non-spinose varix, orthocline, its edge thin and dentate, internally thickened and dentate. Growth lines serrate on forward-facing side of varices.

REMARKS. *Pterynotus* (*Pteropurpura*) *tricarinatus* (Lamarck) has the varices upturned and spinose adapically.

Family BUCCINIDAE

Genus ***BENDEIA*** nov.

TYPE SPECIES. *Liomesus africanus* Newton.

GENERIC CHARACTERS. Of small-medium size, buccinoid, intermediate in general form between *Cominella* and *Strepsidura*, oval-conic. Protoconch naticoid, of two to two and a half smooth, moderately convex whorls. Last whorl forming slightly less than three-quarters of the height of the shell. Spire consisting of about two and a half gently convex whorls with conspicuous, deep sutures, slightly stepped; two incised spiral lines close to the adapical suture define two raised cords. Last whorl inflated-oval, ornamented like the spire whorls, base well excavated and with 11–13 spiral threads which are narrower and stronger abapically; neck moderately long and swollen. Aperture rather narrowly oval, with an adapical channel, and with a siphonal canal of moderate length which is inclined to the left and notched. Columellar callus not thick or extensive; columella with a fairly strong fold limiting the canal, and a series of wrinkles where the spiral threads of the base pass under the columellar callus. Siphonal fasciole only moderately swollen, carrying five to eight longitudinal threads, limited above by a strong, sharp, raised thread. Outer lip thin, internally smooth, almost orthocline, slightly prosocline adapically.

REMARKS. Although superficially resembling *Liomesus*, this genus is more strepsiduriform (i.e. it has a shorter spire, and is more produced abapically), has a longer and more inflected canal, a less callous inner lip, and a distinct siphonal fasciole limited above by a fine, raised carina; moreover, spiral ornament is present on the upper part of the whorls, the base of the last whorl is more excavated, the aperture is narrower, and there is a distinct columellar fold in an abapical position. The relationships evidently lie more with *Cominella* than with *Liomesus* or *Strepsidura*.

Bendeia africana (Newton)

(Pl. 7, figs. 2*a*, *b*)

1922. *Liomesus africanus* Newton, p. 38, pl. 3, figs. 20–21.

MATERIAL. Several specimens, including the lectotype (G.42096, Newton's fig. 21) here selected.

Genus ***LACCINUM*** nov.

TYPE SPECIES. *Athleta lugardi* Newton.

GENERIC CHARACTERS. Attaining a large size, thick-shelled, conic to buccinoid, with a low spire. Protoconch (worn in available specimens) evidently not large and bulbous as in many Volutidae. Shell completely smooth except for growth lines which are somewhat accentuated on the siphonal fasciole, although extremely vague; fine spirals can sometimes be distinguished. Last whorl forming about ten-thirteenths (younger specimens) to seven-eighths (larger specimens) of the height of the shell. Spire distinctly coeloconoid, composed of about five flattened, very gently convex whorls with distinct, linear sutures, relatively narrower in later stages of growth. Last whorl very large, its shoulder even more sharply rounded in large specimens than in juveniles, flank subcylindrical, base slightly excavated, neck moderately long and swollen by the siphonal fasciole. Aperture narrowly oval, with a broad, flat channel situated adapically at the shoulder, and with a fairly short, poorly-defined siphonal canal which is slightly inclined to the left and deeply notched. Outer lip thin, smooth internally, orthocline as a whole, gently bisinuous. Columella gently concave, vaguely bent at its junction with the canal; inner lip with a thick, moderately wide layer of callus which becomes slightly detached abapically at the extensive siphonal fasciole, and which develops a large, protruding knob of callus beside the adapical channel. No columellar folds.

REMARKS. The above characters indicate that this genus is not related to *Athleta*, nor even a volutid. It is evidently a buccinid, and seems best placed near *Lacinia*, from which it differs in its more cylindrical last whorl, the lack of an umbilicus, and its less ample aperture and better defined siphonal canal.

Laccinum lugardi (Newton)

1922. *Athleta lugardi* Newton, p. 25, pl. 5, figs. 1–3.

MATERIAL. Several specimens, including the lectotype (G.41860, Newton's fig. 1) here selected.

Genus ***JANIOPSIS*** Rovereto, 1899

Janiopsis nigeriensis Newton

1922. *Janiopsis nigeriensis* Newton, p. 41, pl. 4, figs. 22–23.

MATERIAL. Several specimens, including the lectotype (G.42131, Newton's fig. 22) here selected.

Family VOLEMIDAE

Genus ***PSEUDOMAZZALINA*** nov.

TYPE SPECIES. *Bulbifusus nigeriensis* Newton.

GENERIC CHARACTERS. Of large-medium size, rather thin-shelled, inflated-fusiform, entirely smooth. Protoconch unknown. About six moderately convex spire whorls which are broadest a little below the middle, height about two-fifths of the width. Sutures linear. Last whorl forming one-half to three-fifths the height of the shell, inflated, base evenly excavated, neck moderately long, straight, vertical. Aperture oval, with a narrow adapical channel, vaguely constricted abapically where it is extended into a moderately oblique and wide, notched siphonal canal the length of which is about one-half the height of the aperture proper. No siphonal fasciole. Columella gently excavated, rather vaguely bent at the beginning of the canal, with a narrow, thin layer of callus, without columellar folds. Outer lip thin, strongly convex in its median and anterior parts, receding strongly adapically at an angle of about 45° and becoming nearly orthocline close to the suture. Some 10–12 irregular, elongate lirae are developed well inside the aperture in its upper half.

Remarks. Compared with *Mazzalina* (of which *Bulbifusus* is a synonym) this genus is less inflated and more fusiform, and has a higher spire, a narrower aperture and canal, no columellar folds, no spiral ornament on the base, and an outer lip which is deeply excavated adapically. *Levifusus* is distinctly ornamented and has a longer canal. *Sycostoma* is less fusiform and has heavier columellar callus; its outer lip is less excavated adapically.

Pseudomazzalina nigeriensis (Newton)

1922. *Bulbifusus nigeriensis* Newton, p. 35, pl. 4, figs. 1–2.

Material. Several specimens, including the lectotype (G.42057, Newton's fig. 2) here selected.

Family Fusinidae

Genus ***CLAVILITHES*** Swainson, 1840

Subgenus ***AFRICOLITHES*** nov.

Type species. *Rhopalithes africanus* Newton.

Subgeneric characters. Of large-medium size, fusiform. Protoconch not preserved. Last whorl forming about half the height of the shell. Spire conic (apex rather cyrtoconoid), of about eight gently convex whorls, with a slight spiral depression just below the suture. First five or six whorls with moderately fine spiral threads crossing strong nodular ribs which are not in alignment from whorl to whorl. In the later stages the ribs become obsolete adapically, and on the last two whorls are absent completely, the spiral threads also becoming feebler. Base of last whorl excavate; neck long, straight, vertical. No siphonal fasciole. Imperforate. Aperture oval, with a small adapical channel and a long, straight siphonal canal only slightly inclined to the left. Outer lip thin, broadly concave, internally smooth. Columellar callus not widely spread, detached externally. Columella straight, joining the canal without any twist. No columellar folds.

Remarks. *Clavilithes* is considerably less fusiform. *Rhopalites* has rather shouldered whorls, a more oblique canal, and a heavier adapical apertural callus, and it tends to have a siphonal fasciole and small pseudumbilicus. *Chiralithes*, from the Upper Eocene of Peru, is somewhat similar, but has a considerably broader aperture. *Perulithes*, also from the Upper Eocene of Peru, has a higher spire, and its later whorls are quite smooth.

Clavilithes (Africolithes) africanus (Newton)

1922. *Rhopalithes africanus* Newton, p. 32, pl. 2, figs. 9–10.

Material. Several specimens, including the lectotype (G.42004, Newton's fig. 10) here selected.

Genus ***LEUCOZONIA*** Gray, 1847

Leucozonia pseudominax sp. nov.

(Pl. 6, fig. 8)

1922. *Cornulina minax* (Solander) : Newton, p. 34, pl. 3, figs. 6–7.

Material. The holotype (G.42052, Newton's figs. 6–7).

Description. Of medium size, similar in form to *Cornulina minax*. Protoconch not preserved. Last whorl forming a little more than half the height of the shell. Probably about four spire whorls forming a conic spire ; whorls angulated at about one-third of their height, cylindrical or with sides inclined slightly inwards abapically, sloping and gently concave adapically. Ornament of spiral threads crossing vague, broad ribs which form blunt, slightly upturned spines on the keel. Last whorl large, base excavated, lower portion missing ; spines well developed and protruding both on the main keel and on a subsidiary one developed abapically, with a narrow slit on their forward-facing side and thus evidently hollow. Aperture rounded-oval, with a small adapical channel limited below by a small spiral ridge ; evidently with a fairly short siphonal canal distinctly inclined to the left. Columella concave, with at least two strong columellar folds abapically. Outer lip thin, gently parasigmoidal, orthocline as a whole, coarsely but vaguely fluted internally. The broken lower end of the columella is solid.

Remarks. Apart from the fact that the ornament on the lower part of the last whorl differs from that of *Cornulina minax* in consisting of widely-spaced, sharp spiral threads instead of numerous closely-spaced threads of several orders, the presence of strong columellar folds indicates that the Nigerian form is not a *Cornulina*. Since the genus *Fascioplex* has an umbilicus, a lower spire, and a last whorl which is less inflated adapically, the Nigerian form seems best placed in the genus *Leucozonia*.

Family Volutidae

Genus ***VOLUTOCORBIS*** Dall, 1890

Volutocorbis multispinosa (Newton)

1922. *Volutospina multispinosa* Newton, p. 28, pl. 3, figs. 3–5.

Material. Numerous specimens, including the lectotype (G.41949, Newton's fig. 3) here selected.

Remarks. This species is now removed from *Volutospina*, as the more scabrous ornament, less spinose ribs, and more oval form indicate that it is a *Volutocorbis*.

Genus ***BENDELUTA*** nov.

Type species. *Volutospina conicoturrita* Newton.

Generic characters. Of medium size, not very thick-shelled, in general form somewhat similar to *Volutospina* and related genera. Protoconch conical, not large, of about three smooth, moderately convex whorls. Spire conic. Four flat-sided spire whorls, a little wider than high, ornamented with rather weak and narrow, straight axial ribs crossed by low, flat spiral ribbons; whorls shouldered above, shoulder bearing increasingly prominent but short, upturned, hollow spines, both shoulder and horizontal sutural ledge free of spiral ornament; sutures linear, undulatory. Last whorl large, inflated, with a second row of short, laterally directed spines at the level of the adapical end of the aperture, this level forming the widest part of the whorl; ribs dying out below and spiral ornament obsolete on flanks; base moderately sharply excavated at its junction with the rather broad neck at the middle of which a vague spiral depression demarcates the slightly swollen siphonal fasciole; base, neck and siphonal fasciole with irregular spiral threads. Aperture elongate, rather irregular in shape on account of the constriction of the shell above the neck and on the flank, rather deeply notched below, and with a moderately short, oblique, poorly-differentiated siphonal canal. Columella oblique, well set off above, slightly convex, its upper half with three spiral folds of which the upper one is a little weaker and is a little closer to the median fold than is the lower one. Parietal callus spread adapically over half the ventral surface of the last whorl as a very thin glaze, almost absent medially and abapically. Lip straight and orthocline as a whole, slightly receding and sinuous abapically, strongly prosocline on the narrow shoulder, thin-edged, internally smooth.

REMARKS. The more globose last whorl (the widest part of which bears the lower row of spines), the thicker neck, and the shorter and more irregularly shaped aperture, together with the other characters mentioned above, readily distinguish this from *Volutospina*.

Bendeluta conicoturrita (Newton)

1922. *Volutospina conicoturrita* Newton, p. 27, pl. 3, figs. 1–2.

MATERIAL. Several specimens, including the lectotype (G.41901, Newton's fig. 1) here selected.

Family OLIVIDAE

Genus ***PSEUDOLIVA*** Swainson, 1840

Subgenus ***BUCCINORBIS*** Conrad, 1865

Pseudoliva (Buccinorbis) kitsoni (Newton)

1922. *Buccinorbis kitsoni* Newton, p. 37, pl. 3, figs. 16–19.

MATERIAL. Many specimens, including the lectotype (G.42069, Newton's fig. 16) here selected.

REMARKS. The umbilicus is mostly covered by the umbilical callus, but the presence of such a distinct depression as is present in this species is more a feature of *Buccinorbis* than of *Pseudoliva*.

Family Strepsiduridae

Genus *STREPSIDURA* Swainson, 1840

Subgenus *STREPSIDUROPSIS* nov.

Subgeneric characters. Like *Strepsidura*, but with one strong spiral fold on the columella at the beginning of the canal, and above it a convex pad on which are grouped six more folds; anterior part of shell more constricted, siphonal canal a little longer and more twisted; outer lip internally thickened and weakly crenulated.

Remarks. *Mazzalina* has no carinate siphonal fasciole, and its canal is shorter and less oblique.

Strepsidura (Strepsiduropsis) spirata Newton

(Pl. 7, fig. 3)

1922. *Strepsidura spirata* Newton, p. 33, pl. 3, figs. 24–25.

Material. Many specimens, including the lectotype (G.42008, Newton's fig. 25) here selected.

Family Cancellariidae

Genus *SVELTIA* Jousseaume, 1887

Subgenus *AFRICOSVELTIA* nov.

Type species. *Cancellaria multiplicis* Newton.

Subgeneric characters. Of small-medium size, having the form of *Sveltia* or *Sveltella*, but with a rather shorter spire. Protoconch unknown. Spire conic; three to four spire whorls which are convex and tend to be slightly subangular just above the middle; sutures linear, undulatory. Ornament consisting of strong, widely-spaced spiral threads crossing solid axial ribs which are narrower than their intervals; ribs fairly strong, becoming very solid on the last whorl, gently prosocline. Last whorl oval, narrower abapically, base declivous. Aperture oval, narrower and gently emarginate (not channelled) abapically. Columella straight, with three columellar folds of which the uppermost is the strongest. Columellar callus moderately widely spread adapically, narrower and detached abapically, leaving a narrow but distinct pseudumbilicus which is limited externally by a broad, vague swelling rather than by a siphonal fasciole. Lip straight to gently concave, slightly prosocline, thin-edged, with a strong varix close behind it, lirate and slightly thickened internally.

Remarks. The aperture has no siphonal notch as in *Cancellaria*. Compared with *Sveltia* s.str., in the new subgenus the spire is lower, there is a distinct pseudumbilicus, and there are three (not two) columellar folds. *Sveltella* has no noticeable umbilicus, a higher spire, and only two columellar folds.

Sveltia (Africosveltia) multiplicis (Newton)

(Pl. 7, figs. 4*a–c*)

1922. *Cancellaria multiplicis* Newton : p. 42, pl. 3, fig. 26.

MATERIAL. The holotype (G.42137).

Genus ***BONELLITIA*** Jousseaume, 1887

Subgenus ***ADMETULA*** Cossmann, 1889

Bonellitia (Admetula) amekiensis sp. nov.

(Pl. 7, figs. 5*a–c*)

1922. *Bonellitia* cf. *evulsa* (Solander) : Newton, p. 44, pl. 5, figs. 14–15.

MATERIAL. The holotype (G.42171, Newton's fig. 15) and several other specimens.

DESCRIPTION. Small, like *Admete* and *Admetula* in form. Protoconch unknown. Last whorl slightly less than half the height of the shell. Spire conic, consisting of about four strongly convex whorls with deep, linear, undulatory sutures. Ornament consisting of solid axial ribs, practically straight and gently prosocline, equal to or slightly narrower than their intervals, occasionally varicose, crossed by spiral threads. Last whorl swollen-ovate, narrower abapically, base declivous and with the ribs feebler. Aperture rounded-oval, not notched abapically, but with a broad, slightly emarginate channel inclined to the left. Columella vertical, with three well-developed columellar folds of which the lower two are the more closely spaced. Parietal callus thin ; columellar callus narrow, its outer edge separated from the region of the neck by a well-marked, linear, vertical depression, but not by an umbilicus. No siphonal fasciole. Outer lip fairly straight, gently prosocline, blunt, limited behind by a varix, internally thickened and lirate, the lirae continuing over the floor of the aperture.

REMARKS. Although *Admetula* is placed in the synonymy of *Bonellitia* by Wenz, the name seems worth retaining for those forms with less muricate ornament. The Nigerian form differs from *B.* (*A.*) *evulsa* in its more oval-conic outline and less inflated form, its relatively finer and more numerous spiral threads, and its more callous and more detached columellar lip.

Subgenus ***AFRICOSTOMA*** nov.

TYPE SPECIES. *Trigonostoma decorata* Newton.

SUBGENERIC CHARACTERS. Small, having the general form of a *Bonellitia* except for the marked, canaliculate ramp behind the shoulder. Protoconch naticoid, of two smooth, convex whorls. Last whorl forming slightly less than half the height of the shell. Spire conic, of two and a half subcylindrical, gently convex whorls which are slightly inturned below and have a sharp, upturned, undulatory carina on the shoulder angle ; ramp horizontal as a whole, gently concave, smooth except for irregular continuations of the ribs. Ornament consisting of delicate, gently prosocline axial ribs crossed by spiral threads, both being narrower than their intervals; the occasional very strong varices develop even stronger lobes on the upturned carina than do the ribs. Last whorl large, slightly convex abapically, ornamented like the spire whorls. No neck or siphonal fasciole. Aperture oval-pyriform, wider adapically, slightly emarginate abapically (not notched), with a slight projection at the shoulder carina. Columella vertical, with a double fold abapically (limiting the very short, oblique siphonal canal), and with a well-separated median fold. Parietal callus thin and not widely spread above, thicker and tending to be slightly detached below. Lip straight, gently prosocline, thin-edged but with a broad, strong varix just behind it, internally thickened and lirate.

Remarks. The absence of an umbilicus together with other characters described above indicate that this species is not a *Trigonostoma*; it seems best regarded as belonging to a new subgenus of *Bonellitia*.

Bonellitia (Africostoma) decorata (Newton)

(Pl. 7, figs. 6*a–c*)

1922. *Trigonostoma decorata* Newton, p. 43, pl. 5, figs. 18–19.

Material. Several specimens, including the lectotype (G.42138, Newton's fig. 18) here selected.

Family Conidae

Genus ***CONUS*** Linné, 1758

Subgenus ***LEPTOCONUS*** Swainson, 1840

Conus (Leptoconus) amekiensis sp. nov.

(Pl. 7, figs. 7*a–c*)

1922. *Conospirus* cf. *parisiensis* (Deshayes): Newton, p. 24, pl. 3, figs. 8–9.

Material. Several specimens, including the holotype (G.41837, Newton's fig. 9).

Description. Of small-medium size, biconic. Protoconch rather tectiform, of three smooth, slightly convex whorls. Last whorl forming at least five-eighths of the height of the shell. Spire gently coeloconoid, of five to five and a half whorls with small nodes on an angulation close to the abapical suture; the narrow portion below the angulation vertical or sloping slightly inwards and causing a slightly imbricate appearance; upper part flattened or vaguely concave, shelving, with four or five spiral threads on its abapical two-thirds, the threads being slightly crenulated where crossed by the deeply concave growth-lines. Last whorl inverted-conic, shoulder with small, low nodes, base slightly excavated and neck slightly swollen; coarse, irregular spiral ribbons, which have narrow intervals and are fainter adapically, are vaguely beaded where crossed by low, flat ribs extending from the small nodes on the shoulder; the ribs are of about the same width as their intervals. Aperture narrow and parallel-sided, vaguely constricted near the abapical end, emarginate but not notched terminally.

REMARKS. *Conus parisiensis*, with which Newton compared this species, is more produced abapically and has compound crenulations on the uppermost thread of the spire whorls (not small nodes on the lower angulation) ; its spiral ornament is not beaded and is restricted to the abapical half of the last whorl.

Family TURRIDAE

Genus ***EOPLEUROTOMA*** Cossmann, 1889

Eopleurotoma nigeriensis Newton

1922. *Eopleurotoma nigeriensis* Newton, p. 23, pl. 2, figs. 11–12.

MATERIAL. A few specimens, including the lectotype (G.41829, Newton's fig. 12) here selected.

Genus ***TURRICULA*** Schumacher, 1817

Subgenus ***SURCULA*** H. & A. Adams, 1853

Turricula (Surcula) africana (Newton)

1922. *Surcula africana* Newton, p. 22, pl. 2, figs. 6–8.

MATERIAL. Several specimens, including the lectotype (G.41809, Newton's fig. 7) here selected.

Genus ***SURCULITES*** Conrad, 1865

Subgenus ***CLINURA*** Bellardi, 1875

Surculites (Clinura) ingens (Mayer-Eymar)

1922. *Surcula ingens* (Mayer-Eymar) : Newton, p. 20, pl. 2, figs. 3–5 (*cum syn.*).

MATERIAL. Two specimens.

Genus ***MITRELLOTURRIS*** nov.

TYPE SPECIES. *Asthenotoma* (*Endiatoma*) *casteri* Chavan.

GENERIC CHARACTERS. Having the general form of *Mitrella*, elongate oval-conic to rather turriculate-conic. Protoconch unknown. About six spire whorls (only four preserved), which are flat-sided, their height a little more than half their width. Sutures linear, slightly stepped. A narrow, flat, slightly raised juxtasutural band is limited abapically by a vague, narrow, spiral depression ; whorls otherwise smooth. Last whorl about two-fifths of the height of the shell, narrowly oval, base narrowly and gently excavated, the neck of moderate length and swollen. Base and neck with spiral threads becoming increasingly stronger and more closely spaced abapically.

Aperture narrow and parallel-sided, with a short, distinct siphonal canal notched at the end. Columellar callus not extensive, smooth. Small adapical channel present. Outer lip (broken) evidently thin, not varicose, internally smooth, gently convex abapically, orthocline or slightly prosocline at the suture, with a broad, shallowly V-shaped sinus at a position corresponding to two-thirds of the height of the spire whorls. The two last whorls with a very vague angulation of the surface at the apex of this sinus.

Remarks. Although obviously related to *Asthenotoma* and *Endiatoma*, this genus differs in the complete lack of axial ornament, the reduced spiral ornament, the smooth columella, and the absence of folds inside the outer lip.

Mitrelloturris casteri (Chavan)

(Pl. 7, figs. 8*a*, *b* ; Pl. 8, fig. 1)

1952. *Asthenotoma* (*Endiatoma*) *casteri* Chavan, p. 80, text-fig.

Material. The holotype (G.69600).

Genus ***AMEKICYTHARA*** nov.

Type species. *Cominella douvillei* Newton.

Generic characters. Of small-medium size, form resembling that of the *Cythara* group of the Turridae. Protoconch naticoid, consisting of two and a half smooth, convex whorls. Last whorl forming four-sevenths of the height of the shell. Spire conic, consisting of three to four gently convex whorls which are moderately angulated at about two-thirds of their height ; sutures linear. Ornament delicately cancellate, *Ficus*-like, with tiny crenulations at the intersections of the axial and spiral elements. Last whorl oval, gently angulated adapically like the spire whorls and similarly ornamented ; base declivous and gently excavated at the origin of the moderately short neck ; axial ornament obsolete and spiral ornament irregular abapically. Aperture narrowly oval, with a short siphonal canal which is gently inclined to the left and flares a little at its deeply emarginate end. Columella gently concave, with one prominent fold (well inside the aperture) at half the height of the aperture proper. Columellar lip with thin callus which is moderately widely spread adapically but narrow abapically. No siphonal fasciole. Imperforate. Outer lip thin at edge, moderately convex medially, slightly concave at a level corresponding with that of the columellar fold, receding adapically, and with a very shallow, rounded sinus adjacent to the suture; thickened internally and with prominent, short lirae.

Remarks. The above characters indicate that the species is a member of the Turridae. *Cominella*, in which genus Newton placed the species, is a buccinid genus with fundamentally different characters.

Amekicythara douvillei (Newton)

(Pl. 8, figs. 2*a*–*c*)

1922. *Cominella douvillei* Newton, p. 39, pl. 2, figs. 18–19.

MATERIAL. Several specimens, including the lectotype (G.42100, Newton's fig. 19) here selected.

LAMELLIBRANCHIA

Family NUCULIDAE

Genus ***NUCULA*** Lamarck, 1799

Nucula costaeimbricatis Newton

1922. *Nucula costaeimbricatis* Newton, p. 73, pl. 6, figs. 10–11.

MATERIAL. The holotype (L.48096, Newton's figs. 10–11).

Family GLYCYMERIDAE

Genus ***AFRICARCA*** nov.

TYPE SPECIES. *Glycimeris nigeriensis* Newton.

GENERIC CHARACTERS. Of small-medium size, moderately thick-shelled, moderately strongly inflated, oval-subtrapezoidal in outline. Beaks submedian, almost orthogyrous. Hinge-line almost straight, forming only about two-thirds of the length of the shell. Greatest height anterior to the median line, at about two-thirds of the length, the shell being slightly produced antero-ventrally. Cardinal area inclined mainly at an angle of about 45° to the surface of the hinge-plate. Hinge-plate fairly solid, straight medially, gently arched downwards on the flanks. Teeth taxodont, numerous, anterior ones slightly more numerous than the posterior, the eight most anterior and six most posterior ones larger and oblique; a minute gap between anterior and posterior series. Muscle scars fairly large, not buttressed. No byssal sinus. Numerous low, square-cut ribs. Surface without carina. Ventral margin internally fluted.

REMARKS. Although the hinge is somewhat like that of *Glycymeris*, the subtrapezoid (rather *Arcopsis*-like) outline and other characters described above readily distinguish this genus.

Africarca nigeriensis (Newton)

(Pl. 8, figs. 3*a*, *b*)

1922. *Glycimeris nigeriensis* Newton, p. 72, pl. 8, figs. 8–10.

MATERIAL. Several specimens, including the lectotype (L.48441, Newton's fig. 8) here selected.

Supplementary characters. Beaks very slightly anterior to the middle line, the extreme tips tending to be slightly prosogyrous. Hinge-line sloping vaguely downwards and outwards away from the beak. Dorso-lateral angles obtusely rounded, the anterior a little the more angular. Anterior end gently convex, joining the ventral margin in a well-rounded curve. Ventral margin gently convex. Posterior end obliquely truncated, slightly convex, joining the ventral margin in a rounded, blunt angle. Cardinal area moderately narrowly triangular, placed symmetrically beneath the beak, slightly concave where abutting against the slight projecting ridges constituting the dorsal margin of the shell, carrying fairly numerous ridges, slightly wider than their intervals medially and narrower than their intervals on the flanks, at right angles to the hinge-line. Adult with 24 anterior and 20 posterior teeth, distally converging ventrally; median 30 teeth all small, especially medially. Surface with nearly 70 rather low, square-cut, finely beaded ribs of about the same width as their intervals, rather finer on the flanks. Surface evenly convex.

Family Noetiidae

Genus ***PROTONOETIA*** MacNeil, 1938

Protonoetia nigeriensis (Newton)

1922. *Anadara nigeriensis* Newton, p. 70, pl. 8, figs. 4–7.
1938. *Protonoetia nigeriensis* (Newton): MacNeil, p. 25, pl. 4, figs. 1–3.

Material. Several specimens, including the lectotype (L.48544, Newton's fig. 4) here selected.

Remarks. This is the type species of *Protonoetia*.

Genus ***ARCOPSIS*** von Koenen, 1885

Arcopsis africana (Newton)

(Pl. 8, fig. 4)

1922. *Fossularca africana* Newton, p. 68, pl. 8, figs. 14–17.

Material. Several specimens, including the lectotype (L.48113, Newton's fig. 14) here selected.

Remarks. *Fossularca* is a synonym of *Arcopsis*.

Genus ***RECTANGULARCA*** nov.

Type species. *Striarca africana* Newton.

Generic characters. Of small-medium size, not very thick-shelled, rather strongly inflated, subrectangular in outline. Beaks median, practically orthogyrous, the extreme tips slightly opisthogyrous. Cardinal area narrowly triangular, the portion anterior to the beak slightly the shorter; with one fine chevron-shaped groove very close to the two shorter sides, the remainder of the surface with numerous, fine, closely-spaced ridges perpendicular to the hinge-line ; when the valves are in contact the two areas are in one plane, occasionally pouting slightly along the line of junction. Hinge-line straight, forming about seven-ninths of the length of the shell. Dorso-lateral angles obtuse, the anterior a little the more so. Anterior end gently convex near the dorso-lateral angle, rather sharply rounded below. Ventral margin almost straight, gently upturned near the ends. Posterior end fairly straight, joining the ventral margin in a sharply rounded curve. No byssal depression. Hinge-plate very narrow, straight, its base horizontal, slightly expanded at the extreme ends ; a small, narrow gap, slightly depressed, beneath the beak, with 22–23 taxodont teeth on each side, the teeth being short and vertical except for the five or six flanking ones which are slightly longer and oblique (converging ventrally). Surface not carinate, with fine, very numerous radial riblets of three orders minutely beaded by fine concentric threads. Muscle scars large, subequal, not buttressed. Valve margins smooth.

REMARKS. The more elongate and subrectangular form, characters of the hinge, lack of a buttress to the posterior muscle scar, and smooth valve margins distinguish this genus from *Striarca*. *Breviarca* is much shorter and has a much more convex ventral margin.

Rectangularca africana (Newton)

(Pl. 8, figs. 5*a*, *b*, 6)

1922. *Striarca africana* Newton, p. 69, pl. 8, figs. 11–13.

MATERIAL. Several specimens, including the lectotype (L.48172, Newton's fig. 11) here selected.

DIMENSIONS. Height 9·6 mm., length 18·3 mm., thickness (two valves) 7·8 mm.

Family PLICATULIDAE

Genus ***PLICATULA*** Lamarck, 1801

Plicatula polymorpha Bellardi

1922. *Plicatula polymorpha* Bellardi : Newton, p 65, pl. 6, figs. 6–9 (*cum syn.*).

MATERIAL. Fourteen specimens.

Family OSTREIDAE

Genus ***OSTREA*** Linné, 1758

Ostrea amekiensis sp. nov.

(Pl. 8, fig. 7)

1922. *Ostrea* cf. *ludensis* Deshayes : Newton, p. 61, pl. 8, figs. 2–3.

MATERIAL. The holotype (L.48195, Newton's figs. 2–3).

DESCRIPTION. The single specimen is a right valve, rounded-subtriangular, a little narrower in the upper third near the ligament area which (although worn) is much enrolled forward but otherwise typical. The valve is almost flat, very slightly concave medially, vaguely out-turned laterally and at the rounded end. Outer surface, apart from growth lines, with numerous, fine vermicular riblets like those of *Placuna* (about six to the mm. near the rounded end). Muscle scar slightly posterior to the middle. Valve margin smooth internally.

Dimensions. Height 28·7 mm., length 26·3 mm.

Remarks. Although known only by a right valve, this species is well characterized by its *Placuna*-like ornament. As shown by Deshayes's illustration, the right valve (called " left valve ") of *O. ludensis* is larger and less transverse, and has a larger ligament area and ornament of a different type (not *Placuna*-like).

Ostrea pseudomarginidentata sp. nov.

(Pl. 8, fig. 8)

1922. *Ostrea* cf. *marginidentata* S. V. Wood : Newton, p. 60, pl. 6, figs. 2–5.

Material. Several specimens, including the holotype (L.48203).

Description. Of medium size, moderately thick-shelled, linguiform. Left valve (incomplete) with a large, flattened attachment area occupying most of the surface, leaving a narrow area, inturned ventrally almost at right angles, with numerous rather small radial ribs of about the same width as their intervals (four occupying 5·2 mm. ventrally, where they are widest). Valve margin correspondingly frilled.

Right valve irregularly flat. Outer surface smooth except for growth lines and a few irregularities. A narrow, inturned margin, flanking the ligament area, has rather prominent, short ribs which are irregularly spaced but normally narrower than their intervals ; further from the umbo these merge into relatively coarse, much wider-spaced crenulations on the inner margin of the valve. Muscle scar fairly large, posterior to the middle.

Dimensions. Holotype (a left valve) : height (incomplete) 24·3 mm., length 19·6 mm. Topotype (Newton's illustrated right valve, L.48202) : height, 36·5 mm., length 22·8 mm.

Remarks. While showing some superficial similarity to *O. marginidentata* S. V. Wood, this species differs not only in being smaller, but in being usually higher, and in having a larger attachment area, and plications which are finer on both valves.

Subgenus ***CRASSOSTREA*** Sacco, 1897

Ostrea (Crassostrea) lugardi (Newton)

1922. *Crassostrea lugardi* Newton, p. 62, pl. 6, fig. 1 ; pl. 7, fig. 1 ; pl. 8, fig. 1.

Material. Several specimens, including the lectotype (L.48217, Newton's pl. 6, fig. 1 and pl. 7, fig. 1) here selected.

Family CARDITIDAE

Genus *GLANS* M. von Mühlfeldt, 1811

Glans nigeriensis sp. nov.

(Pl. 8, figs. 9*a*, *b*)

1922. *Cardita* cf. *planicosta* J. Sowerby : Newton, p. 80.

MATERIAL. The holotype (L.48318).

DESCRIPTION. The solitary right valve is small, subtrapezoidal in outline, and rather strongly inflated. Umbo moderately prominent, distinctly prosogyrous, situated at about one-third of the length from the anterior end. Lunule small, indistinct, limited in its early stages by a fine, raised thread. Escutcheon well defined. Antero-dorsal margin gently convex, more steeply descendent than the longer, straight postero-dorsal margin. Anterior end rather sharply rounded, situated rather low down. Ventral margin almost straight. Posterior end truncated slightly obliquely, joining the ventral margin in a rounded angle which is only a little more than a right angle, and the postero-dorsal margin in a rounded angle of about 155°. Surface ornamented with 23 rather low, moderately broad, rather vaguely beaded ribs which are slightly wider than their intervals over the main body of the shell but more closely spaced at the extreme ends; they have rather square-cut, shallow intervals, and are flattened on top, although slightly depressed along the middle line. Valve margins coarsely fluted. Right valve hinge : AI small, pointed, with a small, shallow socket above it; 3a broken, evidently thin and moderately oblique; 3b solid, rather narrowly triangular, its dorsal pointed portion projecting into the shell cavity; a small PIII may have been present, but cannot be observed as the margin of the shell is rather worn posteriorly.

DIMENSIONS. Height 11·9 mm., length 14·7 mm.

REMARKS. From its general form and ornamentation, as well as from the characters of the hinge, it is evident that this specimen is not a juvenile of the large *Venericardia* (*Venericor*) *planicosta* (Lamarck).

Subgenus ***BENDEGLANS*** nov.

TYPE SPECIES. *Cardita costaeirregularis* Newton.

SUBGENERIC CHARACTERS. Of small-medium size, only moderately thick-shelled, subtriangular-cuneiform, moderately strongly inflated; anterior and posterior parts of surface with flat ribs separated by linear intervals, median portion with only three very wide, rather high and flat-topped ribs separated by broad intervals, the intervals showing as raised broad ridges on the inner surface of the shell; right valve with small AI, low 3a, solid 3b, lamellar 5b, and small PIII; left valve with AII, fairly solid 2 and 4b, PII, and small PIV.

Glans (Bendeglans) costaeirregularis (Newton)

(Pl. 9, figs. 1, 2)

1922. *Cardita costaeirregularis* Newton, p. 81, pl. 9, figs. 30–31.
1944. *Cyclocardia costaeirregularis* (Newton) : Chavan, p. 35.

MATERIAL. Many specimens, including the lectotype (L.48324, Newton's fig. 30) here selected.

SUPPLEMENTARY SPECIFIC DESCRIPTION. Beaks pointed, rather high, prosogyrous, situated anterior to the middle line at about two-thirds of the length. Lunule small, cordiform, concave. Escutcheon rather short, narrow. Anterior part of surface with nine depressed, flatly rounded, unbeaded ribs separated by linear intervals ; posterior part with 11 similar but rather narrower ribs ; median part with three very broad, elevated, flat-topped, unbeaded ribs separated by broad, subrectangular intervals ; the anterior ribs increase in size posteriorly, the ninth being almost as large as the adjacent one on the median part and separated from it by a linear interval ; the most anterior of the posterior group is a little larger than the remainder ; valve margins fluted according to the ribbing, the three main depressions of the outer surface showing as ridges on the inner surface. Posterior adductor impression of normal shape, anterior one rather elongate. Right valve : AI small, low, close to the end of 3a ; 3a obscure, thin, low, more or less fused to the valve margin, only slightly inclined forwards ; 3b solid, elevated, not very broadly triangular, inclined slightly backwards ; 5b long, thin and lamellar, almost straight, fused to the lower edge of the nymph from which it is separated by a narrow groove ; PIII lamellar, moderately long, fused to the continuation of the ridge limiting the escutcheon. Left valve : AII short, fused to the ridge limiting the inner margin of the lunule ; 2 solid, elevated, narrowly triangular, slightly inclined forwards ; 4b solid, elevated, rather more narrowly triangular, oblique ; PII small ; apparently a still smaller tooth (PIV) above and behind PII. Nymph narrow, relatively short. Escutcheon of right valve with a groove outside it, radiating from beneath the beak and enlarging with growth.

REMARKS. Chavan placed this species in *Cyclocardia*, but in *C. borealis* (Conrad), as represented by specimens in the British Museum (Natural History), the shell is suborbicular and has beaded ribs in youth, and vague, flatly V-shaped ribs in the adult, with no median enlarged ribs ; there are no posterior lateral teeth, and the cardinal teeth of the right valve differ in orientation. The hinge of *Cardita* (*Cyclocardia*) *granulata* Say, as figured by Chavan, differs in a similar manner. The greatly enlarged median ribs and the hinge characters warrant the placing of the Nigerian species in a new subgenus.

Subgenus ***AMEKIGLANS*** nov.

TYPE SPECIES. *Cardita costaenodulosis* Newton.

SUBGENERIC CHARACTERS. Of small-medium to medium size, very thick-shelled, oval-subtriangular to cuneiform, inflation moderate ; extreme posterior ribs flat and rather low, slightly wider than their intervals, the remainder very narrow and high, with rounded tops, finely beaded, with deep, broader, smooth, U-shaped intervals; right valve with AI, low 3a, solid 3b, lamellar 5b, and distinct PIII; left valve with short, pointed AII, solid triangular 2, narrower and longer 4b, and distinct PII.

Glans (Amekiglans) costaenodulosis (Newton)

(Pl. 9, figs. 3, 4)

1922. *Cardita costaenodulosis* Newton, p. 82, pl. 9, figs. 22–25.
1938. *Cossmannella costaenodulosis* (Newton): Chavan, pp. 3–10, fig. 1.
1944. *Cossmannella costaenodulosis* (Newton): Chavan, p. 35.

MATERIAL. Many specimens, including the lectotype (L.48360, Newton's figs. 24–25) here selected.

SUPPLEMENTARY SPECIFIC DESCRIPTION. Beaks pointed, rather high, prosogyrous, situated anterior to the middle line at about two-thirds of the length. Lunule small, narrowly cordiform, depressed, bulging medially. Escutcheon narrow, rather short. Extreme posterior end with five rather flattened, unbeaded ribs with slightly narrower intervals, the remainder of the surface with 14 very narrow and high, finely beaded ribs with rounded tops, separated by smooth, broadly U-shaped intervals of nearly three times their width. Valve margins coarsely fluted. Right valve: AI rather small, fairly close to and in line with the end of 3a; 3a low, not very long, sloping forwards at about 45°, partially fused to the inner margin of the lunule, from which it is separated by a slight groove; 3b solid, elevated, triangular, its anterior edge vertical; 5b rather long, very thin and lamellar, fused to the lower edge of the nymph; PIII distinct, moderately long, rather distant, situated fairly near the valve margin. Left valve: AII small, pointed, situated at the forward end of the inner edge of the lunule; 2 solid, elevated, triangular, its posterior edge vertical; 4b solid, more narrowly triangular, oblique at about 45°; PII distinct. Posterior adductor impression tending to be obliquely subrectangular; anterior adductor impression moderately elongate.

REMARKS. Chavan placed this species in *Cossmannella*. None of the specimens of *Cardita fayumensis* Oppenheim (*C. aegyptiaca* Fraas *non* Monterosato), the type species of *Cossmannella*, in the British Museum (Natural History), shows the hinge. It is not recorded as having any lateral teeth, but Chavan has intimated to me that the hinges of the two species are identical as judged from specimens in his own collections. The ribs of *C. fayumensis* are recorded as being " few, strong, sharp, slightly tripartite ", but while specimens in the British Museum (Natural History) do occasionally show tripartite ribs, this is due to wear. The ribs are considerably more numerous and less high than in *costaenodulosis*, the intervals being much less conspicuous, and the shell is not normally so pointed posteriorly, often being truncated. In view of the doubts concerning the exact characters of the hinge of *Cossmannella*, and since its form and ribbing apparently differ appreciably from those of the Nigerian species, a new subgeneric name seems warranted for the latter.

Subgenus **DIVERGIDENS** nov.

Type species. *Cardita triparticostata* Newton.

Subgeneric characters. Of small to small-medium size, fairly thick-shelled, rather strongly inflated, outline subtriangular, moderately high. A few simple, narrow ribs posteriorly, the remainder of the surface with broad, low, square ribs with deep, narrow, almost linear, square-cut intervals, the middle third of each rib bearing a strong, rounded, beaded cord. Right valve with AI, obsolete and very oblique 3a, solid and rather broadly triangular 3b, and distinct PIII ; left valve with AII, strongly divergent 2 and 4b (the latter the more oblique), PII and weak PIV.

Glans (Divergidens) triparticostata (Newton)

(Pl. 9, figs. 5*a*, *b*, 6, 7)

1922. *Cardita triparticostata* Newton, p. 83, pl. 9, figs. 26–29.
1938. " *Venericardia* " *triparticostata* (Newton) : Chavan, p. 7.

Material. Several specimens, including the lectotype (L.48319, Newton's fig. 26) here selected.

Supplementary specific description. Beaks pointed, prominent, moderately prosogyrous, situated anterior to the middle line at about three-fifths of the length. Lunule rather small, moderately broadly cordiform, smooth, not much sunk. Escutcheon short. Extreme posterior end with seven low, gently rounded, unbeaded ribs with rather narrower intervals, the remainder of the surface with 18 low, flat, broad ribs with deep, narrow, almost linear, square-cut intervals, the middle third of each rib carrying a strong, rounded, beaded cord. Valve margins coarsely fluted. Right valve : AI small but distinct, slightly elongate ; 3a obscure, long, low, thin, lamellar, very oblique and only gently descendent, fused to the inner margin of the lunule ; 3b solid, elevated, rather broadly triangular, its anterior edge sloping gently forwards, its posterior edge sloping more obliquely backwards ; PIII distinct. Left valve : AII distinct, slightly elongated ; 2 and 4b strongly divergent, solid, elevated, narrowly triangular, their inner margins forming an angle of about 80°, 4b slightly more oblique than 2 ; PII distinctly elongated ; PIV similar but weaker. Nymph rather narrow, moderately long. Posterior adductor impression normal in shape ; anterior adductor impression moderately elongate.

Remarks. Chavan tentatively referred this species to *Glyptoaxis*, but the right cardinal is not curved and elongate ; he has recently suggested to me that it may be a *Cardiocardita* (group of *Cardita beaumonti*), but *Cardiocardita* has no anterior laterals. In its form, ornament, and hinge characters the Nigerian species appears to belong to a new subgenus.

Family Lucinidae

Genus **PHACOIDES** Gray, 1847

Phacoides eaglesomei Newton

1922. *Phacoides eaglesomei* Newton, p. 75, pl. 8, figs. 18–20.

Material. Numerous specimens, including the lectotype (L.48237, Newton's fig. 18) here selected.

Genus *GIBBOLUCINA* Cossmann, 1904

Subgenus *EOMILTHA* Cossmann, 1910

Gibbolucina (Eomiltha)* (?) *subrhomboidalis (Newton)

1922. *Phacoides subrhomboidalis* Newton, p. 77, pl. 7, figs. 4–5.

MATERIAL. The holotype (L.48244).

REMARKS. The characters of the hinge are unknown since the valves of the single specimen available cannot be separated. Chavan (in correspondence) has suggested that the species may be an *Eomiltha*.

Genus *POMPHOLIGINA* Dall, 1901

Subgenus *EODIVARICELLA* Chavan, 1951

Pompholigina (Eodivaricella) oppenheimi (Newton)

1922. *Divaricella oppenheimi* Newton, p. 78, pl. 7, figs. 2–3.
1951. *Pompholigina* (*Eodivaricella*) *oppenheimi* (Newton) : Chavan, p. 23, fig. 27.

MATERIAL. A few specimens, including the lectotype (L.48097, Newton's fig. 2) here selected.

REMARKS. This is the type species of *Eodivaricella*.

Family CARDIIDAE

Genus *FRAGUM* (Bolten MS.) Röding, 1798

Subgenus *AFRICOFRAGUM* nov.

TYPE SPECIES. *Cardium* cf. *obliquum* Lamarck : Newton = *Fragum* (*Africofragum*) *newtoni* sp. nov.

SUBGENERIC CHARACTERS. Small, outline *Fragum*-like, length and height nearly equal, posteriorly subcarinate. Ornament of flattened ribs which have rather narrower intervals, and are smooth except for the most anterior four or five which bear small prickles ; ribs on posterior area more irregular and producing short spines at the margin. Postero-dorsal margin, of left valve only, with a row of six short, upturned and outward-bent spines. Hinge less arched than in *Fragum*, anterior lateral teeth a little closer to cardinals than posterior lateral teeth. Nymph short.

Fragum (Africofragum) newtoni sp. nov.

(Pl. 9, figs. 8*a*–*c*)

1922. *Cardium* cf. *obliquum* Lamarck : Newton, p. 74, pl. 7, figs. 6–9.

MATERIAL. Many specimens, including the holotype (L.48416, Newton's fig. 6).

DESCRIPTION. Beaks moderately prominent, not large, prosogyrous, situated slightly anterior to the median line. Antero-dorsal margin short, straight or slightly convex, joining the anterior end in an obtusely rounded angle. Anterior end well rounded, receding a little ventrally. Ventral margin convex, its posterior part the straighter, joining the posterior end in a blunt angle of a little more than 90°. Posterior end obliquely truncated, gently convex. Postero-dorsal margin short, nearly straight. About 34 ribs. Left valve : AII obscure, below the forward end of a well-developed AIV ; 2a massive, upturned, pointed ; 2b small ; PII and PIV small. Right valve : AI larger than AIII ; 3a small ; 3b massive, upturned, pointed ; PI well developed ; no PIII below the straight shell margin, above which are the spines. Valve margins fluted.

REMARKS. *Cardium obliquum* Lamarck appears to be a *Loxocardium*, and is quite different from the Nigerian form in that it is transversely oval in outline, not subcarinate, and has distinct transverse scales or beads on the ribs, but no spines.

Family VENERIDAE

Genus ***TIVELINA*** Cossmann, 1886

Tivelina newtoni sp. nov.

(Pl. 9, figs. 9*a*, *b*, 10*a*, *b*)

1922. *Tivelina* cf. *sphenarium* (Bayan) : Newton, p. 90, pl. 9, figs. 7–10.

MATERIAL. Many specimens, including the holotype (L.48504, Newton's fig. 7).

DESCRIPTION. Small to small-medium. Moderately thick-shelled, oval-subtriangular. Beaks small, prosogyrous, high, situated anterior to the middle line at about two-thirds of the length. Inflation moderate ; greatest height anterior to the middle line, at the position of the beaks. Lunule large, narrowly cordiform, limited by a fine raised thread. Escutcheon narrow, rather short. Antero-dorsal margin gently convex, steeply descendent. Anterior end well rounded, a little produced antero-ventrally. Ventral margin convex, straighter (even vaguely emarginate) posteriorly. Posterior end moderately produced, situated rather low down, sharply rounded. Postero-dorsal margin long, slightly convex, rather steeply descendent. Surface with numerous strong, rather irregular, fairly sharp, concentric threads. Right valve : AI and AIII small, short, lamellar ; 3a rather short, simple, thin, inclined forwards ; 1 vertical, narrowly triangular, simple ; 3b oblique, deeply grooved. Left valve : AII prominent ; 2a thin, simple, inclined forwards ; 2b narrowly triangular, simple, inclined backwards ; 4b oblique, thin, lamellar, simple, moderately long. Nymph moderately long, thin. Pallial sinus subtriangular, rather short, its apex not reaching the middle line, its upper arm subhorizontal, its lower arm steeply descendent. Valve margins smooth.

REMARKS. Comparison with specimens in the British Museum (Natural History) shows that this is not Bayan's species ; the ornament is more serrate and less *Costacallista*-like, the pallial sinus is larger, and the hinge-plate has no rectangularly ending projection beneath the anterior lateral teeth, as in *T. sphenarium*.

Genus ***PITAR*** Roemer, 1857

Pitar amekiensis sp. nov.

(Pl. 9, figs. 11*a–c*, 12 ; Pl. 10, fig. 1)

1922. *Cordiopsis incrassata* (J. Sowerby) : Newton, p. 85 (pars).

MATERIAL. The holotype (L.48253) and two topotypes (L. 48245–6).

DESCRIPTION. Of medium size, moderately thick-shelled, rather strongly inflated, equivalve, subtriangular in outline. Beaks rather prominent, prosogyrous, situated anterior to the middle line at about one-fifth of the length. Escutcheon moderately long, narrow. Lunule large, rather narrowly cordiform, limited by a vague incised line. Antero-dorsal margin straight, steeply descendent. Anterior end rather sharply rounded. Ventral margin convex, with a gentle median bulge, straighter anteriorly and posteriorly. Posterior end vaguely truncated, joining the ventral margin in an obtusely rounded angle. Postero-dorsal margin moderately long, gently convex. Surface with irregular concentric threads, often with noticeably narrower intervals. Right valve : AI and a smaller, shorter AIII ; 3a vertical, rather thin, its forward face less perpendicular to the surface of the hinge-plate than its posterior face ; 1 sloping slightly backwards, its posterior face the less nearly perpendicular to the hinge-plate ; 3b oblique, moderately long, deeply grooved. Left valve : AII prominent, pointed ; 2a thin, lamellar, vertical ; 2b oblique at about 45°, narrowly triangular, higher posteriorly ; 4b moderately long, simple, gently curved downwards near its end. Nymph of medium length (about twice as along as the posterior cardinal tooth). Muscle impressions not very large. Pallial sinus rather acutely triangular, its upper arm gently ascendent, its apex narrowly rounded and situated slightly less than half-way across to the anterior adductor impression, its lower arm very steeply descendent. Valve margins smooth.

DIMENSIONS. Holotype : height 27·0 mm., length 30·7 mm. Topotype (L.48245) : height 30·9 mm., length 35·0 mm.

REMARKS. These three specimens, which were labelled " *Cordiopsis incrassata* " by Newton, together with those here recorded as *Sinodiopsis coxi* sp. nov., are quite different from that species ; they are more inflated and more triangular, the beaks are much higher and less anterior in position, the hinge-plate is placed less forward and less inclined, the pallial sinus is a little shorter and more ascendent, the nymph is shorter, the teeth differ in the details of their orientation, the ventral margin is more bulging, and the concentric ornament is less serrate.

Genus ***CHIONELLA*** Cossmann, 1886

Subgenus ***COSTACALLISTA*** Palmer, 1927

Chionella (Costacallista) elongatotrigona (Newton)

1922. *Callista elongatotrigona* Newton, p. 88, pl. 9, figs. 1–5.

MATERIAL. Many specimens, including the lectotype (L.48065, Newton's fig. 3) here selected.

Subgenus **MICROCALLISTA** Stewart, 1930

Chionella (Microcallista) kitsoni (Newton)

(Pl. 10, figs. 2*a*, *b*, 3)

1922. *Callista kitsoni* Newton, p. 89, pl. 9, figs. 6, 11–14.

Material. Several specimens, including the lectotype (L.48069, Newton's fig. 11) here selected.

Remarks. The left anterior cardinal tooth (2a) is simple, not grooved as in "*Callista*" auct. (= *Costacallista* Palmer, 1927).

Genus **SINODIA** Jukes-Browne, 1908

Sinodia heward-belli Newton

1922. *Sinodia heward-belli* Newton, p. 86, pl. 9, figs. 18–21.

Material. Several specimens, including the lectotype (L.48102, Newton's fig. 21) here selected.

Remarks. The left anterior cardinal tooth (2a) is not faintly grooved as in *Sinodia*, but in all other characters the species agrees with that genus and seems best retained in it.

Genus **SINODIOPSIS** nov.

Type species. *Cordiopsis incrassata* (J. Sowerby) : Newton = *Sinodiopsis coxi* sp. nov.

Generic characters. Of medium size, moderately well inflated, transversely oval-subquadrate in outline, equivalve. Beaks rather small, prosogyrous, not prominent, well recurved, situated anterior to the middle line at about one-quarter to one-fifth of the length. Escutcheon fairly long, narrow. Lunule vague, large and moderately narrowly cordiform, limited by a fine incised line. Surface ornamented with rather irregular, strong, closely-spaced concentric threads. Hinge-plate moderately well developed ; not as thick, as inclined, or as high as in *Cordiopsis* and *Sinodia*. Right valve : AI rather solid and triangular ; AIII small ; 3a thin, lamellar, gently inclined forwards ; 1 rather triangular, its forward edge vertical, high, lamellar, its surface shelving downwards posteriorly ; 3b oblique and deeply bifid. Left valve : AII very prominent and pointed ; 2a thin, lamellar, vertical ; 2b not so thin as 2a but lamellar at the apex, oblique at about 45° ; 4b simple, thin, long, gently arched. Nymph long, narrow, gently arched. Muscle impressions rather large, situated relatively more dorsally than in *Cordiopsis* and *Sinodia*. Pallial sinus bluntly and moderately acutely triangular, its upper arm horizontal or slightly ascendent, its apex sharply rounded, its lower arm descendent at about 45°, the apex situated at about mid-length of the shell. Valve margins smooth.

Sinodiopsis coxi sp. nov.

(Pl. 10, figs. 4, 5)

1922. *Cordiopsis incrassata* (J. Sowerby) : Newton, p. 85 (pars), pl. 9, figs. 15–17 (*non* J. Sowerby).

1938. *Macrocallista palmerae* Caster, p. 66 (pars) (*non* pl. 1, figs. 9–10 ; pl. 8, fig. 7).

MATERIAL. The holotype (L.48250) and several topotypes.

REMARKS. This form is quite distinct from *Sinodia* (*Cordiopsis*) *orbicularis* (Goldfuss) (= *Venus incrassata* J. Sowerby *non* Brocchi) in its outline, hinge, and pallial sinus ; the species was erroneously referred by Caster to the Angola Miocene species *Macrocallista palmerae*, but it differs still more from *Macrocallista*. While the hinge and pallial sinus are of the same type as in *Sinodia*, the form is quite different, the hinge-plate is less massive and less inclined, and tooth 2a is not grooved. *Cordiopsis*, which also has a much more massive and more inclined hinge and a different outline, has a shorter pallial sinus. The species is named after Dr. L. R. Cox.

Family MACTRIDAE

Genus ***SPISULA*** Gray, 1837

Subgenus ***CREPISPISULA*** nov.

TYPE SPECIES. *Mactra semisulcata* Lamarck: Newton = *Spisula* (*Crepispisula*) *amekiensis* sp. nov.

SUBGENERIC CHARACTERS. Of medium size, moderately thin-shelled, subtriangular, rather *Hecuba*-like in outline, rather strongly inflated, subcarinate anteriorly and posteriorly. No lunule or escutcheon. Ornament of coarse incrementals. Left valve : AII rather short, prominent ; 2a and 2b meeting in a right angle dorsally, projecting ; resilium pit moderately narrowly triangular, its anterior side limited by a high, thin lamella, its posterior side by a very slight ridge ; PII prominent, a little longer than AII ; posterior and anterior lateral teeth at about equal distances from the cardinal teeth. Right valve : AI a little larger and stronger than AIII ; 3a and 3b simple, divergent, 3a a little the more oblique ; resilium pit as in the left valve ; PI and PIII better developed than the opposing anterior lateral teeth. A narrow ligament slit extends from the dorsal side of the hinge-plate to the tip of the beak. Pallial sinus narrow, forming a gently ascending tongue with its apex at mid-length of the shell. Valve margins smooth.

Spisula (Crepispisula) amekiensis sp. nov.

(Pl. 10, figs. 6*a*, *b*, 7)

1922. *Mactra semisulcata* Lamarck : Newton, p. 93, pl. 7, figs. 10–13.

MATERIAL. Several specimens, including the holotype (L.48224, Newton's figs. 10–11).

Supplementary specific description. Beaks rather high, narrow, prosogyrous. Antero-dorsal margin long, straight. Anterior end narrowly rounded, even bluntly pointed. Ventral margin straightest posteriorly, bulging somewhat downwards along its anterior half. Posterior end sharply and narrowly rounded to bluntly pointed. Postero-dorsal margin arched, obtusely angulated in two places. Anterior carination formed by a vague depression anterior to which the concentric ornament becomes less closely spaced than on the middle of the shell. Posterior angulation formed of two very obtuse carinae, the ornament behind the posterior one being likewise relatively less closely spaced.

Remarks. Although this form is somewhat similar in outline to the Recent genus *Scissodesma* Gray, it has definite concentric ornament, its posterior carina is less marked, the ligament slit from the dorsal side of the hinge-plate to the tip of the beak is distinctly smaller, and the lateral teeth are not crenulated. *Mactra semisulcata* Lamarck, a Paris Basin Eocene species with which Newton identified the Nigerian form, possesses a similar ligament slit, but its outline differs in being less triangular and less bulging antero-ventrally, it has a less definite anterior ridge, and its ornament is weaker.

Family Tellinidae

Genus ***MACOMA*** Leach, 1819

Subgenus ***BENDEMACOMA*** nov.

Type species. *Peronaea nigeriensis* Newton.

Subgeneric characters. Of large-medium size, rather thick-shelled, transversely oval-subtriangular, length considerably exceeding height, inflation moderate. Beaks small, moderately prominent, prosogyrous. Surface ornamented with accentuated growth-lines, posteriorly with two very vague carinae. Escutcheon long, narrow. Lunule narrow, shorter than escutcheon, limited by a fine incised line. Left valve: 2a vertical, distinctly grooved dorsally; 2b moderately oblique, very thin and lamellar, simple; no lateral teeth. Right valve: 3a rather solid, directed moderately forwards, grooved dorsally; 3b a little longer than 3a, directed backwards moderately obliquely, well grooved; no lateral teeth. Nymph long and rather narrow. Pallial sinus rather narrowly tongue-shaped, its upper part rising slightly for a short distance from the posterior adductor impression, then gently descendent for most of its length, narrowly rounded at its apex, its lower part coalescent with the pallial line posteriorly for nearly half its length. Valve margins smooth.

Macoma (Bendemacoma) nigeriensis (Newton)

1922. *Peronaea nigeriensis* Newton, p. 91, pl. 11, figs. 1–3.

Material. Several specimens, including the lectotype (L.48513, Newton's fig. 1) here selected.

Remarks. The characters of the hinge and the form of the pallial sinus indicate that this species is not a *Peronaea*; it appears to belong to a new subgenus of

Macoma characterized by the shape of the shell, the grooved 3a, and the form of the pallial sinus.

Family MYIDAE

Genus ***RAETOMYA*** Newton, 1919

Raetomya schweinfurthi (Mayer-Eymar)

1922. *Raetomya schweinfurthi* (Mayer-Eymar) : Newton, p. 96, pl. 10 (*cum syn.*).
1942. *Raetomya schweinfurthi* (Mayer-Eymar) : Rossi, p. 182, pl. 11, fig. 3.
1952. *Labiosa* (*Raeta*) *schweinfurthi* (Mayer-Eymar) : Tessier, pp. 350–351, pl. 29, figs. 7–8.
1954. *Labiosa* (*Raeta*) *schweinfurthi* (Mayer-Eymar) : Dartevelle & Roger, pl. 5 fig. 4.
1955. *Raeta schweinfurthi* (Mayer-Eymar) : Dartevelle & Roger, pp. 164–167.

REMARKS. This is the type species of *Raetomya.* Tessier placed it as a subgenus of the mactrid genus *Labiosa* Schumacher, 1817, which is evidently a synonym of *Anatina* Lamarck, 1816. *Raeta* is also a mactrid genus, but *schweinfurthi* has been well described by Newton and is undoubtedly a myid. Since it was recorded from Egypt and Nigeria, it has also been recorded from the Eocene of Tripolitania and the Cameroons and from the (reputed) Lower Lutetian or Ypresian of Senegal ; the horizon stated in the latter record is rather low, and it might be advisable to re-investigate the evidence on which the age was assigned. The Angola Miocene specimens referred to this species by Caster actually belong to *Platyodon klinghardti* (J. Böhm) ; Dartevelle & Roger express doubts concerning the generic assignation of the latter species, and it may well be that it is a distinct Miocene species of *Raetomya.*

Family CORBULIDAE

Genus ***VARICORBULA*** Grant & Gale, 1931

Varicorbula amekiensis sp. nov.

(Pl. 8, figs. 10, 11 ; Pl. 10, figs. 8*a–c*)

1922. *Corbula rugosa* Lamarck : Newton, p. 98, pl. 7, figs. 14–18.

MATERIAL. Many specimens, including the holotype (L.48264, Newton's fig. 14).

DESCRIPTION. Small, thick-shelled, inequivalve, right valve larger and more strongly inflated than the left, beaks submedian (on the right valve a little anterior to the middle line on account of the greater rostration), prosogyrous, right valve umbo strongly enrolled. Outline subtriangular.

Right valve very strongly inflated, umbo prominent but not broad, posterior end with a moderately short, slightly upturned rostrum, with two blunt carinae posteriorly, limiting the upper and lower portions of the rostrum. Anterior end sharply rounded. Ventral margin gently convex, straighter posteriorly. Ornament consisting of strong, rounded concentric folds of about the same width as or slightly wider than their intervals, regularly increasing in size with growth. Valve margin internally smooth, with a fine incised line some distance from the edge for the reception of the margin of the smaller left valve. Tooth 1 solid, triangular, strongly upturned and pointed, with a deep, triangular chondrophore behind it ; PI short, lamellar. Pallial sinus widely rounded, reaching about one-third of the distance towards the anterior adductor impression. Inner half of rostrum with two short grooves extending downwards and outwards, one near the top, the other half-way down ; these are not associated with a left valve siphonal plate (such as is present in *Caestocorbula*), no trace of which has been found on any of the specimens.

Left valve fitting within the margin of the right, inner portion of right valve rostrum remaining visible. Valve oval-subtriangular, inflated (a little flattened posteriorly near the blunt carina), beak narrow, umbo with fine concentric folds, main portion of surface with growth-lines only, apart from four very fine, widely-spaced radial threads on its middle third. Tooth 2b oblique, simple, with a deep, triangular chondrophore in front of it ; there is a trace of a very small, pointed AII at the anterior corner of the chondrophore. Pallial sinus as in the right valve. Valve margin smooth.

REMARKS. The illustrations of Cossmann & Pissarro, and specimens from France in the British Museum (Natural History), suggest that the name *Corbula rugosa* Lamarck has been applied to two forms, one relatively finely ornamented, the other (probably a *Varicorbula*) more strongly ornamented, higher, and more inflated. The Nigerian form is not conspecific with either of these ; the rostrum and umbonal region are narrower, the shell is more triangular, and there is no distinct initial stage separated off by a constriction.

Family KITSONIIDAE nov.

TYPE GENUS. *Kitsonia* gen. nov.

FAMILY CHARACTERS. *Lithophaga*-like in form. No gape. Not nacreous externally. Sinupalliate. Internally, that part of the surface behind the pallial sinus is highly polished and nacreous. Ligament external. No hinge-plate, the two right valve teeth and the one left valve tooth, all cardinals, project markedly beyond the plane of commissure. Apparently a boring form.

REMARKS. This form belongs to a new family which is provisionally regarded as being related to the Clavagellidae and is placed in the Clavagellacea.

Genus ***KITSONIA*** nov.

TYPE SPECIES. *Coralliophaga eocenica* Newton.

GENERIC CHARACTERS. Small, thin-shelled, equivalve, very elongate, ventral margin slightly excavated, posterior end slightly curved downwards. Beaks small, low, prosogyrous, situated slightly behind the anterior end. Surface smooth except for growth lines. Anterior adductor impression moderately broad and large ; posterior adductor impression situated medially just below the dorsal margin. Pallial sinus apparently extending for two-fifths of the length of the shell. That part of the surface anterior to the pallial sinus dull, white, with obscure, raised, rather vermicular, radial markings (reminiscent of the Lucinidae), that part posterior to the sinus highly polished and nacreous. No lunule or escutcheon. Ligament narrow, rather long, external. Right valve: two lamellar subumbonal teeth, subhorizontal and slightly ascending posteriorly, the anterior one relatively short, highest distally; posterior tooth very obliquely bifid, its posterior portion very close to the anterior portion and largely behind it. Left valve: one long, lamellar, simple, subumbonal tooth, highest distally, subhorizontal, and slightly ascending posteriorly. No other teeth. Valve margins smooth internally.

REMARKS. As noted by Newton, this form is quite different from the edentulous and gaping *Gastrochaena* and from the mytilid genus *Lithophaga*, which is integripalliate and likewise edentulous. However, the lack of a hinge-plate, the entirely different dentition, and the lack of radial ornament and of wide-spaced concentric frills distinguish it readily from *Coralliophaga*.

Kitsonia eocenica (Newton)

(Plate 9, figs. 13, 14)

1922. *Coralliophaga eocenica* Newton, p. 99, pl. 11, figs. 4–5.

MATERIAL. Two specimens (a right valve and a left valve); lectotype (L.48192, Newton's fig. 5) here selected.

III. ACKNOWLEDGMENTS

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PLATE 5

Fig. 1. *Turritella amekiensis* sp. nov. Holotype (G.42215). × 1.

Fig. 2. *Turritella amekiensis* sp. nov. Paratype (G.42222). × 3.

Figs. 3*a–c*. *Architectonica* (*Nipteraxis*) *bendeica* sp. nov. Holotype (G.42373). × 3.

Fig. 4. *Architectonica* (*Stellaxis*) *bicingulata* (Newton). Syntype (G.42356). × 1.

Figs. 5*a–c*. *Architectonica* (*Solariaxis*) *amekiensis* sp. nov. Holotype (G.42361). × 1.

Fig. 6. *Acrilla nigeriensis* sp. nov. Holotype (G.42285). × 2.

Figs. 7*a*, *b*. *Calyptraea newtoni* sp. nov. Holotype (G.42438). × 2.

Fig. 8. *Turbocalyptraea scabrosa* gen. et sp. nov. Holotype (G.42437). × 2.

Figs. 9*a*, *b*. *Turbocalyptraea scabrosa* gen. et sp. nov. Paratype (G.42436). × 2.

Figs. 10*a*, *b*. *Semiterebellum* (*Africoterebellum*) *elongatum* Newton. Syntype (G.41761). × 1.


4

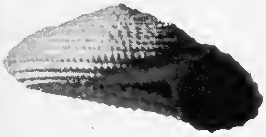

5b


1


2


5a


5c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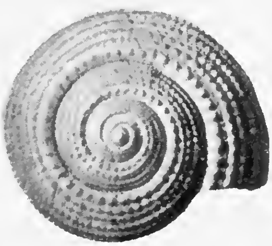
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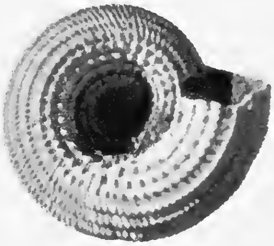
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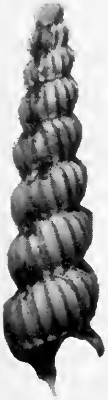
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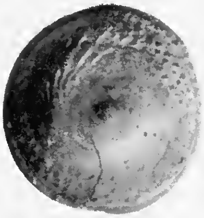
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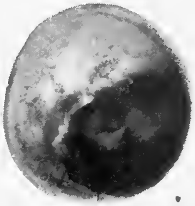
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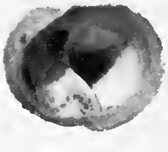
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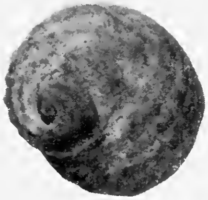
9a


9b


10a


10b

PLATE 6

Figs. 1*a–c*. *Xenophora nigeriensis* (Newton). Lectotype (G.42291). × 2.

Fig. 2. *Eovolva nigeriensis* (Newton). Lectotype (G.41786). × 2.

Fig. 3. *Eovolva nigeriensis* (Newton). Syntype (G.41787). × 2.

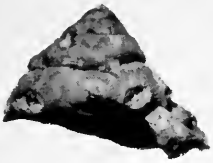
Figs. 4*a*, *b*. *Sphaerocypraea sudanensis* (Schilder). Syntype (G.45778). × 1.

Figs. 5*a*, *b*. *Neverita amekiensis* sp. nov. Holotype (G. 42383). × 1.

Figs. 6*a–c*. *Sinum africanum* Newton. Lectotype (G.42406). × 2.

Figs. 7*a*, *b*. *Sinum nigeriense* sp. nov. Holotype (G. 42390). × 2.

Fig. 8. *Leucozonia pseudominax* sp. nov. Holotype (G.42052). × 1.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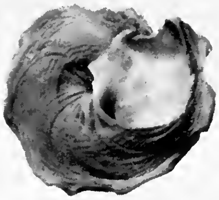
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4a


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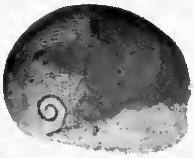
5a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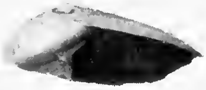
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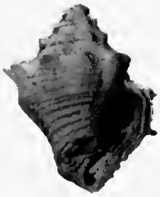
5b


6b


7a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7b

PLATE 7

FIGS. 1*a–c*. *Varicohilda turriculata* (Newton). Lectotype (G.41971). × 2.

FIGS. 2*a, b*. *Bendeia africana* (Newton). Lectotype (G.42096). × 2.

FIG. 3. *Strepsidura* (*Strepsiduropsis*) *spirata* Newton. Lectotype (G.42008). × 2.

FIGS. 4*a–c*. *Sveltia* (*Africosveltia*) *multiplicis* (Newton). Holotype (G.42137). × 1.

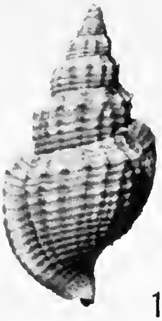
FIGS. 5*a–c*. *Bonellitia* (*Admetula*) *amekiensis* sp. nov. Holotype (G.42171). × 2.

FIGS. 6*a–c*. *Bonellitia* (*Africostoma*) *decorata* (Newton). Lectotype (G.42138). × 2.

FIGS. 7*a–c*. *Conus* (*Leptoconus*) *amekiensis* sp. nov. Holotype (G.41837). × 2.

FIGS. 8*a, b*. *Mitrelloturris casteri* (Chavan). Holotype (G.69600). × 2.


1a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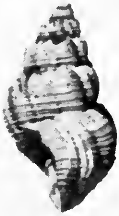
6a


6b


6c


5a


5b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7a


7b


7c


8a

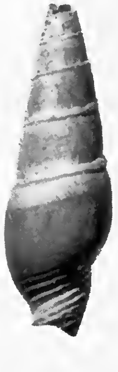
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PLATE 8

FIG. 1. *Mitrelloturris casteri* (Chavan). Holotype (G.69600). × 2.

FIGS. 2*a–c*. *Amekicythara douvillei* (Newton). Lectotype (G.42100). × 2.

FIGS. 3*a*, *b*. *Africarca nigeriensis* (Newton). Syntype (L.48443). × 2. Right valve.

FIG. 4. *Arcopsis africana* (Newton). Syntype (L.48135). × 2. Right valve.

FIGS. 5*a*, *b*. *Rectangularca africana* (Newton). Lectotype (L.48172). × 2. 5*a* : left valve.

FIG. 6. *Rectangularca africana* (Newton). Syntype (L.48173). × 2. Right valve.

FIG. 7. *Ostrea amekiensis* sp. nov. Holotype (L.48195). × 2. Right valve.

FIG. 8. *Ostrea pseudomarginidentata* sp. nov. Holotype (L.48203). × 2. Antero-ventral end of left valve.

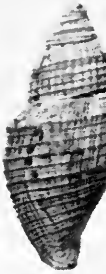
FIGS. 9*a*, *b*. *Glans nigeriensis* sp. nov. Holotype (L.48318). × 2. Right valve.

FIG. 10. *Varicorbula amekiensis* sp. nov. Syntype (L.48265). × 2. Right valve.

FIG. 11. *Varicorbula amekiensis* sp. nov. Syntype (L.48255). × 2. Left valve.


1


2a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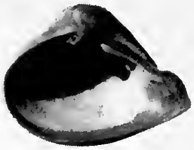
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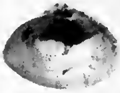
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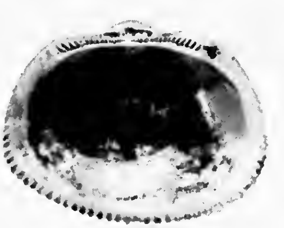
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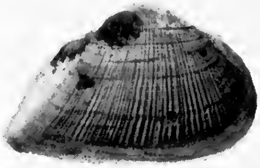
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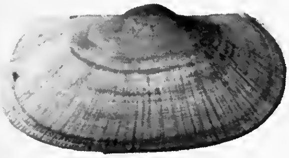
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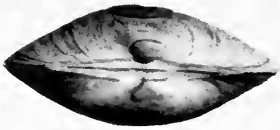
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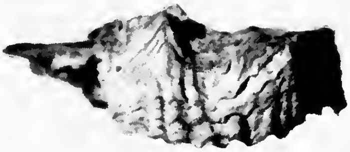

8


9a


9b

PLATE 9

FIG. 1. *Glans* (*Bendeglans*) *costaeirregularis* (Newton). Lectotype (L.48324). × 2. Left valve.

FIG. 2. *Glans* (*Bendeglans*) *costaeirregularis* (Newton). Syntype (L.48325). × 2. Right valve.

FIG. 3. *Glans* (*Amekiglans*) *costaenodulosis* (Newton). Syntype (L.48364). × 2. Left valve.

FIG. 4. *Glans* (*Amekiglans*) *costaenodulosis* (Newton). Syntype (L.48365). × 2. Right valve.

FIGS. 5*a*, *b*. *Glans* (*Divergidens*) *triparticostata* (Newton). Syntype (L.48322). × 2. 5*a* : left valve.

FIG. 6. *Glans* (*Divergidens*) *triparticostata* (Newton). Syntype (L.48321). × 2. Right valve.

FIG. 7. *Glans* (*Divergidens*) *triparticostata* (Newton). Lectotype (L.48319). × 2. Left valve.

FIGS. 8*a–c* *Fragum* (*Africofragum*) *newtoni* sp. nov. Holotype (L48416). × 2. 8*a* : right valve. 8*b* : left valve. 8*c* : right valve.

FIGS. 9*a*, *b*. *Tivelina newtoni* sp. nov. Syntype (L.48498). × 2. Left valve.

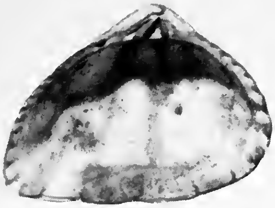
FIGS. 10*a*, *b*. *Tivelina newtoni* sp. nov. Syntype (L.48499). × 2. Right valve.

FIGS. 11*a–c*. *Pitar amekiensis* sp. nov. Paratype (L.48245). × 1. Left valve.

FIG. 12. *Pitar amekiensis* sp. nov. Holotype (L.48253). × 1. Right valve.

FIG. 13. *Kitsonia eocenica* (Newton). Lectotype (L.48192). × 4. Right valve.

FIG. 14. *Kitsonia eocencia* (Newton). Syntype (L.48193). × 5. Left valve.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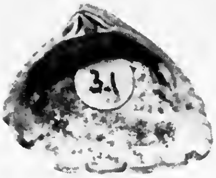
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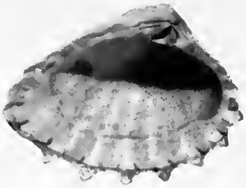
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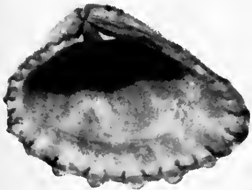
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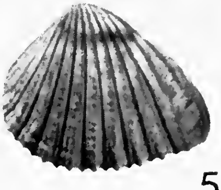
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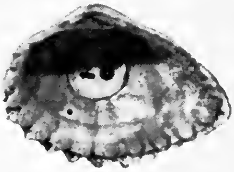
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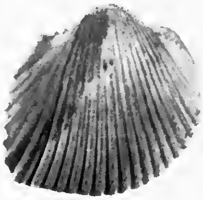
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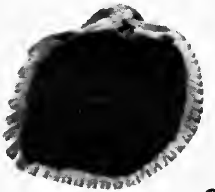
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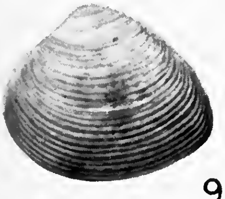
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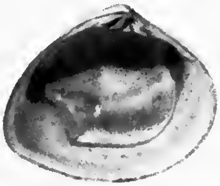
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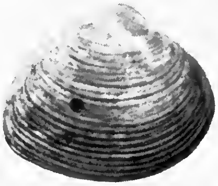
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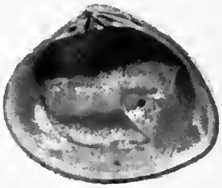
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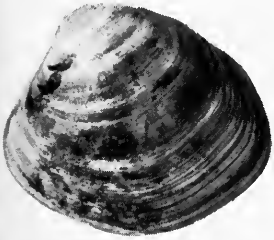
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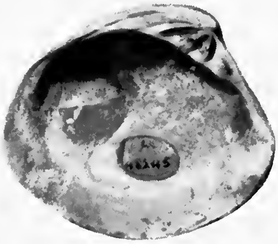
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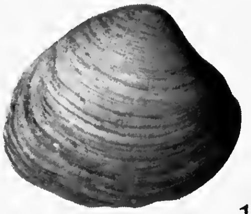
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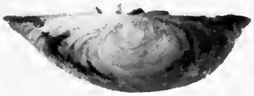
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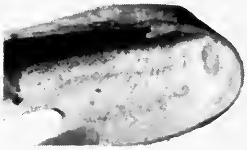

14

PLATE 10

FIG. 1. *Pitar amekiensis* sp. nov. Holotype (L.48253). × 1. Right valve.

FIGS. 2*a, b*. *Chionella* (*Microcallista*) *kitsoni* (Newton). Lectotype (L.48069). × 2. Right valve.

FIG. 3. *Chionella* (*Microcallista*) *kitsoni* (Newton). Syntype (L.48071). × 2. Left valve.

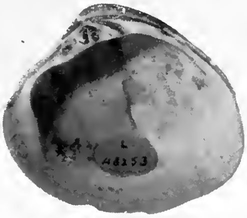
FIG. 4. *Sinodiopsis coxi* gen. et sp. nov. Holotype (L.48250). × 1. Left valve.

FIG. 5. *Sinodiopsis coxi* gen. et sp. nov. Paratype (L.48249). × 1. Right valve.

FIGS. 6*a, b*. *Spisula* (*Crepispisula*) *amekiensis* sp. nov. Holotype (L.48224). × 2. Left valve.

FIG. 7. *Spisula* (*Crepispisula*) *amekiensis* sp. nov. Paratype (L.48219). × 2. Right valve.

FIGS. 8*a–c*. *Varicorbula amekiensis* sp. nov. Holotype (L.48264). × 2. 8*a* : right valve. 8*b* : left valve.



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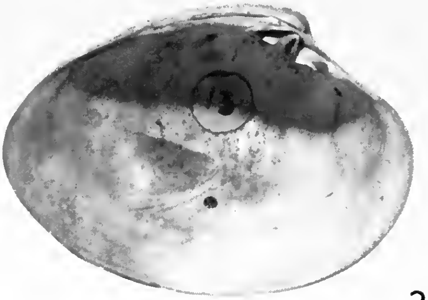

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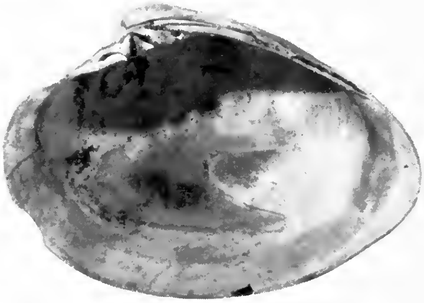

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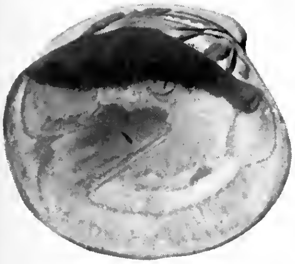

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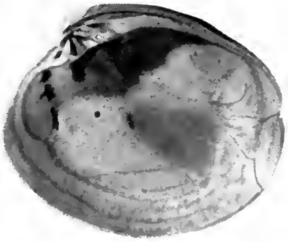

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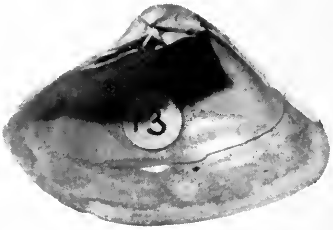

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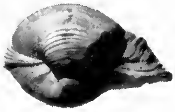
6a

6b

8a

8b



8c

THE OLIGOCENE FLORA OF THE BOVEY TRACEY LAKE BASIN, DEVONSHIRE

M. E. J. CHANDLER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 3 No. 3
LONDON: 1957

BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY)

GEOLOGY

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	Price
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No. 4 (1954). Some Upper Cretaceous and Eocene Fruits from Egypt. Marjorie E. J. Chandler	16s.
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THE OLIGOCENE FLORA OF THE BOVEY TRACEY LAKE BASIN, DEVONSHIRE

BY

MARJORIE E. J. CHANDLER

Pp. 71–123 ; *Pls.* 11–17 ; 3 *Text-figures*

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Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 3, *No.* 3 *of the Geological series.*

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THE OLIGOCENE FLORA OF THE BOVEY TRACEY LAKE BASIN, DEVONSHIRE

By M. E. J. CHANDLER

SYNOPSIS

The Bovey Tracey lignite deposit suggests an accumulation of plant débris much of which was swept from a steep warm valley into an isolated lake basin lying in Palaeozoic strata. The lake was surrounded by marshland and tree-covered slopes which contributed to the fossil flora. Previous work on the beds and their plant remains is shortly reviewed, and in a few instances earlier determinations have been corrected. New material has been identified. The rich abundance of *Sequoia, Osmunda* and *Calamus* is noted and there are a number of other species represented by a few specimens only. Attention is called to the possibilities inherent in the study of pollen from Bovey. Thirty-one families are listed from fruits and seeds and there are at least thirty-eight species.

Many Tertiary species have a long range in time and cannot therefore be useful in determining age. But the slow replacement of some species and genera by others with the passing of successive Tertiary stages may afford a clue. The age which such evidence suggests for Bovey is Middle Oligocene.

INTRODUCTION

A revision of the fossil flora of Bovey Tracey is long overdue. Hitherto, knowledge of the deposit has been based largely on the work of Heer (1862) and Pengelley (1863) and to a lesser extent on that of C. & E. M. Reid (1910). The first-named workers carried out an exhaustive examination of the beds at a time when the coal pit of Bovey Tracey was accessible owing to economic enterprise. Peculiarly good exposures were then available. The sections were described by Pengelley and the flora by Heer.

When the Bovey pit was no longer worked for fuel it became largely obscured owing to flooding and to the growth of vegetation on the upper slopes. Yet C. & E. M. Reid were able to procure material from sections near the surface of the pit to which they added a few fruits collected in a newer pit at Heathfield owned by Messrs. Candy & Co. They also re-examined what remained of Heer's material, and published a revised account of the flora in 1910.

Shortly before the first world war the old Bovey pit was again worked, this time by a German firm, but since 1914 it has remained untouched. E. M. Reid and Chandler visited it again in 1932. Certain species were then available in rich abundance (*Sequoia, Osmunda,* and *Microdiptera* an extinct genus of Lythraceae) in some shaley beds just above the water line. There were also seeds in somewhat greater variety in sandy beds a few feet higher in the section. Both levels were at the western end of the pit where at the very top a few seeds of *Stratiotes* were obtained. The eastern end of the south face was also exposed but was so deeply weathered that it yielded nothing. In a pit at Kingsteignton *Sequoia* was found but here there was little time for prolonged search. In Candy's pit at Heathfield which was still operated there were some good seeds and fruits in clays above a well-marked lignite band. The clays known to the firm as " best black clay " were examined on the spot and blocks kindly supplied later by Messrs. Candy were washed and sifted. Samples supplied from the middle and lower beds at that time exposed were unproductive. Thus almost all the plants at present known come from the two large pits at Bovey and Heathfield.

These Devonshire lignitic beds differ from all other plant-producing localities in the South of England Tertiary Beds in that they occur in isolation in a deep rock-basin formed of Palaeozoic strata. Other plant beds lately examined are interbedded among marine strata and so can be dated within certain limits at least by marine organisms. The Bovey basin is shown in the 1-inch Geological Survey Map (26th sheet), reproduced by Pengelley, as about 8 miles in length with a maximum breadth of about 3½ miles. It is filled by gravel, sand, and pottery clays with abundant seams of lignite. The nature of these deposits indicates their derivation from decayed Dartmoor granites. C. & E. M. Reid (1910) state that the tectonic rock-basin is " surrounded on every side by steep bluffs which immediately to the northwest slope upwards into the heights of Dartmoor ".

Examination of borings by Reid suggested that throughout the great thickness of the beds, exceeding 500 feet, the same flora occurs so that they appear to belong to a single geological series. The beds near the surface at Bovey appeared to be equivalent to those near the base of the boring at Heathfield which penetrated for 526 feet without reaching the bottom of the basin. Among the sediments are masses of wood and other plant remains. Some may have been swept down from higher ground, but the greater part are presumed by the Reids to have been derived from the slopes of a forest-clad steep warm valley leading from Dartmoor and disgorging, in the neighbourhood of the Bovey pit, into the old lake basin. *Sequoia* is easily the dominant element in the vegetation of this valley. Ferns, such as *Osmunda*, apparently flourished in the ravine or around the lake. Recent work shows the presence of other marsh plants e.g. *Caricoidea* (Cyperaceae), *Myrica, Microdiptera* and *Lysimachia*. True aquatics are represented by *Salvinia, Stratiotes, Potamogeton* and *Brasenia*. Climbing plants are represented by vines and *Rubus*. Trees and shrubs such as *Nyssa*, the Lauraceae, *Symplocos, Carpinus, Magnolia* and *Meliosma* probably overhung the water and dropped their fruits into it. The Heathfield pit which lay nearer to the centre of the lake is less rich in *Sequoia* than the Bovey pit, and shows a greater variety of types. Prolonged collecting by a local enthusiast might prove very profitable here.

On the whole the flora is very limited but there is a great abundance of some few forms, rarer species being represented by one or a few individuals only. This may well be because dense *Sequoia* forests and *Calamus* jungle do not provide a congenial habitat for a wide range of plants.

PREVIOUS WORK ON THE FLORA

Although Heer described nearly sixty species, many of his determinations are unsatisfactory as judged by modern standards. Some because his material was poorly preserved or fragmentary as in the case of many of his leaves. This was recognized by Heer himself as a cause of some uncertainty. In certain instances his study of better material was too superficial, the possibilities inherent in intensive detailed research being then not so well understood as they are at the present time. Again to some extent comparable living forms were probably unknown. In spite of these disadvantages, and to his lasting credit, a number of Heer's species have stood the test of later critical study while it has now been possible to correct a few erroneous determinations. A revision of Heer's leaves cannot be attempted in this present work more especially as most of his specimens have decayed or seriously deteriorated.

There are a few corrections also of the determinations made by C. & E. M. Reid as will be apparent from the synonyms at the head of some descriptions in the systematic part of this work. One or two plants named by them are omitted—the evidence being inadequate—viz. *Taxodium distichum* (which may have been a peculiarly preserved *Sequoia* cone-scale), *Taxus baccata*, *Calla* cf. *palustris*, *Sagittaria* sp.?, Labiatæ, Genus?, and *Cornus*.

In the following pages only earlier records about which there is additional evidence and new additions to the flora based on fresh and reliable evidence are included.

A recent source of knowledge which calls for a separate study may be mentioned, namely pollen. In 1932 Reid and Chandler obtained a few anthers from which pollen grains were extracted, identified and photographed by Dr. J. B. Simpson. These are included in this paper.

In 1950 the late Nils-Erik Ross examined a sample of lignitic clay. He wrote from Uppsala (June, 1950) " The sample from Bovey contained an interesting micro-flora. There are plenty of pollen-grains of *Calamus* indicating a dense *Calamus* jungle at the time of the sedimentation of the clay. Other specimens of pollen and spores I have provisionally determined as ? *Picea*, *Pinus* (several spp.), *Podocarpus*, *Engelhardtia* (pollen-grains and star hairs from the cuticle), *Myrica*, *Symplocos* (2 spp.), *Ilex*, *Quercus* (comparable with some evergreen spp., e.g. *Q. ilex*), cf. *Tilia*, Ericaceae, Ulmaceae, Caprifoliaceae, ?Anacardiaceae, *Osmunda*, Schizaeaceae, etc."

Although Ross's evidence has not been published, it is interesting to note in passing that it confirms the determination of *Calamus*, *Myrica* and *Symplocos* from other organs, gives support to Simpson's *Tilia* and confirms Heer's *Quercus* and Ericaceae (the two last based on leaves).

The record of *Engelhardtia* is of interest because of its occurrence in the Oligocene Bembridge Beds. Schizaeaceae range from the Palaeocene to the Bembridge but it may be recalled that the Oligocene species of *Anemia* is different from that of the Lower Bagshot and Lutetian (Bournemouth Freshwater Beds). It would be helpful to know what genera and, if possible, what species Ross found of this family at Bovey. Dr. J. W. Franks of the British Museum (Natural History) is presently continuing the study of Bovey pollen and it is hoped that the important results of Ross's investigations will be included in a forthcoming paper with additional evidence.

THE MODE OF PRESERVATION OF THE FOSSILS

All specimens collected in recent years are carbonaceous entities. In the majority of cases they are separable from the matrix of clay or sand only after prolonged boiling with soda. All appear to have undergone intense compression so that they are not only distorted and flattened but frequently the carpellary coats or testa have been so carbonized that they break with a glassy fracture and the cell structure may be more or less obliterated in many cases. So far as the fruits and seeds are concerned the best specimens are not found in the lignite bands themselves but are associated with the interstratified beds. It should, however, be noted that in Ross's letter he asked for samples of pure lignite in which, he stated, the pollen grains are much better preserved than in clays. It was clear when collecting in the Bovey pit in 1932 that the richest variety of fruits and seeds occurred in the coarser sandy beds. This is commonly the case in Tertiary deposits, for in sandy beds the seeds and other remains are less distorted and more readily released and therefore less liable to be damaged. Unfortunately sandy exposures are very restricted in extent.

The laminated clay beds chiefly enclosed masses of matted *Sequoia* and *Osmunda* at the horizons lately available, and very little else. Prolonged search of the washings from such layers were rarely rewarded by any new discovery and were discontinued.

The leaves described by Heer were, in all probability, impressions with mummified leaf-substance. Such at least is suggested by the mode of preservation of the abundant *Sequoia* and *Osmunda* remains.

A revised list of Bovey plants is given below:

Family and its approximate climatic range, after R. Good. ct = tropical or chiefly tropical. tc = temperate or chiefly temperate. *b* = both tropical and temperate.		Genus and species	Other fossil occurrences in the South of England
Osmundaceae	b	*Osmunda lignitum* Giebel	Bournemouth Freshwater.
Salviniaceae	b	*Salvinia boveyana* n. sp.	Genus, Lower Headon.
Taxodineae	tc	*Sequoia couttsiae* Heer	Palaeocene? Lower Bagshot (Studland) to Hamstead Beds (Hamstead).
Potamogetonaceae	b	*Potamogeton tenuicarpus* C. & E. M. Reid	Hamstead Beds.
Hydrocharitaceae	b	*Stratiotes websteri* (Bgt.)	Hamstead Beds.
Cyperaceae	b	*Caricoidea nitens* (Heer)	
Calameae (Palmae)	ct	*Calamus daemonorops* (Ung.)	Bournemouth Freshwater; Cliff End, near Mudeford.
Zingiberaceae	ct	*Spirematospermum wetzleri* (Heer)	Lower Headon to Bembridge.
Myricaceae	b	*Myrica boveyana* (Heer)	
Betulaceae	tc	*Corylus* sp.	
		Carpinus boveyanus (Heer)	Bournemouth Marine; Cliff End; Lower Headon.
Fagaceae	tc	*Fagus minima* n. sp.	
Ulmaceae	tc	*Zelkova boveyana* n. sp.	

Family and its approximate climatic range, after R. Good. ct = tropical or chiefly tropical. tc = temperate or chiefly temperate. *b* = both tropical and temperate.		Genus and species.	Other fossil occurrences. in the South of England.
Moraceae	ct	*Moroidea boveyana* n. gen. et sp.	Genus, Lower Headon.
Nymphaeaceae	b	*Brasenia ovula* (Bgt.)	Bournemouth Marine to Hamstead.
Magnoliaceae	b	*Magnolia boveyana* n. sp.	Genus, London Clay and Bournemouth Freshwater Beds.
Lauraceae	ct	Various genera not determined	Palaeocene to Lower Headon, Bembridge.
Capparidaceae	ct	*Capparidispermum boveyanum* n. gen. et sp.	Family, Lower Bagshot to Bartonian.
Hamamelidaceae	tc	2 spp. or genera	Family, Palaeocene to Lower Headon.
Rosaceae	tc	*Rubus microspermus* C. & E. M. Reid	Upper Headon.
Leguminoseae	b	Genus ?	
Rutaceae	ct	*Rutaspermum exaratum* (Heer).	Genus, London Clay to Upper Headon.
Sabiaceae	ct	*Meliosma reticulata* (C. & E. M. Reid)	Genus, London Clay; Lower Bagshot (Lake); Bournemouth Freshwater Beds.
Vitaceae	ct	*Parthenocissus britannica* (Heer)	Genus, London Clay to Lower Headon.
		Parthenocissus boveyana n. sp.	
		Vitis hookeri Heer	Genus, Palaeocene to Lower Headon.
		Vitis stipitata n. sp.	
Tiliaceae	tc	*Tilia* sp.	Bournemouth Freshwater.
Lythraceae	b	*Microdiptera parva* n. gen. et sp.	Bournemouth Marine Bed Lower and Upper Headon.
Nyssaceae	b	*Nyssa boveyana* n. sp.	Genus, London Clay.
Myrtaceae	ct	*Myrtospermum boveyanum* n. gen. et sp.	Family, Palaeocene to Upper Headon.
		Myrtospermum dubium n. sp.	
		Myrtospermum sp.	
Mastixioideae	ct	*Mastixia boveyana* n. sp.	Family, London Clay to Lower Headon. Genus, London Clay.
Primulaceae	tc	*Lysimachia boveyana* n. sp.	
Symplocaceae	ct	*Symplocos anglica* n. sp.	Genus, Oldhaven to Lower Headon.
		Symplocos headonensis Chandler	Species, Lower Bagshot to Lower Headon.
Solanaceae	b	*Solanispermum reniformis* n. gen. et sp.	Lower Bagshot to Bournemouth Marine and Cliff End Beds.

The grouping of the families into tropical or chiefly tropical, temperate or chiefly temperate, and both tropical and extratropical is based on R. Good's classification (1947). It is inevitably to some extent arbitrary. Thus it might be argued should the Magnoliaceae, Lauraceae and Vitaceae be classified as chiefly tropical or wide-ranging in that they have extensions into cooler regions ? or should the Rosaceae and Hamamelidaceae be grouped as temperate or wide-ranging for they have limited extensions into warmer areas? On the whole, however, the grouping appears to give a representative picture and suggests a warm flora, for of thirty-one families, eleven are chiefly tropical and only eight temperate. But for reasons shortly to be stated these figures should not be unduly stressed. In this connexion it may be noted that certain genera of temperate type e.g. *Sequoia*, *Carpinus*, are associated in Eocene beds with a well-defined warm flora so that, in the past, they may have had extensions into subtropical or tropical climates which have been lost at the present day. Families such as Hamamelidaceae still retain limited extensions; hence their presence in a warm flora is not surprising. Further, the constant association in the fossil record [in part awaiting publication] of the genus *Microdiptera* and the species *Solanispermum reniformis* with warm floras points to them as warm representatives of the wide-ranging families Lythraceae and Solanaceae.

THE AGE OF THE BOVEY FLORA

Palaeobotanists have differed considerably in their views on the age of this isolated undated deposit.

Heer, although on slender evidence, equated the Bovey lignites with the Middle Oligocene Hamstead Beds of the Isle of Wight (1862*a*). Gardner (1879 : 18) regarded the flora as identical with the Eocene Bournemouth Freshwater Beds with which, it is true, they have a number of genera in common e.g. *Osmunda*, *Calamus*, *Stratiotes*, *Magnolia*, *Rubus*, *Meliosma*, *Vitis*, *Mastixia* and *Symplocos*.

C. & E. M. Reid (1910) compared the flora with that of the Wetterau. Reid & Chandler (1926 : 25–28) used the percentages of *European* genera present in a series of floras ranging from Eocene to Pliocene among which was Bovey with 38% (so far as it was then known). They reached the conclusion that the Bovey flora was approximately of Middle Oligocene age and was considerably younger than the Upper Eocene Hordle flora, and older than the Mio-Pliocene and Pliocene floras of Pont-de-Gail and Reuver. The figure for Bovey would now be more like 44% still well below that for the Pliocene (47–58%). It cannot, however, be stressed too emphatically that in dealing with small floras of relatively few genera and species statistical methods may not be wholly satisfactory. A few new finds or fresh determinations can alter the figures appreciably. It therefore seems inadvisable to lay too much stress upon such methods in cases where the element of chance may influence results to a large extent.

Another point to be borne in mind is this : The utmost caution is needed in attempting to date one of the older Tertiary floras by its plant remains. Long research on Eocene and Oligocene plants has underlined the fact that many species have a far longer range in time than was once supposed. There are indications of this in the Bovey table given on pp. 76, 77. Some examples are quoted here, using species found at Bovey.

Sequoia couttsiae is a typical instance. The species is well known from twigs, cones, seeds and cuticle. Its cuticular structure is distinctive. Its range in England is certainly from the Lower Bagshot to Hamstead Beds and may be from the Palaeocene.

Carpinus boveyanus is known in the Bournemouth Marine Beds, the Cliff End Beds and the Lower Headon, possibly also in the Upper Headon.

Solanispermum reniformis ranges from the Cuisian, through the Bournemouth Freshwater and Marine Beds to the Cliff End Beds.

A number of species not found yet at Bovey could also be used to illustrate the long range of some older Tertiary types. For example the following awaiting record or description which have been found in the Lower Bagshot of Lake or Arne, the Lower Headon of Hordle, and sometimes in intermediate beds: *Caricoidea obscura* (Cyperaceae), *Protoaltingia* (Hamamelidaceae), *Phellodendron, Natsiatum, Myrtoidea, Myrtospermum variabile, Styrax, Eomastixia, Mastixicarpum.*

It may be dangerous to rely on the presence or absence of particular species in trying to assess age, for it is impossible to determine the part played by chance preservation and discovery in the records of a flora.

Nevertheless time and further research may throw fresh light on the problem of Tertiary plants as time-indicators. There is already some hint that although long range of species is a common phenomenon, there is also a gradual replacement of some species or genera by others during a long period.

Up to the present (and it is necessary to stress this qualification) *Spirematospermum wetzleri* has not been found in this country below the Lower Headon (or possibly the Barton Beds). It occurs at Hordle, and in the Middle Oligocene Bembridge Beds. It also occurs at Bovey.

Brasenia ovula (Bgt.) appears in the Bournemouth Marine Beds and Hengistbury Beds and persists through the Barton, Lower and Upper Headon, Bembridge and Hamstead Beds. Below the Bournemouth Marine Beds in the Freshwater (Lutetian?) series and the Lower Bagshot, its place appears to be taken by another characteristic and readily recognizable water-lily (awaiting description) which disappears after the Lutetian. It is *Brasenia ovula* which occurs at Bovey.

Similarly, *Microdiptera parva*, an extinct genus of Lythraceae, occurs in the Bournemouth Marine Beds and the Lower and Upper Headon. In the Bournemouth Freshwater Beds there is a different species of *Microdiptera*. It is *M. parva* which occurs at Bovey.

These records suggest that the Bovey flora is not older than the Bournemouth Marine Series.

Again *Potamogeton tenuicarpus* is known in the Hamstead Beds (possibly also in the Upper Headon). On the other hand a highly distinctive spiny species, *P. pygmaeus* ranges, according to present knowledge, from the Bournemouth Marine Beds, through the Lower Headon only up to the Bembridge Beds, after which *P. tenuicarpus* is found. *P. tenuicarpus* is the species found at Bovey.

Stratiotes is a characteristic common Tertiary genus where water-plants are preserved. The successive species appear to have a very limited range in time (Chandler, 1923). *S. websteri* (Bgt.), which occurs at Bovey, is found in the Hamstead Beds, also in the Oligocene Cyrena-Marls of Offenbach on the Main. It does not, so far as is known, range into the Miocene which is characterized by *S. kaltennordheimensis* Zenker. It is markedly different from the somewhat older Lower and Upper Headon species *S. headonensis* Chandler. In deposits older than the Lower Headon a much smaller species has now been found. It will be described as a variety of *S. zinndorfi* Kirch.

S. zinndorfi was thought by Kirchheimer to be Oligocene. The variety is of Eocene age and disappears before the Lower Headon. The occurrence of the large typical *S. websteri* at Bovey therefore supports a Middle Oligocene age for the deposit.

On the whole such evidence as there is indicates an Oligocene, and perhaps a Middle Oligocene age for the Bovey flora.

One other genus perhaps deserves special mention, viz. *Mastixia.* It, or its close allies, are among the most abundant Eocene plants ranging from the London Clay through the Lower Bagshot, Bournemouth Freshwater and Marine, Cliff End and Hengistbury Beds to the Bartonian and Lower Headon. So far they have not been found in the Upper Headon or younger beds.

According to Kirchheimer (1936 : 125), who based his conclusions on evidence from successive beds of the German Brown Coal, the genus disappeared in Europe after the Oligocene. The sparse occurrence of a species, quite specifically distinct from any of the British Eocene species, indicates, therefore, a pre-Miocene and post-Eocene age for the Bovey lignites.

Further work on Bovey pollen may serve to throw more definite light on this problem of age. At present there appears to be no other source from which information is likely to come.

In conclusion it should be recorded that the writer had the advantage of collaboration with E. M. Reid in the study of some at least of the material collected in 1932. The Introduction to this paper was seen and approved by the late Mr. W. N. Edwards shortly before his death and Mr. F. M. Wonnacott has given invaluable help in the preparation of the manuscript for the press.

PTERIDOPHYTA

Order FILICALES

Family OSMUNDACEAE

Genus ***OSMUNDA*** Linnaeus

Osmunda lignitum (Giebel)

(Pl. 11, figs. 1–6)

1862. *Pecopteris* (*Hemitelia* ?) *lignitum* Giebel : Heer, p. 1047, pl. 56, figs. 2–8.
1882. *Osmunda lignitum* (Giebel) : Gardner, p. 49 (reference to Bovey material).

DESCRIPTION. *Pinnules :* These have been fully described by Heer (1862).

Sporangia : Sub-globular, dehiscing longitudinally on one side from pole to pole, the margins of the sutures formed by about three rows of narrow elongate longitudinally aligned cells. Walls elsewhere formed of a layer of thick-walled, usually longitudinally elongate cells, often about 0·025 by 0·05 mm. in diameter. Annulus a raised patch of thicker-walled more opaque cells at one pole adjacent to the distal end of the split, occupying about half the length of the sporangium. Diameter of sporangium about 0·45–0·55 mm.

Spores : Finely granular, sub-globular, tetrahedral, about 42 to 62 μ in diameter (actual measurements, 50 × 45 μ and 62 × 42 μ).

REMARKS AND AFFINITIES. Almost as abundant in the Bovey coal pit as *Sequoia* with which it is mixed in certain seams forming matted masses. Slabs of matrix from such seams are very fissile on drying so that they quickly disintegrate. In addition to a number of such blocks with barren fronds there are scanty remains of fruiting organs in the washed residues. The disc-like annulus points to the family Osmundaceae and to the genus *Osmunda*. Spores of the living *O. regale* appear to be somewhat thinner-walled with finer spines than those seen in the fossil. They measured 45 μ in diameter. Heer found no sori in spite of repeated search (1862 : 1047). Later his work was criticized by Gardner (1882 : 49) who identified the Bovey barren pinnules with similar specimens from Bournemouth, and with others from continental localities. Gardner pointed out that the absence of sori on the pinnules should have directed Heer's attention to *Osmunda* in which the fertile pinnules are segregated at the ends of the fronds.

The name *O. lignitum* has been used frequently for indistinguishable barren pinnules from widely scattered European localities. Probably, like *Sequoia couttsiae*, the species was wide-ranging in space and time in the older Tertiary. There seems no reason why the barren pinnules and isolated sporangia should not belong to a single species.

Family SALVINIACEAE

Genus *SALVINIA* Linnaeus

Salvinia boveyana n. sp.

(Pl. 11, figs. 7–11)

1910. Spadix of aroid ? C. & E. M. Reid, p. 173, pl. 16, fig. 57.

DIAGNOSIS. Sporocarps sub-globular enclosing at least twenty to fifty globular male sporangia. Microspores tetrahedral, the majority 0·025 mm. (25 μ) in diameter, ranging from 0·02 to 0·03 mm. Vegetative parts unknown.

HOLOTYPE. A sporocarp. Brit. Mus. (N.H.), No. V.33834.

DESCRIPTION. *Vegetative parts :* Unknown.

Sporocarps : Sub-globular (incomplete). Walls thin, as shown by the manner in which the sporangia distort the wall (Pl. 11, fig. 7), structure obscure, but small equiaxial cells 0·006–0·009 mm. in diameter can be detected on the much corroded surface. In many places abrasion has actually exposed the sporangia so that their cell-structure and contents tend to obscure and confuse the cell-structure of the sporocarp. As preserved the sporocarps enclose from about twenty to fifty sporangia, but there must originally have been more for all are incomplete.

Sporangia: Globular, thin-walled, 0·15–0·2 mm. in diameter, walls apparently one cell thick, formed of coarse polygonal cells. The cell-walls are obscure either because they have decayed so that they are represented by impressions only, or else because they are very thin. The sporangia are hollow in the middle, formed of a frothy substance within which the microspores occur in fours, each spore with characteristic triradiate markings. The average spore diameter is 0·025 mm. (25 μ) but some are as much as 0·03 mm., others 0·028 mm., a few only are smaller than 0·02 mm. and those are probably immature.

REMARKS AND AFFINITIES. Five sporocarps with numerous sporangia. The microspores agree closely in size with an unnamed species described by Kirchheimer (1931 : 102–113) from the Upper Miocene Brown Coal of Beuern in Vogelsberg (spore diameter 25 μ), also with *Salvinia hassiaca* Kirchh. from Garbenteich (spore diameter 26 μ), a species of similar age (1930*a* : 203). Among living species of which spore measurements are available, the nearest to the fossil is *S. auriculata* Aubl. (spore diameter 27 μ), a species from Central and South America and the West Indies. In the living *S. natans* (Linn.) the microspores measure only 18 μ, and in *S. ancillata* Roxb. 22 μ, while in *S. oblongifolia* Mart they measure 23 μ. These measurements are taken from Kirchheimer's detailed researches on the fruiting organs of fossil *Salvinia* in German Brown Coal (1931); there are other papers by this author on the fossil occurrence of the genus (1928; 1929; 1930; 1932; 1937). His investigations are concerned chiefly with Miocene material, but an Oligocene species was figured from the Niederpleis Brown Coal in 1937 (p. 897, text-fig. 4); unfortunately it does not permit of satisfactory comparison; the dimensions of the microspores were not given.

No fruiting organs have been described previously from Britain, but vegetative parts are known from the Lower Headon of Hordle (Chandler, 1925: 10, pl. 1, figs. 1*a–d*; text-fig. 1) and also occur in numerous continental localities (Florin, 1919 : 243).

The living genus *Salvinia* is distributed throughout the north temperate zone in the Old and New Worlds. It occurs also in the East Indies, Tropical Africa, the Mascarene Islands, South and Central America and the West Indies.

GYMNOSPERMAE

Order CONIFERALES

Family TAXODINEAE

Genus ***SEQUOIA*** Endlicher

Sequoia couttsiae Heer

1862. *Sequoia couttsiae* Heer, p. 1051, pl. 59; pl. 60, figs. 1–46; pl. 61.
1862*a*. *Sequoia couttsiae* Heer: Heer, p. 372, pl. 18, figs. 1–7.
1883. *Sequoia couttsiae* Heer: Gardner, p. 36, pl. 6, figs. 7, 10–17.

1910. *Sequoia couttsiae* Heer : C. & E. M. Reid, p. 170, pl. 15, figs. 23–27.
1921. *Sequoia couttsiae* Heer : Chandler, p. 457.
1922. *Sequoia couttsiae* Heer : Chandler, p. 385.
1923. *Sequoia couttsiae* Heer : Bandulska, p. 257, pl. 21, figs. 31, 32.

The external morphology has been well described and figured by Heer (1862, 1862*a*) and by C. & E. M. Reid (1910). It may be added here that the seed-body can be either straight or curved whereas Heer referred only to curved seeds. Twigs, cones, detached cone-scales and seeds are common at Bovey, and occur less frequently at Heathfield and Kingsteignton. The cuticle has been described and figured by C. & E. M. Reid (1910) and Bandulska (1923). New details of cuticular structure are here recorded.

The stomata are borne on both sides of the leaf.

Cuticle of upper surface : This has two well-marked stomatal bands one on each side of the midrib showing thickly scattered stomata variously oriented, a few being longitudinal or transverse but the majority oblique. They have a tendency to be arranged in short longitudinal rows, but this is not a conspicuous feature. In the broader parts of the leaves three or four, sometimes more, stomata may be arranged abreast. Three bands of epidermal cells occur outside the stomatal bands, a narrow band frequently about eight cells wide at each margin, and a broad median band over the midrib which may be about twenty-five cells wide at the leaf base. The marginal bands unite with one another and sometimes with the median band also at the apex of the leaf. Occasionally the median band dies out a short distance below the apex and then the two stomatal bands unite, or almost unite, just below the apex. Towards the leaf-tip the epidermal cells nearest the margin tend to diverge in a fan-like manner. Epidermal cells between the stomata very variable in form and size, frequently more or less equiaxial, not infrequently transversely elongate and aligned especially between stomata in the same longitudinal row. Stomata rarely share any auxiliary cells but are often sufficiently close together for the auxiliaries of adjacent stomata to be in contact without intervening epidermal cells. Stomatal pores oval to sub-quadrangular except on the decurrent flanges of the leaf where they may be sub-circular or broadly oval. Guard cells thinly cuticularized, the slit between them conspicuous, occasionally they show fine granulation. The outer pore ("aussere atemhöhle" of Florin) is normally about 0·02 mm. long, occasionally 0·03 mm. The auxiliary (= subsidiary) cells are considerably thickened where they unite with the guard cells, they vary from four to six and are arranged in a ring around the guard cells, often end to end, but there is a tendency to vary in size and shape so that the regularity of the ring is sometimes destroyed. Sometimes two concentric cells (or a cell which has divided into two by a longitudinal partition) occur in parts of the ring. The epidermal cells outside the stomatal bands are longitudinally elongate and aligned, in some leaves parallel-sided with rectangular or oblique end walls, in others tending to be broader at the middle than at the ends but such frequently have flat straight end walls. Cells brown and much cutinized with a fine inconspicuous reticulate thickening at least in some cells. At the base of the leaf the walls are always thin and colourless. Cells of the marginal epidermal band often appreciably broader than those of the middle. Typical leaves measured :

(1) length, 0·7 mm.; breadth, 1 mm.; (2) length, 0·64 mm.; breadth, 0·48 mm.

Cuticle of lower surface: Also has two stomatal bands which are broader and less sharply defined than those of the upper surface and do not extend so far towards the tip of the leaf. The bands broaden considerably towards the base where sometimes they almost merge, but at the extreme base they are reduced to one or two rows of large oblique stomata adjacent to the leaf margin separated by a wide triangle of thin-walled epidermal cells with large cavities. The stomata are more distant and widely scattered than those of the upper surface with a tendency to occur in short longitudinal lines often separated from neighbouring lines by several rows of longitudinal ordinary epidermal cells; they are transversely, obliquely, and longitudinally oriented, but on the whole oblique orientation appears to predominate. The "outer pore" may be oval but is frequently narrow-oval, usually about 0·02 mm. long or a little longer. The slit between the guard cells is clear. Auxiliary cells vary from four to six and are arranged in a ring around the "outer pore", but there is a much more marked tendency for the cells in the ring to be uneven in length, shape, and size than on the upper surface. There is also a marked tendency for one or two of the cells to be prolonged into a row of ordinary epidermal cells adjoining the stoma and from these they can scarcely be distinguished. Auxiliary cells of adjacent stomata may be contiguous and are occasionally shared by adjacent stomata, more often, epidermal cells intervene. There is sometimes a double ring of auxiliary cells in part of the circumference. The auxiliary cells are not more conspicuously cutinized than the ordinary epidermal cells except where they abut on the guard cells; here there is a thickening of the wall. The ordinary epidermal cells in the stomatal bands are often irregularly arranged and are frequently as broad as long, sometimes longitudinally elongate and aligned, but often between two stomata in the same linear series transversely elongate and aligned. Marginal and median bands of ordinary epidermal cells unite below the apex to form a broad triangular apical area without stomata. The epidermal cells are frequently parallel-sided, longitudinally elongate and aligned; in the median band they often have rectangular or oblique end walls; in the marginal bands they are less frequently rectangular, usually also narrower and longer than in the median. Also in the median band they tend to be shorter at the apex of the leaf than below. In one slide they appeared to be beset with small pits, about 0·002 mm. broad, irregular in shape and distribution. They are occasionally very slightly sinuous, especially their transverse walls. Such sinuosities are seen often on the decurrent leaf base in the median band.

There is a greater resemblance to *Sequoia gigantea* in the arrangement of the stomata on the upper-side of the leaf than to *Sequoia sempervirens* owing no doubt to the greater similarity of form.

REMARKS. The species has lately been recognized at Studland (Lower Bagshot), the Bournemouth Marine Beds of Southbourne, the Cliff End and Hengistbury Beds. It is also represented in the Lower Headon at Hordle, and the Upper Headon at Colwell Bay.

Detailed accounts and illustrations of these cuticles are included in a forthcoming monograph on the Lower Bagshot flora where the species is fully discussed.

ANGIOSPERMAE

Class MONOCOTYLEDONES

Family POTAMOGETONACEAE

Genus *POTAMOGETON* Linnaeus

Potamogeton tenuicarpus C. & E. M. Reid

(Pl. 11, figs. 12–14)

1910. *Potamogeton tenuicarpus* C. & E. M. Reid, p. 173, pl. 16, figs. 53, 54.

DESCRIPTION. *Endocarp:* Broadly obovate, originally somewhat inflated (now much flattened), curved through almost a complete circle about a circular or oboval central depression, the curved area forming the locule; dorsal margin semicircular, ventral margin convex above and below, conspicuously indented between the ends of the limbs i.e. between the convexities at a distance of about one-third of the length from the base of the fruit; sometimes remains of a small spine can be seen just above the indentation. Style small, patent, terminal on the ventral margin. Surface conspicuously ridged, one ridge outlining the central depression, another the dorsal margin adjacent to the keel, a third down the middle of the keel; ridges sharp, forming small flanges. Keel broad reaching from the base almost to the apex, with a groove on each side of the median ridge. Surface cells irregular in shape with the long axes diverging from the central area but also showing an alignment parallel with the curvature of the endocarp; cells averaging in size about 0·012 by 0·02 mm. Length of endocarp, about 1–1·5 mm.; breadth, 0·75–1·2 mm.

Seed: (Formerly described as the embryo, C. & E. M. Reid, 1910.) Narrow, elongate, curved in accordance with the curvature of the locule; testa smooth, shining, light brown, semi-translucent, the square cells measuring 0·017 mm. across and aligned parallel with the direction of curvature.

Pollen: Preserved in detached anthers and determined by Dr. J. B. Simpson. Smaller than that of *P. natans*, finely reticulate all over with a marked invagination on one side of the grain exposed when the intine had been cleaned out (Pl. 11, fig. 14). Probably belongs to this species; the only one present.

REMARKS AND AFFINITIES. This species is re-described above in greater detail. The form and structure of endocarp, seed (and according to Dr. Simpson, pollen also) indicate the presence of a species of *Potamogeton*. The living *P. cristata* Regel & Maack is almost equally small but does not otherwise resemble the Bovey fruit. The breadth of the dorsal keel in the Bovey fossil shows that in life the locule was probably more or less triangular in cross-section, but the thin though coriaceous carpel has collapsed and been variously distorted by pressure in fossilization. The same species occurs in the Hamstead Beds of the Isle of Wight.

P. pygmaeus Chandler from the Upper Eocene of Hordle and the Oligocene Bembridge Beds, Isle of Wight, is distinguished by the normally smaller size, the convexity of the ventral margin with median prominence, and especially by the spines on the keel (bases only preserved except in impressions).

Family HYDROCHARITACEAE

Genus ***STRATIOTES*** Linnaeus

Stratiotes websteri (Brongniart)

(Pl. 11, figs. 15–19)

1862. *Carpolithes websteri* (Brongniart) : Heer, p. 1075, pl. 70, fig. 6.
1910. *Stratiotes websteri* (Brongniart) : C. & E. M. Reid, p. 172.
1920. *Stratiotes kaltennordheimensis* (Zenker): E. M. Reid, p. 60, pl. 3, figs. 8, 9.
1923. *Stratiotes websteri* (Brongniart) : Chandler, p. 128, pl. 5, figs. 10, 11 ; pl. 6, figs. 2, 3.

DESCRIPTION. *Seed :* Oblong with rounded ends, hooked or slightly sigmoidal in outline, laterally flattened. Keel narrow, beaked at the apex in sigmoidal seeds, usually rounded externally, not continued round the base but merging gradually into the collar. Collar usually large, rounded, testa woody ornamented over the body with interrupted longitudinal ridges which run from neck to apex where they curve towards the keel and converge to the raphe ; pitting fairly uniform on body, collar and sides of keel, typical pits measuring about 0·05 mm.; along the dorsal margin of the keel the pits are much finer. Keel broadening gradually towards the apex as seen in longitudinal section of the seed (Pl. 11, figs. 18, 19).

Micropyle basal or sub-basal, very slightly oblique, hilum dorsal, associated with the beak at the apex of the keel in the few specimens available. Raphe short, transverse. Digitate cells of the interior of the keel straight, parallel to the length of the keel.

Length of a large seed in Sedgwick Museum, Cambridge, 6·8 mm.; breadth, 2·75 mm. Length of a seed in the Geological Survey Collection 6·4 mm.; breadth, 3 mm. Length of a seed recently found at Bovey by the author, 5·25 mm.; maximum transverse measurement of a seed flattened dorsi-ventrally, 3 mm.

REMARKS AND AFFINITIES. One seed and fragments of three others showing respectively the raphe and the collar have been found lately at Bovey. Several specimens from other collections have also been examined. The seeds have been compared with specimens of *Stratiotes websteri* from the Hamstead Beds of the Isle of Wight and are indistinguishable from that species.

Family CYPERACEAE

Section CARICOIDEAE

Genus ***CARICOIDEA*** nov.

A form-genus for fruits or endocarps belonging to the section Caricoideae of the family Cyperaceae of which the nearer relationship is not known.

Caricoidea nitens (Heer)

(Pl. 11, figs. 20–23 ; Text-fig. 1)

1862. *Carpolithes nitens* Heer, p. 1078, pl. 70, figs. 15–23.
1910. *Taxus ? nitens* (Heer) C. & E. M. Reid, p. 172.

DIAGNOSIS. Originally globose with triangular calyx about 2·4 mm. in diameter ; apex pointed, base with aperture closed by a plug about 0·8–0·9 mm. in diameter. Epicarp shining, formed by longitudinally aligned cells with straight or sinuous outlines. Endocarp 0·5–1 mm. thick. Diameter (crushed dorsi-ventrally), 4–5 mm.

HOLOTYPE. A laterally compressed fruit ; also figured by Heer (1862, pl. 70, fig. 20). Brit. Mus. (N.H.), No. V.33842.

DESCRIPTION. *Fruit :* Originally globose (now compressed sometimes laterally, at others dorsi-ventrally), apex somewhat pointed, base somewhat truncate having a triangular impression (as of a non-accrescent calyx), about 2·4 mm. in maximum diameter, at the centre of which is a circular scar closed by a plug about 0·8–0·9 mm. in diameter. Surface of fruit and triangular impression (except over the plug) shining, longitudinally striate (fine parallel striae varying in direction are the result of tensions in compression). This coat (epicarp) formed of irregular longitudinally aligned cells with straight or sinuous outlines, 0·05 mm. or less in length, 0·016–0·025 mm. in breadth. This coat appears vitreous as seen in section and is intimately fused with the subjacent wall. Endocarp, 0·5–1 mm. thick, formed of regular parenchyma ; cells, 0·012 mm. in diameter, the layers lining the cavity being vitrified. Locule small, often flattened by pressure, lined by irregular, slightly sinuous, thin-walled cells, 0·25–0·5 mm. in diameter, and in one specimen by a series of parallel transversely aligned cells (impression of testa or adherent testa). The locule communicates with the exterior by a canal about 0·5–0·8 mm. broad and is closed by the plug described above. Diameter of fruits, 4–5 mm.

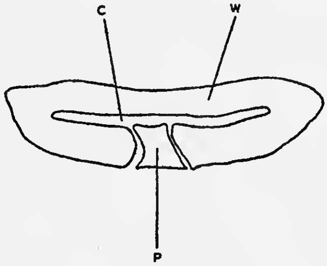

FIG. 1. *Caricoidea nitens* (Heer). Diagrammatic longitudinal section through specimen dorsiventrally crushed, showing the cavity (*c*), thick wall (*w*) and the plug (*p*) filling the basal canal. × 10.

REMARKS AND AFFINITIES. Seven fruits, two now broken. They are stated by C. & E. M. Reid in their photographic records to be the originals of Heer's figures (1862, pl. 70, figs. 15–23). It has been possible to identify the originals of figs.

16, 18 and 20, but the other drawings are too inaccurate in detail to permit of further identification of types.

In describing this species under the name *Carpolithes nitens*, Heer draws a comparison with seeds of *Taxus*. Later, C. & E. M. Reid (1910 : 172) refer the specimens tentatively to this genus. The evidence does not support this ascription. The characters indicate relationship with Cyperaceae, section Caricoideae (the shining exocarp, basal triangular scar, basal canal and plug, and thick parenchymatous wall). Similar surface cells occur in *Cladium mariscus* which differs in having a much smaller fruit. No genus which corresponds closely with the fossil has been found, while in most of the Caricoideae the exocarp is distinct from the wall of the nut and not indistinguishable from it. The apparent fusion of the two in the fossil is no doubt the result of the intense compression which has occurred.

Family PALMAE

Sub-section LEPIDOCARYINAE

Genus ***CALAMUS*** Linnaeus

Calamus daemonorops (Unger)

(Pl. 12, figs. 24–42)

1862. *Palmacites daemonorops* (Unger) Heer, p. 1056, pl. 55, figs. 7–15 ; pl. 60, figs. 50–53 ; pl. 62.

1910. *Palmacites daemonorops* (Unger) : C. & E. M. Reid, p. 172, pl. 16, figs. 44–49.

DESCRIPTION. *Spines :* (Pl. 12, figs. 38–41). Common, either single or attached to a piece of stem, especially at Bovey ; a few occur at Heathfield. They are black, shining, thin, tapering to a fine point, varying in length from 4 to 50 mm., the longest being only 3 mm. broad at the base. The spine has a shallow longitudinal furrow on one surface ; frequently the spines are grouped in threes of which the middle one is the longest. Often they are two, or solitary, while four, five, or even more may occur in a group. Heer stated that they were distributed on a finely striate, flat, minutely warty surface (Heer, 1862, pl. 55, figs. 11, 12 ; pl. 62, fig. 7). In the specimens recently examined this surface appears rough, formed of equiaxial cells about 0·025 mm. in diameter.

Fruiting axes (Pl. 12, figs. 35, 36) : Abundant, some with scars only to which bracts were formerly attached, others still carry striate overlapping bracts which are usually broken at their free edges.

Flowers : Dioecious, surrounded by stiff coriaceous bracts and bracteoles as in an amentaceous inflorescence. Male flowers (Pl. 12, figs. 32–34) with three pointed-oval bracts having valvate aestivation. Usually the stamens have been shed but one flower contained stamens with pollen. This was examined and photographed by Dr. J. B. Simpson. In letters of 27.iii.38 and 1.iv.38 he provided the following facts : " *Pollen.* Grains smaller than those of *Trachycarpus excelsis* (the only recent pollen available for examination) having a single furrow lined by a thin membrane as in *Trachycarpus*, the membrane sometimes preserved in the fossils but at other times destroyed. Also having the same type of irregular reticulations in the exine " (see Pl. 12, fig. 42). In his preliminary statement on Bovey pollen grains the late Nils-Erik Ross reported abundant *Calamus*.

Female flowers or immature fruits : Numerous. One-loculed with three stigmas (Pl. 12, figs. 24–31). Better-developed specimens are ovoid or sub-globular (but much compressed in fossilization), having six bracts, usually free with imbricate convolute aestivation, arranged in two alternate whorls. Bracts longitudinally striate through the occurrence of sub-parallel conspicuous nerves. Surface of fruit formed by characteristic recurved scales of the Rotang palm type, frequently almost obliterated owing to the highly compressed state of the material. Surface of scales of oblong cells aligned in rows forming striae which diverge from the proximal end of the scales and fan out to their thin slightly fringed edges. Inner wall of fruit compact, formed of equiaxial cells 0·012–0·016 mm. in diameter.

Seeds : Not seen in a fully developed condition, but C. & E. M. Reid (1910, pl. 16, fig. 48) figured a seed partially enclosed by a fruit 6 or 7 mm. long. Heer, moreover, stated that he had seen a drawing (natural size) by Pengelley, of a fruit which measured 13 mm. in length and 10 mm. in breadth. The drawing is reproduced by Heer (1862, pl. 60, fig. 50). Another fruit, recently examined by the author, enclosed an immature seed (Pl. 12, fig. 37) 1·75 mm. long and 1·5 mm. broad. The seed was obovoid with two irregular longitudinal crumples on the dorsal face, and with a sunk median area (chalaza ?) on the ventral face surrounded by a broad, marginal, horse-shoe shaped, inflated area over which the cells radiate from the centre. Cells from 0·025 to 0·03 mm. broad. No embryo-scar was seen.

REMARKS AND AFFINITIES. The evidence from all organs points to relationship with the group Calameae of the sub-section Lepidocaryinae, family Palmae.

The fruits although so small and probably immature suggest *Calamus* as do the pollen grains. Heer regarded the prickles as identical with organs from Laubach in the Wetterau which Unger (1860) described as *Palaeospathe daemonorops* on account of their resemblance to the spines on the spathes of living *Daemonorops*. Heer also identified them with similar organs from Salzhausen and Hessenbrücken described by Ludwig (1860 : 86, pl. 20, figs. 2, 3) as *Chamaerops teutonica*. *Palmacites*, however, is a form-genus containing different organs of palms which cannot yet be ranged in well-defined genera. In view of the relatively full information now available about the Bovey species it appears reasonable to place it in the palaeotropical genus *Calamus*. Whether it should be referred to Unger's species *Daemonorops* is open to question. But for the present it is retained in the species after Heer.

Calamus daemonorops (Unger) ?

(Pl. 12, figs. 43, 44)

An obovoid seed, evidently immature, with two irregular longitudinal folds on the dorsal side, and a narrow spathulate chalazal area on the ventral side, may possibly be an isolated seed of *Calamus*. It appears to be related to Palmae as evidenced by the general structure, possibly also by the presence close to the base on the dorsal side of a small raised sub-circular scar, 0·3 by 0·2 mm. in diameter, which may mark the embryo. The walls are 0·05 mm. thick, coarsely columnar in section, the columns are about 0·016 mm. broad, but as the texture is very vitreous they may not show their true structure. The surface is irregularly rugose, but its cells are indistinct. Length of seed, 2·87 mm.; breadth, 1·6 mm.

Family ZINGIBERACEAE

Genus ***SPIREMATOSPERMUM*** Chandler

Spirematospermum wetzleri (Heer)

1862. *Gardenia wetzleri* Heer : Heer, p. 1069, pl. 69, figs. 1–6.
1925. *Spirematospermum wetzleri* (Heer) Chandler, p. 17, pl. 1, figs. 8*a–c* ; text-fig. 5.

The characteristic spirally striate seeds were described and figured by Heer from Bovey and referred by him to the genus *Gardenia* (Rubiaceae). More recent researches by Chandler (1925) on similar material from the Eocene of Hordle demonstrated that the true relationship lay with Zingiberaceae, a conclusion subsequently corroborated by Kirchheimer (1936*a* : 98 ; 1937*a* : 50 ; 1939*a* : 275). No further specimens have been found in the Bovey Basin since Heer's discovery. The species is also known from the Bembridge Beds (Reid & Chandler, 1926 : 84, pl. 5, figs. 6, 7).

DICOTYLEDONES

Family MYRICACEAE

Genus ***MYRICA*** Linnaeus

Myrica boveyana (Heer) pars

(Pl. 12, figs. 45–48)

1862. *Carpolithes boveyanus* Heer, p. 1077, pl. 70, ? figs. 7–14 (in part).

Under the name *Carpolithes boveyanus* Heer may have included several species or genera which in their highly compressed state are difficult to distinguish. All are black, more or less flattened (sometimes laterally or marginally, sometimes dorsi-ventrally). Heer's description and figures are inadequate although his figures 8 and 12 with " longitudinal furrow " suggest seeds of Zanthoxyleae showing the typical hilar scar. The sections in figures 9 and 13, possibly also in figures 10 and 14 suggest either *Myrica* or *Carpinus*, probably the former.

In his description Heer points out that they are of " two different dimensions ; some are 3 millims. long and 2½ millims. wide ; others are 4–4½ millims. long and 3½ millims. wide".

An examination of hundreds of these small carpels suggests that while many specimens cannot at present be sorted there is clear evidence in the material of two genera viz. *Myrica* and *Carpinus*.

Typical *Carpinus* shows the longitudinal fibre grooves of the persistent perianth. The fibres terminate against a large basal scar where the fruit was formerly attached to a wing-like bract. The surface of such specimens is usually smooth and shining.

Typical *Myrica* shows a more irregularly rugose dull surface with no clearly defined large basal scar. Between these two types are others variously distorted, which might belong to one or other. They cannot at present be separated with certainty. Some, indeed, may be seeds, not fruits, and belong to other genera or families not yet recognized.

The fruit of living *Myrica* is superior, the seed is erect and orthotropous, solitary. There is a conspicuous basal placenta scar on the locule, and chalaza scar on the seed. The form of the locule when the two valves have separated, as in germination, is similar to that of *Carpinus*, urceolate in outline, somewhat compressed at right angles to the plane of dehiscence, but the wide sutures are very flat and more close-textured in *Myrica* than in *Carpinus*. Unfortunately the fossil seeds, when preserved at all, are much crumpled and do not well display the chalaza although there are hints of its presence. The locule surface is usually much corroded so that the placentation is not clear while evidence of a superior fruit is lacking. The texture of the endocarp and the sutures nevertheless appear to point to *Myrica* in many instances.

There may be more than one species of *Myrica* at Bovey. Some of the endocarps, as Heer noted, appear so much smaller and more inflated than others. As there is no clear line of demarcation under the conditions of preservation, all are grouped for the present as *Myrica boveyana* (Heer). The relationship of these endocarps to *Myrica* was recognized by Kirchheimer (1938 : 327, footnote).

DIAGNOSIS. Endocarp bisymmetric, sub-ovoid, usually somewhat compressed and angled in the plane of symmetry. Locule not emarginate at the base. Basal part of wall not thickened. Length about 3·5–4 mm.; breadth in plane of symmetry, 3–3·8 mm. Smaller specimens, length about 2·5 mm.; breadth in plane of symmetry, 2 mm.

NEOTYPE. Valve from a broad fruit. Brit. Mus. (N. H.), No. V.33868.

DESCRIPTION. *Endocarp:* One-loculed, somewhat rugose externally, rounded to sub-ovoid but somewhat angled at the margins, bisymmetric, often but not invariably compressed at right angles to the plane of symmetry. Dehiscing in this plane into equal valves showing the sub-urceolate locule on the inner surface which is not emarginate at the base. Locule narrowing into an apical stylar canal. At the base the wall is pierced by a short straight vascular canal and is not here thickened. No clear evidence of the attachment of the seed is yet available. Sutures wide, flat, close-textured. Endocarp wall compact in structure, formed of hard parenchyma, cells small, more or less radially aligned on the sutures. Locule surface smooth (always much corroded), longitudinally striate due to finely toothed cells which are oblong at the extremities of the locule to which they converge, equiaxial over the middle. A second coat sometimes overlies the locule-lining (= testa ?) and shows larger equiaxial cells about 0·05 mm. in diameter. Length of typical fruit, 3·5–4 mm.; breadth in plane of symmetry, 3–3·8 mm. Small specimens, length, 2·5 mm.; breadth in plane of symmetry, 2 mm.

Remarks. It is impossible to say how many of the variously distorted fruits should be referred to this species. A laterally crushed example is shown in Pl. 12, fig. 46 which may belong, but distorted specimens of this type are most difficult to sort and determine.

The presence of *Myrica* is confirmed by Ross from pollen (p. 75). The Recent genus has a wide range in the northern Hemisphere. It also occurs in South Africa and the Andes. It is especially sub-tropical. It is also a widespread Tertiary genus. The smaller Bovey specimens resemble endocarps found in the London Clay of Nursling. The species appears to be distinct from the large much-inflated *Myrica suppani* Kirchheimer (1938; 1939) from the German Brown Coal (spherical endocarps 2·3–5 mm. long, locule cordate at the base, carpel wall basally thickened).

Family Betulaceae

Genus *CORYLUS* (Tourn.)

Corylus sp.

(Pl. 13, figs. 49–51)

Part of a male inflorescence with anthers (Pl. 13, figs. 49, 50) enclosing pollen examined and determined by Dr. J. B. Simpson. The pollen, which was flattened, contained no intine; its condition made it clear that it was a true fossil, not Recent material accidentally introduced. The grains, like those of *Corylus*, show the typical thickening of the exine in the neighbourhood of the pores, and the zone of granules around each pore, the granules being longer and not so close-set as in other regions of the exine.

Various modern species of *Corylus* differ slightly from one another in the size and prominence of the zone of granules, but Dr. Simpson has not determined the nearest living species.

Genus *CARPINUS* Linnaeus

Carpinus boveyanus (Heer) pars

(Pl. 13, figs. 52–67)

1862. *Carpolithes boveyanus* Heer, p. 1077, pl. 70, figs. 7–14 (in part).

Diagnosis. Fruits sub-ovoid, 2·5–4 mm. long, 1·75–2·5 mm. broad. Sometimes twinned.

Neotype. A fruit showing fibres and scar of attachment. Brit. Mus. (H. N.), No. V.33870.

Description. *Fruit:* Attached to a bract rarely preserved and then only as a fragment at the base. Very variable in shape and size, enclosed by the abraded accrescent perianth rarely with remains of short superior perianth segments (Pl. 13, fig. 57). On the whole sub-ovoid, bisymmetric and slightly compressed. Scar of attachment to bract basal, large, sub-circular (Pl. 13, figs. 52–54). Surface in the better-preserved specimens showing slender longitudinal vascular bundles which arise from the margin of the basal scar; the strands themselves are often abraded but their position may be indicated by furrows (Pl. 13, figs. 52, 54, 56). Surface smooth, formed of small, oblong, longitudinally aligned cells about 0·008 mm. in diameter.

A few specimens show two fruits grown together. If, as appears likely, they really belong to *Carpinus* they may be due to the rare development of two fruits in a bract, for two female flowers are present in the early stages in living *Carpinus*. I have not been able to find any living twinned fruits to bear out this suggestion. Twinned fossils are shown in Pl. 13, figs. 59–65).

Endocarp: One-loculed, agreeing with the fruit in shape, style terminal forming a mucro when well preserved, showing remains of two style bases. Dehiscence along a marginal suture in the plane of symmetry. Cavity not well seen.

Seed: When preserved much shrivelled, its placentation obscure.

Length of best preserved fruits, 2·5–4 mm.; breadth, 1·75–2·5 mm. Scar breadth, 0·9–1 mm.

REMARKS AND AFFINITIES. A few fruits among a mass of small, black, crushed fruits and seeds are attributable beyond doubt to *Carpinus*. Possibly some of these were included in Heer's *Carpolithes boveyanus* which certainly included specimens of *Myrica*. The presence of an undoubted accrescent superior perianth, and the basal scar of attachment to a bract make the relationship to *Carpinus* clear. It is unfortunate that there is no evidence so far of the pendulous anatropous seeds which together with perianth and scar serve to distinguish this species from *Myrica*.

The same or a closely allied species of *Carpinus* occurs in the Bournemouth Marine Beds, at Cliff End near Mudeford, and in the Lower Headon of Hordle.

Family FAGACEAE

Genus ***FAGUS*** Linnaeus

Fagus minima n. sp.

(Pl. 13, figs. 68–70)

DIAGNOSIS. Endocarp unusually small, 3·75–4·5 mm. long; lateral faces, 2·5 mm., 2·2 mm. and 1·1 mm. broad respectively.

HOLOTYPE. An endocarp. Brit. Mus. (N. H.), No. V.33886.

DESCRIPTION. *Endocarp:* Trigonous with three unequal flat or concave sides. Broadest outline semi-oval, style apiculate, base with scar of attachment, 1 mm. in diameter, reaching the margin of the narrow face but not continued on to it as in the case of the other two faces, thus showing it to be one of a pair of nuts which abutted along the narrow face; angles sharp but not flanged. Surface smooth, but cell walls raised so as to form minute, irregular, sinuous, longitudinal crumples 0·008 mm. apart, also having irregularly rounded dimples 0·012–0·019 mm. in diameter which are so crowded towards the apex as to produce a rough surface; they may represent hair-bases. Length of endocarp, 3·75 mm.; breadth of broadest side, 2·5 mm.;

maximum breadth of narrowest side, 1·1 mm. (? originally about 1·75 mm. now folded in); maximum breadth of medium side, 2·2 mm. Length of endocarp found by C. & E. M. Reid (see below), 4·5 mm.

Remarks and affinities. One endocarp. Two others were figured by C. & E. M. Reid from Bovey (1910, pl. 16, figs. 67, 68). The angled form, character of attachment scar and surface, position and character of style, all indicate relationship with *Fagus*. The small size distinguishes it from any living species seen. No other fossil species so small has been recognized. The compressed form consequent on the narrowness of one side, and the correspondingly narrow triangular scar which terminates at the margin of the narrow side suggest that the endocarp was developed in a laterally compressed cupule. *Fagus* leaves are of common occurrence in Cretaceous and Tertiary deposits. Leaves of *Fagus* and of *Nothofagus* (Bandulska, 1924) occur in the Bournemouth Freshwater Beds.

Family Ulmaceae

Section Celtidoideae

Genus ***ZELKOVA*** Spach.

Zelkova boveyana n. sp.

(Pl. 13, figs. 71–73)

Diagnosis. Endocarp much inflated. Maximum diameter, 1·5 mm.; maximum diameter in plane of symmetry, 0·9 mm.; maximum diameter at right angles to plane of symmetry, 1·25 mm.

Holotype. An endocarp. Brit. Mus. (N. H.), No. V.33887.

Description. *Endocarp:* Approximately bisymmetric about a plane through the attachment and style, marked by a conspicuous marginal ridge (Pl. 13, figs. 72 73); asymmetric in this plane of symmetry about a line between the attachment and style so that the outline is gibbous on one margin near the attachment, and on the other near the apex (Pl. 13, fig. 71). The endocarp is much inflated producing a rounded-quadrilateral outline at right angles to the plane of symmetry (Pl. 13, fig. 72). Attachment indicated by a small depression from which obscure ridges diverge, a few also diverge from the marginal ridge. Surface rough with indefinite depressions that give rise to an obscure network, wall formed of small equiaxial cells 0·012 mm. in diameter.

Maximum diameter, 1·5 mm.; maximum diameter in plane of symmetry, 0·9 mm.; maximum diameter at right angles to plane of symmetry, 1·25 mm.

Remarks and affinities. One endocarp. The form and structure so far as it has been seen, relate the fruit to *Zelkova*, a genus represented by about six living species in North Temperate regions.

All species seen are much larger than the fossil, but they vary much in size, so that the relationship in size between the fossil and *Z. keaki* (for example) is comparable with that between *Z. keaki* (3 mm. maximum diameter) and *Z. sinica* (7 mm.). Size alone could not therefore exclude the fossil from this genus. *Z. sinica* resembles the fossil closely in form, but most living species are more markedly curved, and some are actually hooked in the stylar region. The apparent absence of superficial fibres in the fossil may be due to its worn condition. There appear to be no other grounds for excluding it from the genus *Zelkova.*

Family MORACEAE

Section MOROIDEAE

Genus ***MOROIDEA*** nov.

DIAGNOSIS. Unidentified genera of the section Moroideae, family Moraceae.

Moroidea boveyana n. sp.

(Pl. 13, fig. 74)

DIAGNOSIS. Fruit markedly asymmetric in plane of symmetry. Stylar projection narrow. Length incomplete; breadth in plane of symmetry, 1·5 mm.; thickness, 0·7 mm.

HOLOTYPE. A fruit, broken at the rounded base. Brit. Mus. (N. H.), No. V.33888.

DESCRIPTION. *Fruit:* Sub-circular in outline, somewhat flattened laterally but sub-cuneate in transverse section, the narrower edge crested along the whole length preserved, the opposite edge and base of the fruit rounded. Style prominent, terminal at the apex of the crested margin, closely adjacent to a sub-terminal curved projection which marks the point of entry of the funicle to the sub-apical placenta inside the rounded margin. Carpel wall 0·05–1 mm. thick, formed of a few layers of small cells aligned radially so as to give a columnar appearance in section, producing superficially a closely punctate surface with pits 0·012–0·016 mm. in diameter.

Length of fruit, incomplete; breadth, 1·5 mm.; thickness, 0·7 mm.

REMARKS. One fruit, broken at the rounded base. The interior and structure of the seed have not been seen. A similar fruit was found at Hordle giving evidence of both internal structure and of seed structure. In the Hordle specimen the relation to Moraceae was clear, and the evidence indicated a connexion either with the section Moroideae or with Artocarpoideae, probably with the former.

The chief distinctions between the Bovey and Hordle fossils lie in the style which is a narrow projection in the Bovey fruit, and a broad flat one with a broad flat stylar canal in the fruit from Hordle, and in the greater symmetry of the Hordle fruit. Such differences are probably of specific value, but this conclusion can only be established when a greater range of living and fossil material is available for comparison. In the meantime the Bovey and Hordle fruits are treated as specifically distinct.

Family NYMPHAEACEAE

Genus *BRASENIA* Schreber

Brasenia ovula (Brongniart)

(Pl. 13, fig. 75)

1862. *Nymphaea doris* Heer, p. 1072, pl. 70, figs. 32–37.
1925. *Brasenia* sp. (*B. ovulum* Brongn. ?) Chandler, p. 23, pl. 3, figs. 7*a–d*.
1926. *Brasenia ovula* (Brongn.) : Reid & Chandler, p. 99, pl. 6, figs. 15–18.

DESCRIPTION. *Seed :* Obovoid, now much crumpled and distorted, having an aperture at one end, measuring 0·45 mm. in diameter, from which the embryotega has come away. Surface black, glistening, with longitudinal corrugations about 0·075 mm. in breadth at the middle of the seed. Surface cells, 0·05–0·075 mm. in diameter, with interlocking digitations, the length of individual digitations often more than one-third of the total diameter of a cell ; surface of cells finely punctate.

Length of seed, 2·25 mm.; breadth, 1·5 mm.

REMARKS. One seed from Heathfield. Heer recorded numerous seeds from Bovey under the name *Nymphaea doris*. His seeds were 2·5–3·5 mm. long and 2–3 mm. broad, the diameter being slightly increased no doubt by the flattening of the the seeds. The species ranges in the British Tertiary from Bournemouth Marine to Hamstead Beds.

Family MAGNOLIACEAE

Genus *MAGNOLIA* Linnaeus

Magnolia boveyana n. sp.

(Pl. 13, figs. 76–80)

1910. *Magnolia attenuata* Weber : C. & E. M. Reid, p. 165, pl. 15, figs. 1, 2.

DIAGNOSIS. Seeds longer than broad. Length 6–7 mm., breadth 2·75–4·5 mm.

HOLOTYPE. Brit. Mus. (N. H.), No. V.33890.

DESCRIPTION. *Seed :* Anatropous, ovate in outline, narrow, longer than broad, much compressed (compression doubtless emphasized by fossilization), gently convex, angled longitudinally on one face with a shallow longitudinal depression on the other (the raphe side). Chalaza terminal at the broad end, marked by a small plug or scar which is pierced at the centre. Surface marked by a fine " fingerprint " pattern due to polygonal cells, 0·01 mm. in diameter, cells aligned in rows, the rows being grouped in clusters. Testa (represented only by the inner hard coat) 0·4 mm. thick at the middle of the seed, formed of equiaxial cells arranged radially in a columnar manner, the columns about 0·016 mm. broad. Tegmen thin, translucent, longitudinally striate, structure obscure.

Length of a seed, 6 mm.; breadth, 2·75 mm. Length of a second seed, 6 mm.; breadth, 4 mm. Length of a seed found by C. & E. M. Reid (1910 : 165), 7 mm.; breadth 4·5 mm.

REMARKS AND AFFINITIES. Six seeds and several fragments. They resemble *Magnolia* seeds of the American longer-than-broad type. The species is larger, more ovate in outline, and less triangular in transverse section than *M. angusta* from the London Clay (Reid & Chandler, 1933 : 177, pl. 5, figs. 6–8).

Comparable living species are *M. grandiflora* Linn., and *M. glauca* Linn., but the former is a large, and the latter is a smaller species. C. & E. M. Reid (1910 : 165) named these seeds *M. attenuata* Weber, identifying them with *Magnolia* seeds found abundantly in the Rhine lignite; but they were careful to indicate that as the type of *M. attenuata* was a leaf, and as another *Magnolia* species also occurred in the same deposit, the connexion of the Rhineland seeds with the leaves was not conclusively established.

On this account Kirchheimer (1936*a* : 85–86) recently instituted a new specific name *M. sinuata* for a species from Salzhausen in which he included the relatively narrow seeds of *M. attenuata* Weber and a broader-seeded species *M. hoffmani* Ludwig on the grounds of histological identity. *M. sinuata*, although some of its forms resemble the Heathfield specimens, appears to exhibit much greater variation both of form and size. On the whole it is appreciably larger, the length of the seed, 6–10 mm.; breadth, 5–9 mm., whereas the maximum length of the Heathfield seeds is 7 mm.; maximum breadth, 4·5 mm. Hence a distinct specific name, *Magnolia boveyana*, has been given to the seeds from the Bovey basin.

Family LAURACEAE

Genus *CINNAMOMUM* Blume

Cinnamomum is represented at Bovey, according to Heer, by three species, two based on leaves (*C. rossmassleri* and *C. lanceolatum*), the third on leaves and flowers (*C. scheuchzeri*). Probably some of the cupules and berries hereafter recorded may belong to *Cinnamomum*. At present, however, they are referred to the family Lauraceae only, the evidence being insufficient for definite determination.

C. rossmassleri Heer was represented by two leaf-fragments both with the apex missing. Hence Heer himself regarded the determination as doubtful. The species is therefore omitted in the list on p. 77 as the figures (Heer, 1862, pl. 67, figs. 17, 18) are inconclusive and not distinguishable with certainty from those of *C. scheuchzeri*.

C. scheuchzeri and *C. lanceolatum* are better represented, and there can be no reason to doubt the occurrence of the genus *Cinnamomum* in the Bovey Lake deposits. No new leaves of either species have been found and the genus is not therefore included in the plant list on p. 77.

VARIOUS GENERA AND SPECIES

(Pl. 14, figs. 81–91)

In addition to the genus *Cinnamomum*, the Lauraceae are represented by leaves referred to *Laurus primigenia* Unger and to *Daphnogene ungeri* (Heer, 1862 : 1064, pl. 65, figs. 1, 2, 6). Neither of these determinations are wholly satisfactory. There are a number of cupules and berries also. These were never seen by Heer or their affinities were not recognized.

C. & E. M. Reid (1910, pl. 16, figs. 64–66) figured three small wrinkled cupules clearly belonging to Lauraceae. Similar specimens (all small) are common both at Bovey and Heathfield. They vary from about 1·75–3 mm. in diameter. Sometimes they are cup-like with simple margins, sometimes they are notched or divided above into sepals. In a few the small unripe berry still lies within the calyx. In all the skin is much wrinkled, shining, formed of very small cells which may produce a finely striate effect.

The flattened skins or epicarp of larger, detached, formerly ovoid berries are also common. The epicarp is leathery, shining, often yellowish-brown and semi-translucent, mainly formed of equiaxial cells which may vary considerably both in form and size ; they are often about 0·025 mm. in diameter.

In some specimens, overlying these cells at the apex is a thin layer of polygonal cells about 0·05 mm. long and 0·025 mm. broad. These diverge from the apical scar, but quickly die out and become obscure so that they cannot be traced a short distance below the apex. Remains of the mesocarp commonly adhere to the epicarp and in some specimens enclose numerous ovoid or globular yellow oily (?) bodies about 0·05 mm. in diameter. The largest berry seen is 6 mm. long (incomplete) by 5·25 mm. broad (breadth increased by flattening).

It is possible, but unlikely in view of the immature condition, that detailed comparative study of cuticle and mesocarp structure in living and fossil material might serve to distinguish some at least of the genera represented, but it would require very long research and an abundance of living material for comparison. The berries and cupules can therefore only be referred to the family Lauraceae without suggestions as to the generic relationship.

Family CAPPARIDACEAE

Genus ***CAPPARIDISPERMUM*** nov.

DIAGNOSIS. A form-genus to embrace seeds of Capparidaceae of which the nearer relationship is unknown.

Capparidispermum boveyanum n. sp.

(Pl. 14, figs. 92–96)

DIAGNOSIS. Seeds transversely oboval about 2–3 mm. in minimum and 2·75–3·75 mm. in maximum diameter. Contiguous walls of the curved limbs form a condyle, they appear to be fused for most of its length. Testa tubercled, the tubercles oriented parallel with the margin of the seed. Surface cells equiaxial.

HOLOTYPE. Brit. Mus. (N. H.), No. V.33904.

DESCRIPTION. *Seed :* Woody, transversely oboval in outline, almost flat, approximately bisymmetric, splitting for germination in the plane of symmetry.

Locule with curved unequal limbs separated by a narrow curved condyle, the micropylar limb longer and narrower than the other (Pl. 14, fig. 96). The sutures in the plane of dehiscence are smooth finished surfaces both along the margins of the seed and on the condyle. Marginal suture variable in breadth, 0·18 mm. broad at the distal end of the seed ; 0·4 mm. broad near the proximal end on the concave outer curve of the short limb. Hilar scar large, oval, marginal between the limbs, sometimes sunk in an emargination (Pl. 14, fig. 94). Micropyle small, terminal on the longer limb. The walls which form the condyle appear to be completely fused for the greater part of their length except at the hilar end where they enclose a shallow V-shaped cavity (Pl. 14, fig. 96), 0·8 mm. long, 0·3 mm. wide at the margin.

The condyle is sometimes indicated externally by an elongate prominence which is smoother than the rest of the surface (Pl. 14, fig. 92). Testa tubercled externally, the tubercles often elongate parallel with the margin of the seed ; breadth of bases of tubercles, 0·05–1·5 mm.; height, 0·025–0·05 mm., surface cells equiaxial about 0·025 mm. in diameter giving the margins of the tubercles a clawed or digitate appearance. Testa in section formed of equiaxial cells, 0·017 mm. in diameter. Lining cells of seed-cavity, 0·017 mm. in diameter, equiaxial, in rows transverse to the length of the cavity.

Dimensions of four seeds respectively : 2·75 by 2 mm., 3·75 by 3 mm., 3·5 by 2·25 mm., 3·5 by 2·25 mm. (the last represented by one valve only).

REMARKS. Four seeds and two fragments. The curvature of the locule, marginal hilum between the limbs and the long narrow condyle indicate relationship with Capparidaceae.

No living genus seen combines the characters of form, size and ornamentation, hence the reference to a form-genus *Capparidispermum.* It is possible that the specimen shown in Pl. 14, fig. 95, represents a second species, it is larger, flatter, and the short limb has a more marked spiral incurve. In the absence of more evidence it is regarded as a slightly abnormal seed of the same species.

Family HAMAMELIDACEAE

Genus ? sp.

(Pl. 14, figs. 97, 98)

DESCRIPTION. *Seed :* Sub-oboval in outline, rounded at the apex, slightly excavated at the base, laterally compressed (compression exagerrated by fossilization), with a large, bilobed, slightly concave hilar scar lying across the base having one lobe on each flat face ; the lobes are unequal in length and breadth but occupy about half the length of the seed. The arrangement of the other organs has not been seen. Surface much abraded, rough as preserved, the polygonal cells being about 0·03 mm. in diameter and somewhat sinuous. In a few places the testa has cracked transversely on drying owing to the transverse alignment of one or more of its layers. As seen in section near the apex it is 0·25 mm. thick but its cells cannot here be distinguished although at one point there is a false appearance of curved columns, 0·016 mm. broad, the results of the fracture of tissue which has become vitrified in fossilization. Lining of seed-cavity formed of equiaxial cells 0·012–0·016 mm. in diameter.

Length of seed, 5·25 mm.; breadth, 3·25 mm.; thickness, 2 mm.

Remarks and affinities. One seed. The form and the large lobed hilar scar extending over the base and continued on each side, indicate a seed of Hamamelidaceae. Although many seeds in this family show similar hilar scars, no living genus seen has so large a scar as the fossil, while in many it is considerably smaller. In certain living genera there are two distinct scars one on each side near the base, but not united over it. *Sinowilsonia* (length of seed, 6·5 mm.; breadth, 4 mm.) has a similar scar occupying almost half the length of the seed. *Fortunearia*, with a scar extending about one-third of the length, has a much larger seed as have many species of *Hamamelis*. While the relationship of the fossil to the family Hamamelidaceae is certain, the evidence is insufficient to determine the generic position, but perhaps the closest living genus is *Sinowilsonia*.

It is interesting to note that Dr. J. B. Simpson (1936 : 99) records the occurrence of pollen belonging to *Bucklandia*, *Corylopsis*, *Fortunearia*, *Loropetalum*, *Dicoryphe* and *Distylium* in the Scottish Tertiary coals of Ardnamurchan and Mull.

Genus ? sp.

(Pl. 14, fig. 99)

Description. *Fruit :* Represented only by a fragment of septum and fibrous axis adhering to the seed near its apex.

Seed : Originally ovoid (much compressed in fossilization). Hilar scar sunk, long and narrow, lateral but continued across the base where it terminates without extending on to the opposite face. Testa black, shining, showing the cell-structure fairly clearly ; around the scar the cells are elongate, approximately parallel with its margin, but over most of the surface there are fine parallel striations diverging obliquely from the middle which appear to be a secondary consequence of compression.

Length of seed, 4·75 mm. ; maximum breadth, 2·5 mm. Length of scar on lateral face, 2 mm.; breadth, 0·3 mm.

Remarks and affinities. One seed from Heathfield. The form, hilar scar, and surface all indicate relationship with Hamamelidaceae. It has not been possible to relate it to a genus. In *Hamamelis* the hilar scar is shorter and the seed larger. In *Corylopsis*, which has a long, sunk scar, there is also a marked facetting on the opposite side. *Fothergilla* has a small, sunk scar and the walls of the surface cells are much thicker.

The second species here described is quite distinct from the first in which the hilar scar is large, broad and bilobed.

Family Rosaceae

Genus *RUBUS* Linnaeus

Rubus microspermus C. & E. M. Reid

(Pl. 14, figs. 100–109)

1910. *Rubus microspermus* C. & E. M. Reid, p. 169, pl. 15, figs. 13–17.

Description. *Endocarp:* Laterally compressed, semi-circular, semi-oval or sub-ovate in outline, ventral margin straight or almost straight, dorsal margin semi-circular or markedly convex, base rounded, margin rimmed all round. Surface reticulate with conspicuous pits, angular in outline, separated by thin, sharp, clearly defined ridges, occasionally the ridges are prolonged on to the margin. Carpel wall formed superficially of small equiaxial cells 0·01 mm. in diameter.

Length of endocarp, 1–2·5 mm. (commonly 2·25 mm.); breadth, 1–1·8 mm. (commonly 1·25 mm.).

Remarks and affinities. Endocarps of this species are common at Bovey and Heathfield. Their relationship to *Rubus* was discussed by C. & E. M. Reid (1910: 169) but a larger range of material is here shown (Pl. 14, figs. 100–109) to demonstrate variation in size and form. Prickles of *Rubus* which were reasonably assumed to belong to the same plant were also described and figured by C. & E. M. Reid (1910: 169, pl. 15, figs. 16, 17). The endocarps have been compared with *Rubus acutiformis* Chandler which occurs at Hordle, Cliff End, Sandbanks, Branksome Dene and Studland, but the two species are clearly distinguishable although both are of unusually small size. *Rubus acutiformis* is commonly more pointed and narrower at the apex, and is therefore more ovate in outline as a rule, while the ventral margin is not infrequently very slightly concave, the apex being curved somewhat towards the ventral side. The well-marked marginal flange is most conspicuously developed on the ventral margin.

Family Leguminosae

Genus ?

(Pl. 15, figs. 110–112)

Description. One perfect compressed seed, and fragments of three others must be referred to Leguminosae. The original shape was probably lensiform (but the seeds are now flat owing to compression), the marginal hilar scar (obscured by marginal cracking) must have been small. The surface is formed of inconspicuous concave equiaxial cells 0·02 mm. in diameter, the walls are 0·25 mm. thick as seen in one of the incomplete specimens, 0·45 mm. thick around the hilar aperture, the cells being arranged in a columnar manner, the radial columns about 0·012 mm. broad; a shallow pocket, presumably connected with the radicle, lies immediately beneath the hilum, it is delimited on the surface of the cavity by elongate cells. Lining of main seed-cavity of convex equiaxial cells 0·012 mm. in diameter. Diameter of the perfect seed, 3·5–3·75 mm.; other specimens larger but incomplete.

Family RUTACEAE

Section ZANTHOXYLEAE

Genus ***RUTASPERMUM*** nov.

DIAGNOSIS. A form-genus to include seeds of Rutaceae of which the nearer relationship is unknown.

Rutaspermum exaratum (Heer)

1862. *Carpolithes exaratus* Heer, p. 1079, pl. 70, figs. 24–27.

The seed was described by Heer as 3·5 mm. long, 3·3 mm. broad; the figures showed it as sub-circular in outline, much inflated, with a long, narrowly-triangular, sunk hilar scar (the "umbilical fissure" of Heer). The surface was ornamented with nodular ridges aligned parallel with the rounded dorsal margin, much as in a species to be described from Sandbanks, and ornamented also with fine polygonal cells or pits (the "innumerable dots" of Heer); but the species is larger than the Sandbanks seeds. The characters are clearly those of Zanthoxyleae, of the type referred to the form-genus *Rutaspermum*. In the absence of actual specimens and of more accurate figures than the diagrammatic illustrations given by Heer, the species cannot be clearly defined. Available evidence, however, suggests that it is of a very distinctive type.

Family SABIACEAE

Genus ***MELIOSMA*** Blume

Meliosma reticulata (C. & E. M. Reid)

(Pl. 15, figs. 113–118)

1910. *Calvarinus reticulatus* C. & E. M. Reid, p. 169, pl. 15, figs. 18–20.

DIAGNOSIS. Endocarp about 5–5·25 mm. long, 3·75–4 mm. in maximum transverse diameter. External surface with about eighteen to twenty raised ribs over the proximal half which branch and anastomose to form a sharp network over the distal half.

NEOTYPE. A perfect but laterally compressed endocarp. Brit. Mus. (N. H.), No. V.33924.

DESCRIPTION. *Endocarp:* Woody, obovoid, slightly compressed laterally (compression increased by fossilization), the transverse diameters being in the proportion of 7 : 10; bisymmetric about a plane which passes through the attachment, funicular canal and a marked marginal angle; splitting in the plane of symmetry into two valves. Funicular canal oblique, about 1 mm. long, placenta basi-lateral or subbasal. External surface ornamented with about eighteen to twenty raised ribs diverging from the attachment over the lower half of the fruit and uniting, branching, and anastomosing, to form a network over the upper half of the fruit. Surface formed of polygonal cells 0·01 mm. in diameter. Walls 1·25–1·5 mm. thick. Surface of locule rough, cell-structure very obscure, but the centipede-type of cells with interlocking walls characteristic of *Meliosma* can be traced oriented parallel with the lateral ribs on one small fragment; the length of individual cells is obscure, but near the base their width is about 0·037 mm.

Length of endocarp, 5·25 mm.; breadth, 4·25 mm. Length of a second endocarp, 5 mm.; breadth, 3·75 mm.

Remarks and affinities. Six endocarps or valves and a number of fragments. The form, surface ornamentation, structure, and short oblique funicular canal relate these fossils to *Meliosma*. So far as it has been possible to study the different living species, the Bovey fossils are unique in the number of their longitudinal ribs and the fineness and sharpness of the apical network, also in the narrow oboval form. In living species the three diameters (two transverse and one longitudinal) are usually approximately equal but occasionally the transverse diameters may be slightly longer or shorter than the longitudinal. The considerable differences in the diameters of the fossil which give rise to the elongate form and lateral compression have not, however, been seen in the living forms.

C. & E. M. Reid (1910) described the species under the generic name *Calvarinus*, and referred it to the family Boraginaceae. There were two specimens from Heathfield and one from Bovey. Reid and Chandler also obtained endocarps from both localities.

Family VITACEAE

There are several types of vine seeds at Bovey and Heathfield. Heer (1862 : 1070, pl. 69, figs. 25–29) distinguished two species which he named *Vitis britannica* and *V. hookeri*. The figures are poor and the descriptions inadequate but the outstanding features are clear.

C. & E. M. Reid (1910 : 165, pl. 15, figs. 3–6) distinguished three species, *V. hookeri* Heer, *V. teutonica* A. Br. and *V. ludwigi* A. Br. The greater number of specimens are now referred to *Parthenocissus britannica* (Heer). One imperfect seed appears to belong to *V. hookeri* Heer. The specific relationship is discussed in the following pages where the species are described.

Two new species have been added, *Parthenocissus boveyana* from Bovey, and *Vitis stipitata* from Heathfield.

Genus ***PARTHENOCISSUS*** Planchon

Parthenocissus britannica (Heer)

(Pl. 15, figs. 119–122)

1862. *Vitis britannica* Heer, p. 1071, pl. 69, figs. 25, 26.
1910. *Vitis ludwigi* A. Br. : C. & E. M. Reid, p. 166, pl. 15, fig. 6 (not fig. 4 as in text).
1910. *Vitis teutonica* A. Br. : C. & E. M. Reid, p. 166, pl. 15, figs. 4, 5 (not fig. 6 as in text).

Diagnosis. Seed pointed-obovate in outline, smooth dorsally, slightly emarginate at the apex, chalaza elongate-ovate, surface grooved between chalaza and base; sharply angled ventrally with infolds occupying more than half the length, deep, narrow, straight but diverging upwards. Length, 4·75 mm.; breadth, 2·25–2·8 mm.; thickness, 1·5–2 mm.

NEOTYPE. A typical seed. Brit. Mus. (N. H.), No. V.33927.

DESCRIPTION. *Seed:* Pointed-obovate in outline, slightly emarginate at the apex, pointed at the base, with smooth contours, ventral and dorsal faces meeting at an acute angle, ventral face sharply facetted so as to form a conspicuous raphe ridge extending almost the whole length of the seed, the facets being flat or concave and meeting approximately at a right angle; at the apex the ridge gives place to the shallow channel which produces the slight apical emargination. Ventral infolds deep, narrow, straight, occupying more than half the length of the seed arising near the base, diverging upwards so that the raphe ridge is broader above than below. Dorsal face flat, slightly emarginate at the apex having a shallow groove along which the raphe passes into the narrow elongate-ovate chalaza which lies above the middle of the seed. From the chalaza a well-marked groove passes to the base. Testa formed of two coats, the outer thin, its irregular elongate polygonal cells about 0·02 mm. in shortest diameter producing transverse striations which diverge from the chalaza and ventral infolds to the margin. The inner coat is hard, averaging 0·1 mm. in thickness, formed of cells 0·016 mm. in diameter arranged in radial columns. These cells give a finely pitted surface to the coat.

Length of seed, 4·75 mm.; breadth, 2·25–2·8 mm.; thickness, 1·5–2 mm. (somewhat distorted).

REMARKS AND AFFINITIES. Ten seeds and several fragments from Bovey. The smooth seed with long divergent infolds suggests relationship with the living *Parthenocissus*. The same species was apparently described by C. & E. M. Reid (1910) under the name *Vitis teutonica* A. Br. They state that " Heer's type specimens of *V. britannica* appear to be nothing but badly compressed seeds of this vine [*V. teutonica*], though his figures are scarcely recognisable ". Their description is " ovate-acuminate, gradually narrowed into the beak, granulate all over, inner face with long shallow pits, outer convex longitudinally sulcate with a narrow pyriform chalaza, length 4 mm."

The identity of these specimens with *Vitis teutonica* A. Br. from the German lignite cannot now be maintained. *V. teutonica* was originally based on leaves, but as seeds were associated with them, Unger applied the name to the seeds also (Braun, 1845 : 172; Unger, 1860 : 23, pl. 9, figs. 1–8). Unfortunately neither Unger's figures or diagnosis really define the species. Later German workers have also referred a variety of seeds from the Brown Coal to *V. teutonica.* Thus Kräusel (1920, pl. 25, figs. 1, 2) illustrates seeds with short, wide, divergent lateral infolds, a marked apical groove on the ventral side, a short elongate-obovate chalaza and shallow furrow between the chalaza and base on the dorsal side (pl. 24, figs. 20–23). His seeds appear more inflated than the Bovey specimens, and are sometimes fluted. Kirchheimer (1934 : 35, pl. 9, figs. 3–6) describes and figures a somewhat fluted seed under the name *V. teutonica.* It has a relatively small oval chalaza and appears quite distinct from the Bovey seeds. Later Kirchheimer (1938, pl. 4, figs. 12–15; 1939, pl. 2, fig. 3) figures other seeds under this name. The first shows a small median oval chalaza and very wide sub-parallel ventral infolds. The second shows a much larger chalaza which is elongate-oval in shape occupying the upper half of the seed, while wide and divergent ventral infolds and a markedly stipitate base arise out of the rounded, smooth, lower half of the seed.

The Bovey fossil appears to be sufficiently distinctive in its shape and chalazal character and in the narrow upwardly divergent infolds to merit a distinct specific name and *Parthenocissus britannica* (Heer) is here retained for this purpose.

Another Bovey seed described and figured by C. & E. M. Reid (1910 : 166, pl. 16, fig. 6) as *V. ludwigi* ? is also probably a differently distorted specimen of *P. britannica*, although in the description it is said to have a more slender form with an oval, not pyriform, chalaza. Such individual differences may, however, occur among living seeds within a species.

Parthenocissus boveyana n. sp.

(Pl. 15, figs. 123–125)

DIAGNOSIS. Seed obovate in outline, not emarginate at the apex, contours smooth, chalaza median oval, angle of raphe ridge about 135°, ventral infolds markedly divergent upwards. Length, 3·5 mm.; breadth, 2·75 mm.; thickness, 1 mm.

HOLOTYPE. Brit. Mus. (N. H.), No. V.33929.

DESCRIPTION. *Seed :* Obovate in outline, not emarginate at the apex, pointed at the base, contours smooth, ventral face facetted, the facets being slightly concave and meeting at an angle of about 135° so that the raphe-ridge is not very sharp or conspicuous ; the raphe itself—a stout cord—is preserved above the middle on the ventral face and is continued on to the dorsal face passing into the external chalaza. Ventral infolds deep and narrow, extending from near the base to a quarter of the length from the apex, they diverge above and are slightly convex towards the raphe-ridge which is therefore triangular. Dorsal face almost flat, very slightly convex, not emarginate at the apex, or if it is grooved, the groove is obscured by the preservation of the raphe ; there is a shallow median groove between the chalaza and the base. Chalaza oval situated rather above the middle of the seed, gradually narrowing above into the raphe. Surface rather rough especially at the base and apex and on the chalaza, cells diverging from the lateral infolds and from the chalaza, many of them elongate in the direction of divergence, others polygonal 0·012 mm. in diameter. Wall as seen in section columnar, the columns about 0·012 mm. in diameter. Thickness of wall, 0·1 mm.

Length of seed, 3·5 mm.; breadth, 2·75 mm.; maximum thickness, 1 mm.

REMARKS AND AFFINITIES. One seed, and an imperfect specimen possibly referable to this species. The seed is relatively broader than seeds of *V. britannica*, and has a larger, broader chalaza, and more divergent lateral infolds. It is less rounded and stipitate than Kirchheimer's figures of *V. teutonica* (1939, pl. 2, figs. 3*a–e*) and lacks the emarginate apex. Its chalaza is much larger than that in Kirchheimer's figure (1938, pl. 4, fig. 14).

Genus *VITIS* Linnaeus

Vitis hookeri Heer

(Pl. 15, figs. 126, 127)

1862. *Vitis hookeri* Heer, p. 1070, pl. 69, figs. 27–29.
1910. *Vitis hookeri* Heer : C. & E. M. Reid, p. 165, pl. 15, fig. 3.

Description. *Seed :* Broadly obovate in outline but scarcely emarginate at the apex, pointed at the base, contours smooth and rounded. Ventral face facetted so as to form a conspicuous raphe-ridge, ventral infolds broad widening upwards, about half as long as the seed. Dorsal face rounded with slight flutings diverging from the ovate chalaza which is situated above the middle of the seed. Between chalaza and base is a deep median groove. Testa, 0·075 mm. thick, formed of cells 0·0125 mm. in diameter which have a columnar radial arrangement ; they give rise superficially to a finely and evenly but deeply punctate surface.

Length of seed, 3·75 mm.; estimated breadth (actually incomplete), 3·5 mm.

Remarks and affinities. One incomplete seed from Heathfield ; also a second from Bovey which may possibly be referred to this species. This second specimen is much distorted being compressed from base to apex, but its features can be seen and measured, and agree with those described above. It is slightly stipitate.

Except that the better preserved specimen is not stipitate, it shows characters which agree with those of *Vitis hookeri* Heer of which Heer found one seed at Bovey. There is general agreement in size with Heer's specimen (length, 3·5 mm; breadth, 3 mm.), the contours are in general similar to those in Heer's inadequate figure ; the chalaza is of comparable size and, although not round, occupies a very similar position on the dorsal surface when due allowance is made for its displacement by distortion which has brought it nearer to the apex than it originally lay. In the second much distorted specimen, the chalaza is round and but slightly above the middle. Comparison of the ventral face cannot be satisfactorily made both because of the distortion of the new material and because Heer's figure cannot really represent the ventral aspect of any vine. While, therefore, identity with Heer's species *V. hookeri* is not indisputably established, it seems probable that the new specimens should be referred to that species. The presence or absence of stipitation is not in itself of great importance, for Recent grape-seeds show that this character varies considerably in a single species. C. &. E. M. Reid (1910 : 165, pl. 15, fig. 3) described as *V. hookeri* Heer a seed which is probably correctly so named, although its chalaza is somewhat smaller than that shown in Heer's type. But variation in size of the chalaza also occurs in living species. The ventral side of this seed was not shown.

Family Tiliaceae

Genus *TILIA* Linnaeus

Tilia sp.

(Pl. 15, figs. 130–132)

Two groups of anthers were obtained from Heathfield and were sent to Dr. J. B. Simpson for examination. In a letter (27.iii.38) he reported that they yielded typical pollen of *Tilia*, adding " I am not well acquainted with the pollen of many of the tropical genera of Tiliaceae, and so cannot positively exclude the other genera except *Grewia* and *Luhea*, but certainly they [the pollen grains] agree so perfectly with *Tilia*, that I feel sure it must be this genus they represent ". A further report after a greater variety of living material had been obtained and examined was expected but has not come to hand. But in a letter dated 1.iv.38 Dr. Simpson adds in writing of the fossil pollen " The furrows are short and deep and have the appearance of pits and occur in the middle of the sides not at the rounded corners of the triangular grain. The exine . . . is irregularly reticulate with a fine mesh ".

Ross, working quite independently of Simpson recorded " cf. *Tilia* " based on pollen.

Family LYTHRACEAE

Genus ***MICRODIPTERA*** nov.

DIAGNOSIS. Fruit many-seeded. Seeds anatropous, compressed at right angles to the germination valve and in the plane of symmetry. Valve an oval operculum as in *Diclidocarya menzeli* E. M. Reid in the lower part of the dorsal surface. Seed-body flanked by two thin lateral wings with spongy internal tissue. Wings more or less equally developed.

TYPE SPECIES. *Microdiptera major* n. sp. from the Eocene of Sandbanks (awaiting full description). Brit. Mus. (N. H.), No. V.34249.

Microdiptera parva n. sp.

(Pl. 15, figs. 133–149 ; Text-fig. 2)

DIAGNOSIS. Lateral wings very thin, markedly concave on the ventral side, raphe straight and narrow, triangular form of seed rare. Maximum length of seed so far recorded, 1·25 mm.; maximum breadth, 1·75 mm. (2 mm. in Cliff End specimen).

HOLOTYPE. A seed. Brit. Mus. (N. H.), No. V.33934.

DESCRIPTION. *Seed :* Anatropous, much compressed dorsi-ventrally ; oboval, sub-circular, transversely oval, irregular in outline, or occasionally broadly triangular, differentiated into a median elongate-oval body and thin lateral wings, convex on the dorsal surface, concave on the ventral. Raphe prominent, linear, median longitudinal on the ventral face flanked by the marked concavities of the wings, hilum marginal. Germination by an oval operculum on the lower half of the dorsal face, associated with the basal micropyle. Internal chalaza circular at the apex of the seed (Text-fig. 2). Testa formed superficially of a shining, black coat giving a netted surface with large cells or pits equiaxial at the apex, more irregular and elongate below. Over the operculum the cells are very regular, equiaxial, about 0·05 mm. in diameter, arranged in about seven regular longitudinal rows. Some specimens show in addition evidence of small cells, 0·01–0·012 mm. in diameter, also aligned in longitudinal rows. Within the superficial coat and clearly seen on abraded seeds is a layer of fine cells 0·012 mm. in diameter; they are arranged so as to give rise to striations which curve around the operculum, across on to the wings, and lie parallel with the margin of the wings near the circumference of the seed. Near the margin, the wings are only 0·025 mm. thick, but they thicken towards the seed-body close to which they measure 0·06 mm. in thickness. The external coats are close-textured and no cells can be distinguished in section ; near the body the dorsal coat is 0·025 mm. thick, the ventral 0·012 mm., the middle layer is 0·025 mm. thick and is much less compact than the outer layers, but its cell-structure cannot be clearly seen. The coat surrounding the seed-cavity is hard and compact, it is 0·05 mm. thick on the dorsal side, 0·037 mm. thick on the ventral side. The seed-cavity is finely striate longitudinally. The tegmen is semi-translucent and is fused with the testa at the large black chalazal scar.

FIG. 2. *Microdiptera parva* n. gen. et sp. Diagrammatic longitudinal section through seed-cavity. × 45 approx.

The dimensions of a series of seeds are as follows :

	Length (mm.)	Breadth (mm.)
(1)	1·25	1·75
(2)	1·0	1·25
(3)	1·0	1·5
(4)	1·0	1·75
(5)	1·25	1·0

Typical dimensions of germination opercula are respectively 0·5 by 0·3 mm., 0·5 by 0·4 mm., 0·6 by 0·4 mm., 0·5 by 0·4 mm., 0·55 by 0·35 mm., 0·4 by 0·3 mm.

REMARKS AND AFFINITIES. The characters are those of Lythraceae, more especially the position of the organs, the form of the anatropous seed and the structure and arrangement of the wings. The systematic position will be discussed in greater detail when the type species from Sandbanks is described in a forthcoming catalogue. At Bournemouth not only isolated seeds, but some still in the position of growth in a fragment of fruit were found.

Family NYSSACEAE

Genus *NYSSA* Gronov.

The genus *Nyssa* from Bovey is in urgent need of revision. Four supposed species, truncate at one end, must now be referred to *Symplocos*. They are *Nyssa europaea* Unger (Heer, 1862 : 1066, pl. 69, figs. 11–17 ; C. & E. M. Reid, 1910 : 67, pl. 15, fig. 9), *Nyssa laevigata* Heer (1862 : 1066, pl. 69, fig. 18), *Nyssa microsperma* Heer (1862 : 1067, pl. 69, fig. 24 ; C. & E. M. Reid, 1910 : 167) and *Nyssa obovata* Weber (C. & E. M. Reid, 1910 : 168, pl. 15, fig. 10).

One specimen figured as *Nyssa ornithobroma* Unger by C. & E. M. Reid (1910 : 168, pl. 15, fig. 11) does not agree with Unger's species and may be a *Mastixia*.

Others are of uncertain relationship: *N. striolata* (Heer, 1862 : 1067, pl. 69, figs. 20–23). The figures show an ovoid ribbed fruit with finer, closer, more regular ribbing than that of *N. boveyana* (now to be described). Heer's fig. 23 shows a mass of fruits lacking both the finer ribbing seen in his figs. 20–22, and the coarser ribbing of *N. boveyana*. The types in the Geological Survey Museum were so decayed in 1910 that the true nature of this endocarp could not be discovered, all finer features being obliterated.

There remains in these earlier records *Nyssa vertumni* Unger (C. & E. M. Reid, 1910 : 168, pl. 15, fig. 12) which is undoubtedly *Nyssa*.

There is indeed abundant evidence of the genus which occurs both at Bovey and Heathfield but the evidence is of one species only, now described as *N. boveyana* n. sp.

Nyssa boveyana n. sp.

(Pl. 16, figs. 150–157)

DIAGNOSIS. Endocarp sub-ovoid or less commonly sub-obovoid, tending to be arched, the dorsal side being less convex than the ventral, ventricose in the upper part of the ventral face. Germination valve triangular, relatively narrow in proportion to its length, 2·5–4·5 mm.; breadth, 2·5–3·25 mm. Length of endocarp, 6·8–11·5 mm.; breadth, 3·1–5·5 mm.

HOLOTYPE. Brit. Mus. (N. H.), No. V.33944.

DESCRIPTION. *Endocarp:* Sub-ovoid or less commonly sub-obovoid with a tendency to be less convex on the dorsal than on the ventral side, frequently ventricose in the upper part of the ventral surface, inflated and rather narrowed towards the base (but now usually flattened and often distorted in fossilization). The surface shows conspicuous, broad, rounded, longitudinal ribs and thin strands of fibres in the intervening narrow furrows ; the ribs, six to twelve in number, extend from base to apex on the ventral and lateral faces, are in general smoothly rounded but have a tendency to become nodular especially over the ventricosity, they are symmetrically placed, four or five being ventral and two lateral; along the crests of the lateral pair at the top of the endocarp are the sutures of the dorsal germination valve. Valve sub-triangular, gaping at the apex and along the sides which are slightly incurved towards the base, breaking irregularly along its base which is also that of the triangle.

On the dorsal surface there is a thin thread-like median rib, sometimes flanked on each side near the base by a broad scarcely raised rib, these die out before reaching the valve.

Length of endocarp, 6·8–11·5 mm.; breadth, 3·1–5·5 mm.

The dimensions of a series of endocarps, in millimetres, are as follows: 9·5 × 4·6, 10 × 4·6, 10 × 4, 9 × 5·1, 9 × 6, 11 × 3·1, 9 × 4·2, 11 × 4·2, 7·2 × 4·2, 9·8 × 4·5, 8 × 3·8, 9·8 × 5·5, 9 × 4, 10·5 × 4·8, 9 × 4·6, 7·4 × 4·9, 8 × 4, 7·2 × 4·1, 8 × 3·7, 9·5 × 5, 11·5 × 5, 6·8 × 8·9, 8·4 × 4.

Remarks and affinities. One of the most abundant fossils in the Bovey lignite basin occurring in profusion in the upper beds at Heathfield and in the lower beds at Bovey (C. & E. M. Reid, 1910 : 167). The structure of the endocarp and the characteristic short dorsal germination valve place them beyond doubt in *Nyssa*. Although now almost invariably flattened they were obviously much inflated in life. The many directions of distortion and compression show that originally they were but slightly compressed dorsi-ventrally below the valve. The valve itself was flat or slightly concave while there was considerable ventricosity in the corresponding part of the ventral face. Some specimens have been folded upon themselves from top to bottom, the folding always being towards the dorsal side. A few have been flattened laterally; these show the difference in curvature of the two surfaces described. The position of crushing has affected the appearance of the ridges which may be almost obliterated or folded longitudinally so as to appear as sharp ridges.

The specific determination of fossil *Nyssa* presents great difficulties as was recognized by Kräusel (1920) and later, in a series of papers by Kirchheimer.

Initially Kirchheimer (1934) regarded the abundant Brown Coal species described by Kräusel (1920), Gothan & Sapper (1933) and himself as agreeing both in morphology and histology with the Recent *Nyssa sylvatica* Marsh and indistinguishable from it. In later reviews of the subject (1938, 1939) he included all the Brown Coal " species " (including Middle Oligocene to Pliocene forms) in a single " form-species ", *Nyssa disseminata* (Ludwig), on the grounds that the characters did not permit of true specific determination. The length of *N. disseminata* was given as 0·8–1·9 cm.; breadth as 0·5–1·2 cm. (1938 : 339); length, 1–2 cm.; breadth, 0·5–1·2 cm. (1939*a* : 270).

It has not been possible to make a study from actual Brown Coal material and it is abundantly clear that at present species cannot be distinguished on histological grounds. It may, however, be possible to separate some species at least by size and shape of the endocarp plus shape of the germination valve. Thus the Pliocene Reuverian endocarps recorded as *N. sylvatica* by C. & E. M. Reid (1915) are distinguishable on these grounds from the Bovey species although apparently agreeing closely with the living *N. sylvatica*.

	N. sylvatica (Recent)	*N. sylvatica* var. *biflora* (Recent)	*N. sylvatica* (Pliocene; Reuver)	*N. disseminata* (Brown Coal)	*N. boveyana*
Number of specimens used	40	12	49	Kirchheimer's measurements (1938; 1939*a*)	42
Length of endocarp	6·9–8 mm.	7·5–10·5 mm.	5·5–11 mm.	8–20 mm.	6·8–11·5 mm.
Breadth of endocarp	4·5–6 mm.	5·2–7 mm.	3·5–6 mm.	5–12 mm.	3·1–5·5 mm.
Length of valve	3–3·5 mm. (5 specimens only)	3·5–3·6 mm. (2 specimens only)	2·25–3·25 mm. (8 specimens)	—	2·5–4·5 mm. (13 specimens)
Breadth of valve	4–5 mm.	4·5–5 mm.	3–4 mm.	—	2·5–3·25 mm.

The valve measured in Kirchheimer's figure of a Brown Coal *Nyssa* (Kirchheimer, 1938, pl. 4, fig. 24) appears to be: length about 4·5 mm.; breadth, 3·5 or 4 mm.

It will be noted that the Bovey endocarps are relatively longer, and narrower than those of *N. sylvatica* while the valves have a relatively narrow triangular form. These characters can be seen in the published figures.

It is possible, basing the suggestion on experience of the wide range shown by many other Eocene and Oligocene genera and species, that the Brown Coal species of *Nyssa*, at least in the older beds, may indeed be a true single species. Whether it should in that case be referred to *N. disseminata* Ludwig (1857) or to *N. rugosa* Weber (1852) is not within the scope of this paper. It does, however, raise the question of the relationship of the Bovey *Nyssa* to the Brown Coal forms, for it might be reasonably supposed that the same wide-ranging species occurred in Germany and Britain.

The figures already quoted, together with an examination of the published illustrations of *N. disseminata* (or *N. rugosa*) suggest that the Bovey *Nyssa* should provisionally be regarded as distinct. The germination valve in the two species is of similar narrow triangular character differing markedly from that of *N. sylvatica* from any source. On the other hand the Bovey *Nyssa* is appreciably smaller on the whole than the Brown Coal endocarps judging by Kirchheimer's measurements quoted above. Moreover if his figures (1938, pl. 4, figs. 21–24) are typical they show that *N. disseminata* tends to produce endocarps which are normally broadest above the middle: those from Bovey show a majority which are broadest at the middle. In view of these features a distinct name, *Nyssa boveyana*, has been given to the British material. But it obviously more closely resembles *N. disseminata* than *N. sylvatica* whether Recent or Pliocene.

Family MYRTACEAE

Section MYRTINAE

Genus ***MYRTOSPERMUM*** nov.

DIAGNOSIS. Seeds referable to the family Myrtaceae and probably to the section Myrtinae, with curved or U-shaped cavities, marginal hilum at the end of a condyle between the limbs of the curved cavity. Chalaza close to the hilum, terminal or sub-terminal on the inner side of one limb, micropyle adjacent to the hilum, terminal on the other limb.

TYPE SPECIES. *Myrtospermum variabile* n. sp. Bournemouth Freshwater Beds (awaiting description). Brit. Mus. (N. H.), No. V.34248.

Myrtospermum boveyanum n. sp.

(Pl. 16, figs. 160–168)

1910. "compressed winged seed" C. & E. M. Reid, p. 173, pl. 16, figs. 61, 62.

DIAGNOSIS. Seed of variable shape, much compressed, glossy, with thin testa. External surface ornamented with very regular concentric rows of cells 0·05–0·1 mm. in diameter (pits or convexities). Diameters of seeds, 1·25–2 mm.

HOLOTYPE. Brit. Mus. (N. H.), No. V.33950.

DESCRIPTION. *Seed:* Bisymmetric, flat (the degree of compression emphasized by fossilization, sometimes distorted and folded on itself), sub-oval, transversely-oval, sub-circular, or rounded-triangular, sometimes slightly emarginate at the hilum; limbs of the U-shaped cavity somewhat unequal in length and breadth, the micropylar limb being the longer and narrower. Hilar-scar elongate-oval, marginal between the limbs, micropyle small terminal on one limb, chalaza small sub-terminal on the other. Surface shining, ornamented externally with polygonal or hexagonal pits 0·05–0·1 mm. in diameter, but a few specimens give clear evidence that the pits are actually highly convex areas which have now collapsed; the pits are aligned parallel with the margin of the seed except near the middle where they diverge from the narrow median area between the limbs. In this median area individual pits are usually very obscure but when visible they are longer and narrower in this part of the testa than over the rest of the surface. In certain specimens the outlines of the surface pits are confused possibly owing to the presence of fine parenchymatous cells which form their walls as in other species of *Myrtospermum.* Testa only about 0·075 mm. thick in section. The outer part is formed by the coarsely pitted coat, the inner part shows evidence of equiaxial or rectangular cells 0·012–0·016 mm. in diameter; its structure is often obscure owing to intense compression. Diameter of seeds, 1·25–2 mm.

REMARKS AND AFFINITIES. Numerous seeds, all much crushed so that they are reluctant to split in the plane of symmetry. Fortunately one imperfect seed had split naturally and shows the U-shaped cavity and marginal germination. The form of the cavity was confirmed in other specimens by treatment with nitric acid, potassium chlorate and ammonia which rendered them semi-translucent. The curved form and unequal limbs are also clearly indicated by the alignment of the surface sculpture. The species occurs both at Bovey and Heathfield.

The relationship of the fossil to Myrtaceae is fully discussed in a forthcoming catalogue on the Bournemouth flora.

The species here described as *M. boveyanum* differs from others from Bovey, Heathfield, the Bournemouth Beds and elsewhere in its extreme degree of compression which must be, in part at least, original. It differs also in its thin walls, glossy surface and in the extreme regularity of its surface sculpture. It is also larger than the common Tertiary species awaiting description in a forthcoming catalogue as *Myrtospermum variabile*. Two specimens were figured and described by C. & E. M. Reid (1910 : 173, pl. 16, figs. 61, 62) but not named.

Myrtospermum dubium n. sp.

(Pl. 16, figs. 169–172)

DIAGNOSIS. Seed sub-circular or irregular in outline. Surface pits 0·025–0·05 mm. in diameter near the circumference, smaller near the hilum and between the limbs. Diameter of seed, 1·25–2 mm.

HOLOTYPE. Brit. Mus. (N. H.), No. V.33957.

DESCRIPTION. *Seed :* Sub-circular or irregular in outline, somewhat inflated, approximately bisymmetric but with a tendency to be more convex on one side than on the other. Two specimens have a slight elevation over the condylar area between the limbs of the U-shaped seed-cavity ; the exact form of the cavity is not exposed. Marginal hilum large, oval, micropyle small. Surface pitted, pits polygonal or hexagonal, about 0·025–0·05 mm. in diameter near the circumference, smaller and more obscure towards the hilum and between the limbs, tending to be arranged in rows parallel with the margin and to diverge from the area between the limbs. Tegmen thin and translucent, cells not seen.

Diameter of four seeds respectively, 1·6 mm., 1·6 by 1·25 mm., 2 mm., 1·75 by 1·25 mm.

REMARKS. Five seeds all much compressed and carbonized. One was fractured transversely whereupon it showed the two limbs of the cavity in transverse section; owing to the mode of preservation, the structure of the wall is obscure. The diameter is twice as great as that of typical seeds of *M. variabile.*

Myrtospermum sp.

(Pl. 16, figs. 173, 174)

DESCRIPTION. *Seed :* Bisymmetric, broadly sub-oval in outline, slightly truncate at the hilar end, inflated, but having a somewhat depressed median area ; U-shaped cavity with a maximum diameter of 0·35 mm.; micropylar limb longer and narrower than the chalazal limb, micropyle terminal at the end of the longer limb, chalaza sub-terminal on the other. Surface deeply pitted, pits equiaxial and hexagonal near the margin where they are 0·07 mm. in diameter, becoming irregular in form and size away from the margin, narrow and elongate over the condylar area between the limbs where they may measure 0·1 by 0·03 mm. Their walls appear not to be built of small cells. They form thick ridges with a median groove along which there is a marked tendency for splitting to occur. Testa thick, maximum thickness at the end opposite to the hilum (0·12 mm.). The outer part of the testa as seen in section is a single coat of large simple prismatic cells with their longest axes (0·09 mm.)

at right angles to the surface. The collapsed outer ends of these cells form the surface pits. Inner part of testa formed of uniform parenchyma, the cells being 0·025 mm. in diameter and radially arranged.

Diameter of seed, 1·1 by 0·9 mm.

REMARKS. One seed (V.33960), now broken at the hilar end and split marginally (irregularly) so as to expose the internal structure.

It differs in its small size from *M. boveyanum* and *M. dubium.* From *M. boveyanum* it also differs in its inflated form and less regular pitting. From *M. dubium* it also differs in its surface sculpture.

The single layer of prismatic cells forming the outer coat of the testa is characteristic. There is no indication, as in *M. variabile* from Cliff End, Sandbanks, Woolwich and Reading Beds, that it was formed of fine parenchyma. The middle lamella between the prismatic cells is clearly indicated by the narrow grooves along the middle of the ridges between the pits.

Family CORNACEAE

Section MASTIXIODEAE

Genus ***MASTIXIA*** Blume

Mastixia boveyana n. sp.

(Pl. 17, figs. 175–178)

1910. *Mastixia* n. sp. C. & E. M.Reid, p. 166, pl. 16, figs. 73, 74.

DIAGNOSIS. Endocarp with smoothly rounded, interrupted, longitudinal external ribs; median infold broad, rounded; wall with an external coat of parenchyma. Length about 11 mm. (estimated).

HOLOTYPE. A broken endocarp showing the infold. Brit Mus. (N. H.), No. V.33961.

DESCRIPTION. *Endocarp:* One-loculed, ribbed longitudinally, the ribs (about nine at each end, the number in the middle doubtful) smoothly rounded, interrupted, and with additional intercalated short ribs like elongate nodulations towards the middle of the endocarp. A large longitudinal germination valve occupies nearly half the breadth of the nut bearing on its inner surface a broad, rounded, median, longitudinal infold (0·4 mm. across, 0·8 mm. deep in the one specimen in which it could be measured); the length of the valve cannot be determined from the imperfect material available. Endocarp wall hard and woody, variable in thickness from about 0·4 mm. as measured through the grooves, to 0·5 mm. through the ribs, the locule being smooth, not ribbed in agreement with the external surface of the endocarp. In section the walls show the following structure: An inner coat of horizontally aligned sclerenchyma many layers thick giving a transversely striate locule-surface; the cells forming the outer layers of this coat gradually pass from a horizontal to an oblique, and from an oblique to a radial alignment, the radially aligned portion forming the main thickness of the wall. Along the margins of the valve, however, the oblique alignment is never lost but passes across the walls to the periphery constituting planes of weakness along which the valve separates ; outside the radial cells are a few peripheral layers of parenchyma, superficially the cells which form the layers are irregularly polygonal with an average diameter of about 0·025 mm., and no definite alignment. These cells give a smooth surface to the endocarp.

Length of endocarp unknown, estimated to be about 11 mm.; diameter of one fragment (probably basal end), 2·7 mm. (possibly increased by distortion).

Seed : Not seen ; cells of the testa, 0·03–0·05 mm. in diameter, preserved as impressions on the locule wall superposed on the transverse striations of the locule-lining.

REMARKS AND AFFINITIES. Two fragments of *Mastixia* endocarp were figured and briefly described by C. &. E. M. Reid (1910 : 166, pl. 16, figs. 73, 74) but no attempt was made at specific diagnosis. Six more fragments have now been recognized in their collection, two are the ends of nuts showing the complete circumference, both being distorted obliquely. Another fragment is from the middle of a nut with both ends and the valve missing ; a fourth, incomplete at the ends, appears to have broken along the edge of the valve. It suggests a length of about 11 mm. for the perfect specimen. All fragments are recognizable by their ribbing and microscopic structure, they therefore appear to offer a sufficient basis for specific determination.

Detailed histological studies of *Mastixia* and allied fossil genera from the Brown Coal of Germany have been published by Kirchheimer in papers from 1934 to 1939. Many details of the sclerenchyma and parenchyma of the endocarps are shown. The genus *Mastixia* was first recognized as a fossil by C. & E. M. Reid (1910). It has also been recorded more recently from the London Clay (Reid & Chandler, 1933 : 448, pl. 25, figs. 1–17).

Family PRIMULACEAE

Section LYSIMACHINAE

Genus ***LYSIMACHIA*** (Tourn.)

Lysimachia boveyana n. sp.

(Pl. 17, figs. 179, 180)

DIAGNOSIS. Seeds as in *Lysimachia*, 0·8–0·85 mm. long, 0·62–0·7 mm. broad. Surface rugosities forming small areoles with nodular boundaries. There are also semi-translucent tubercles especially well seen around the margin.

HOLOTYPE. Brit. Mus. (N. H.), No. V.33964.

DESCRIPTION. *Seed :* Rounded triangular in outline, originally gently convex on the dorsal face, facetted on the ventral face the two facets meeting to form a longitudinal median angle extending from margin to margin. Hilum elongate about the middle of this angle. Surface rugose, rugosities forming small areoles with nodular boundaries about 0·032 mm. in diameter on the ventral side, and 0·032 mm. or larger in diameter on the dorsal side. On the ventral side they are aligned in rows directed from the median angle to the margin, on the dorsal side no such definite arrangement is apparent. Around the margin semi-translucent tubercles, 0·025 mm. long and 0·022 mm. broad, are visible. Similar tubercles, or their remains can also be seen over parts of the surface but they are less prominent than around the margin.

Length of seed, 0·8–0·85 mm.; breadth, 0·62–0·7 mm.

Remarks and affinities. Two seeds. The form, character of testa, and median hilum as described, are only to be found combined in the family Primulaceae. Seeds of this shape with a simple hilar ridge extending from edge to edge have been seen only in the Lysimachinae and closely comparable structure in the genus *Lysimachia.*

The majority of species have larger seeds, but in *L. japonica* some seeds are comparable in size (0·85 by 0·65 mm. and 0·9 by 0·65 mm. for example) although average sized seeds are larger (1·05 by 0·9 mm and 0·9 by 0·75 mm.).

The genus *Lysimachia* is distributed through the temperate and sub-tropical regions of the whole world.

Family Symplocaceae

Genus ***SYMPLOCOS*** Jacquin

Symplocos anglica n. sp.

(Pl. 17, figs. 181–186)

1862. *Nyssa europaea* Unger : Heer, p. 1066, pl. 69, figs. 11–17.
1910. *Nyssa europaea* Unger : C. & E. M. Reid, p. 167, pl. 15, fig. 9.

Diagnosis. Endocarp ovoid to obovoid or oblong, three-loculed, apical depression with gently sloping edges markedly truncating the apex of the endocarp. Base rounded. Outer surface finely wrinkled longitudinally. Length, 3·5–6·7 mm.; breadth, 2·2–4·4 mm.

Holotype. A somewhat compressed endocarp. Brit. Mus. (N. H.), No. V.33965.

Description. *Endocarp :* Syncarpous, three-loculed, locules arranged around a central canal, one or two occasionally being abortive, opening by wide apertures into the large apical depression the edge of which slopes gently inward being neither thickened nor rounded. At the rounded base is a small attachment scar from which the funicle passes into the central canal. The endocarp may be either obovoid, oblong with rounded base, or ovoid, markedly truncated at the top by the apical depression, but the truncation may be obscured either by the persistent base of the style or by oblique distortion when it appears ovoid. Wall possibly formed of fused mesocarp or endocarp (the former preserved only in part if present), or the mesocarp may be entirely absent ; thickness of wall averaging about 0·25 mm.; its outer surface is finely wrinkled longitudinally, it usually shows about twelve to sixteen irregular, sometimes interrupted and nodular rather obscure longitudinal ribs; surface cells mostly very small with obscure outlines but occasionally (when the mesocarp is abraded ?) the wall is finely and evenly pitted.

Length of endocarp, 3·5–6·7 mm.; breadth, 2·2–4·4 mm. Average length, 4·8 mm.; average breadth, 3·3 mm.; average breadth if uncompressed, about 2·1 mm.; breadth of apical depression as compressed, 1·5–2 mm.

REMARKS AND AFFINITIES. About thirty-four specimens, all much crushed, some symmetrically others obliquely. The species was described and figured as *Nyssa* both by Heer and by C. & E. M. Reid. However it is clear that such truncated specimens could not be *Nyssa* whereas they agree in character and size with the species of *Symplocos* here described. Other fossil species based on fruits are commonly much larger and differ in other ways. *S. gregaria* Unger (1866 : 31, pl. 11, figs. 1*g–h*) is one of the more comparable species but is more variable in size ranging from 4·1–12·5 mm. in length, and from 2·1–6·2 mm. in breadth (Kirchheimer, 1936*a* : 95, pl. 9, figs. 5*a*, *b*) gives the dimensions as 4–10 mm. length, 2·5–6 mm. breadth. The fruits of *S. gregaria* are represented as larger, more markedly truncate, with finer, more regular and numerous grooves and with thicker walls. *S. kirstei* Kirchheimer (1939 : 285, pl. 3, fig. 3) is also similar but larger (length, 5·5–11 mm.; breadth, 3·5–6 mm.) and relatively longer and narrower.

A new name, *Symplocos anglica*, has therefore been given to the Bovey fruits.

Symplocos headonensis Chandler

(Pl. 17, figs. 187, 188)

1910. ? *Nyssa obovata* Weber : C. & E. M. Reid, p. 168, pl. 15, fig. 10.
1926. *Symplocos headonensis* Chandler, p. 40, pl. 7, fig. 3 ; text-fig. 24.

DESCRIPTION. *Endocarp :* Syncarpous, four-loculed, the locules arranged around a central canal and opening above by wide apertures into a large apical depression ; broadly ovoid, urceolate, or sub-globular, conspicuously truncated by the apical depression ; margin of the apical depression thickened, somewhat rounded ; attachment indicated by a small sunk scar at the base, thickness of wall, 0·2 mm.; thickness of septum, 0·05 mm. Surface without ribs, but uneven, surface cells angular, unequal in size, with a tendency to be aligned in longitudinal rows near the base thus producing obscure fine striations.

Length of an obscurely four-lobed and slightly urceolate specimen (possibly immature), 6 mm.; breadth, 5·5 mm. Length of a second well-developed specimen, 7 mm.; breadth, 5·5 mm. Estimated diameter when uncompressed, 3·5 or 3·6 mm.

REMARKS AND AFFINITIES. Three specimens one of which is in the Geological Survey Museum if the specimen figured by C. & E. M. Reid (1910, pl. 15, fig. 10) really is of this character. The illustration indicates a larger, broader form than *S. anglica*. This species is near in size, form, and general appearance to *S. headonensis* Chandler from Hordle which see for the probable relationship of this species to living forms. The species occurs both at Bovey and Heathfield.

Family SOLANACEAE

Genus ***SOLANISPERMUM*** nov.

DIAGNOSIS. Seeds of unknown generic relationship agreeing with Solanaceae in form and structure.

Solanispermum reniformis n. sp.

(Pl. 17, figs. 189–191)

1910. *Carpolithus* sp. 5 C. & E. M. Reid, p. 174, pl. 16, fig. 72.

A number of seeds of Solanaceae with distinctive rugose surface which characteristically weathers into fibres occur in the Lower Bagshot, Bournemouth Freshwater and Marine Beds, and the Cliff End Beds near Mudeford as well as at Bovey. The most perfect specimen was found at Branksome Dene and an extremely good seed showing the hilar aperture was found at Sandbanks.

In order that the description should be as complete as possible it has been largely based on material from the Bournemouth area.

DIAGNOSIS. Seed transversely oval or reniform in outline, occasionally hooked, surface normally with coarse, interrupted, sinuous rugosities or tubercles which produce a pitted effect in places. An outer coat, rarely preserved, shows " pits " with sinuous outlines. The rugose coat shows fine striae at right angles to the tubercles. Splitting along the striae on drying produces a fibrous effect. Inner coat spongy formed of equiaxial cells. Maximum diameter of seeds about 3·5–4·8 mm.

HOLOTYPE. A perfect seed figured by C. & E. M. Reid (1910, pl. 16, fig. 72). Geol. Surv. Colln. No. 1805.

DESCRIPTION. *Seed:* Bisymmetric, flattened or slightly inflated, transversely oval or reniform in outline, occasionally hooked. Hilum usually marginal occupying part of the concave margin in reniform seeds and one of the longer margins in oval seeds, large and gaping, elongate-oval leading into a small cavity separated from the main seed-cavity by a thin curved partition seen in longitudinal sections of the seed. Probably the funicle lay close to this partition within the hilar cavity. A few seeds are distorted (in growth) so that a gaping hilum is twisted on to one of the broad surfaces. Dorsi-ventral flattening of such distorted seeds may have occurred. Micropyle usually marginal, adjacent to the hilum. Its position is most apparent in hooked seeds where it occupies the extremity of the hook. Surface occasionally showing traces of an outer coat with coarse digitate cells, but in most specimens this is worn away. As normally preserved ornamented with interrupted sinuous rugosities which diverge from the hilum. They produce a pitted effect in places, the pits being about 0·05–0·1 mm. in diameter. The rugose seed-coat is about 0·1 mm. thick ; it appears striate, the striae crossing the rugosities more or less at right angles and lying parallel with the margin near the circumference of the seed. Splitting tends to occur along the striae in weathered or dried specimens producing a fibrous effect. Close examination of the " fibres " shows them to be formed of fine equiaxial cells 0·012 mm. in diameter. Several layers of such " fibres " occur in this integument. Within it is a spongy coat, 0·4 mm. thick, formed of compact soft parenchyma. The lining of the seed-cavity is striate, the striae diverging from the neighbourhood of the hilum (actually from the closely associated chalaza).

Maximum diameter of seeds, 4·8 mm.; commonly 3·5 mm.; diameter at right angles to it, 2·25–3·6 mm.

REMARKS AND AFFINITIES. One seed figured by C. & E. M. Reid (1910) from Heathfield and another (now broken) from the same pit collected by E. M. Reid and Chandler in 1932. The curved outline, flattened seed, large gaping marginal hilar cavity and even the mode of distortion which brings the gaping hilar cavity on to one of the broad surfaces all suggest Solanaceae. Seeds of *Capsicum* and allied genera show a general resemblance but the succession of coats cannot be matched exactly in any genus examined. Striate fibrous coats, or striate fibrous outgrowths of the testa are found in *Lycopersicum* and *Cyphomandra.*

Reference to a living genus cannot be made and even the reference to the family is somewhat tentative until living seeds with a closely comparable succession of coats have been found. Meanwhile these readily recognizable specimens are referred to a new genus *Solanispermum* as it is in Solanaceae that the closest resemblance has so far been traced.

INCERTAE SEDIS

Carpolithus sp.

(Pl. 17, figs. 192–194)

Fruit : Inferior with remains of three small triangular patent perianth segments at the apex. Elongate having three broad surfaces two of which are ventri-lateral and one dorsal. Surfaces separated by longitudinal angles, the lateral angles sharp and almost flanged, the ventral one fibrous. The broad perianth segments each lie opposite one of the broad surfaces. In profile the fruit is long and narrow. The ventral angle is straight. The dorsi-lateral angles are convex hence the two ventri-lateral surfaces are more or less semi-oval (but unequal). The dorsal face is narrowly oval. Ventral surfaces smooth formed of fine, close, elongate, obliquely aligned fibres, 0·008 mm. broad. Dorsal surface with similar fibres transversely aligned. Fibrous surfaces often concealed by a rough coat of equiaxial cells, 0·025 mm. in diameter.

Length, 2·25–3·5 mm.; breadth, 1–1·3 mm. Breadth of ventral faces in one specimen, 1 and 0·3 mm. respectively, and in a second specimen, 0·5 and 0·52 mm. respectively.

REMARKS. Thirteen endocarps from Heathfield. The relationship of these small fruits has not been established. The difference in form of the dorsal and two ventral faces or facets suggests that the fruits grew in close association with one another, the ventral faces possibly in actual contact.

Carpolithus sp.

(Pl. 17, figs. 195–197)

A three-, four- or possibly five-partite capsule, the segments united still at the base. Segments lanceolate, three only preserved, two being attached, the third represented by a detached distal end. They diverge from one another and have strongly incurved tips. The length of one segment, 4·2 mm.; breadth, 0·9 mm. (but the full length is not shown owing to the strong incurving of the tip). The second (attached) segment 3·6 mm. with deeply incurved tip by 1·5 mm. The number of segments in the perfect fruit can only be guessed by the angle between existing segments.

Segments highly rugose and even nodular on both surfaces; margins greatly thickened and almost revolute. Hence the segments are concave externally, the broader one having a slight median ridge which makes it biconcave. All show traces of spines near the base, one each side of the median line in the shorter of the two attached segments. Cells of outer surface equiaxial, about 0·016 mm. in diameter.

Carpolithus sp.

(Pl. 17, figs. 198, 199)

Endocarp (?) *:* Syncarpous, sub-ovoid, three-lobed and three-carpelled, or two-lobed and two-carpelled by suppression, the base being sunk between the lobes. Dehiscing loculicidally from the apex (which is always broken irregularly), almost to the base. No central axis seen. Wall close-textured, hard, 0·033 mm. thick (cells indistinct owing to intensely carbonized condition in section). Surface smooth, of equiaxial cells 0·016 mm. in diameter usually evenly distributed but occasionally aligned in obscure longitudinal rows. Septa very thin, columnar in section. Locule lined by equiaxial cells, 0·012 mm. in diameter.

Length of longest specimen, 5·5 mm. (incomplete at apex); breadth, 3·25 mm. Length of second specimen, 4 mm.; breadth, 2·1 mm.

Seed (lying within the locule near the broken apex) : Linear with a median ridge on the concave side at one end, somewhat tufted at the other end, too decayed to show cell-structure. Length, 2·7 mm.; breadth, 0·6 mm. at the broadest estimate, but actually bent so as to appear only 0·5 mm. broad.

REMARKS. Two specimens from Bovey, one from Heathfield. Also three very imperfect specimens from Bovey which may belong to this species. The relationship is undiscovered.

Carpolithus sp.

(Pl. 17, figs. 200–202)

Several much collapsed and immature fruits are narrow-obovoid or urceolate, three-lobed, three-loculed, the lobes being rather slender and much smaller than those figured in Pl. 17, figs. 198, 199. Base sunk between the lobes. Apex in best preserved specimens with three minute patent persistent perianth segments one corresponding to each lobe. Dehiscence by loculicidal splitting from the apex downwards showing apical canals (or canal) (style ?). Surface dull, finely rugose, cells aligned in obscure longitudinal rows. Locule transversely striate, striae 0·0125–0·017 mm. apart due to small cells aligned in transverse rows. Thickness of walls about 0·025 mm.; thickness of septum (where seen near the apex), 0·016 mm. Length and breadth of four specimens respectively: 4·6 mm. (broken at one end) × 2·4 mm., 4·2 mm. × 2 mm., 4·2 × 2 mm., 4·6 mm. × 2 mm.

Seed: Occupying the whole length of the locule, flattened. Longitudinally striate.

REMARKS. The form of this tiny fruit and the three minute patent perianth segments recall the rather larger, flattened, immature fruits of *Eomastixia bilocularis* found in the Bournemouth Beds and the considerably larger immature specimens of another *Eomastixia* from Lake (awaiting description). There is nothing in the limited evidence available to exclude such a relationship although it should be noted that living *Mastixia* perianth segments are four- to five-partite. A species of *Mastixia* occurs in the Bovey lignites but any suggestion as to the relationship must be regarded as tentative only.

Carpolithus sp.

(Pl. 17, fig. 203)

An elongate ovoid seed with a few longitudinal angles or crumples. No definite organs are visible but the alignment of cells at the pointed end and crumples at the broad end suggest the presence of organs in these positions. Surface formed of inflated longitudinally aligned cells about 0·025 mm. long and 0·001 mm. broad, but over much of the surface the cells have been abraded so that no cell-structure can be seen.

Length of seed, 2·6 mm.; breadth, 0·9 mm.

Bulbil ?

(Pl. 17, fig. 204; Text-fig. 3)

Two sub-spherical bodies, slightly flattened on one side with a large deep depression at the middle of the flat surface, and a second similar depression on one side, may

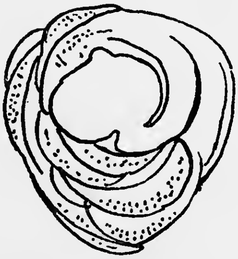

FIG. 3. Bulbil ? Diagrammatic section showing overlapping layers of thick bracts. × 4 approx.

be bulbils or buds. They show superficially an obscure network of shallow furrows. When fractured they reveal overlapping layers of thick bracts. Diameter about 6·6–7 mm. Relationship not known.

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PLATE 11

Osmunda lignitum (Giebel)

FIG. 1. Two sporangia which have burst and become interlocked. × 28. (V.33833.)

FIG. 2. Diagram to explain Fig. 1. Annulus at (*a*).

FIG. 3. The same pair of sporangia, opposite surface. × 28.

FIG. 4. Diagram to explain Fig. 3. Annulus at (*a*).

FIG. 5. A single burst sporangium showing the annulus at (*a*). × 60 approx. (V.33833.)

FIG. 6. A group of spores embedded in remains of sporangium from the specimen in Figs. 1, 3. The spores show the fine granulations of the surface. × 400. (V. 33833*a*.)

All the above are from Bovey.

Salvinia boveyana n. sp.

FIG. 7. A sporocarp showing the globular thin-walled sporangia projecting through the wall. × 28. (V.33834.)

FIG. 8. Another less mature specimen showing a closely compacted mass of sporangia. Also figured C. & E. M. Reid, 1910, pl. 16, fig. 57. × 12. Geol. Surv. Mus. Colln. No. 76682.

FIG. 9. A sporangium showing spores embedded in a froth-like mass. × 150. (V.33835.)

FIG. 10. Another sporangium with stalk. × 150. (V.33835.)

FIG. 11. Part of another. × 400. (V.33835.)

All the above are from Bovey.

Potamogeton tenuicarpus C. & E. M. Reid

FIG. 12. An endocarp, side, with keel on the right beginning to gape. The seed (*s*), protrudes at the apex. × 15. (V.33836) Bovey.

FIG. 13. Another endocarp showing the gap between the ends of the curved carpel. × 15. (V.33837) Bovey.

FIG. 14. Pollen-grain probably belonging to this species. × 1000. J. B. Simpson Colln. Heathfield.

Stratiotes websteri (Brongniart)

FIG. 15. A seed, ventral side, (*c*) collar. × 6·5. (V.33838.)

FIG. 16. The same, dorsal, looking on to the keel. The specimen is somewhat crushed dorsiventrally. × 6·5.

FIG. 17. Part of a seed which has begun to split and burst. It shows the smooth rounded collar and the keel (*k*) arising out of it. × 6·5. (V.33839.)

FIG. 18. Valve of a seed, broken at the micropylar end, inner surface showing the short transverse raphe (*r*). × 6·5. (V.33840.)

FIG. 19. Another broken valve as in Fig. 18. × 6·5. (V. 33841.)

All the above are from Bovey.

Caricoidea nitens (Heer)

FIG. 20. A laterally compressed fruit, truncate at the base. Also figured Heer (1862, pl. 70' fig. 18). × 6 approx.

FIG. 21. Another fruit. The impression of the calyx is clearly seen in profile at the base. Also figured Heer (1862, pl. 70, fig. 16). × 6 approx.

FIG. 22. Base of a dorsiventrally compressed fruit showing the basal calyx scar in the centre of which is the plug closing the passage to the locule. × 6 approx.

FIG. 23. Holotype. Figured Heer (1862, pl. 70, fig. 20). A laterally compressed fruit from which a tangential slice had been cut to display the small locule. × 6 approx. (V.33842.)

All the above are from Bovey.

Figs. 8, 20–23: *Photo C. Reid;* Figs. 9–11: *Photo W. N. Croft;* Fig. 14: *Photo J. B. Simpson.*


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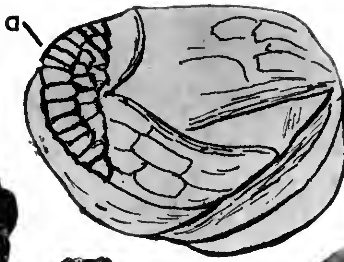

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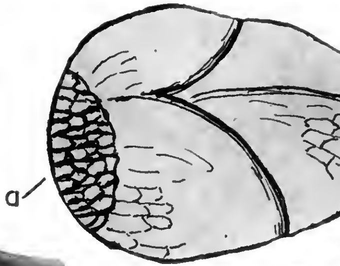

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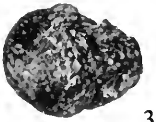
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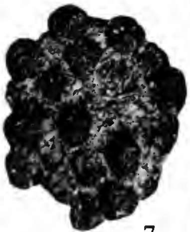
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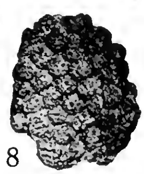
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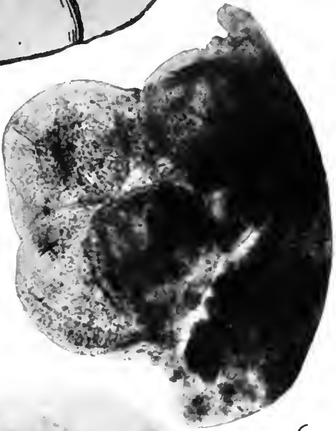
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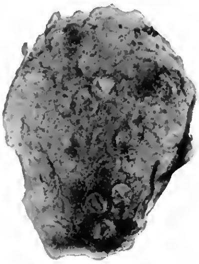
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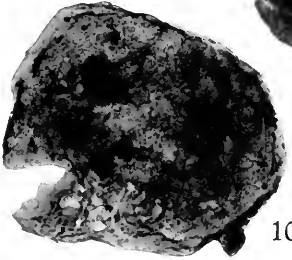
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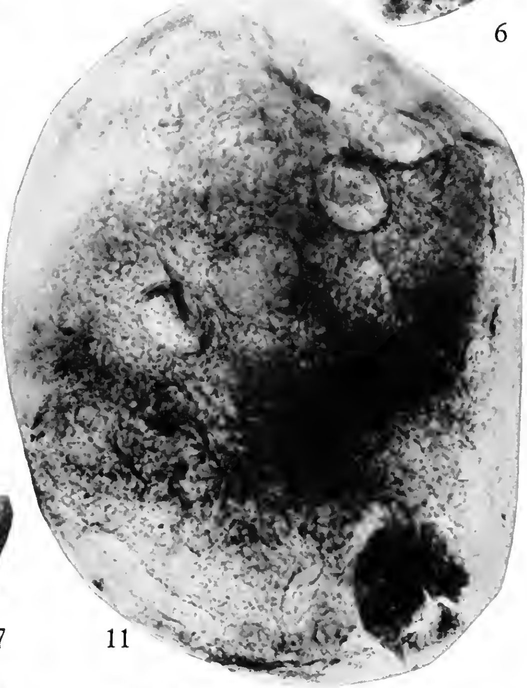
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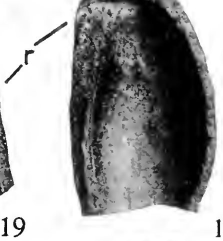

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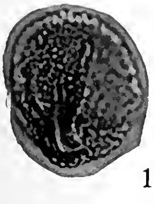
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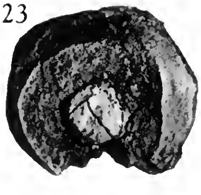
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OSMUNDA, SALVINIA, POTAMOGETON, STRATIOTES, CARICOIDEA

PLATE 12

Calamus daemonorops (Unger)

FIGS. 24, 25. Two young fruits or female flowers showing three styles. × 15. (V.33846—47.)

FIG. 26. Somewhat older fruit; style bases are preserved but the three-fid style has disappeared. × 15. (V.33848.)

FIG. 27. A fruit showing clearly the inner and outer perianth segments. × 15. (V.33849.)

FIG. 28. A better developed fruit also showing the two whorls of persistent perianth segments. × 15. (V.33850.)

FIG. 29. Base of immature female fruit, the striate bracts in two whorls each of three bracts. × 15. (V.33851.)

FIG. 30. Small immature fruit showing overlapping reflexed scales. × 15. (V.33852.)

FIG. 31. A larger, better developed but much compressed fruit showing the overlapping reflexed scales. × 15. (V.33853.)

FIG. 32. The three-partite bract-like perianth of a male flower. × 15. (V.33854.)

FIG. 33, 34. Two more male flowers. × 15. (V.33855–56.)

FIG. 35. Fragment of a fruiting axis. × 6·5. (V.33857.)

FIG. 36. A smaller fragment of an axis. × 6·5. (V. 33858.)

FIG. 37. Immature seed extracted from a fruit. × 15·5 (V.33859.)

FIGS. 38–41. Spines and spine bases. × 2·8. (V.33860–63.)

FIG. 42. A pollen-grain (doubled on itself). × 1000. J. B. Simpson Colln.

FIG. 43. A crumpled immature seed possibly belonging to this species. × 15·5. (V.33864.)

FIG. 44. The same, opposite side. × 15·5.

All the above (except Figs. 37 and 42 from Heathfield) are from Bovey.

Myrica boveyana (Heer)

FIG. 45. An endocarp showing somewhat rugose surface. × 6·5. (V.33865.)

FIG. 46. A laterally flattened endocarp which may belong to this species. × 6·5. (V.33866.)

FIG. 47. One valve of an endocarp, internal surface, showing coat of equiaxial cells: (*f*) funicle, (*st*) stylar canal. × 15. (V.33867.)

FIG. 48. Neotype. Another valve from a broader fruit. Interior. Lettering as above. × 15. (V.33868.)

All the above are from Bovey.

Fig. 42: *Photo J. B. Simpson.*


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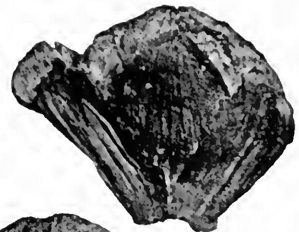
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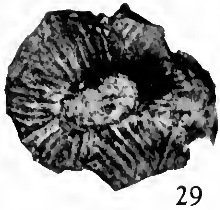
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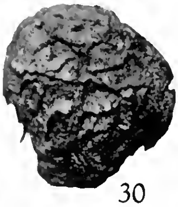
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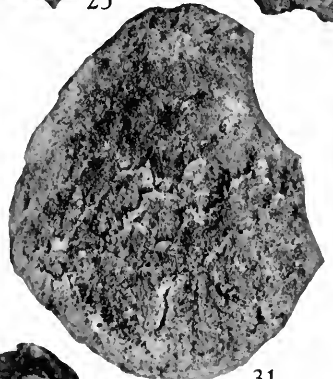
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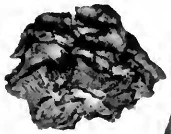
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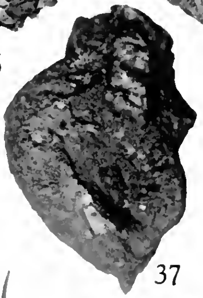
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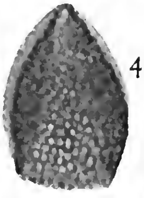
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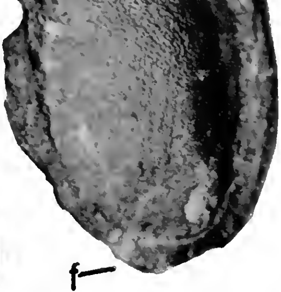

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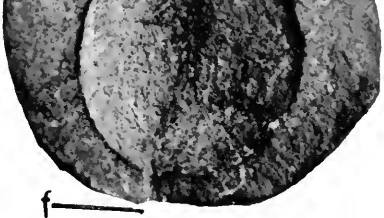

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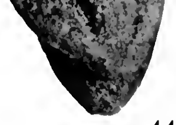
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CALAMUS, MYRICA

PLATE 13

Corylus sp.

FIG. 49. Fragment of an inflorescence of male flowers with anthers. × 15. (V.33869.) Heathfield.

FIG. 50. The same, opposite side. × 15.

FIG. 51. Pollen grain from the above. × 1000. J. B. Simpson Colln.

Carpinus boveyanus (Heer)

FIG. 52. Neotype. Fruit with accrescent calyx preserved showing longitudinal furrows associated with fibres which arise from the margin of the basal scar (*s*) of attachment to the wing-like bract. × 6·5. (V.33870.)

FIG. 53. Another longer, narrower fruit ; (*s*) as above. × 6·5. (V.33871.)

FIG. 54. Another fruit. × 6·5. (V.33872.)

FIG. 55. Another. × 12. (V.33873.) Heathfield.

FIG. 56. Another. × 15. (V.33874.)

FIG. 57. A small fruit with remains of superior perianth at the apex of the accrescent calyx ; one of the two styles is preserved. × 6·5. (V.33875.)

FIG. 58. A specimen with styles preserved. Perianth much worn. × 6·5. (V.33876.)

FIG. 59. A fruit, the lateral scar near the base indicates that it was one of a pair of fruits, the other being but little developed. × 12. (V.33877.) Heathfield.

FIG. 60. A twinned fruit. × 12. (V.33878.) Heathfield.

FIG. 61. A small twinned fruit. × 12. (V.33879.) Heathfield.

FIGS. 62–65. Four twinned fruits. In Fig. 62 part of the basal end of one of the pair is broken away exposing the locule. The upper part is splitting in the plane of symmetry. Fruits in Figs. 64, 65 very unequally developed. × 6·5. (V. 33880–83.)

FIG. 66. Base of dorsiventrally compressed fruit. *Carpinus* ? × 6·5. (V.33884.)

FIG. 67. One valve (interior) of another dorsiventrally compressed fruit probably *Carpinus*. × 6·5. (V.33885.)

Fagus minima n. sp.

FIG. 68. Holotype. An endocarp : (*s*) basal scar of attachment. × 6·5. (V.33886.)

FIGS. 69, 70. Two endocarps. × 6. The figures are reproduced from C. & E. M. Reid (1910, pl. 16, figs. 67, 68). Geol. Surv. Mus. Colln. No. 76683.

Zelkova boveyana n. sp.

FIG. 71. Holotype. Endocarp, lateral aspect : (*st*) style, (*a*) attachment. × 15. (V.33887.)

FIG. 72. The same, marginal view. × 15.

FIG. 73. The same, as in Fig. 72 but more tilted to show the attachment (*a*). × 15.

Moroidea boveyana n. sp.

FIG. 74. Holotype. Fruit, side. The rounded base is broken, (*st*) style ; (*f*) projection marking the point of entry of the funicle to the sub-apical placenta. × 15. (V.33888.)

Brasenia ovula (Brongniart)

FIG. 75. A somewhat crumpled and distorted seed showing longitudinal corrugations of the surface due to effects of contraction and alignment of the cells : (*e*) position of embryotega. × 15. (V.33889.) Heathfield.

Magnolia boveyana n. sp.

FIG. 76. Holotype. A seed, concave surface with raphe : (*ch*) chalaza. × 6·5. (V.33890.) Heathfield.

FIG. 77. The same, opposite convex surface. × 6·5.

FIG. 78. Another seed, raphe side. × 6·5. (V.33891.) Heathfield.

FIG. 79. The same, opposite side. × 6·5.

FIG. 80. A seed longitudinally sectioned showing the canal (*ca*) through the chalaza-plug. × 6·5. (V.33892.) Heathfield.

Unless otherwise stated all the above are from Bovey.

Fig. 51 : *Photo J. B. Simpson* ; Figs. 55, 59–61, 70 : *Photo C. Reid.*


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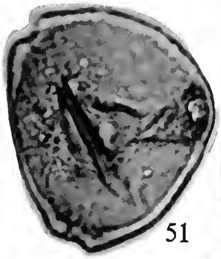
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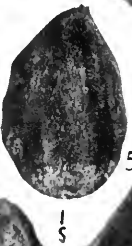
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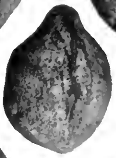
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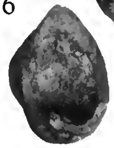
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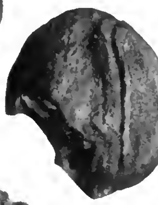
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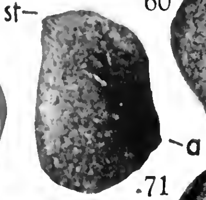
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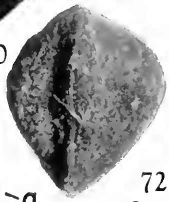
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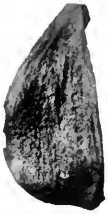
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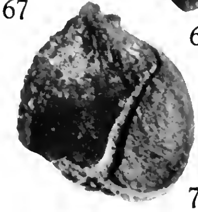
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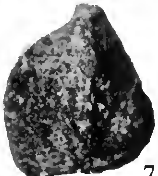
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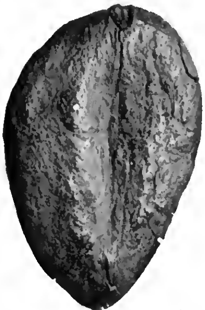
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CORYLUS, CARPINUS, FAGUS, ZELKOVA, MOROIDEA, BRASENIA, MAGNOLIA

PLATE 14

LAURACEAE

FIG. 81. An empty cupule with simple rim tilted to show the inner surface and scar of attachment of the berry. × 6·5. (V.33893.)

FIG. 82. Another. × 6·5. (V.33894.)

FIG. 83. A wrinkled leathery type of cupule with entire rim. × 6·5. (V.33895.)

FIG. 84. Leathery cupule with distinct sepals at the rim. × 6·5. (V.33896.)

FIG. 85. Another of similar type but much more slender. × 6·5. (V.33897.)

FIG. 86. Small cupule with distinct sepals enclosing berry. × 6·5. (V.33898.)

FIG. 87. Cupule with entire rim, berry enclosed. × 6·5. (V.33899).

FIG. 88. Small cupule with berry. × 6·5. (V.33900.) Bovey.

FIG. 89. A detached berry, imperfect below. × 6·5. (V. 33901.)

FIG. 90. Incomplete berry having glandular secretions beneath the skin. × 6·5. (V.33902.) Bovey.

FIG. 91. Another. × 6·5. (V.33903.) Bovey.

Unless otherwise stated all the above are from Heathfield.

Capparidispermum boveyanum n. sp.

FIG. 92. Holotype. A seed showing curved form and ornamentation : (*h*) hilum. × 15. (V.33904.)

FIG. 93. The same, opposite side. × 15.

FIG. 94. Another seed showing the hilar aperture (*h*) very clearly. × 15. (V.33905.)

FIG. 95. A larger but more compressed seed in which the cotyledonary limb is somewhat more incurled. × 15. (V.33906.)

FIG. 96. One valve of a seed, inner surface, showing the curved cavity. The form of the partition between the limbs is highly characteristic of Capparidaceae. × 15. (V.33907.)

All the above are from Bovey.

HAMAMELIDACEAE Genus ?

FIG. 97. A seed, side, showing a lobe of the large hilar scar at (*l*). × 6·5. (V.33908.) Bovey.

FIG. 98. The same seed at right angles to Fig. 97. The hilar scar (*h*) crosses the proximal end of the seed and has a lobe on each of its broad faces. × 6·5.

FIG. 99. A seed of another species showing the long narrow hilar scar (*h*). At the opposite end of the seed a small portion of the septum between two locules adheres and shows a strand of fibres from the axis of the carpel. × 6·5. (V.33909.) Heathfield.

Rubus microspermus C. & E. M. Reid

FIGS. 100–105. Six endocarps showing variations in form and size. × 15. (V.33910–15.) Bovey.

FIGS. 106–109. Four endocarps. × 15. (V.33916–19.) Heathfield.


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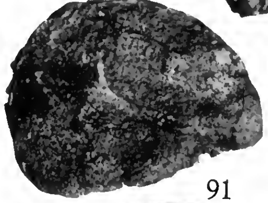
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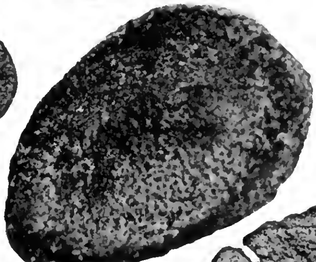

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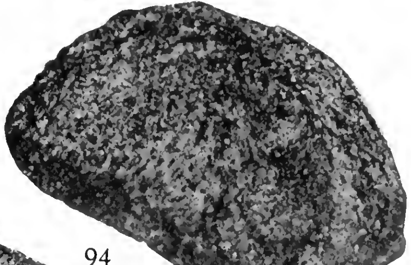

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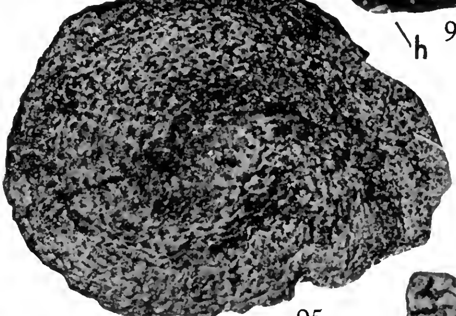
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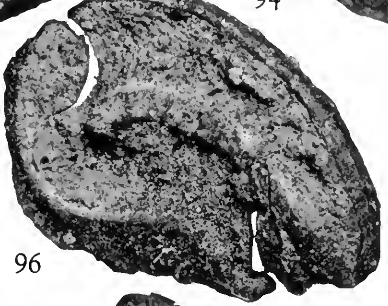
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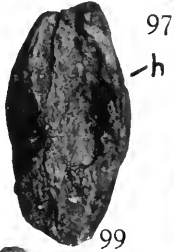

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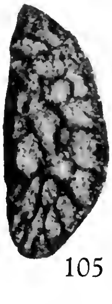
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LAURACEAE, CAPPARIDISPERMUM, HAMAMELIDACEAE, RUBUS

LEGUMINOSAE Genus ?

FIG. 110. A crushed seed. × 6·5. (V.33920.)
FIG. 111. Another. × 6·5. (V.33921.)
FIG. 112. Part of a third seed showing hilum and the testa in section. × 6·5. (V.33922.)

The above are from Heathfield.

Meliosma reticulata (C. & E. M. Reid)

FIG. 113. Valve of an endocarp, external surface showing reticulations. × 6·5. (V.33923.)
FIG. 114. The same, interior: (*f*) funicular canal. × 6·5.
FIG. 115. Neotype. A perfect but laterally compressed endocarp. × 6·5. (V.33924.)
FIG. 116. The same, opposite surface. × 6·5.
FIG. 117. A dorsiventrally compressed endocarp, looking on to the attachment (centre of figure). × 6·5. (V.33925.)
FIG. 118. The lower part of one valve of an endocarp, interior showing the attachment and short funicular canal (*f*). × 6·5. (V.33926.)

All the above are from Bovey.

Parthenocissus britannica (Heer)

FIG. 119. Neotype. A typical seed, dorsal, showing long narrow chalaza. × 6·5. (V.33927.) Bovey.
FIG. 120. The same, ventral, showing lateral infolds diverging upwards. × 6·5.
FIG. 121. Another seed, dorsal. × 6·5. (V.33928.) Bovey.
FIG. 122. The same, ventral. × 6·5.

Parthenocissus boveyana n. sp.

FIG. 123. Holotype. Seed, dorsal. × 6·5. (V.33929.) Bovey.
FIG. 124. The same, ventral. × 6·5.
FIG. 125. Another seed with outer coat removed, dorsal (base broken). × 6·5. (V.33930.) Bovey.

Vitis hookeri Heer

FIG. 126. Seed (imperfect above on the left), dorsal × 6·5. (V.33931.) Heathfield.
FIG. 127. The same, ventral. × 6·5.

Vitis stipitata n. sp.

FIG. 128. Seed (imperfect on the left), dorsal. × 6·5. (V.33932.) Heathfield.
FIG. 129. The same, ventral. × 6·5.

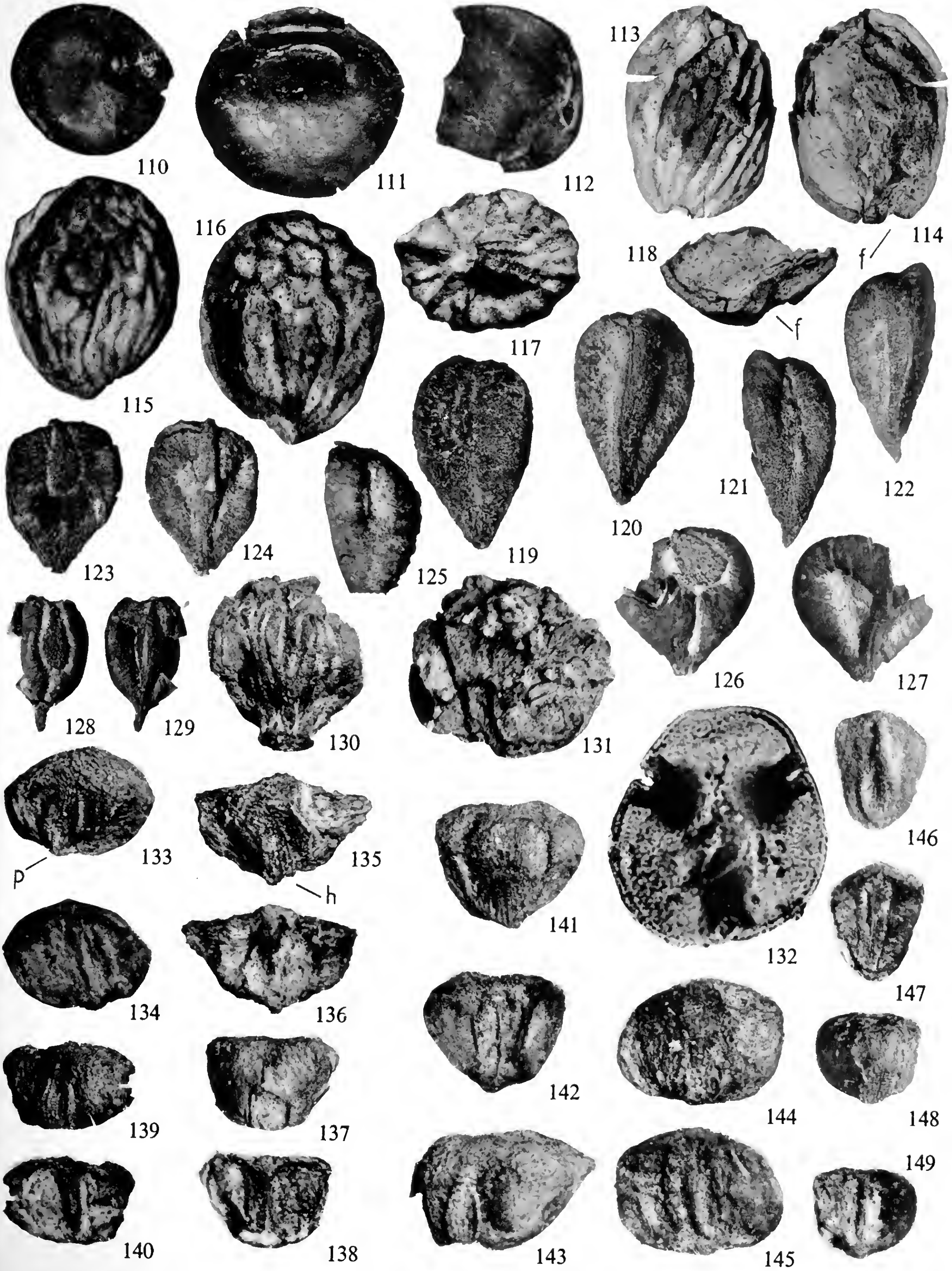
Tilia sp.

FIG. 130. A group of anthers. × 15. (V.33933.)
FIG. 131. Another group of anthers. × 15.
FIG. 132. A pollen grain from anthers in Fig. 131. × 1000. J. B. Simpson Colln.

The above are from Heathfield.

Microdiptera parva n. gen. et sp.

FIG. 133. Seed, dorsal, with pitted oval germination valve and striate wing surface. × 15·5. (V.33934.)
FIG. 134. The same, ventral, showing median longitudinal raphe ridge also a furrow on each side of it flanked by a wing. × 15·5.
FIG. 135. Seed with pointed wings, dorsal: (*h*) hilum. × 15·5 (V.33935.)



LEGUMINOSAE, MELIOSMA, PARTHENOCISSUS, VITIS, TILIA, MICRODIPTERA

FIG. 136. The same, ventral. × 15·5.

FIG. 137. Seed, dorsal. The germination valve has come away and the cavity is full of sand. × 15·5. (V.33936.)

FIG. 138. The same, ventral, showing wings and raphe ridge very clearly. × 15·5.

FIG. 139. Seed, dorsal, pitted valve very clear. × 15·5. (V.33937.)

FIG. 140. Same, ventral. × 15·5.

FIG. 141. Seed, dorsal. × 15·5. (V.33938.)

FIG. 142. Same, ventral. Cavities flanking raphe ridge show clearly as they are filled with sand. × 15·5.

FIG. 143. Seed with asymmetrically developed wings and clearly defined valve beginning to gape. × 15·5. (V.33939.)

FIG. 144. Seed, dorsal. Symmetric wings show striations very clearly. × 15·5. (V.33940.)

FIG. 145. Same, ventral. × 15·5.

FIG. 146. Small narrow seed, dorsal. × 15·5. (V.33941.)

FIG. 147. Same, ventral. × 15·5.

FIG. 148. Small seed, dorsal. × 15·5. (V.33942.)

FIG. 149. Same, ventral. × 15·5.

All the above are from Bovey.

Fig. 132 : *Photo by J. B. Simpson.*

PLATE 16

Nyssa boveyana n. sp.

FIG. 150. Holotype. Endocarp, dorsal, showing the valve (*v*). × 6·5. (V.33944.)

FIG. 151. Same, ventral. × 6·5.

FIG. 152. Another endocarp, dorsal, valve beginning to open. × 6·5. (V.33945.)

FIG. 153. The same, ventral. × 6·5.

FIG. 154. An endocarp, dorsal, valve detached exposing part of locule. × 6·5. (V.33946.)

FIG. 155. The valve removed from the above. × 6·5.

FIG. 156. Apical end of an endocarp showing valve in position exceptionally clearly. × 6·5. (V.33947.)

FIG. 157. A large laterally compressed endocarp. × 6·5. (V.33948.)

FIG. 158. Detached valve from endocarp of *Nyssa sylvatica* var. *europaea* for comparison. × 6·5. (V.33949.) Pliocene; Reuver.

FIG. 159. Detached valve from *N. sylvatica* var. *biflora* for comparison. × 6·5. Recent.

Myrtospermum boveyanum n. sp.

FIG. 160. Holotype. Seed showing curved form and characteristic pitting. × 15. (V.33950.)

FIG. 161. Typical seed, usual preservation, showing indications of curved form and condyle between the limbs. × 15. (V.33951.)

FIG. 162. Same, opposite side. × 15.

FIG. 163. Another seed with clear indications of curved cavity. × 15. (V.33952.)

FIG. 164. Seed showing clear indications that the pits were originally inflated. × 15. (V.33953.)

FIG. 165. Somewhat distorted seed. × 15. (V.33954.)

FIG. 166. Incomplete seed, internal surface of one valve showing condyle: (*h*) hilum leading into raphe cavity in condyle. Structures are rarely seen in these highly compressed seeds of which the valves are reluctant to separate. × 15. (V.33955.)

FIG. 167. Two closely adpressed seeds in position of growth, one ? abortive. × 15. (V.33956.)

FIG. 168. The same pair of seeds, opposite side. × 15.

Myrtospermum dubium n. sp.

FIG. 169. Sub-circular seed. × 15. (V.33957.)

FIG. 170. Opposite side of same seed. × 15.

FIG. 171. Seed of irregular form. × 15. (V. 33958.)

FIG. 172. Another somewhat larger seed. × 15. (V.33959.)

Myrtospermum sp.

FIG. 173. Seed, imperfect at hilar end. × 15. (V.33960.) Heathfield.

FIG. 174. One valve of the above, internal surface, showing curved cavity, broad triangular canal in condyle and columnar testa cells as seen in section. × 15.

Unless otherwise stated all the above are from Bovey.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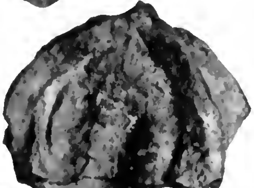
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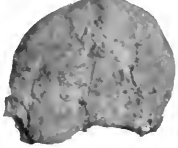
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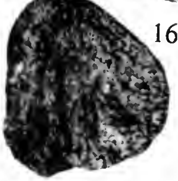
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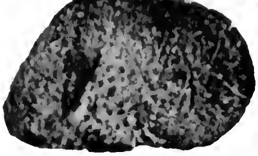
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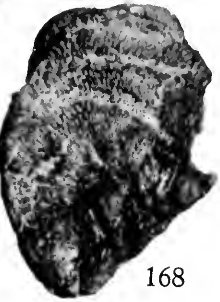
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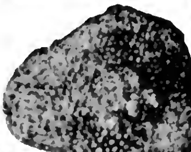
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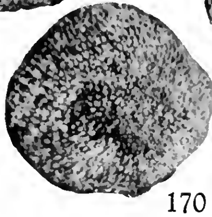
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NYSSA, MYRTOSPERMUM

PLATE 17

Mastixia boveyana n. sp.

FIG. 175. Holotype. One end of an endocarp. × 6·5. (V.33961.)

FIG. 176. Opposite aspect of same fragment showing locule in transverse section with its valve and infold. × 6·5.

FIG. 177. One end of another endocarp, side. × 6·5. (V.33962.)

FIG. 178. Fragment of endocarp, external surface, at about the middle showing ribbing. × 6·5. (V.33963.)

The above are from Heathfield.

Lysimachia boveyana n. sp.

FIG. 179. Holotype. Seed, ventral, showing two facets and ridge on which the attachment lies. × 28. (V.33964.)

FIG. 180. The same, dorsal. The longitudinal shadow marks a crack in the testa. × 28.

Symplocos anglica n. sp.

FIG. 181. Holotype. An endocarp somewhat compressed and showing the apical depression. × 6·5. (V.33965.)

FIG. 182. Endocarp, side, slightly distorted so as to show part of the apical depression. × 6·5. (V.33966.)

FIG. 183. The same, more tilted, so as to show the three apical apertures. × 6·5.

FIG. 184. Another, side, showing truncated apex and wrinkled surface. × 6·5. (V.33967.)

FIG. 185. Small endocarp, distorted so that two of the three apical apertures are shown. × 6·5. (V.33968.)

FIG. 186. A broader endocarp, probably belonging to this species. × 6·5. (V. 33969.)

Symplocos headonensis Chandler

FIG. 187. Endocarp somewhat distorted so as to show the apex with four apertures. × 6·5. (V.33970.)

FIG. 188. Another, side. The apical depression is seen in profile. × 6·5. (V.33971.)

All the above are from Bovey.

Solanispermum reniformis n. gen et sp.

FIG. 189. Perfect seed. × 6. Geol. Surv. Mus. Colln. No. 76684.

FIGS. 190–191. Two fragments of one seed which broke on removal from the matrix. × 15·5. (V.33972.)

Carpolithus spp.

FIG. 192. A carpel, side, showing one of the ventral facets. Ventral angle on the right. Note three-fid perianth at apex. × 15. (V.33973.) Heathfield.

FIG. 193. Another, dorsal side, dorsiventral compression shows part of one of the ventral facets on the right. × 15. (V.33974.) Heathfield.

FIG. 194. The same, ventral side, showing two facets and ventral angle. Persistent superior perianth can be seen. × 15.

FIG. 195. Two lobes of a dehisced capsule, inner surface. × 8. (V.33975.)

FIG. 196. The same, outer surface. × 8.

FIG. 197. Outer surface of a third detached lobe from the same specimen. × 8.

FIG. 198. Endocarp, incomplete at one end, broken so as to show one of the septa. × 6·5. (V.33976.) Heathfield.

FIG. 199. Another, broken at one end. × 6·5. (V.33977.)

FIG. 200. A three-lobed slender fruit. × 6·5. (V.33978.)

FIG. 201. Another somewhat broader specimen. × 6·5. (V.33979.)

FIG. 202. Another fruit with three minute patent perianth segments. × 6·5. (V.33980.)

FIG. 203. A seed. × 15·5. (V.33981.)

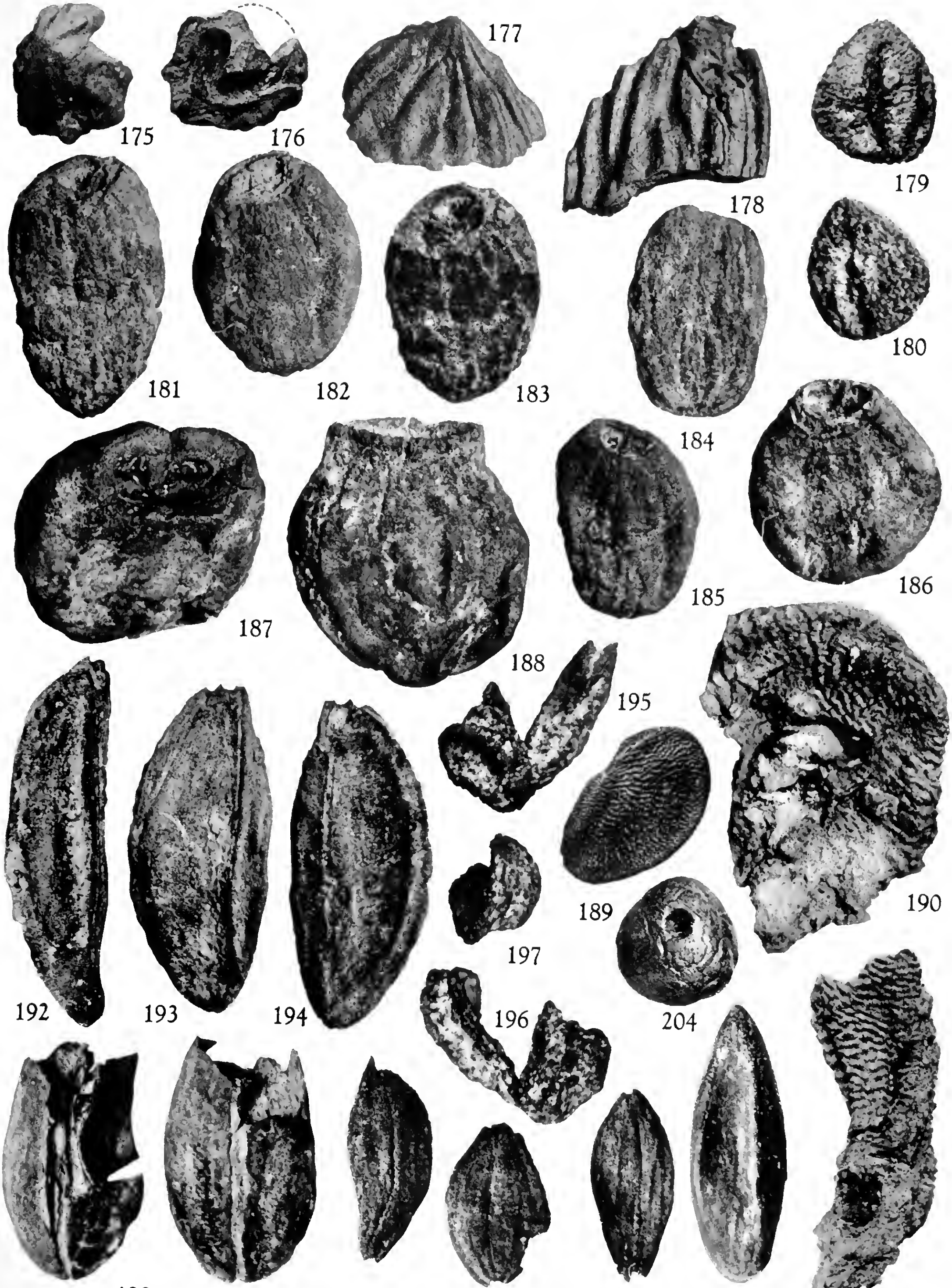
Bulbil ?

FIG. 204. Bud or Bulbil. The large hollow may be the burrow of an insect. × 2·8. (V.33982.)

Unless otherwise stated all the above are from Bovey.

Fig. 189 : *Photo by C. Reid.*

PLATE 17



MASTIXIA, LYSIMACHIA, SYMPLOCOS, SOLANISPERMUM, CARPOLITHUS, BULBIL ?

THE STRUCTURE OF SOME LEAVES AND FRUCTIFICATIONS OF THE GLOSSOPTERIS FLORA OF TANGANYIKA

D. D. PANT

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 3 No. 4
LONDON: 1958

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)

GEOLOGY

The following papers appeared in Volume I (1949–52):

		Price
No. 1	(1949). The Pterobranch *Rhabdopleura* in the English Eocene. H. D. Thomas & A. G. Davis	7*s*. 6*d*.
No. 2	(1949). A Reconsideration of the Galley Hill Skeleton. K. P. Oakley & M. F. Ashley Montagu	5*s*.
No. 3	(1950). The Vertebrate Faunas of the Lower Old Red Sandstone of the Welsh Borders. E. I. White	
	Pteraspis leathensis White, a Dittonian Zone-Fossil. E. I. White	7*s*. 6*d*.
No. 4	(1950). A New Tithonian Ammonoid Fauna from Kurdistan, Northern Iraq. L. F. Spath	10*s*.
No. 5	(1951). Cretaceous and Eocene Peduncles of the Cirripede *Euscalpellum*. T. H. Withers	5*s*.
No. 6	(1951). Some Jurassic and Cretaceous Crabs (Prosoponidae). T. H. Withers	5*s*.
No. 7	(1952). A New *Trochiliscus* (Charophyta) from the Downtonian of Podolia. W. N. Croft	10*s*.
No. 8	(1952). Cretaceous and Tertiary Foraminifera from the Middle East. T. F. Grimsdale	10*s*.
No. 9	(1952). Australian Arthrodires. E. I. White	15*s*.
No. 10	(1952). Cyclopygid Trilobites from Girvan. W. F. Whittard	6*s*.

The following papers appeared in Volume II (1953–56):

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THE STRUCTURE OF SOME LEAVES AND FRUCTIFICATIONS OF THE GLOSSOPTERIS FLORA OF TANGANYIKA

BY

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SYNOPSIS

The epidermal and cuticular structure of three new species of *Glossopteris*, a species of *Rhabdotaenia* gen. nov. (*Taeniopteris* in part), some scale leaves, microsporangia and two new species of seeds (*Spermatites* Miner) from the Mhukuru Coalfield, Tanganyika are described. *Taeniopteris danaeoides* Royle from India is referred to *Rhabdotaenia* on the basis of its epidermal structure. Two discs bearing microsporangia, from Newcastle, New South Wales, are described and their sporangia compared with those from Africa.

I. INTRODUCTION

THE study of the cuticular structure of fossil plant compressions has rapidly advanced but comparatively little work has yet been published on the structure of plants of the *Glossopteris* flora. The cuticular structure of *Glossopteris* itself, the most widespread genus of the flora, is but briefly described for only two leaves, *G. indica* Schimper (Zeiller, 1896 : 369, fig. 13) and *G. angustifolia* Bgt. (Sahni, 1923 : 277, pl. 17, figs. 2, 3). These cuticles are, however, so dissimilar that they have always pointed to the need for more extensive work on the subject and the present paper is an attempt in this direction.

The material described here was obtained from six borehole cores from the Mhukuru Coalfield in Tanganyika. The cores have been described by Harkin (1953) and in the same paper Professor J. Walton (Appendix IV : 28) gave a preliminary report on their flora, a typical *Glossopteris* assemblage. Professor Walton later handed the cores to me for detailed study. The work was begun in his laboratory in Glasgow and completed at Professor Harris's laboratory in Reading.

The cores are only about 5 cm. in diameter, hence the specimens are small, but the matrix is fine and is entirely unoxidized and the plants are beautifully preserved compressions. An unexplained feature of the preservation is that while some leaves are complete, as is ordinarily the case, others show only one epidermis with more or less of the mesophyll adherent to it ; the veins may be present or they may be missing and merely represented by the epidermal cells. It looks as though the leaf had split through the middle before preservation and the two halves were preserved separately. As a result the single epidermis is thin enough to be transparent and it shows its cell outlines very clearly, often far more clearly than can be seen in the cuticle. It is easily removed from the rock by celloidin pulls. It also shows the lignine thickenings of the guard cells which are destroyed when the cuticle is prepared.

The smaller fossils (scale leaves, microsporangia and seeds) described in this paper owe their interest to the excellent preservation of their cuticles. One of the small *Vertebraria* axes which show their tracheids and ray tissue has already been described (Pant, 1956).

The other fossils occurring in the cores consist of a single fragment of a leaf sheath of *Schizoneura*, some equisetaceous stems, a few megaspores, abundant two-winged pollen grains, a few three-winged, one-winged and unwinged examples and numerous slender roots showing scalariform metaxylem and spiral and annular protoxylem with or without a surrounding sheath of fibres. These are not described here. Walton (1953 : 30) had, in addition, recorded the occurrence of two specimens of *Noeggerathiopsis* in these cores (a third is a counterpart) but after examining the specimens and preparing their cuticles I think that they are poorly preserved midrib regions of *Glossopteris* leaves.

According to Harkin (1953 : 9) the plant-bearing shales at Mhukuru belong to the " Upper Coal Measures " and to the " upper part of K_3 bed " regarded as corresponding to the upper part of the Ecca Series in South Africa (see Harkin, 1953 : 7, Table 2). Walton (1953 : 28) also regards the age as Ecca. His determinations were, however, based on a preliminary identification of the fossils which are here regarded as new species and therefore do not indicate a precise age.

Genus *GLOSSOPTERIS* Brongniart

The epidermis of the various species described here is of a single general type and it may well be that all these species belong to one true genus. *Glossopteris indica*

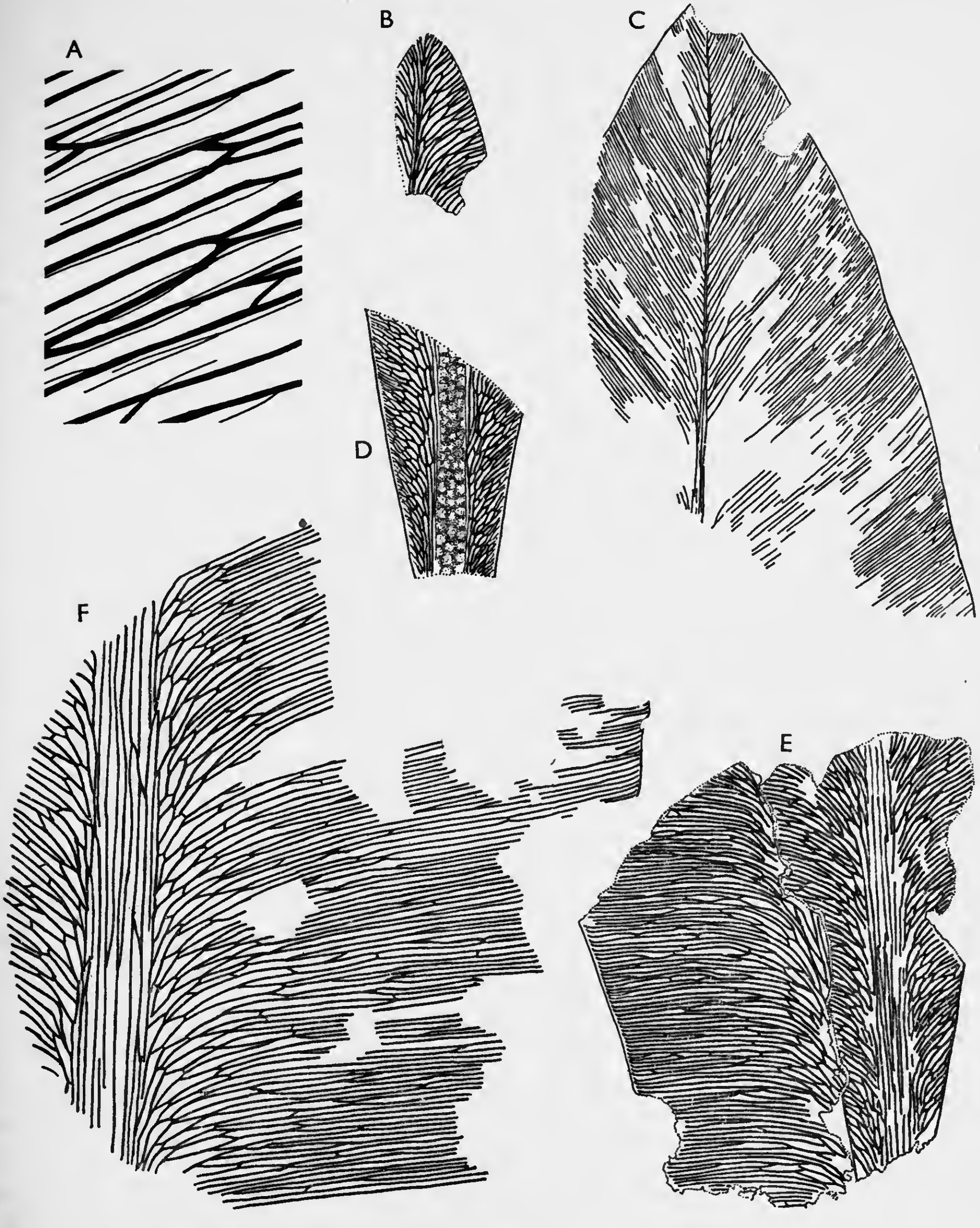

Fig. 1. A–E, *Glossopteris fibrosa* n. sp.; F, *G. hispida* n. sp. A, details of venation of a typical leaf showing fibres in certain meshes. V.34444. × 10. B, leaf apex with short meshes. V.34444. × 2. C, leaf apex with long meshes; a few anastomoses may have been missed. V.34446. × 2. D, leaf base showing narrow meshes near the margin. The midrib shows lumps but no bundles. V.34447. × 2. E, two leaf fragments, on the left, middle region, on the right, near base; some anastomoses may have been missed. Holotype, V.34440*a*. × 2. F, middle region of leaf showing veins, midrib and part of the margin. Holotype, V.34450*a*. × 2.

of Zeiller (1896) however, appears from the figure to be different in cuticle and may belong to another genus; (I was unable to find Zeiller's original slide in Paris). The fructifications described by Zeiller (1902) as *Ottokaria*, and by Plumstead (1952, 1956) as *Scutum* and *Lanceolatus* also suggest generic differences but at present I consider it premature to make new genera out of *Glossopteris*.

Glossopteris fibrosa n. sp.

(Pl. 18, figs. 1–5; Pl. 19, fig. 1; Text-figs. 1, A–E; 2, 3)

Diagnosis. Leaf long lanceolate, average length estimated at between 13 and 30 cm.; width in middle region 4–6 cm. Basal part tapering very gradually, margins becoming almost parallel to midrib at base, two sides of lamina often of unequal width. Apex more or less obtuse. Petiole not known. Midrib up to 0·5 cm. wide below, persisting to apex but becoming narrow, probably depressed above and convex below. Midrib sometimes showing small lumps. Margins normally entire or slightly undulate, rarely lobed, slightly curved downwards and thickened. Veins arising from midrib at a very acute angle in all parts of the leaf but soon bending outwards for about 1 cm. and then continuing at an angle of 60°–80° to the midrib except in basal and apical parts where veins less arched making angles of 40°–50° only with midrib. Veins crossing lamina at a concentration of about 20–30 per cm. near midrib and 32–44 per cm. near margin (measured at right angles to majority of veins). Veins anastomosing in all parts of lamina but more frequently near midrib. Average width of meshes 0·5 mm. (ranging from 0·4 to 0·9 mm.) near midrib and 0·3 mm. near margin. Meshes in middle of lamina of varied length, average length 7 mm.; extreme base of leaf with lamina only one or two short meshes wide. Veins bending forwards at margin. Veins normally 90–160 μ thick (some up to 250μ), prominent on underside.

Substance of lamina rather thin, meshes showing elongated fibres running parallel with main veins, about 5–14 μ wide, fibres occasionally crossing connecting veins or moving to join main veins; also showing palisade-like cells 15–30 μ wide and spongy mesophyll cells elongated transversely to the veins averaging 60 μ long and 20 μ wide.

Upper epidermis of lamina usually without stomata. Cells between veins averaging 86 μ long and 44 μ wide tending to form rows parallel with veins. Lateral (anticlinal) walls about 3 μ thick, arched or nearly straight, never sinuous. Surface wall either without any papilla but appearing finely mottled or occasionally with several small papillae with or without an obscure larger median papilla. Sometimes numerous small papillae tend to be in longitudinal rows or are replaced by longitudinal striations. Cells over veins and often above fibres somewhat narrower and longer. In basal part of leaf and near margin upper epidermal cells become isodiametric but elongated along the margin itself. Cells over midrib with thicker walls (about 6 μ thick), elongated or short, rectangular or polygonal, tending to occur in longitudinal rows, stomata present but rare. Midrib cells often with a moderately conspicuous papilla. Trichomes absent.

Upper cuticle of lamina rather thick (up to 3 μ thick). Cell outlines thin, straight,

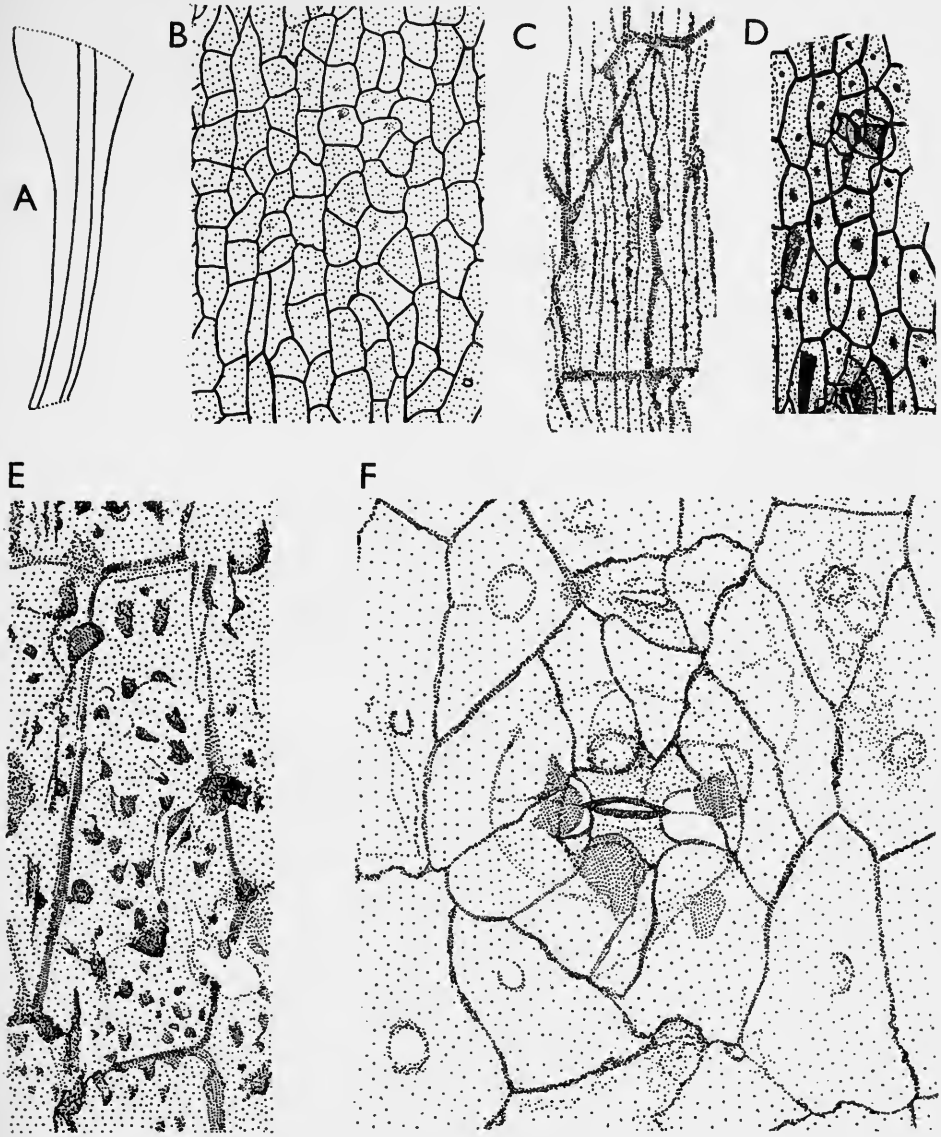

FIG. 2. *Glossopteris fibrosa* n. sp. A, leaf base showing slight asymmetry at the top, venation mentioned on p. 130. V.34445. × 1. B, upper cuticle of lamina showing cells arranged in longitudinal rows parallel with the veins. V.34448. × 125. C, cell of upper epidermis over vein showing longitudinal striations with small papillae arranged along them at some places. V.34449*a*. × 800. D, epidermis (? upper) of midrib showing stomata and thick-walled cells with median papillae. V.34444*a*. × 125. E, a cell of upper epidermis showing papillae of various sizes. V.34449*a*. × 800. F, lower cuticle showing stoma with outlines of guard cells distinctly marked at the poles but less distinct at the sides (see also Pl. 18, fig. 4). V.34443. × 800.

not bordered; surface of cells finely mottled, sometimes with obscure median papilla or several small papillae; otherwise as epidermis.

Lower epidermis of lamina showing isodiametric polygonal cells or cells somewhat elongated in various directions between veins, but longitudinally elongated cells over veins. Average width of cells about 44 μ. Lateral walls nearly straight or curved, never sinuous, sometimes unevenly thickened. Surface wall finely mottled, often showing a single ill-defined more or less prominent median papilla. Cells over midrib as on upper side but stomata absent. Trichomes absent.

Stomata frequent in vein meshes, rarely over veins; concentration typically about 125 per sq. mm. Orientation inconstant, tending to be longitudinal near veins and transverse between them.

Stomata haplocheilic, partly or completely amphicyclic but sometimes monocyclic. Guard cells about 45 μ long and 25 μ wide; sunken, usually aperture alone exposed in a small pit about 30 μ deep. Subsidiary cells 4–8, forming a very irregular ring; often slightly smaller than ordinary epidermal cells, polar cells unspecialized; surface usually somewhat thicker than that of other epidermal cells; usually showing a rather prominent thickened papilla or with a thickened rim on the inner side, papilla more or less hollow. Papillae pointing over the stomatal pit or pointing outwards; often a second faint papilla occurs in the middle of the cell. Encircling cells unspecialized, sometimes tangentially elongated.

Lower cuticle rather thinner than upper (up to about 2 μ thick), anticlinal cell walls thin without uneven thickenings. Cell surface finely mottled, usually with a faint median papilla. Guard cells slightly thickened round aperture, outlines clearly marked at poles, less clear at the sides. Lower cuticle otherwise like lower epidermis.

HOLOTYPE. Brit. Mus. (N.H.) Palaeont. Dept. no. V.34440 (Text-fig. 1, E).

LOCALITY AND HORIZON. Mhukuru Coalfield, Songea District, Tanganyika; Ecca Series (" Upper Coal Measures ").

DESCRIPTION. *G. fibrosa* is by far the commonest of all *Glossopteris* remains in the borehole cores. There are in all 146 fragments of different parts of its leaves (including 16 apices and 15 bases). The diameter of the cores being about 5 cm. no complete leaves can be seen.

In about half the specimens the midrib forms a fairly deep groove and the veins are distinctly sunken. In the others the midrib is only very slightly raised and the veins flat. I regard the first set as leaves preserved with the lower surface downwards, the second set, preserved upside down (Walton, 1936). I conclude that the midrib and veins were very prominent on the lower side but on the upper side the midrib was slightly sunken and the veins flat. The margin also is slightly curved downwards.

The veins and midrib contain abundant scalariform tracheids from 14–26 μ wide. Tracheids with uniseriate or multiseriate bordered pits also occur in the midrib; some pits show crossed apertures (see Text-figs. 3, B, C).

In epidermal pulls, the guard cells of the more exposed stomata show lateral and polar lignine lamellae of Gymnosperm type but these dissolve on maceration.

There is great variety in the surface of the upper epidermal cells of specimens referred to *G. fibrosa*. A very common state is a finely mottled wall but other speci-

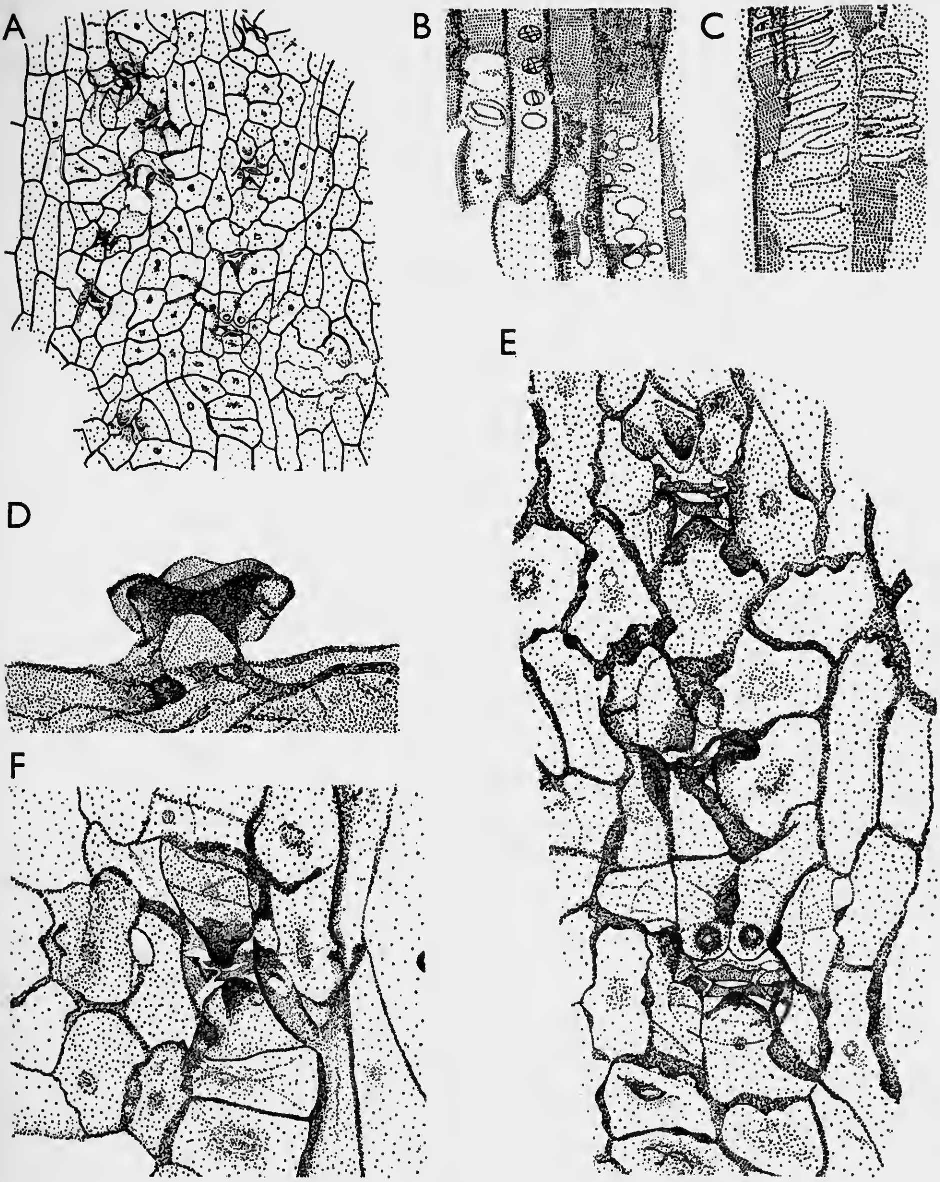

Fig. 3. *Glossopteris fibrosa* n. sp. A, lower epidermis showing a stomatal area between two veins. V.34440*d*. × 125. B, tracheids of midrib showing bordered pits; some of them show crossed apertures. V.34440*d*. × 400. C, scalariform tracheids from a vein. V.34440*d*. × 800. D, stoma at a fold of the lower epidermis, seen from inner side (see also Pl. 18, fig. 2). V. 34441. × 400. E, part of A, more magnified, showing more and less exposed stomata. × 400. F, a stoma with four subsidiary cells and lateral and polar lignine lamellae in guard cells. V.34440*d*. × 400.

mens show a faint papilla and others several moderately developed small papillae, a state which grades into mottling and also grades into longitudinal striations. One leaf showed striations in cells over a vein and close to them cells with several small papillae and one faint larger papilla. In some leaves the lower cuticle is thin and looks much like that of *G. hispida* (details are however obscure), but differs in the absence of hair bases.

The only additional characters to be noted are those seen in exceptional specimens and which may be the result of peculiar preservation. The upper epidermis of a leaf shows pale cell walls and dark cell contents, the cells being full of granules of various sizes (Pl. 18, fig. 3).

It was noted that two-winged pollen grains, more commonly varying in size from 40–60 μ across, occur abundantly on both sides of the leaves.

COMPARISON. *G. fibrosa* looks much like many of the figures given by various authors (e.g. Brongniart, 1828; Dana, 1849; Feistmantel, 1878–79, 1879, 1880–81, 1882, 1886; Zeiller, 1896, 1902; Arber, 1905*a*; Walkom, 1922, 1928; Walton, 1929; Plumstead, 1952, 1956) under the names *G. browniana* var. *indica* (*G. indica*), *G. angustifolia*, *G. browniana* var. *australasica* (*G. browniana*) and *G. communis*. I have seen the holotypes of the first two species and a syntype of *G. browniana* var. *australasica* Brong. (No. 507) in the Natural History Museum in Paris. All are clearly different because they lack fibres in vein meshes. None of these has satisfactorily preserved cuticle but there is a little information about *G. browniana* (see Table I). I have examined much other material attributed to these species in the British Museum (Nat. Hist.), École de Mines, Paris and in Oxford University Museum; the only specimens which appear to have fibres are those described by Bunbury (1861) as *G. browniana* var. *indica* (V.19617) and by Walton (1929, pl. C, fig. 19) as *G. indica* (V.20778) both in the British Museum (Nat. Hist.). Two slides showing fragments of *Glossopteris* leaves from Richmond Vale, Australia, sent to the British Museum by Dr. A. B. Walkom, show similar fibres and venation. A cuticle was prepared but cell outlines are very obscure. The only other *Glossopteris* with similar fibres is *G. hispida* described in this paper (see p. 140 for comparison).

Glossopteris cuticles have been described from specimens identified as *G. indica* by Zeiller (1896) and *G. angustifolia* by Sahni (1923). I assume that these determinations are correct. *G. fibrosa* differs clearly in cuticle from both (see Table I). I have examined a few other cuticles of *Glossopteris* leaves with this kind of venation and all are different.

Glossopteris hispida n. sp.

(Pl. 18, figs. 6, 7; Pl. 19, fig. 3; Pl. 20, figs. 1, 2, 7; Text-figs. 1, F; 4–6)

DIAGNOSIS. Leaf 4·3–7 cm wide, elongated, length unknown. Midrib up to at least 0·5 cm. wide, showing numerous longitudinal strands anastomosing at long intervals. Lateral veins departing from midrib at an acute angle (10°–20°) but soon arching outwards and continuing at an angle of 60°–80° to midrib; concentration of veins 19–26 per cm. near midrib, 28–35 near margin (measured transversely to the majority of veins); meshes shorter near midrib, longer towards margin but

TABLE I.—*Comparison of Certain* Glossopteris *Leaves with Narrow Vein Meshes and the Present New Species*

Material	Fibres between veins	Thickness of cell walls	Upper epidermis or cuticle	Lower epidermis or cuticle
1. With type *G. browniana* var. *australasica* Bgt. Mus. Hist. Nat. Paris, no. 507. *Loc.* Hawkesbury River, nr. Port Jackson, N.S.W.	Absent	Thin	Lateral walls straight, surface with several small papillae	Lateral walls sinuous, ordinary cells sometimes with median papillae, subsidiary cells with papillae overhanging stomatal pit. Trichome bases absent.
2. ? With type *G. browniana* var. *australasica* Bgt. Oxford Univ. Mus., no. FW5. *Loc.* " New Holland ". (The type cannot be traced)	,,	,,	Ditto	Lateral walls sinuous, ordinary cells sometimes with median papillae, subsidiary cells ?, trichome bases absent.
3. *Glossopteris* sp. No. V.19164. *Loc.* Burdwan, Bengal, India	,,	,,	Lateral walls straight to wavy, surface with striations or several small papillae (never single)	Lateral walls slightly wavy or almost straight, ordinary cells without median papillae, subsidiary cells with papillae overhanging stomatal pit. Trichome bases absent.
4. *G. angustifolia* (Sahni, 1923). *Loc.* Raniganj, Bengal, India	No data	,,	Lateral walls wavy, surface with " numerous extremely fine punctuations closely arranged along wavy parallel lines "	Lateral walls almost straight, ordinary cells without papillae, some subsidiary cells with median papillae. Trichomes? (probably absent).
5. *Glossopteris* sp. Oxford Univ. Mus., no. FW8. *Loc.* Newcastle, N.S.W.	Absent	,,	Lateral walls straight, surface with single median papilla	Lateral walls slightly wavy, ordinary cells with median papillae, subsidiary cells with papillae overhanging stomatal pit. Trichomes absent.
6. *Glossopteris* sp. No. V.34492. *Loc.* Richmond Vale, N.S.W.	Present	,,	Details and cell outlines very obscure in cuticle	Details and cell outlines very obscure in cuticle.

Table I.—*continued*

Material	Fibres between veins	Thickness of cell walls	Upper epidermis or cuticle	Lower epidermis or cuticle
7. *Glossopteris* sp. A. No. V.34467. *Loc.* Mhukuru Coalfield, Tanganyika (2 specimens)	Absent	Thin	Lateral walls straight or arched, never wavy, bordered, surface with a median papilla or mottled	Lateral walls almost straight, ordinary cells usually with single median papillae, subsidiary cells with papillae overhanging stomatal pit. Trichomes absent.
8. *G. fibrosa* *Loc.* Mhukuru Coalfield, Tanganyika (many specimens)	Present	,,	Lateral walls straight or arched, never wavy, not bordered, surface mottled or with single median papilla or numerous papillae or with longitudinal striations	Ditto
9. *G. hispida* *Loc.* Mhukuru Coalfield, Tanganyika (4 specimens and some small fragments)	,,	,,	Lateral walls straight, never wavy, surface with numerous papillae or mottled	Lateral walls straight to sinuous, ordinary cells without median papillae, subsidiary cells with papillae overhanging stomatal pit. Trichomes and trichome bases present.
10. *G. indica* (Zeiller, 1896). *Loc.* Frances, Johannesburg, S. Africa	No data	Thick	No data	Lateral walls straight, ordinary cells and subsidiary cells without papillae. Trichomes ?
11. *G. colpodes* *Loc.* Mhukuru Coalfield, Tanganyika (many specimens)	Absent	Thin	Lateral walls usually wavy, straight near midrib and margins and over midrib and veins, surface of most cells with a median papilla	Lateral walls markedly wavy but straight near midrib and margins and over midrib and veins, surface often with a median papilla. Trichomes absent.

often the ultimate mesh is again short. Meshes average about 0·8 mm. wide (ranging from about 0·6–1 mm.) near midrib and about 0·3 mm. wide near margin, average length of meshes about 4 mm. Veins and midrib prominent on the lower side, midrib also slightly depressed on the upper. Veins up to 140 μ thick. Margin entire, slightly thickened and slightly curved downwards, occasionally lobed.

Substance of lamina thin, showing spongy mesophyll cells elongated transversely

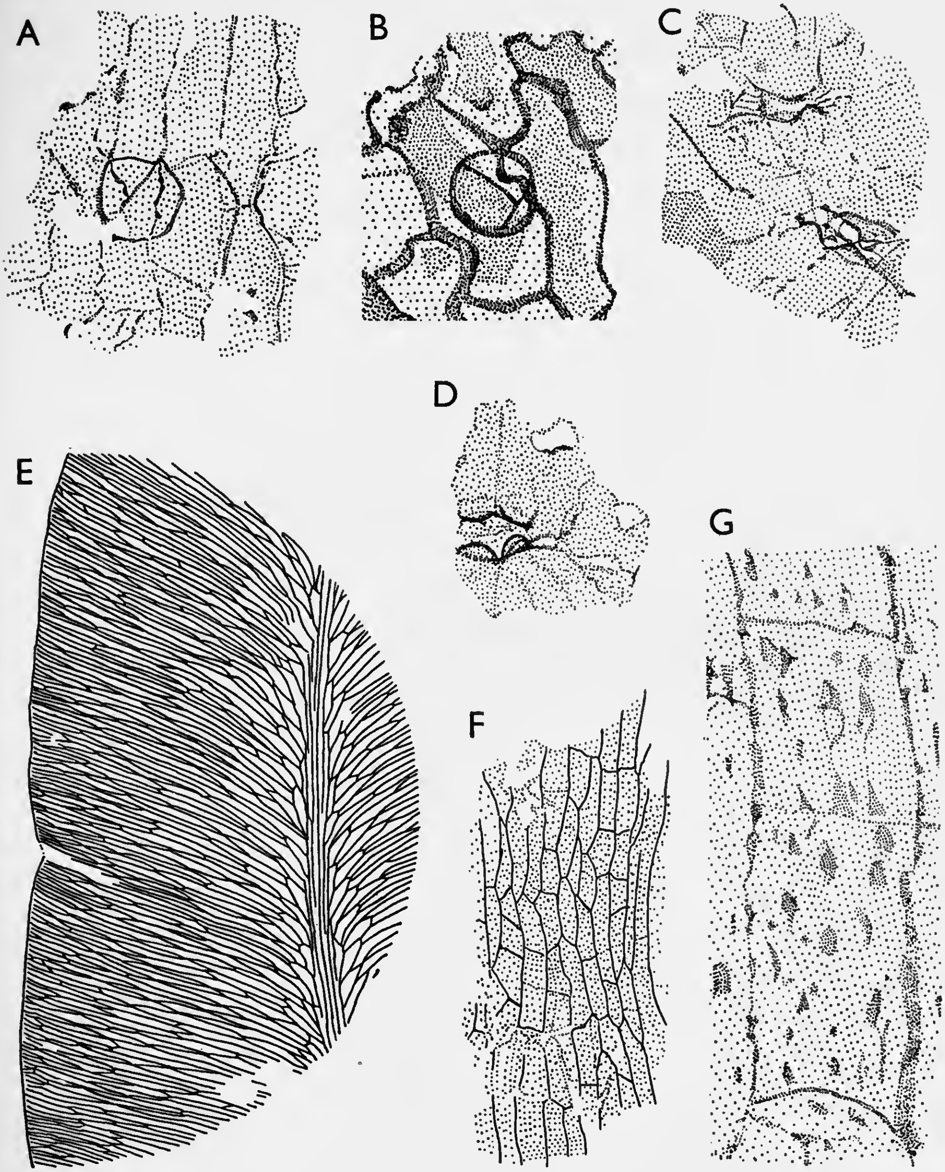

Fig. 4. *Glossopteris hispida* n. sp. A, lower cuticle showing hair base. V. 34451*a*. × 400. B, lower epidermis showing three-celled hair base. V.34450*a*. × 400. C, D. fragments of lower cuticle showing stomata. V.34452. × 400. E, middle part of leaf showing venation and lobed margin. V.34451. × 2. F, upper cuticle showing elongated cells in rows. V.34451*b*. × 125. G, a cell from F further magnified to show its numerous papillae (the small dots represent the substance of the cuticle). V.34451*b*. × 800.

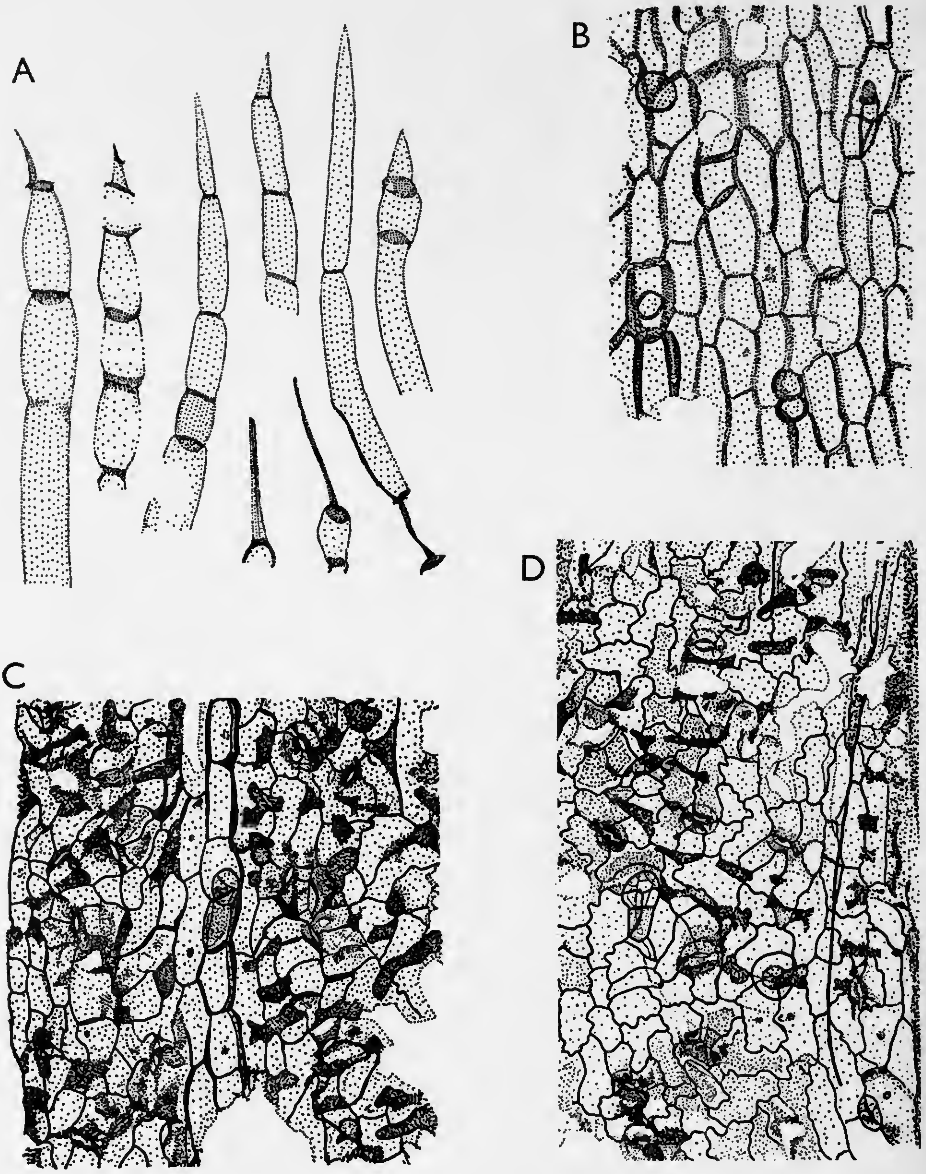

Fig. 5. *Glossopteris hispida* n. sp. A, hairs from matrix in contact with lower side of leaf. B, lower epidermis of midrib showing trichome bases. C, lower epidermis of stomatiferous area between two veins near midrib showing straight-walled cells, stomata and hair bases. The rows of elongated cells in the middle are above a fibre. D, lower epidermis of a mesh away from midrib showing sinuous-walled cells. The elongated cells on the right are above a fibre (see Text-fig. 6 for details of stomata and cells). All from Holotype (V.34450*a*). × 125.

to the veins (about 39–52 μ long × 13–24 μ wide), and palisade mesophyll cells (about 18–30 μ wide) also showing a few isolated fibres running parallel to veins in vein meshes.

Upper cuticle of lamina about 2 μ thick, showing rectangular or polygonal cells. Cells short or frequently elongated in the direction of veins and tending to be in rows parallel to veins, lateral and end walls straight, thin, often obscure. Surface wall with numerous small papillae which tend to be in longitudinal rows, sometimes cell surface irregularly mottled. Cells typically about 30 μ × 57 μ.

Upper cuticle of midrib showing rectangular cells, short or longitudinally elongated, tending to be in longitudinal rows. Surface mottled, papillae absent. Stomata and trichomes absent on the upper side.

Lower epidermis of lamina showing frequent trichomes and trichome bases both along veins and between them, stomata present in areas between veins. Cells in meshes near midrib almost straight walled, polygonal, isodiametric or elongated in various directions; cells in meshes away from midrib irregularly shaped, often more or less elongated in the direction of the veins, cells averaging about 46 μ wide × 62 μ long; lateral (anticlinal) walls slightly to markedly sinuous. Cells above veins and sometimes above fibres in meshes, straight walled, narrow and elongated in the direction of the veins. Lateral walls of lower epidermal cells about 3 μ thick, sometimes unequally thickened. Surface of cells very finely mottled, usually without any papillae.

Lower epidermis of midrib with longitudinally elongated or short, polygonal or rectangular cells, lateral walls straight, about 6 μ thick, surface wall finely mottled, trichomes and trichome bases present, stomata absent.

Trichome bases composed of a single oval or rounded cell, or two or three cells, commonly overlapping a number of ordinary epidermal cells but occasionally overlying a single cell. Trichomes simple, three- to six-celled, tapering, cells short or long, apex of end cell acutely pointed. Trichomes pointing in different directions but usually outwards and backwards on the midrib and backwards on the lamina.

Concentration of stomata about 70 per sq. mm., orientation irregular. Stomata haplocheilic, monocyclic. Guard cells averaging 49 μ long × 21 μ wide, partly overhung by subsidiary cells and their papillae or occasionally exposed. Subsidiary cells 4–6, irregular or forming an irregular ring, like ordinary epidermal cells in shape and size but usually with a prominent thick-walled hollow papilla pointing over the stomatal pit or with a thickened rim towards stomatal aperture. Polar subsidiary cells like lateral ones.

Lower cuticle delicate (about 1 μ thick), cell walls often obscure, thin and straight; surface wall smooth or granular, papillae absent in ordinary epidermal cells but present in subsidiary cells. Lower cuticle otherwise like lower epidermis.

HOLOTYPE. Brit. Mus. (N.H.) Palaeont. Dept. no. V.34450.

LOCALITY AND HORIZON. Mhukura Coalfield, Songea District, Tanganyika; Ecca Series (" Upper Coal Measures ").

DESCRIPTION. The material consists of four good specimens and a few small fragments. In two of the leaves the lamina is torn (see Text-figs. 1, F and 4, E).

The veins and the midrib show abundant scalariform tracheids like those of *G.*

fibrosa. In the epidermal pulls the guard cells show lateral and polar lignine lamellae. These dissolve on maceration. Some cells of the lower epidermis show a dark inner area, slightly smaller than their lumen, which looks like their contracted contents. Dark spots, resembling median papillae, are also seen in a few cells of the lower epidermis. The spot is often placed near one end of the cell. No corresponding structures were observed in the lower cuticle and these spots may be extraneous particles.

FIG. 6. *Glossopteris hispida* n. sp. Part of Text-fig. 5, D further enlarged to show details of stomata and two-celled hair base (see also Pl. 20, fig. 2). × 400.

Two-winged pollen grains of varying sizes are frequently seen overlying the cuticle.

COMPARISON. *G. hispida* agrees with *G. fibrosa* in venation and in the fibres between the veins. Though the vein meshes are usually of similar size, no specimens of *G. hispida* are known with meshes as narrow as in some of *G. fibrosa*.

The conspicous difference is in the hairs on the underside of *G. hispida* (none in *G. fibrosa*). These are seen clearly when the matrix in contact with the underside of the leaf is moistened with oil; their bases are also visible in the epidermis and the cuticle. In *G. fibrosa* the cuticle is rather thicker and usually with clearly marked cell outlines, the cuticle of *G. hispida* is thin and the cell outlines obscure. The cells of the lower epidermis in *G. hispida* have sinuous walls (except over veins and midrib and in meshes near midrib), in *G. fibrosa* they are always almost straight. In *G. fibrosa* the stomata are partly amphicyclic, in *G. hispida* monocyclic. There may be other differences between the two species but their constancy is unknown.

Glossopteris leaves with rather similar veins but whose fine details are unknown have been described under such names as *G. ampla*, *G. musaefolia*, *G. indica*, *G. browniana*, *G. damudica*, and others. I am unable to distinguish any difference between them. A celloidin pull from one of the original specimens of *G. ampla* Dana sent to me by Dr. S. H. Mamay did at least differ in possessing no fibres. I also examined the types of *G. indica* Göppert (*G. browniana*, var. *indica*, Brongniart, 1828, pl. 62, fig. 2) consisting of two separate pieces (No. 506) in the Paris Museum of Natural History; *G. musaefolia* Bunbury (V.19621 and also syntype material), and a specimen attributed to *G. damudica* var. *stenoneura* (V.19577) by Feistmantel (1889, pl. 4, fig. 7) in the Palaeontological Department of the British Museum (Natural History). They all differ from *G. hispida* in lacking impressions of fibres in vein meshes (the original leaf substance is not preserved).

Glossopteris colpodes n. sp.

(Pl. 19, fig. 2; Text-figs. 7–9)

DIAGNOSIS. Leaf elongated (length unknown), average width in middle region about 6 cm. (extremes 4·5–7·5 cm.) basal part tapering with margins approaching midrib at an angle of 10°; apex more obtuse, margins approaching midrib at an angle of 30°. Midrib up to 0·4 cm. wide below, showing numerous longitudinal strands and often small lumps in lower parts, fewer strands and lumps above. Leaf margin entire, undulating or lobed, slightly thickened.

Veins arising from midrib at a small angle but soon bending outwards for about 1 cm. and then continuing at an angle of 45°–65° to midrib (in extreme specimen 75°–80°). Concentration of veins (measured at right angles to majority of veins) 11–15 per cm. near midrib in lower and middle parts of leaf, increasing to about 20 per cm. near midrib in upper part. Near margins veins more crowded, about 30 per cm. (maximum about 36 per cm.). Veins usually up to 140 μ thick, prominent. Veins and midrib raised on the lower side of leaf and midrib also slightly depressed on the upper. Meshes average 4 mm. long (extremes 2–8 mm.) and 0·9 mm. wide (extremes 0·5–1·5 mm.) in lower and middle parts of leaf, longer and narrower in upper part, averaging 7 mm. × 0·5 mm.; ultimate meshes near margin often short and narrow. Veins usually bending slightly forwards at margin.

Upper epidermis of lamina without stomata or trichomes. Cells over veins

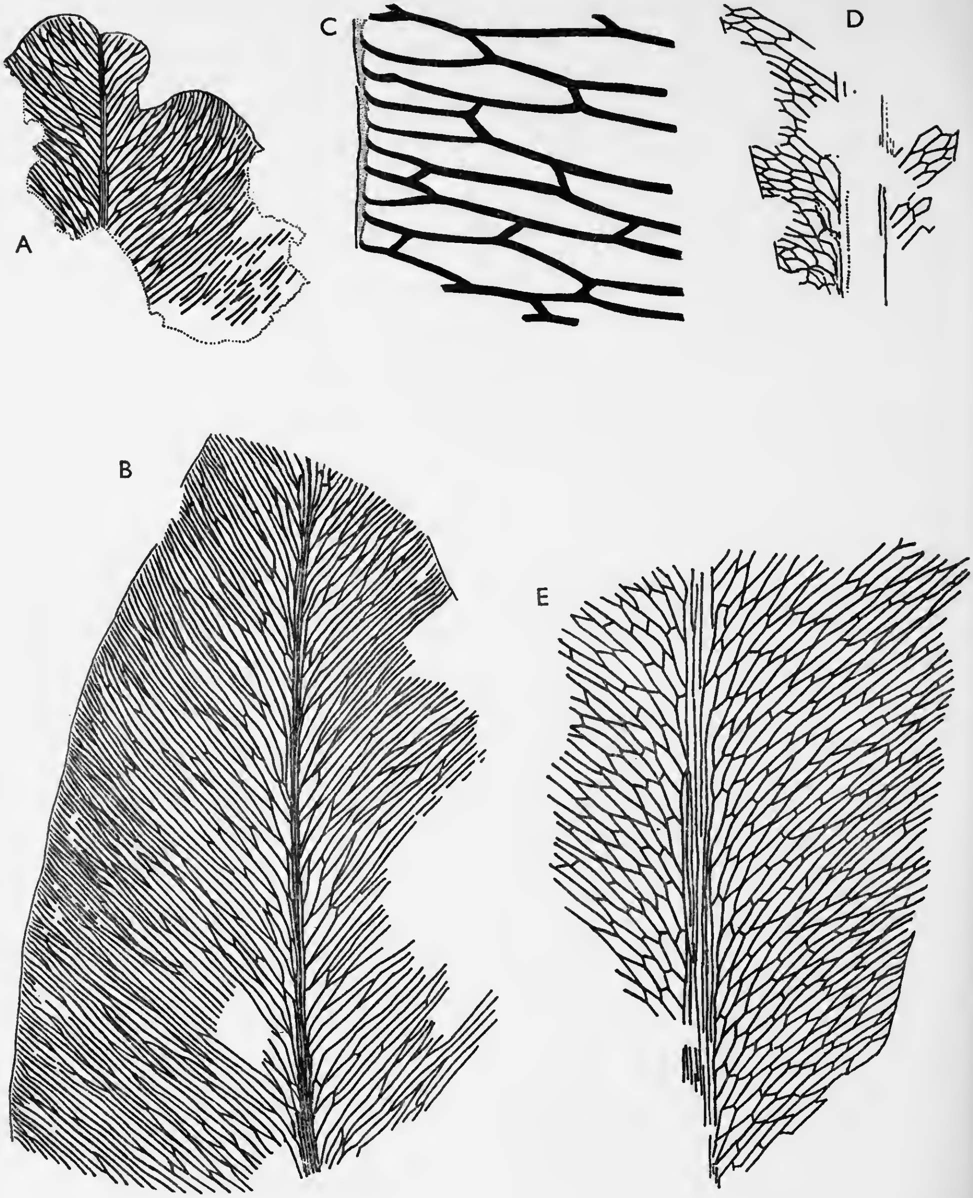

FIG. 7. *Glossopteris colpodes* n. sp. A, lobed apex with narrow elongate meshes. V.34462. × 2. B, apical part of leaf. V.34463. × 2. C, details of venation at margin of a leaf. V.34465. × 10. D, basal part of a leaf. V.34464. × 2. E, middle portion of leaf. Holotype, V.34461. × 2.

narrow, elongated, straight-walled. Cells between veins irregularly shaped or polygonal, short or elongated in various directions, averaging 66 μ long and 40 μ wide. Lateral (anticlinal) walls of cells about 3 μ thick, slightly to markedly sinuous, sometimes appearing nearly straight especially near midrib and margins. Cells at margin longitudinally elongated, nearly straight-walled. Surface of upper epidermal cells always mottled, most cells showing a median papilla about 6 μ wide. Cells over midrib in longitudinal rows, rectangular, short or elongated, lateral walls straight, papilla sometimes seen, trichomes absent.

Upper cuticle moderately thick (about 3 μ), cell outlines between veins obscurely marked, often appearing discontinuous but scarcely showing sinuous waves. Cell walls clearer over midrib and margins, straight or nearly straight but always appearing closely beaded. Papillae sometimes visible.

Lower epidermis of lamina showing narrow straight-walled cells above veins. Cells between veins elongated in various directions or isodiametric, averaging 69 μ × 38 μ, often irregularly shaped, lateral walls more or less sinuous, often unevenly thickened, but nearly straight near midrib and margins. Walls about 3 μ thick. Surface of cells always mottled and often showing a median papilla. Trichomes absent.

Stomata frequent between veins, often unevenly distributed, concentration about 66 per sq. mm., orientation varied. Stomata haplocheilic, monocyclic, occasionally incompletely amphicyclic. Guard cells about 65 μ × 25 μ, sunken, frequently entirely covered by 4–8 subsidiary cells and their papillae, except sometimes from a region near aperture. Subsidiary cells irregular or forming an irregular ring, polar cells resembling lateral ones, size of subsidiary cells almost as large as that of other epidermal cells, but surface sometimes thicker; each subsidiary cell usually with a large hollow but thick-walled papilla pointing over the stomatal pit (papillae often overlapping and completely concealing the stomatal aperture) or papilla pointing upwards. Sometimes a second median papilla also present in subsidiary cells. Encircling cells unspecialized but often tangentially elongated.

Lower cuticle of lamina thin (1–2 μ thick), cell walls between veins faintly marked, usually interrupted and appearing nearly straight but never showing well-marked waves, occasionally walls almost straight. Cell walls over veins more distinct, straight, almost continuous but closely beaded. Papilla and surface mottling often visible. Surface occasionally showing radiating striations extending over several cells. Guard cell outlines clearly marked at the poles but faint on the sides.

Lower cuticle of midrib with short or long polygonal cells arranged in longitudinal rows. Lateral walls straight, surface mottled. Papillae often absent. Stomata and trichomes absent.

HOLOTYPE. Brit. Mus. (N.H.) Palaeont. Dept. no. V.34461.

LOCALITY AND HORIZON. Mhukuru Coalfield, Songea District, Tanganyika; Ecca Series ("Upper Coal Measures").

DESCRIPTION. Sixty-seven fragments were attributed to *G. colpodes*. The difference between the venation in the apical and the basal regions is considerable. These were identified with one another because of their lack of fibres between veins

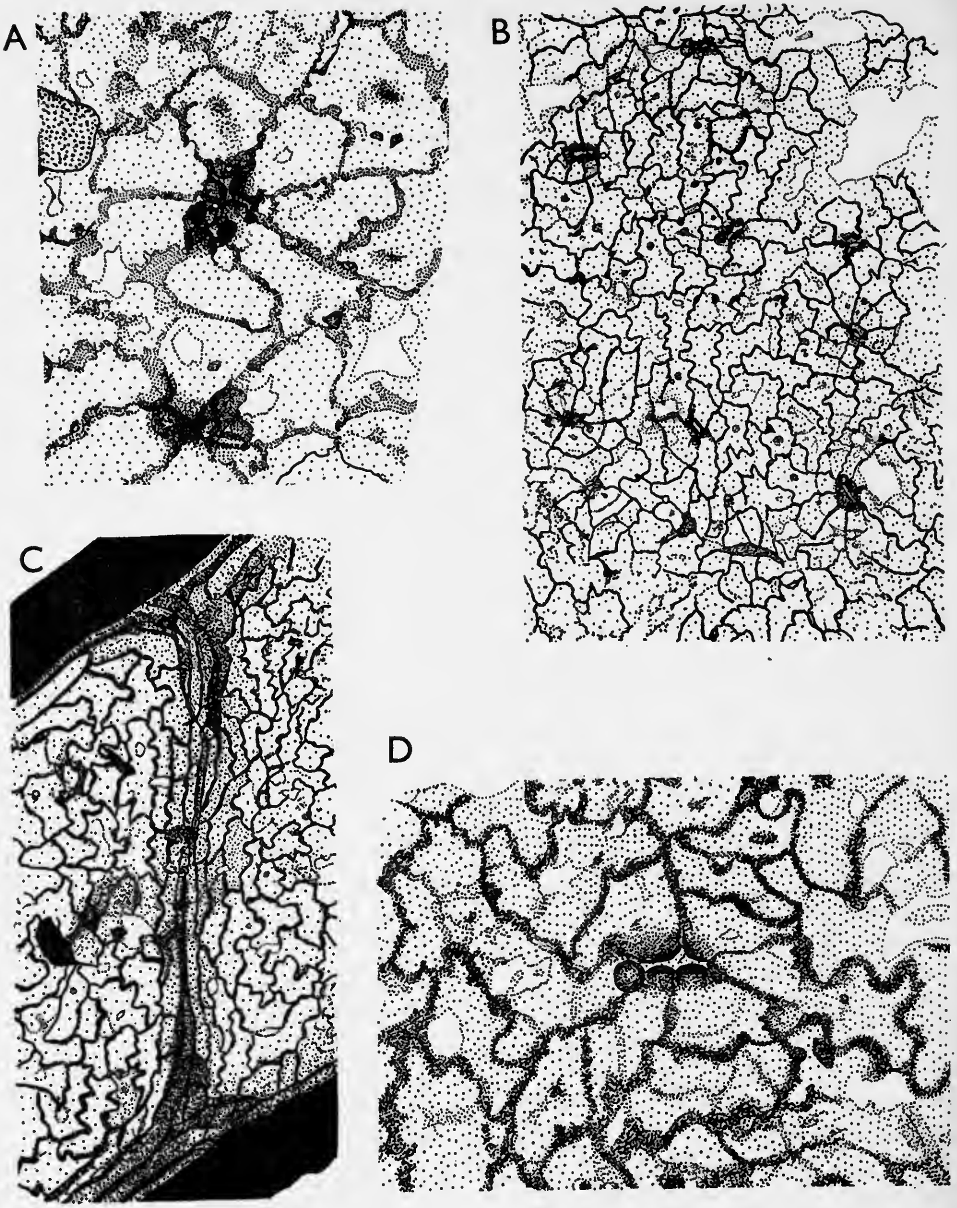

FIG. 8. *Glossopteris colpodes* n. sp. A, two protected stomata. V.34466*a*. × 400. B, lower epidermis of stomatiferous area between two veins. V.34466*b*. × 125. C, lower epidermis. V.34466*b*. × 125. D, relatively exposed stoma from B. × 125.

and also because of their agreement in epidermal or cuticular structure. Fourteen specimens show epidermal cells of the upper or the lower sides and these have sinuous walls, except above the veins and the midrib and in meshes near the midrib and the margins. The other specimens were too thick to show the epidermal cells but they all gave cuticles which showed the characteristic cells with very obscurely marked walls which appear more or less straight but discontinuous (see Text-figs. 9, A; 9, D).

Several epidermal specimens show structures not mentioned in the diagnosis. When sufficiently exposed, the guard cells show lateral and polar lignine lamellae of the Gymnosperm type (these are unrepresented in the cuticle). Some pulls show circles abut 30 μ wide representing flattened palisade cells ; others show less distinct spongy mesophyll cells often elongated transversely to the veins. At a few points in the pulls the veins and the midrib show scalariform tracheids.

The only specimen showing the apex was unfortunately rubbed and damaged. The lamina is lobed (Text-fig. 7, A). There is nothing to show whether this is normal.

Two-winged pollen grains of various sizes ranging between 40–100 μ across are frequently found sticking to the epidermis or cuticle of either side.

Comparison. *G. colpodes* is distinguished from *G. fibrosa* and *G. hispida* by the lack of fibres between the veins and in the lower parts by its wider meshes. The epidermal cells in *G. fibrosa* are never sinuous walled (markedly sinuous in *G. colpodes* except above the veins and the midrib and in the meshes near the midrib and the margins). *Glossopteris* sp. A may have veins as wide as those in *G. colpodes* and also lacks fibres in meshes but differs in the complete absence of sinuous-walled cells. The lower epidermis of *G. hispida* resembles that of *G. colpodes* in having sinuous-walled cells but differs in having trichomes (in *G. colpodes* trichomes are absent).

Among *Glossopteris* leaves of comparable venation are : Dana's Australian leaves of *G. reticulum* and *G. elongata* (Dana 1849), ? *Dictyopteris simplex* Tate (*G. Tatei* Feistmantel, 1889) from S. Africa (Tate, 1867), Feistmantel's Indian leaves of *G. retifera* and *G. conspicua* (Feistmantel, 1880 ; 1881 ; 1886) and various other specimens referred to them by Feistmantel and others, *G. brancai* Gothan (1914), from Portuguese East Africa, and some specimens assigned to *G. browniana* by Arber, (1905*a*), Walton (1929) and others. Most of them differ from *G. colpodes* in the size of meshes and their fine details are unknown (see table II). However, a specimen assigned to *G. browniana* by Arber (1905*a*, : 56, pl. 3, fig. 2) and two others figured by Walton (1929 : 70, pl. C, figs. 21, 22) as *G. cf. browniana* and *G. retifera* respectively are very similar to *G. colpodes* in their venation but like the rest their epidermal or cuticular structure is unknown.

I have also been able to examine some wide meshed undescribed Indian leaves at the Oxford University Museum and an Australian specimen at the British Museum. These yielded pulls showing epidermal cells and stomata very similar to those of *G. colpodes*. The Indian leaves have veins at about the same concentration as in *G. colpodes* (about 10–12 veins per cm. near midrib) and may belong to the same species. The meshes of the Australian leaf are much wider (up to 2·5 mm. wide, concentration of veins about 8 per cm. in lower part) and are therefore outside the range observed in the present material of *G. colpodes*.

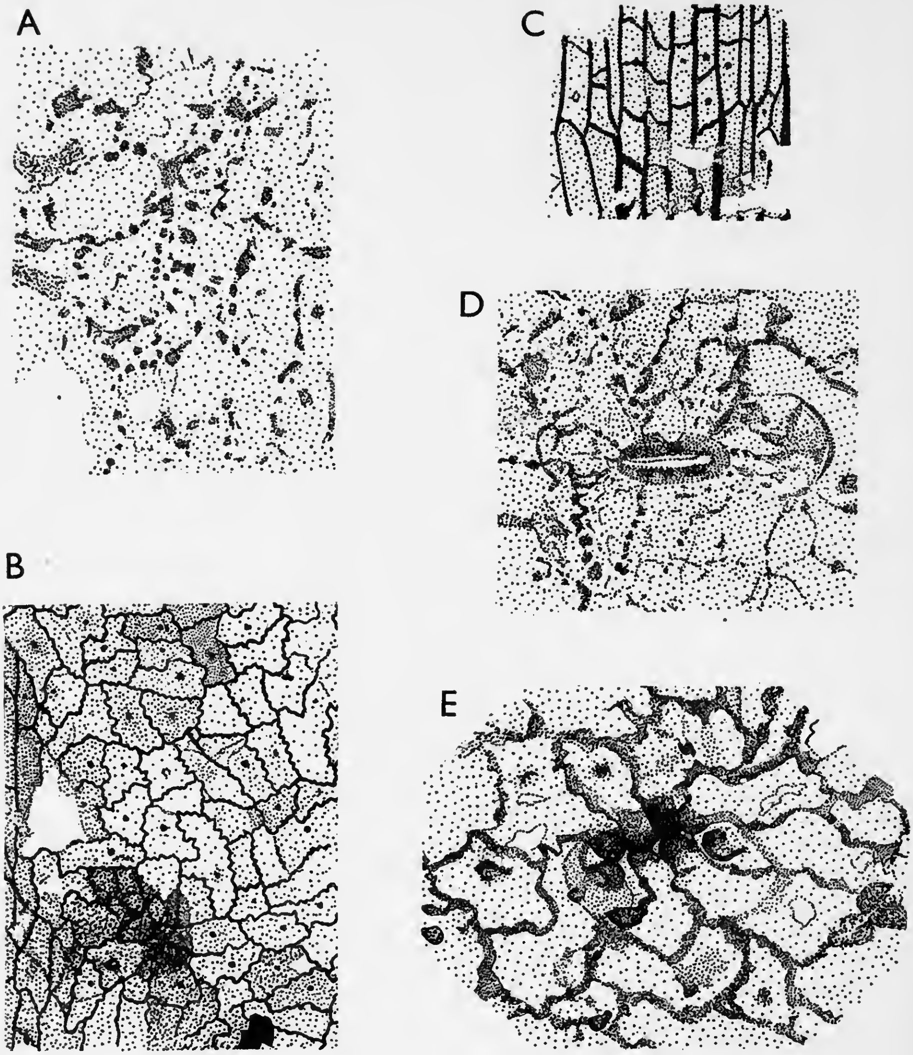

Fig. 9. *Glossopteris colpodes* n. sp. A, upper cuticle as seen under phase contrast microscope. V.34466*c*. × 400. B, upper epidermis showing sinuous-walled cells between veins and straight-walled cells above a vein. V.34466*d*. × 125. C, epidermis over midrib. V.34466*d*. × 125. D, lower cuticle showing a stoma as seen under phase contrast microscope. V.34466*e*. × 800. E, lower epidermis showing a stoma with a ring of eight subsidiary cells and a few encircling cells. V.34466*a*. × 400.

TABLE II.—*Comparison of Certain* Glossopteris *Leaves with Wide Vein Meshes*

Material	Concentration of veins per cm.	Character of meshes	Angle of veins to midrib after 1 cm.	Walls of epidermal cells
1. *G. colpodes* . . *Loc.* Mhukuru Coalfield, Tanganyika, (many specimens)	Near midrib 11–15 in middle and lower parts; up to 20 towards apex; near margin up to 36 .	Short and wide near midrib and base, elongated towards apex and margin .	45°–65° .	Sinuous.
2. *Glossopteris* sp. A. . *Loc.* Mhukuru Coalfield, Tanganyika (2 specimens)	Near midrib 27–30; near margins up to 36 (about 20 in second specimen) .	Elongated but often shorter near midrib and margins .	40°–50° .	Straight.
3. *Glossopteris* sp. Nos. FY 14, 16–21, Oxford University Museum. *Loc.* Raniganj Coalfield, Burdwan, India (15 specimens)	Near midrib 10–12 (veins ill-preserved near margins) .	Shorter and wider near midrib, elongated elsewhere .	60°–70° .	Sinuous.
4. *Glossopteris* sp. No. V.34491 *Loc.* Newcastle, N S.W. (1 specimen)	Near midrib about 9; near margin about 15 in lower parts of leaf .	Ditto	. 80°–85°	,,
5. *G. browniana* (Arber, 1905*a*: 56, pl. 3, fig. 2. No. V.7207. *Loc.* Port Stephens, N.S.W.	Near midrib 14–16 up to 21 near margin (only middle part known) .	Ditto	. 60°–70°	Unknown.
6. *G.* cf. *browniana* (Walton, 1929: 70, pl. C, fig. 21). No. V.20780. *Loc.* Wankie Coalfield, S. Rhodesia	Near midrib up to 15; up to 20 near margin in lower and middle parts. Upper part of leaf unknown .	Short and wide near midrib in upper part, elongated elsewhere; almost uniformly short towards base .	50°–60° .	,,
7. *G. retifera*. (Walton, 1929: 70, pl. C, fig. 22). No. V.20781. *Loc.* Wankie Coalfield, S. Rhodesia	Near midrib 11–16, about 20 near margin (only basal part of leaf known) .	Almost uniformly short and wide .	50°–60° .	,,
8. *G. retifera* (Feistmantel, 1880: 103, pl. 28A, figs. 2, 7, 10; pl. 41A. 1886, pl. 4A, fig. 1). *Loc.* Raniganj Coalfield, Ramkola Coalfield, Nakori River, nr. Gai Nagar, Ganespur River, India	9–14 all over lamina (from figs.) .	Ditto	. 50°–60° .	,,

Table II.—*continued*

Material	Concentration of veins per cm.	Character of meshes	Angle of veins to midrib after 1 cm.	Walls of epidermal cells
9. *G. retifera* (Plumstead, 1952: 300, pl. 49, fig. 5, pl. 51, figs. 1–6, text-fig. 6. *Loc.* Leeukuil, Vereeniging, Transvaal, S. Africa	4 near midrib, 21 near margin in upper part (from description) but 9–12 near midrib, 21 near margin, in Plumstead, 1956, pl. 12, fig. 2	Short and wide near midrib and base, elongated in upper part	"Almost 90°"	Unknown
10. ? *Dictyopteris simplex* (Tate, 1867: 141, pl. 6, fig. 6 — *G. tatei* Feistmantel, 1889: 44, pl. 4, fig. 8). No. V.19579. *Loc.* Bloemkop, S. Africa	7–10 near midrib, about 12 approx. 2 cm. from midrib. Margin not preserved	Short and wide near midrib, elongated, elsewhere.	70°–80°	,,
11. *G. brancai* (Gothan, 1914: 13, pl. 1, figs. 2, 3). *Loc.* Tete, Portuguese East Africa	4–6 near midrib, 10–12 near margin in upper and middle part (from figs.)	Ditto	85°–90°	,,
12. *G. conspicua* (Arber, 1905*a*: 87, pl. 3, fig. 3). No. V.2465. *Loc.* Mill River Drift, Orange River Colony.	9–16 near midrib in various leaves in the slab	Ditto	50°–70°	,,
13. *G. conspicua* (Feistmantel, 1881: 104, pl. 28A. figs. 1, 5, 6, 8, 9). *Loc.* Raniganj, Karanpura, and Auranga Coalfields, India.	7–9 all over lamina (from figs.)	Elongated	50°–60°	,,
14. *G. reticulum* (Dana, 1849: 717, pl. 13, fig. 2). *Loc.* Newcastle, N.SW.	6 near midrib in middle part, 12 near midrib towards apex and near margin. Only upper part of leaf known (from description and fig.)	,,	"About 65°"	,,
15. *G. elongata* (Dana, 1849: 718, pl. 13, fig. 4). *Loc.* Newcastle, N.S.W.	7–11 below. Only basal part of leaf known (from description and fig.)	Almost uniformly short and wide	"60° or more"	,,

Glossopteris sp. A

(Text-fig. 10)

LOCALITY AND HORIZON. Mhukuru Coalfield, Songea District, Tanganyika; Ecca Series (" Upper Coal Measures ").

Only two specimens were recognized. The largest fragment (V.34467) is shown in Text-fig. 10, E, where all the details clearly visible are accurately represented.

The second specimen (V.34493), a fragment with neither midrib nor margin has slightly wider meshes, up to 1 mm. wide. The veins are sinuous but since the epidermal cells show straight veins I have no doubt that the veins have been displaced during preservation.

In both specimens the substance of the lamina is thin. In neither are there any fibres in the vein meshes. The cuticle of both leaves was prepared but the figures are all from the leaf shown in Text-fig. 10, E.

The upper cuticle of the lamina is about 3 μ thick. The cell outlines are clearly marked as shown in Text-fig. 10, C. Lateral walls of cells are thin but have a border on either side (Text-fig. 10, D). The cells tend to be in rows parallel to the veins. The cells above the veins could not be seen in this specimen but in the second specimen they are narrower and more elongated. Stomata are absent.

The lower cuticle is thinner (about 1–2 μ thick). The cell outlines are moderately clear (Text-fig. 10, A). Lateral walls of cells are straight. The cell surface usually shows a median papilla. The cells above the veins are narrow and elongated in the direction of the veins, those between the veins are usually isodiametric or elongated in various directions. Stomata are confined to areas between the veins. Trichomes are absent.

The stomata are haplocheilic and possibly partly amphicyclic. The guard cells are hidden by a ring of five or more subsidiary cells. Each subsidiary cell usually has a prominent thickened papilla covering the stomatal aperture. The cells regarded as encircling cells resemble ordinary epidermal cells but are often tangentially elongated.

The cuticle in the second specimen is very similar but the papillae are very obscure.

Glossopteris sp. A resembles *G. fibrosa* in form, venation and cuticle. The only difference is in the isolated fibres which are here absent but conspicuous in *G. fibrosa*. It differs from *G. hispida* in lacking fibres, hairs and sinuous-walled cells. In the complete absence of sinuous-walled cells it differs also from *G. colpodes*.

It has not been named as a species because too little is known about it.

Genus ***RHABDOTAENIA*** nov.

DIAGNOSIS. Leaf elongated, entire, with a strong midrib, lamina arising from the sides of the midrib, lateral veins arising at a wide angle or at a smaller angle but almost immediately bending outwards and crossing the lamina at a wide angle, lateral veins occasionally forked, anastomoses between lateral veins extremely rare. Stomata usually confined to areas between veins on lower epidermis, subsidiary

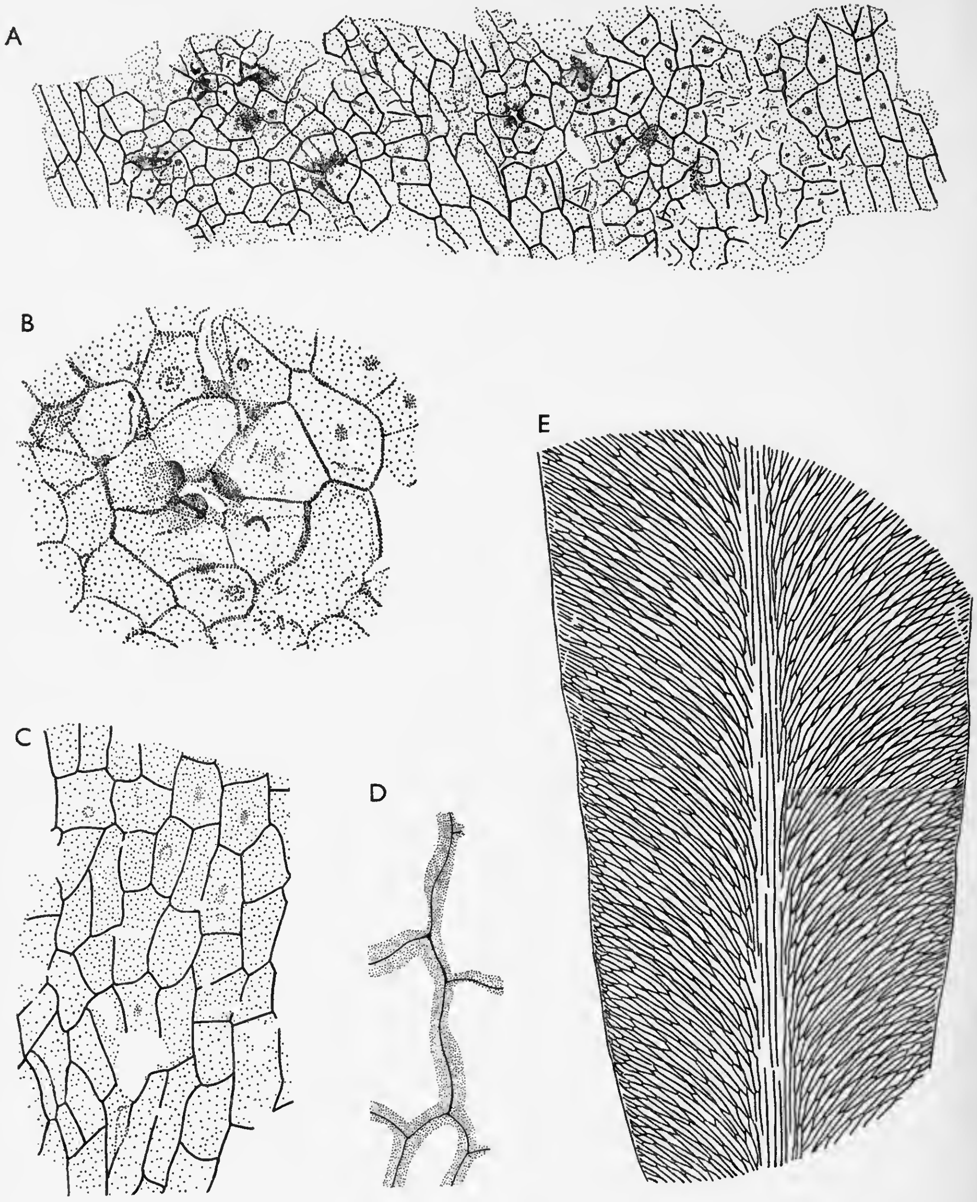

Fig. 10. *Glossopteris* sp.A. A, lower cuticle showing elongated cells above veins and stomatiferous areas between them. V.34467*a*. × 125. B, stoma from A. × 400. C, upper cuticle showing cells in rows parallel to veins. V.34467*a*. × 125. D, part of C more magnified to show bordered walls. × 400. E, middle part of leaf showing venation. V.34467. × 2.

cells haplocheilic, irregular, not forming a definite ring, guard cells exposed or covered by subsidiary cell papillae not situated in a pit. Cuticle rather thin.

TYPE SPECIES. *Rhabdotaenia danaeoides* (Royle) n. comb.

DISCUSSION AND COMPARISON. *Rhabdotaenia* is made for certain fronds of taeniopterid form of which the cuticular structure is known. Among such fronds with haplocheilic stomata are *Bjuvea* Florin (1933 : 48) in which the subsidiary cells are in a rather definite ring and form a pit above the guard cells, and *Doratophyllum* Harris (1932 : 36) where they form a perfect ring arching over the guard cells as a cone. The irregularity of the subsidiary cells distinguishes *Rhabdotaenia.*

The mode of origin of the lamina from the sides of the midrib may be important. In *R. danaeoides* and in *R. harkini* there is no very sharp border to the midrib, certainly no fold such as is seen in *Taeniopteris vittata* where the lamina arises rather above the middle of the rachis and a good deal more rachis is seen from below than from above. In *Nilssonia* it differs even more, arising from the top of the rachis. The precise level of origin in *Doratophyllum* and *Bjuvea* has not been discussed. In *Glossopteris*, from my own observations, the origin of the lamina is purely lateral ; the midrib, however, being slightly depressed on the upperside and prominent below may occasionally show folds at the sides but otherwise it grades imperceptibly into the lamina. The epidermal structure of *Rhabdotaenia* also resembles that of *Glossopteris* and it may be that the two genera are naturally related.

Other genera which may be mentioned are the ill-defined *Macrotaeniopteris* (type *M. major*) which proves to be a Bennettitalean leaf like several other species and may be included in *Nilssoniopteris*, and *Palaeovittaria* (Feistmantel, 1876 : 368, pl. 19, figs. 3, 3*a*, 4, 4*a* ; Zeiller, 1902*a* : 81, pl. 16, fig. 1) which differs in the small angle of the veins from the midrib.

Rhabdotaenia danaeoides (Royle) n. comb.

(Text-fig. 11)

1833. *Glossopteris danaeoides* Royle, p. 29, pl. 2, fig. 9.
1836. *Aspidites danaeoides* (Royle) Goeppert, p. 352.
1850. *Pecopteris danaeoides* (Royle) Unger, p. 170.
1901. *Macrotaeniopteris danaeoides* (Royle) Arber, p. 548 (pars).
1905*a*. *Taeniopteris danaeoides* (Royle) Arber, p. 121, pl. 5, fig. 1.

Similar leaves but with finer details unknown :

1850. *Taeniopteris danaeoides* (Royle) : McClelland, p. 56 pl. 15, fig. 1.
1876. *Taeniopteris danaeoides* (Royle) : Feistmantel, p. 74.
1876*a*. *Macrotaeniopteris danaeoides* (Royle) Feistmantel, p. 137.
1876*b*. *Macroteniopteris danaeoides* (Royle) : Feistmantel, p. 305, pl. 19, figs. 1, 2 ; pl. 21, fig. 1.
1880. *Macrotaeniopteris danaeoides* (Royle) : Feistmantel, p. 88, pl. 20*a*, figs. 1, 2.
1886. *Macrotaeniopteris danaeoides* (Royle) : Feistmantel, p. 24, pl. 4*a*, figs. 2, 3.
1893. *Macrotaeniopteris danaeoides* (Royle) : Oldham, pl. 2.
1905*a*. *Taeniopteris danaeoides* (Royle) : Arber, p. 121 (pars).

EMENDED DIAGNOSIS. Leaf oval-oblong, widest in the middle region, typically 5–7 cm. wide, length possibly about 20 cm.; petiolate. Midrib up to 3 mm. wide

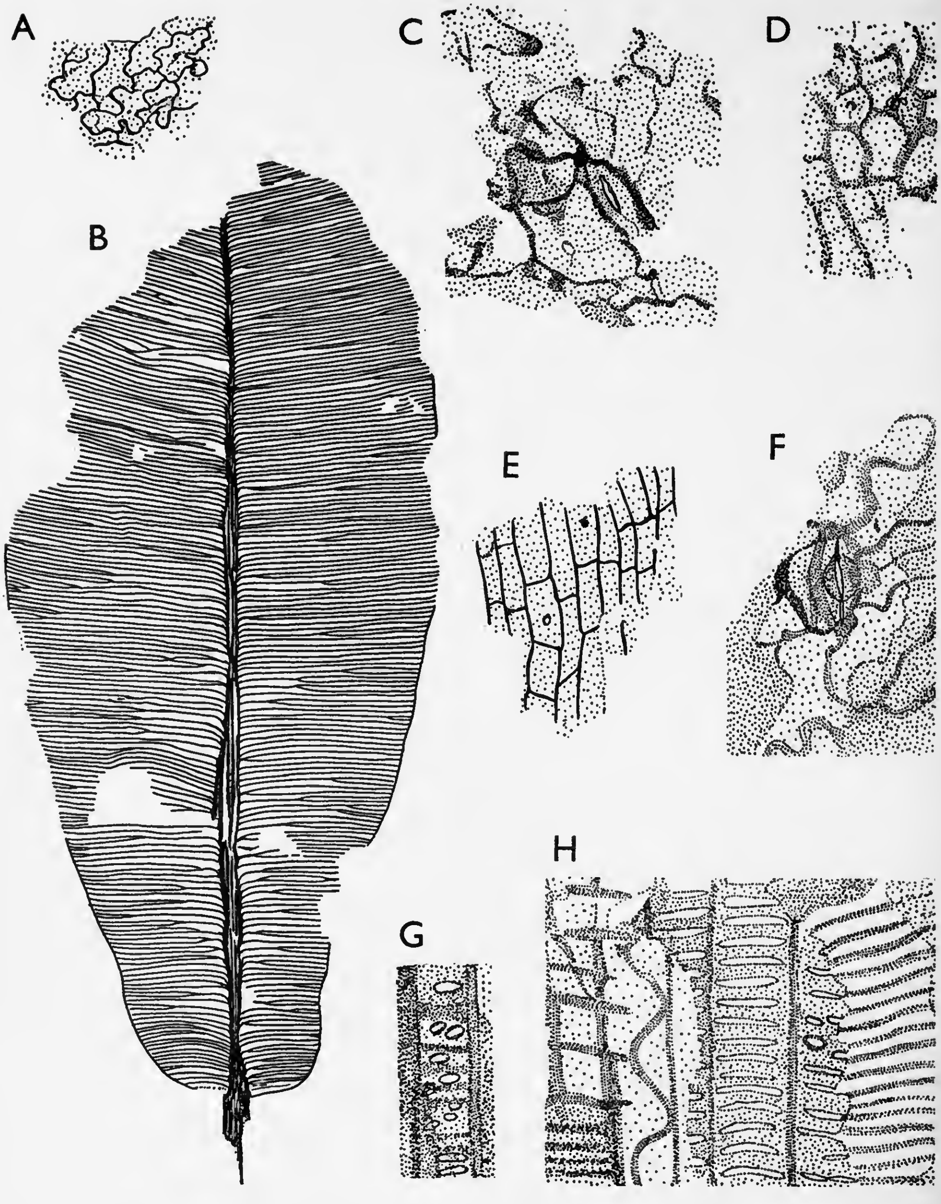

FIG. 11. *Rhabdotaenia danaeoides* (Royle). A, sinuous-walled cells of lower epidermis between veins. V.19598*a*. × 125. B, leaf showing venation. Neotype, V.4191. × 1. C, stoma showing exposed guard cells. V.19598*b*. × 400. D, upper epidermis showing straight-walled cells. V.19598*a*. × 125. E, epidermis of midrib. V.4191*a*. × 125. F, stoma showing lateral lignine lamellae of guard cells. V.19598*a*. × 400. G, tracheid showing both bordered pits and transverse bars, from midrib. V.19598*c*. × 800. H, xylem showing spiral, scalariform and pitted tracheids from midrib. V.19598*c*. × 800.

below, narrower towards the apex, showing numerous longitudinal strands near leaf base, fewer above. Margins entire or slightly undulate. Base more or less abruptly contracted.

Lateral veins parallel, arising at right angles to the midrib or at a smaller angle and almost immediately arching outwards and running at about 90° to midrib. About one-third of lateral veins forked once, rest unbranched. Twice forked veins very rare. Concentration of veins 12–16 per cm. near midrib, 15–20 per cm. near margins.

Upper epidermis of lamina probably without stomata. Cells between veins appearing polygonal with almost straight thick side-walls. Cells tending to be arranged in rows parallel to the side veins. Cells above veins narrower. Upper cuticle rather thick, like upper epidermis, surface showing longitudinal striations.

Upper and lower epidermis of midrib showing straight-walled rectangular cells tending to be arranged in longitudinal rows. Surface sometimes showing longitudinal striations, median papilla occasionally present, stomata absent.

Lower epidermis of lamina thinner than upper, stomatiferous. Cells between veins irregularly shaped, typically about 40 μ wide × 95 μ long, lateral (anticlinal) walls sinuous, about 3 μ thick, becoming gradually straight in the vicinity of midrib, surface occasionally showing striations and a rather obscure median papilla. Cells above veins straight-walled, rectangular, elongated in the direction of veins, surface sometimes with fine longitudinal striations.

Stomata present in areas between veins. Subsidiary cells haplocheilic, numerous (about seven), like ordinary cells, irregular, not forming a ring round guard cells, guard cells exposed, typically 8 μ × 32 μ.

Lower cuticle thin, walls obscure.

NEOTYPE. Brit. Mus. (N.H.) Palaeont. Dept. no. V.4191. Figured Royle (1833, pl. 2, fig. 9) and Arber (1905*a*, pl. 5, fig. 1).

PARATYPE. Brit. Mus. (N.H.) Palaeont. Dept. no. V.19598.

LOCALITY AND HORIZON. Burdwan Coalfield, India; Permo-Carboniferous.

DESCRIPTION. The diagnosis is based on three leaves from Burdwan Coalfield, India, namely Royle's type (V.4191) and a block with two leaves (V.19598). They are very similar indeed but one of the leaves on V.19598 shows more of its petiole which is 3 cm. long.

Without examining the originals it is impossible to say which of Feistmantel's figured specimens belong to the same species; all may well be the same. If so the species includes quite small oval leaves (4 cm. × 2·5 cm.) as well as much wider ones, up to 11 cm. wide and of unknown length.

Two cross connections occur between lateral veins in the neotype. Some guard cells show lateral lamellae. The midrib shows abundant tracheids, sides 14–30 μ wide. Some tracheids show spiral and annular thickenings but most are scalariform (Text-fig. 11, H). A few tracheids also show transverse bars between oval bordered pits (Text-fig. 11, G). There are in addition thick-walled elements showing usually sparsely distributed, small, oval or rounded pinhole-like pits and cells with no pits which may be tracheids or sclerenchyma.

Rhabdotaenia danaeoides is not the only species in the Lower Gondwana Coalfields of India; there is also *Macrotaeniopteris feddeni* figured by Feistmantel (1880 : 89, pl. 21A, fig. 3, pl. 22A, figs. 1–4; 1881 : 255, pl. 2, fig. 1: 1882 : 31, pl. 21, fig. 5; 1886 : 24, pl. 1A, fig. 1). Dolianiti (1953 : 2, pls. 1, 2) has recently reported this species from Brazil.

Macrotaeniopteris feddeni is supposed to be distinguished chiefly by its more crowded veins and thinner midrib. However, several specimens referred to *M. feddeni* agree equally well with others referred to *Macrotaeniopteris danaeoides* e.g. one (Feistmantel, 1882, pl. 21, fig. 5) has as few as 11 veins per cm. according to the figure. I can see no difference in the midrib. No fine details are known. Clearly *M. feddeni* is not, at present, adequately distinguished.

The Brazilian leaf, however, has 25–35 veins per cm. and is clearly distinct from *Rhabdotaenia danaeoides*. The only other Lower Gondwana leaves are *Taeniopteris daintreei* McCoy (1875 : 15, pl. 14, fig. 1, 2), *Angiopteridium spathulatum* Etheridge (1901 : 72), *A.* cf. *mcclellandi* Feistmantel (1880 : 92, pl. 21A, figs. 4–7), *Taeniopteris criciumensis* Dolianiti (1953, pl. 3) and some imperfectly known *Taeniopteris* leaves which are all much narrower.

Rhabdotaenia danaeoides is compared with *R. harkini* below.

Rhabdotaenia harkini n. sp.

(Pl. 20, fig. 5; Text-figs. 12–14)

Diagnosis. Leaf about 6 cm. wide in widest part (presumably from middle region of leaf), length unknown. Midrib at least about 1 mm. wide below, narrower above. Margin entire, probably slightly undulate, very slightly converging towards apex. Lateral veins parallel, arising almost at right angles or at a smaller angle and almost immediately arching outwards and running at 80°–90° to midrib. Veins forked once or twice or unbranched, usually dichotomising near midrib and often elsewhere in the lamina. Cross connections between veins extremely rare. Some veins bent slightly forwards near margin but no marginal vein present.

Concentration of veins 15–18 per cm. near midrib, 23–28 per cm. near margin. Veins usually 145 μ thick but some veins up to 250 μ thick at base. Substance of lamina probably thin.

Upper epidermis of lamina without stomata. Cells between veins polygonal, isodiametric or elongated in various directions typically 60 μ × 45 μ wide, lateral (anticlinal) walls of cells straight, thick (up to 12 μ thick). Cells perhaps tending to be arranged in rows parallel to veins. Surface of cells finely mottled, papillae usually absent.

Upper cuticle about 2 μ thick, outlines of cells somewhat obscure, walls thin, otherwise like upper epidermis.

Lower epidermis of lamina thinner than upper, stomatiferous. Cells between veins irregularly shaped, isodiametric or elongated in various directions, typically about 90 μ long × 60 μ wide, lateral (anticlinal) walls of cells sinuous but gradually becoming straight near midrib. Cells near midrib and those in angles between branches of veins sometimes unusually large and with almost straight walls. Cells over veins narrow, elongated in the direction of veins, rectangular, lateral walls straight. Lateral walls of lower epidermal cells often unevenly thickened, up to 3 μ thick. Cell surface usually showing a large thick-walled median papilla about 10–15 μ in diameter. Papillae in some ordinary epidermal cells and subsidiary cells of stomata (especially near imdrib) about 50 μ long, blunt and often with a rounded top. Cell surface sometimes showing a few ridges, but usually fine striations, radiating from the base of the papilla. Striations often running parallel and continuous between adjacent cells and intervening walls, but usually in no definite direction or arrangement in cells between veins, in cells above veins striations usually parallel and running in the direction of the veins. Striations running longitudinally along the surface of some laterally flattened papillae. Trichomes absent.

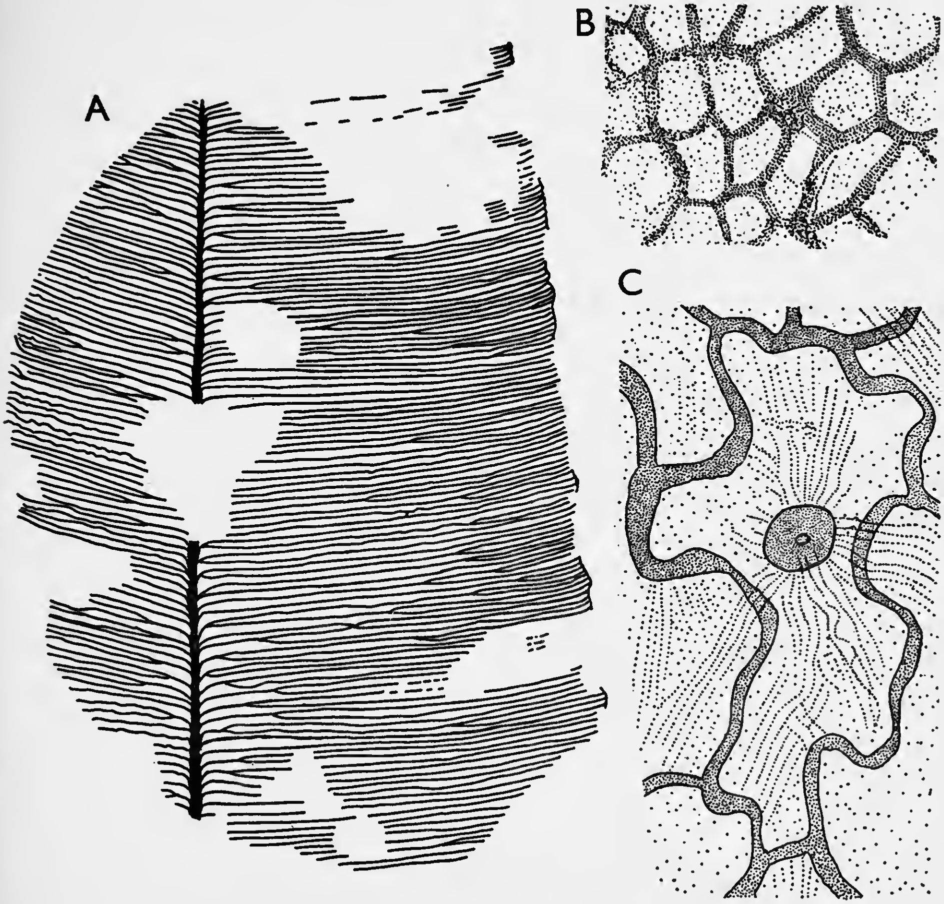

FIG. 12. *Rhabdotaenia harkini* n. sp. A, leaf showing venation. × 2. B, upper epidermis showing straight-walled polygonal cells. × 125. C, a cell of the lower epidermis from Text-fig. 13, B, showing the large median papilla and surface striations. × 800. All from the Holotype (V.34454).

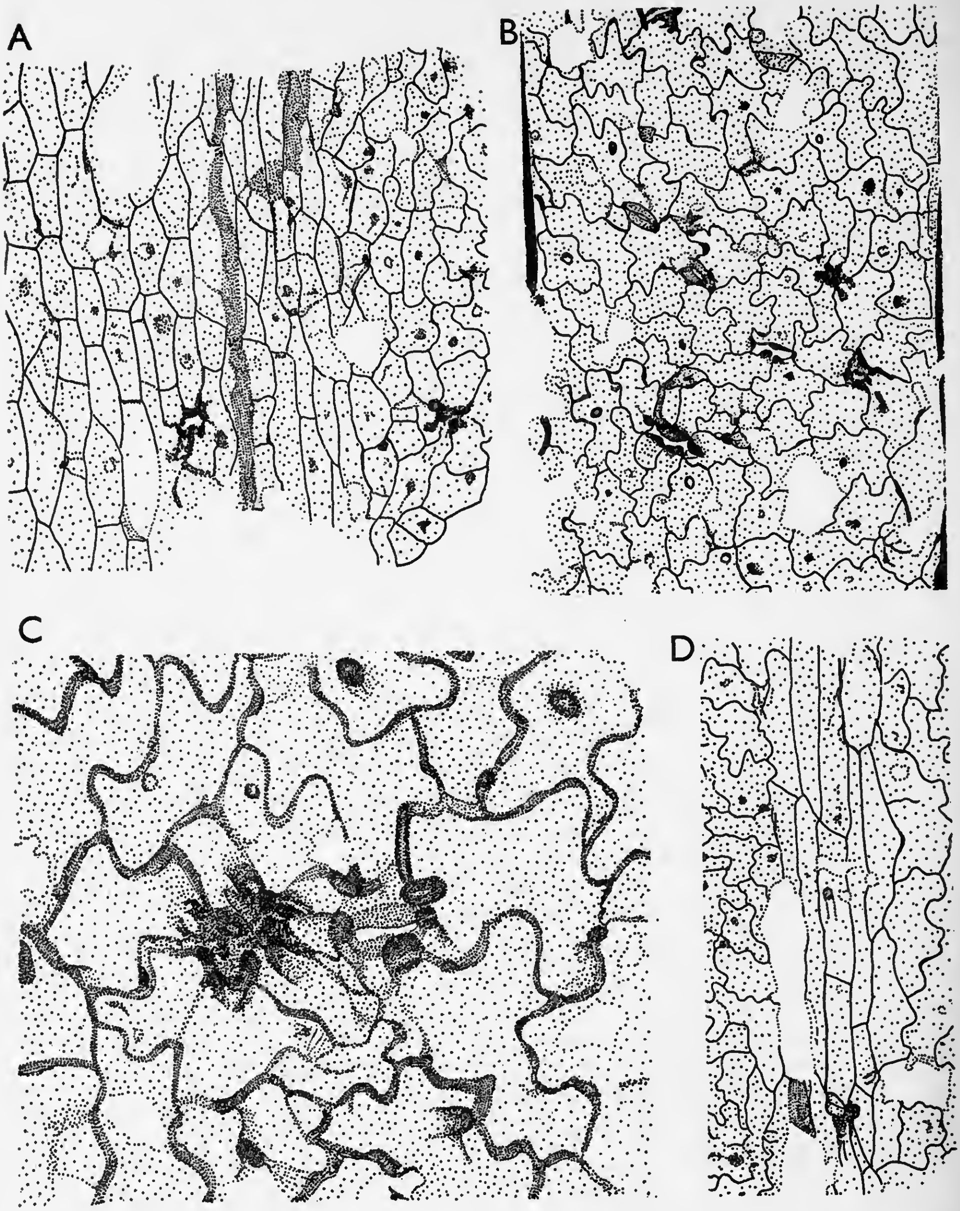

Fig. 13. *Rhabdotaenia harkini* n. sp. A, lower epidermis of midrib (on left) and stomatiferous area between bases of two lateral veins showing sinuous-walled cells on the right. × 125. B, stomatiferous area between two veins. × 125. C, two closely placed stomata, one (right) rather exposed, the other (left) protected by overlapping papillae. × 400. D, cells below vein (lower side). × 125. All from the Holotype (V.34454).

Stomata usually confined to areas between veins, rarely above veins, somewhat unevenly distributed, concentration about 53 per sq. mm., orientation irregular.

Stomata haplocheilic, monocyclic or possibly partly amphicyclic. Guard cells 8–11 μ wide × 32–45 μ long, exposed or more or less covered by subsidiary-cell papillae. Subsidiary cells 3–10, irregular, not forming a ring, polar subsidiary cells like laterals, size and shape of subsidiary cells similar to ordinary epidermal cells but often with a large hollow papilla on the side of the stomatal aperture, sometimes no well-marked papilla present but subsidiary cell margins thickened nearest the guard cells. Papillae pointing upwards or over stomatal aperture. Surface of subsidiary cells sometimes thicker than that of ordinary epidermal cells, showing parallel striations radiating outwards from the side of the stoma.

Lower epidermis of midrib showing rows of straight-walled, longitudinally elongated, polygonal cells, surface mottled, showing longitudinal striations, papillae sometimes present but not prominent, stomata rarely present. Upper epidermis of midrib unknown.

Lower cuticle of lamina thin (about 1 μ thick) walls of cells between veins obscure, usually appearing broken but sometimes showing sinuous waves. Cell walls below veins better marked, straight, thin. Cell surface mottled, occasionally showing a median papilla and striations. Lower cuticle otherwise as lower epidermis.

HOLOTYPE. Brit. Mus. (N.H.) Palaeont. Dept. no. V.34454.

LOCALITY AND HORIZON. Mhukuru Coalfield, Songea District, Tanganyika; Ecca Series (" Upper Coal Measures ").

DESCRIPTION. A single specimen was found (Text-fig. 12, A). The leaf substance appears to have decayed considerably during preservation. It shows only the lower epidermis and the substance of the veins. The upper epidermis is preserved only at a few points (where it overlaps the lower and the intervening leaf substance). In places the veins appear sinuous but this is clearly due to displacement during preservation as the cells above veins run straight. There are two or possibly three anastomoses between lateral veins. Occasionally veins and midrib show scalariform tracheids with sides of varying width but usually about 14 μ wide and spiral tracheids about 10 μ wide. Some exposed guard cells show lateral lamellae of Gymnosperm type and thinner areas at the poles. A few two-winged pollen grains occur on the epidermis.

The species is named after Mr. D. A. Harkin of the Tanganyika Geological Survey who collected the material.

COMPARISON. *Rhabdotaenia harkini* differs from *R. danaeoides* in having a comparatively higher concentration of veins especially near the margin (*R. danaeoides* has 12–16 veins per cm. near the midrib, 15–20 near the margin; *R. harkini* has 15–18 near the midrib, 24–28 near the margin). In *R. harkini* about half the veins are forked and a number of these are forked twice; in *R. danaeoides* only about one-third of the veins are forked and twice-forked veins are very rare. The upper and lower epidermis of the two species are, as far as they are known, similar; the only differences are: (1) the larger and more prominent papillae present in most cells of the lower epidermis of *R. harkini* (in *R. danaeoides* the papillae are rather obscure and only occasionally seen), and (2) in *R. harkini*, while some stomata are fully

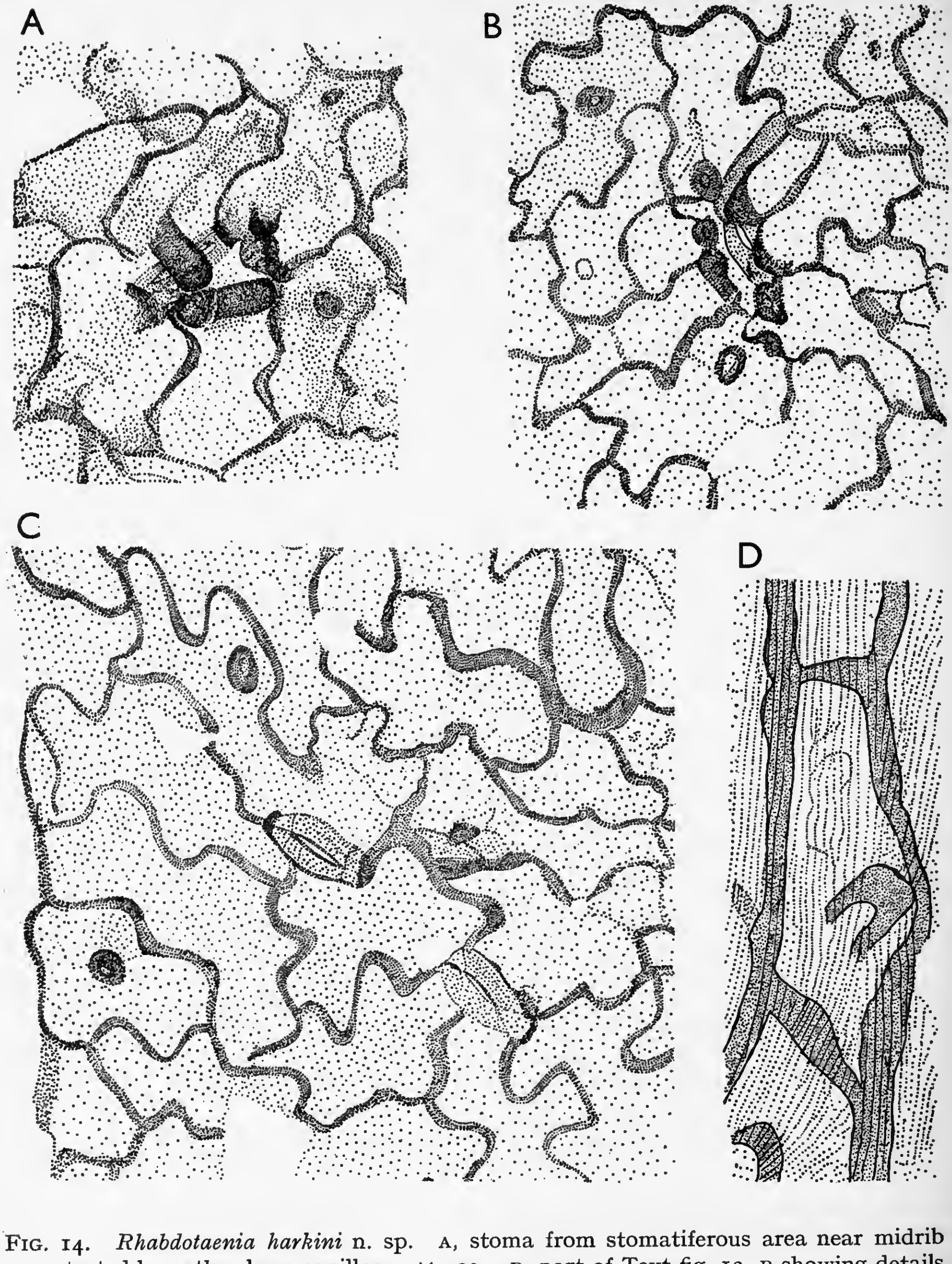

Fig. 14. *Rhabdotaenia harkini* n. sp. A, stoma from stomatiferous area near midrib protected by rather long papillae. × 400. B, part of Text-fig. 13, B showing details of a moderately protected, possibly partly amphicyclic stoma. × 400. C, another part of Text-fig. 13, B, showing details of two exposed stomata. × 400. D, a cell under vein from Text-fig. 13, D, showing parallel longitudinal striations and median papilla. × 800. All from the Holotype (V.34454).

exposed exactly like those of *R. danaeoides*, there are others which are more or less protected by epidermal papillae. No such protected stomata have yet been observed in *R. danaeoides*.

These supposed differences are, however, based on the comparison of a single specimen of *R. harkini* with three very incompletely preserved ones of *R. danaeoides*. Thus the range of variation of neither species is known and, though they may prove to be identical it seems advisable to distinguish them for the present.

Scale Leaves

(Pl. 20, figs. 3, 4; Text-fig. 15)

LOCALITY AND HORIZON. Mhukuru Coalfield, Songea District, Tanganyika; Ecca Series (" Upper Coal Measures ").

DESCRIPTION. Twelve scale leaves of varied form were examined and also some fragments. Text-fig. 15, A shows a lanceolate scale overlying the cordate base of another scale. They are 1·7–2 cm. long and 0·7–1·2 cm. wide, rather convex with an ill-defined broad midrib and diverging veins which occasionally fork and anastomose.

Text-fig. 15, B shows a small rounded scale with a broad base and Text-fig. 15, C shows a group of somewhat larger rounded scales looking like a bud. The veins are more distinct. There is no definite midrib but merely a number of longitudinal strands. Again a few vein anastomoses were seen.

Both broad and lanceolate scales when isolated or transferred and seen in transmitted light show a scarious margin. Some of them show fibres in vein meshes. They usually have short simple hairs, about 300 μ long, on their outer side and at the margins, but some, e.g. the scale in Text-fig. 15, B, show none. The cuticles of the different forms are rather similar. The cuticle of the outer (convex) side is up to 2 μ thick. Its cells are polygonal with straight or arched sides. The cells above veins are narrower. Single-celled hair bases, occasionally with the cutinized hair still attached, are unevenly distributed between the ordinary epidermal cells (Text-fig. 15, D, E). Stomata are absent.

The cuticle of the inner (concave) side is more delicate with rather obscure cell outlines. No definite stomata could be recognized and no hair bases were observed.

REMARKS. Similar scales have been described by Feistmantel (1880, 1882), Zeiller (1896, 1902), Seward (1897, 1904), Arber (1905, 1905*a*) Seward & Sahni (1920), Walkom (1921, 1922, 1928, 1931), Walton (1929) and others. Zeiller (1896, 1902) figured some specimens clearly showing anastomosing veins as in *Glossopteris*. Such scales have usually been attributed to *Glossopteris*, and sometimes to *Noeggerathiopsis*, but with little evidence beyond association. In the cores from Mhukuru they are found in association with leaves of *Glossopteris fibrosa* and *G. colpodes* (as well as seeds, sporangia and roots). No specimens of *Noeggerathiopsis* occur in the flora. The present specimens may be ordinary protective scales of the vegetative bud of *Glossopteris*. Their form is fully consistent with this and their cuticles resemble those of *G. fibrosa*. There is no reason at all to regard them as reproductive organs and certain of these scales when transferred were proved to contain no sporangia, seeds or other bodies.

Sporangia

Similar bodies:

1905. "Sporangium-like organs of *Glossopteris browniana*", Arber, p. 324, pl. 30, figs. 1–3; pl. 31, figs. 1–5.
1905*a*. "Fructification of *Glossopteris*", Arber, p. 39, text-figs. 12–15.
1907. "Sporangia", Seward, p. 68, pl. 8, figs. 7, 7*a*.
1919. "Sporangia", Lundqvist, p. 12, pl. 1, figs. 8, 9.
1928. "Microsporangia of *Glossopteris* (Arber, 1905)", Walkom, p. 561.

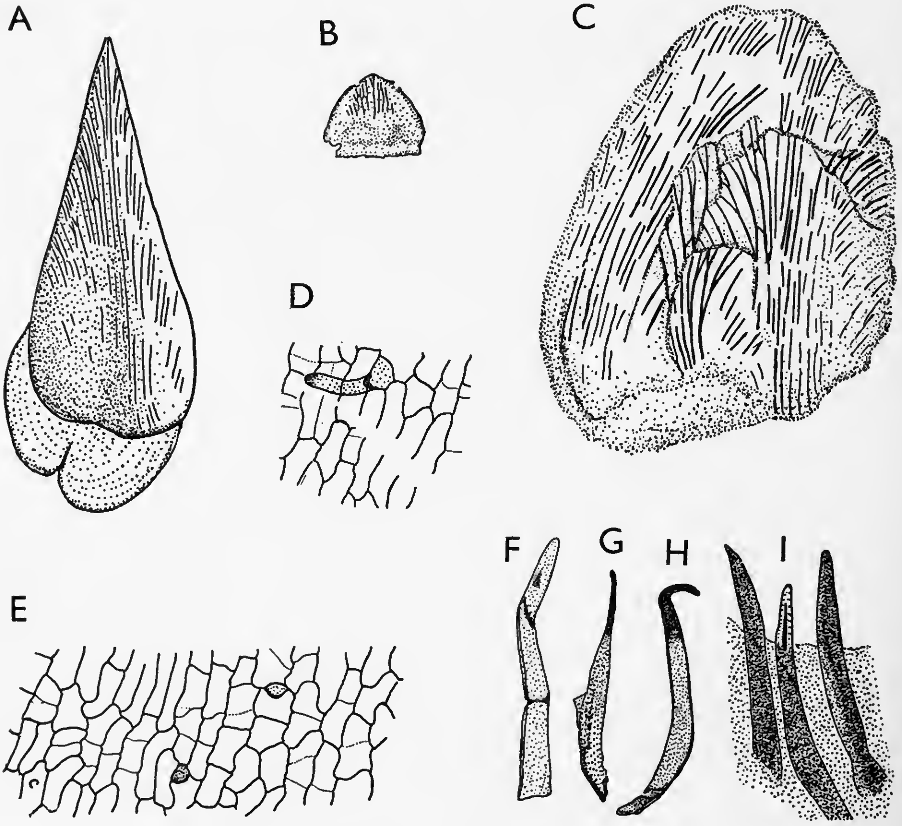

FIG. 15. Scale leaves. A, a lanceolate scale leaf and the cordate base of another. V.34468. B, rounded scale leaf with a broad base (see also Pl. 20 fig. 3). V.34453. C, group of rounded scale leaves resembling a bud. V.34468. D, cuticle of the outer (convex) side of a scale leaf with a cutinized hair and hair base. V.34468*a*. E, cuticle of the outer (convex) side of the same scale leaf showing two hair bases and epidermal cells. F, two-celled hair from a scale leaf. V.34468*b*. G, H, single-celled hairs from the same scale leaf. I, leaf epidermis with attached hairs. V.34468*b*. A–C, × 3; D–I, × 125.

1932. " Sporangia ", Du Toit, p. 384, pl. 40, figs. 9–12.
1955. " Male fructifications referable to *Glossopteris* ", Sen, p. 48, pls. 7, 8.
1956. " New type of fructification referable to *Glossopteris* ", Sen, p. 337, text-figs. 1–3.

Specimens from Mhukuru

(Pl. 21, figs. 1–6 ; Text-figs. 16, 17, A–D)

Seventeen specimens, from Mhukuru Coalfield, Tanganyika, show a large number of sporangia either isolated or occurring in groups. The best specimens were, however, obtained by dissolving pieces of rock in HF. These show slender axes, up to 200 μ thick, branching freely. Each ultimate branch ends in a single sporangium. A longitudinal strand, at some points showing scalariform tracheids about 8 μ wide, is present throughout the axes. Their surface cells are elongated but at a few points in the thicker axes they are short.

Laterally compressed sporangia are oval with one side nearly straight, the other strongly curved (Text-figs. 16, A, E, F, 17, C). They are up to 3 mm. × 1·25 mm. but many are much shorter, some because they were compressed longitudinally (Text-fig. 16, B) but others must have been smaller originally.

Most of the sporangia have dehisced along the whole length of their convex side but the line of dehiscence is often oblique. Two flaps of the wall of such sporangia are either compressed almost flat or contain rock matrix and stray spores. A few sporangia are still closed and full of spores (Pl. 21, figs. 5, 6). These enclosed spores are oval and two-winged, 40–55 μ long and 25–30 μ wide (Text-fig. 17, D). One sporangium, however, which must be another species, contained winged spores measuring about 70 μ by 50 μ. In other respects this sporangium is similar to those with smaller spores.

The wall of the sporangium consists of an outer layer of elongated fibrous cells running lengthwise (parallel with the slit). The wall cells are 150–400 μ long and 6–35 μ wide tending to be narrower towards the apex and base. The surface of the wall cells is thick and uniformly dark ; a few show irregular paler areas probably due to poor preservation. The sides of the cells are straight or slightly sinuous (Text-figs. 16, G, H). The lines where these cells join are often represented by narrow and occasionally by wide gaps (the cuticle, however, is without any corresponding gaps). The outer surface of the sporangial wall cells projects and their walls are sunken. The inner surface of the wall is almost smooth. No specialized cells were recognized along the suture. At the apex of the sporangium the wall cells radiate from a point which is sometimes slightly projecting and marks the apical end of the slit. No specialized cells like an annulus occur anywhere.

At the base of the sporangium the narrowing fibrous cells of the wall converge and enter the stalk which is up to 1 mm. long × 0·1 mm. thick. It is often attached asymmetrically to the straight side of the sporangium (Text-figs. 16, A, E, F, 17, C). The body of some sporangia is bent almost at right angles to the stalk (Text-fig. 16, E, F).

On maceration the sporangium yields two cuticular coats, an outer smooth coat showing the outlines of the fibrous cells and an inner granular membrane showing

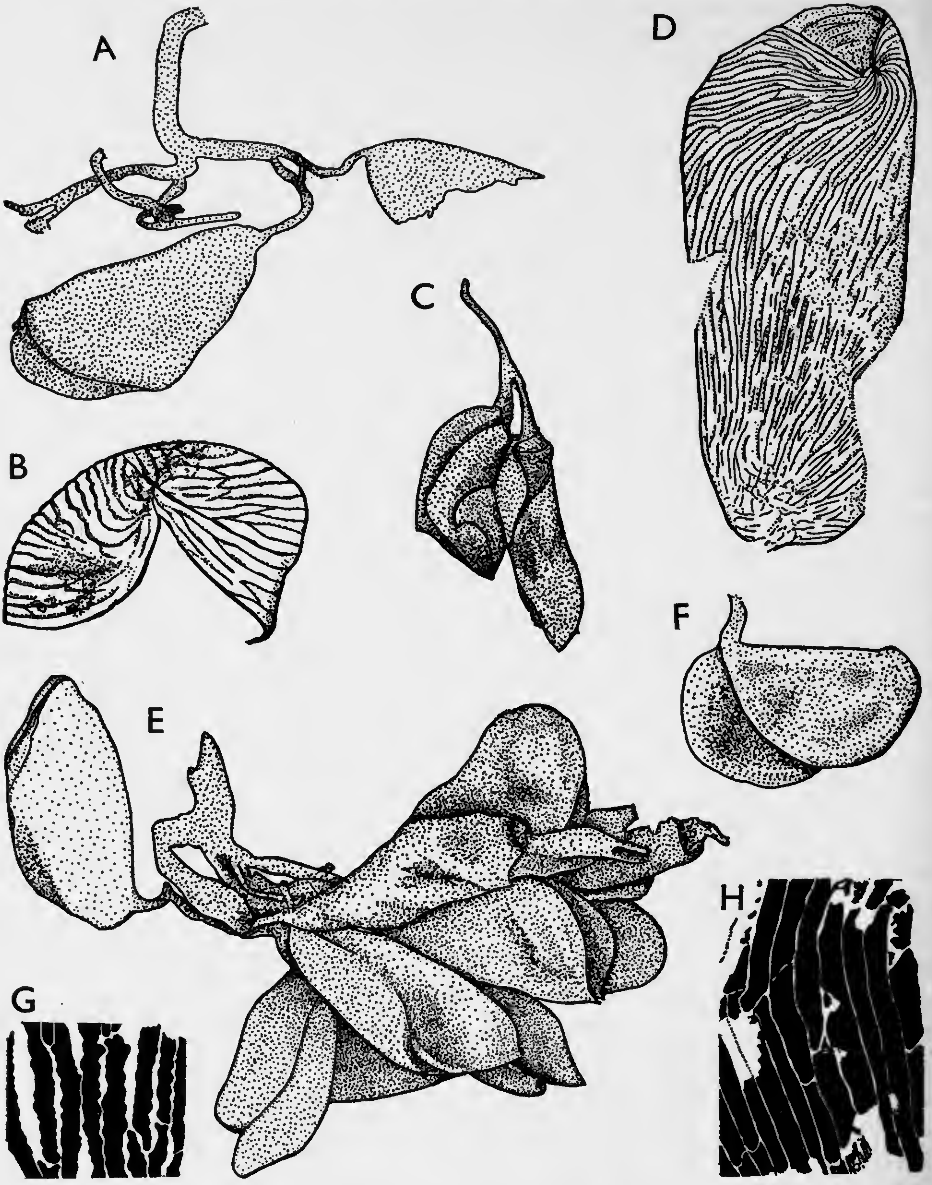

Fig. 16. Sporangia from Mhukuru Coalfield, Tanganyika. A, branching stalks terminating in sporangia; some sporangia have broken off. V.34457. × 25. B, transversely flattened sporangium. V.34469. × 50. C, forked axis bearing terminal sporangia. V.34457. × 25. D, sporangium showing wall-cells radiating from a point at the apex. V.34469. × 50. E, group of sporangia attached to a branching axis (see also Pl. 21, fig. 2). V.34457. × 25. F, sporangium, side view, bent almost at right angles to the stalk. V.34470. × 25. G, sporangium wall showing dark cell-interior from sporangium in Pl. 21, fig. 3. V.34458. × 125. H, wall cells of a sporangium. V.34471. × 125.

straight or slightly sinuous-walled, isodiametric polygonal cell outlines typically about 40 μ across. The cells of the outer membrane, particularly those near the sporangial stalk, may show a median rounded mark (papilla). Some of the dehisced sporangia show spores in great variety which had evidently got in before preservation.

The sporangia occur in association with leaves of *G. fibrosa* and *G. colpodes* (as well as scale leaves, *Spermatites crystallinus*, *S. tetrapterus*, *Vertebraria*, and some thin roots).

Specimens from Australia

(Pl. 21, fig. 7; Text-fig. 17, E, F)

A few sporangia from Newcastle, New South Wales, have been examined and the following notes throw additional light on the African material.

1. *Detached sporangia.* Fourteen specimens from Newcastle (additional to those described by Arber, 1905, 1905*a*) agree very closely with the African ones. None of them is, however, as large as the largest African sporangia. They measure 1–2·5 mm. × 0·6–1·3 mm. A few of them show stalks about 100 μ thick. The wall shows very similar cells to the African ones (projecting outwards but smooth inside) and cuticles were obtained corresponding to the African ones. All have dehisced but a few retain numerous spores, all of one type (Text-fig. 17, F).

The sporangia figured by Arber (1905, 1905*a*) are much like these specimens (Text-fig. 17, E) except that those described by Arber have suffered complete oxidation and no cuticle or other organic matter remains.

2. *Attached sporangia.* Two specimens are available. One (V.24233) is a slightly concave disc (Pl. 21, fig. 7) thickly covered with sporangia compressed in various planes. No stalks were seen and it is not known how the sporangia were attached. The sporangia are empty. A little carbon of the wall remains but the wall cells are replaced by delicate rods of a mineral. The margins of the disc show small epidermal cells arranged in parallel rows. The rows are not concentric but meet the margin at a small angle. The surface of the disc where it is not covered with sporangia is wrinkled.

The other specimen, V.24244, is a fragment of what appears to be a similar disc. Its sporangia are full of spores but they proved ill-preserved. They are represented by rounded outlines about 14 μ wide and they are probably two-winged. This specimen was transferred and the back of it proved to be smooth; its surface shows small epidermal cells arranged in parallel rows, running from what is regarded as the base to the apex, i.e. longitudinally.

Discussion. The Newcastle specimens were finally proved to be sporangia by the discovery of a specimen (V.24244) with sporangia still full of spores. They look very much like the African ones, which also have been proved to be sporangia.

Arber (1905, 1905*a*) who first noticed them believed them to be sporangia; Seward (1907) and Lundqvist (1919) agreed. Thomas, H. H. & Mrs. (1925) and Walkom (1928) thought that they might be ramenta. The presence of spores adhering to empty specimens as noted by du Toit (1932) is not enough to prove them to be sporangia, but the occurrence of nearly ripe specimens full of spores, such as those

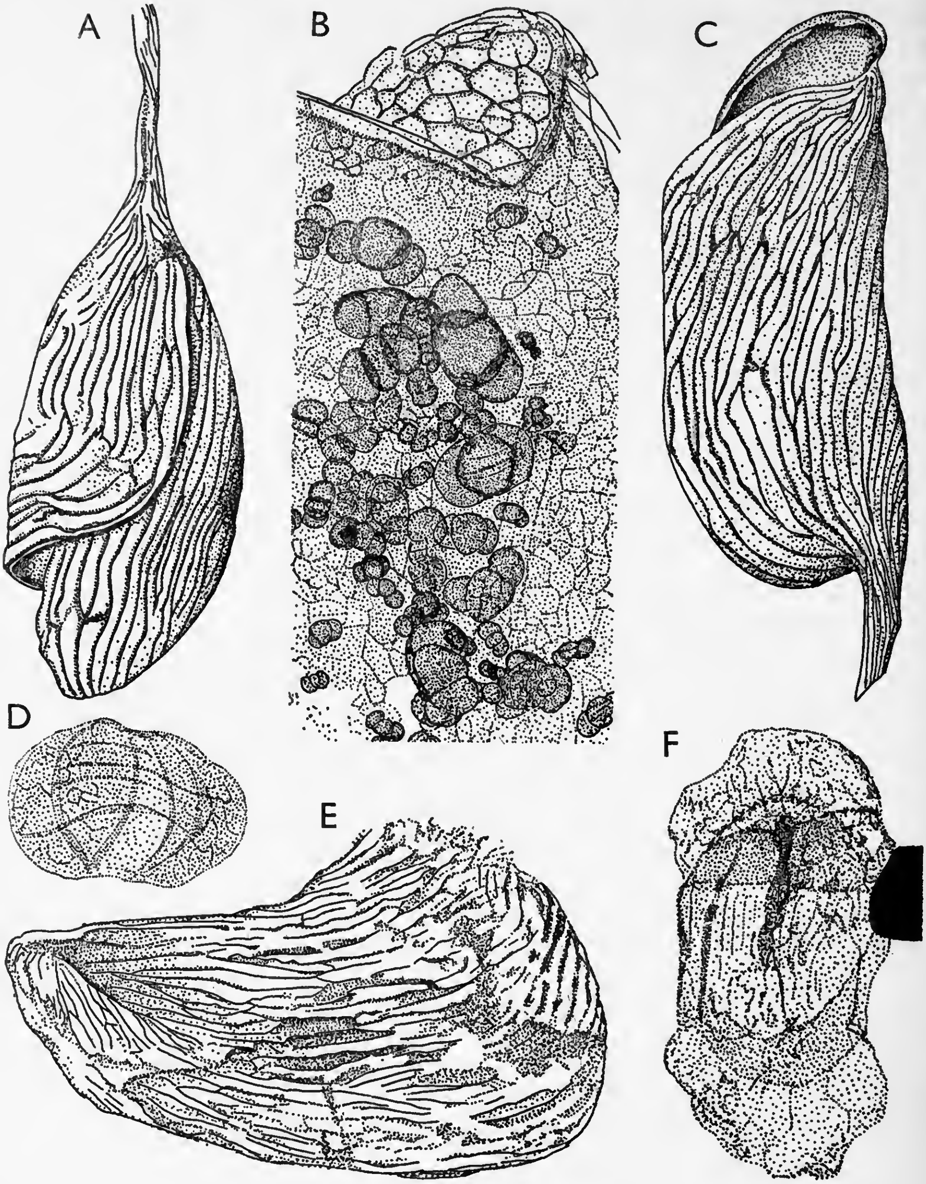

FIG. 17. Sporangia and spores. A, longitudinally dehisced sporangium. V.34457. × 50. B, two-winged spores of diverse sizes adhering to the inner cuticle of a dehisced sporangium (see also Pl. 21, fig. 1). V.34456. × 125. C, dehisced sporangium in side view. The stalk is attached on the flat side. V.34457. × 50. D, two-winged spore from an undehisced sporangium. V.34472. × 800. E, carbonized sporangium as seen in a transfer preparation. V.34491*a*. × 50. F, typical two-winged spore from a dehisced sporangium in a pull. The black spot is part of a wall cell. V.24245*a*. × 800. A–D from Mhukuru Coalfield, Tanganyika. E, F from Newcastle, New South Wales.

in specimen V.24244 and the undehisced African specimens, make their identity certain.

Sen (1955) described a few similar sacs but apparently with transverse dehiscence, which suggests that they are different from the specimens described here. In 1956 he described others with longitudinal dehiscence which are even more similar.

Arber (1905 : 41, 1905*a* : 325) described and figured a specimen, V.7202, in which he believed that these sporangia were borne on a scale (perhaps like one of the scales here regarded as bud scales). There is little of this scale preserved, however. Re-examination of the specimen merely shows that some of the sporangia lie beneath the scale fragment while others are clear. There is no evidence at all of attachment.

No organ exactly like the disc has been described. Several incompletely known fossils may, however, prove similar. These include *Eretmonia natalensis* du Toit (1932, pl. 40, figs. 9–12), *Conites* Seward (1897) and Seward and Leslie (1908) and the scale, " *Glossopteris* sp." (White, 1908, pl. 7, figs. 5, 5*a*, 6), which shows small rounded bodies on its surface. *Ottokaria ovalis* White (1908, pl. 7, figs. 7, 7*a*) and *Ottokaria leslii* Thomas (1921 : 285, text-figs. 1, 2) may be similar.

Ottokaria bengalensis Zeiller (1902) and Seward & Sahni (1920), *Lanceolatus* and *Scutum* Plumstead (1952, 1956) are assumed to be of a different nature. The rather regular arrangement of rounded bodies in *Scutum* is apparently different from the irregular arrangement of sporangia seen in the discs described here. I can see no similarity between the much larger " male bracts " of that organ and the present sporangia.

These Australian sporangia are of particular interest in relation to the African ones because while they look so similar they are probably borne in rather different ways. Not a single African specimen, in the present collection, shows a disc-like structure and it cannot be assumed that the Australian and African sporangia belong to closely related plants. Both of course occur in *Glossopteris* floras in association with various species of *Glossopteris*. It is possible that they belong to the same plants as the associated leaves but so many varied organs have been assigned to *Glossopteris*, on grounds of association, that I refrain from assigning these sporangia to it.

Genus **SPERMATITES** Miner

This non-committal designation is used because the structure of this seed though characteristic is not adequately understood. I feel sure that when it is so understood it will be well worthy of generic rank.

Spermatites crystallinus n. sp.

(Pl. 20, fig. 6 ; Text-figs. 18, 19)

DIAGNOSIS. Seed, flattened, orthotropous, 1·25–1·5 mm. long, 1–1·1 mm. wide and 0·75 mm. thick, oval, micropylar end obtusely pointed, chalazal end rounded, margins often bearing fragments of tissue (wing or possibly fruit substance ?). Surface of seed often showing longitudinal rows of polygonal cells about 30 μ wide. Cuticles : nucellus thickly cutinized showing elongated cells 30–75 μ long and 20–40

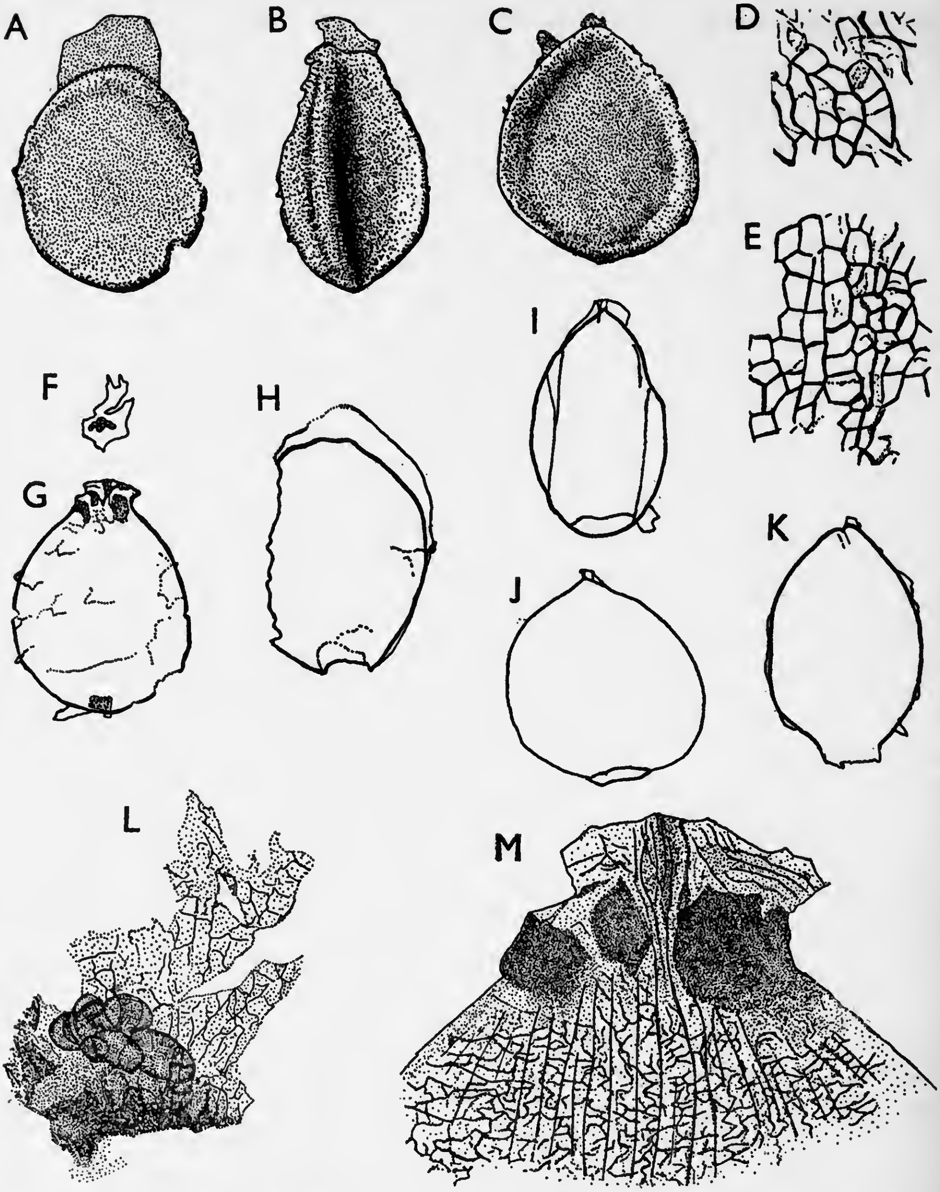

FIG. 18. *Spermatites crystallinus* n. sp. A–C, compressed seeds showing plates of tissue at the margin. B, shows a narrower seed with a longitudinal ridge on the surface. A, Holotype, V.34473. B, V.34474. C, V.34475. D, surface cells of marginal plate of tissue as seen before maceration of seed in A. E, surface cells of seed in A before maceration. F, cuticle of plate of tissue at margin of seed in A (broken while mounting). G, nucellus of seed in A with portions of outer membranes. H, cuticle of seed immediately outside the nucellus (inner cuticle of integument). V.34476. I, J, cuticles of seeds showing micropylar canals and chalaza. V.34477–78. K, cuticle of seed. V.34479. L, cuticle in F more magnified; a few two-winged pollen grains are sticking to it. M, top part of G, more magnified, showing micropylar canal. The three dark masses are unmacerated carbon. A–C, F–K × 25. D, E, L, M × 125.

μ wide, walls thick towards micropylar end, thinner elsewhere, straight or slightly wavy. Micropylar canal 80–90 μ long, chalaza about 300 μ wide. Megaspore membrane absent but nucellus enclosing a dark-coloured tissue often showing polygonal cells typically 15 μ long × 45 μ wide, walls up to 2 μ thick, usually appearing hyaline. Outer cuticles delicate ; immediately outside nucellus a delicate membrane (? inner lining of integument) showing narrow elongated cells which become sinuous near micropyle, cells typically 70 μ long × 15 μ wide.

Stone of integument not very thick, composed of elongated fibres. Outer cuticle (possibly surface of integument) showing short polygonal cells about 30 μ wide, cell surface often showing a rhomboidal, hexagonal or octahedral mark like the imprint of a crystal.

HOLOTYPE. Brit. Mus. (N.H.) Palaeont. Dept. no. V.34473.

LOCALITY AND HORIZON. Mhukuru Coalfield, Songea District, Tanganyika ; Ecca Series (" Upper Coal Measures ").

DESCRIPTION. Thirty-three of these seeds were isolated by dissolving pieces of rock in HF. Most of them are rounded but a few are narrow and show a longitudinal ridge on either surface (Text-fig. 18, B). On maceration their nucellus shows folds corresponding to the surface ridges. I believe these are laterally compressed seeds, they are about 0·75 mm. thick which is perhaps the original thickness of the seed.

Several seeds carry irregular plates of tissue at the margin and these may occur at any point (Text-figs. 18, A–C). The irregular margins of these plates may be original or may have been caused by breakage before preservation or during extraction. This tissue yields a delicate cuticle showing polygonal cells about 30 μ wide. It might represent some sort of wing or may possibly be a relic of the tissue of a fructification.

Maceration always yields the nucellus cuticle and usually fragments of other cuticles around it. Their nature is, however, not as clear as that of the nucellus. The inner cuticle of integument is best seen towards the micropyle. A few seeds yielded internal casts of fibres in the form of rods covered with short outgrowths which must have originally occupied pits. One seed yielded fragments of cuticle showing elongated tracheid-like cells with scalariform marks (Text-fig. 19, I) probably representing impressions of tracheids (cf. Harris, 1941 ; 88, text-fig. 5, F.). The nature of the outer cuticle showing crystalline imprints is not clear and could not be proved to be the same as the cells seen on the outside of the seed though it may be so.

Seven out of twelve seeds showing suitable micropylar ends have pollen grains on the surface of the nucellus around its micropylar end. In two seeds they also occur farther away from the micropyle. They are underneath the delicate inner cuticle of the integument and as far as can be seen most of them are of the same type. Those seen clearly are two-winged, about 30 μ × 50 μ in size (Text-fig. 19, G) but many are so crushed that their shape is obscured ; their texture is, however, similar to the clearer ones. Two exceptional round pollen grains about 60 μ in diameter were also noticed (Text-fig. 19, E). The presence of these numerous pollen grains suggests that they are not accidental but are the result of the normal pollination processes. The grains look just like those of the microsporangia and they provide

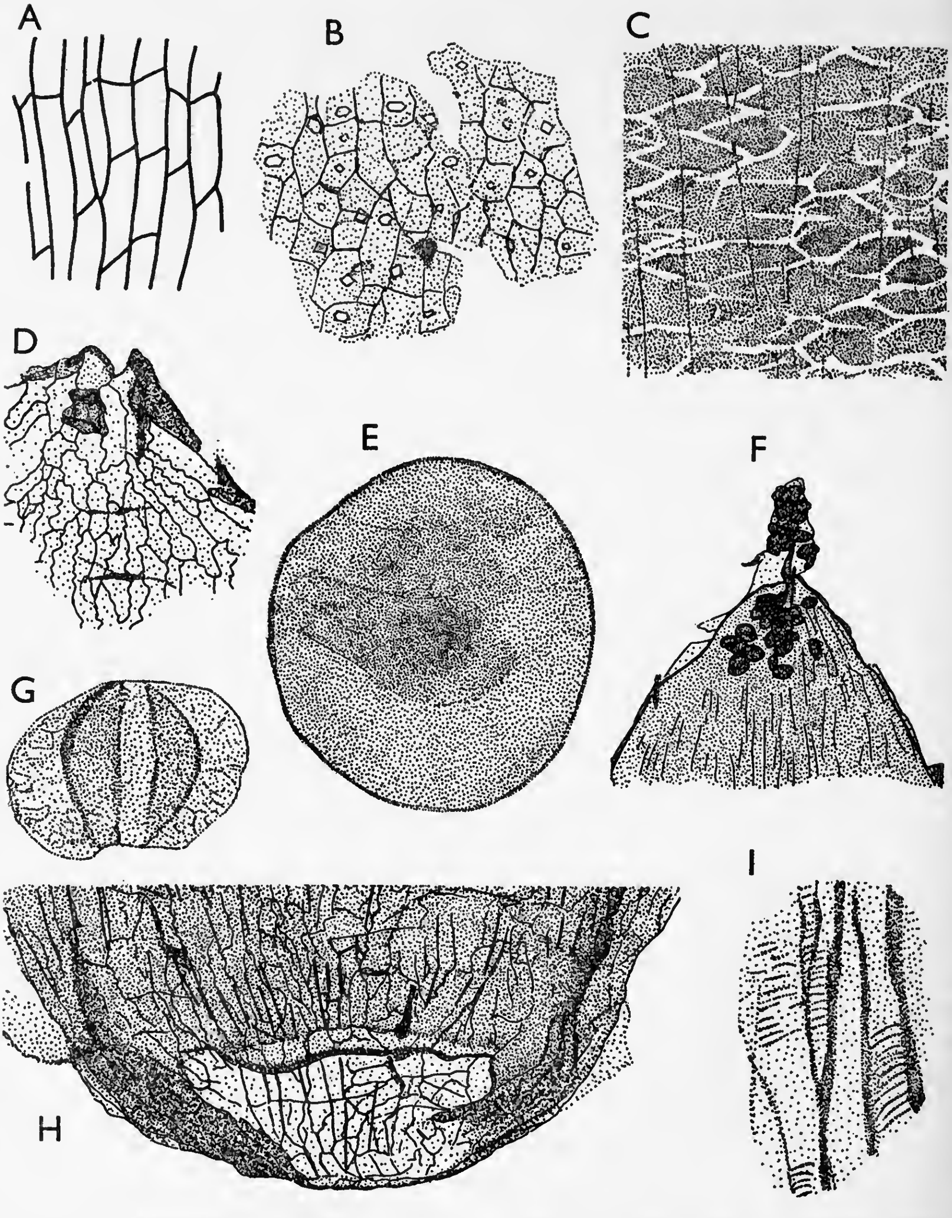

Fig. 19. *Spermatites crystallinus* n. sp. A, nucellar cuticle showing elongated cells. V.34480. × 200. B, outer cuticle of seed showing polygonal cells and crystalline imprints. V.34481*a*. × 200. C, dark tissue inside nucellus showing hyaline cell walls. V.34482. × 200. D, portion of cuticle immediately outside nucellus in Text-fig. 18, H, from near micropylar end of seed showing sinuous-walled elongated cells and a pollen grain. V.34476. × 200. E, unusual rounded pollen grain from the nucellus of a seed. V.34475. × 800. F, part of nucellus of seed showing numerous pollen grains at the micropylar end. A number of pollen grains are also seen sticking to the plate of tissue outside the micropyle. V.34483. × 50. G, pollen grain from the nucellus of a seed showing two wings and a body. V.34483. × 800. H, Chalazal hole of seed shown in Text-fig. 18, I. × 125. I, membrane showing scalariform imprints. V.34479. × 400.

evidence that these seeds and microsporangia probably belong to the same plant species. It is noteworthy that the micropylar canal is shrivelled and narrower than the diameter of a pollen grain. It must have been wider when it admitted them. Clearly the pollination is essentially gymnospermous. Similar pollen is found also on the surface of the seed where, however, it is not significant.

Comparison. The most similar seed of the *Glossopteris* flora is *Spermatites indicus* Srivastava (1954). It differs, however, in having surface cells twice as wide as those in *S. crystallinus*. Certain inner cuticles are present in *S. indicus* which may correspond to those of *S. crystallinus* but their nature is very obscure. There is nothing to suggest that *S. indicus* has any sort of marginal tissue.

Rather similar orthotropous seeds are known in the Mesozoic genus *Caytonia* (Harris, 1940 : 724) where, however, no marginal flange exists, and in the isolated seeds described by Harris (1932 : 14) under the name *Amphorispermum*.

Spermatites tetrapterus n. sp.

(Text-figs. 20, 21)

Diagnosis. Seed, flattened, orthotropous, 3–4·5 mm. long and 2–2·5 mm. wide, oval, micropylar end obtusely pointed, chalazal end rounded. Seed showing two strong ridges on the surface, representing compressed wings, other specimens without surface ridges. Surface showing rows of longitudinally elongated cells about 150 μ long and 25 μ wide. Cuticles : Nucellus moderately thickly cutinized showing elongated cells with straight or nearly straight walls, apical region or nucellar cap sharply distinguished by thick-walled cells with straight or nearly straight walls, up to 2 μ thick, lower part with thinner-walled cells, boundary region between nucellar cap and lower part normally showing scattered round thickenings 6–12 μ across. Micropylar canal very delicately cutinized, about 200 μ long × 100 μ wide, usually collapsed (chalaza not seen).

Megaspore membrane not present, nucellus often enclosing dark matter sometimes showing transversely elongated cell outlines. This tissue extends only as far as the base of the nucellar cap.

Inner cuticle of integument delicate showing obscurely marked longitudinally elongated cells.

Stone of integument not very thick, containing elongated fibres.

Outer cuticle of integument about 1 μ thick, showing cells which are usually elongated and narrow. Typical dimensions 150 μ × 25 μ but sometimes short and broad.

Holotype. Brit. Mus. (N.H.) Palaeont. Dept. no. V.34490.

Locality and horizon. Mhukuru Coalfield, Songea District, Tanganyika; Ecca Series (" Upper Coal Measures ").

Description. Twenty-seven seeds were seen, seventeen of which were obtained by disssolving pieces of rock in HF. Some seeds are filled with rock matrix. If the ridges in the seed represent wings, they may be four-winged. The nucellus of seeds with surface ridges shows deep folds corresponding with the ridges, indicating that the nucellus of the seed was itself angular. In some seeds the cells of the nucellar

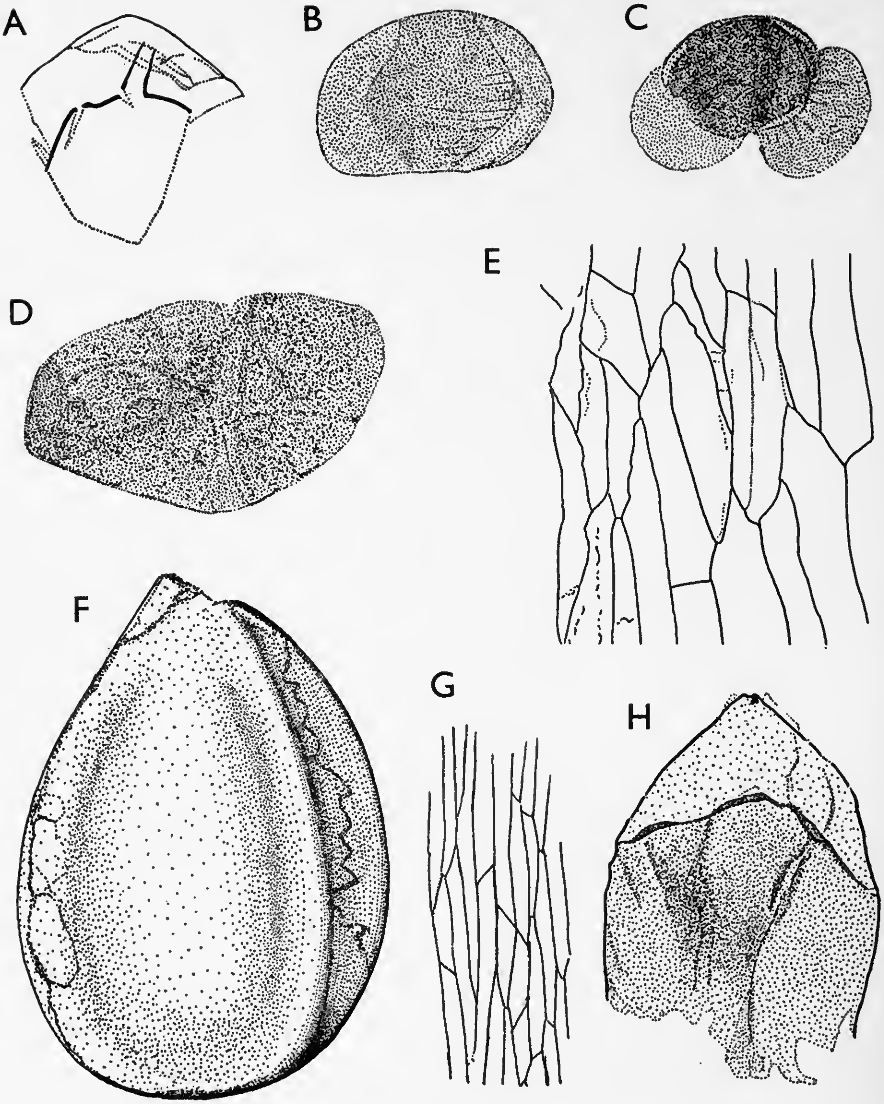

Fig. 20. *Spermatites tetrapterus* n. sp. A, upper part of macerated seed showing nucellus, micropylar canal and outer membrane. V.34484. × 25. B and C, two pollen grains (from inside the nucellus) showing two wings and a striped body. V.34485. × 800. D, unusual pollen grain from inside the nucellus of a seed. V.34486. × 800. E, outer membrane of seed showing straight-walled elongated cells. V.34487. × 200. F, compressed seed showing a ridge on the upper surface. Its interior is filled with rock matrix. Holotype, V.34490. × 25. G, surface cells of seed in F. × 125. H, nucellar cuticle of a seed. The black spot at the top represents pollen grains, a darker tissue is seen below the nucellar cap. V.34486. × 25.

cap form processes (Text-fig. 21, A–C). Text-fig. 21, A shows the top view of a nucellar cap in a seed which is probably obliquely compressed.

Seven out of ten seeds with suitable micropylar ends show numerous oval pollen grains inside the top end of the nucellus. In one seed (Slide V.34494) a mass of pollen grains is also seen inside the micropylar canal. Most of the measureable pollen

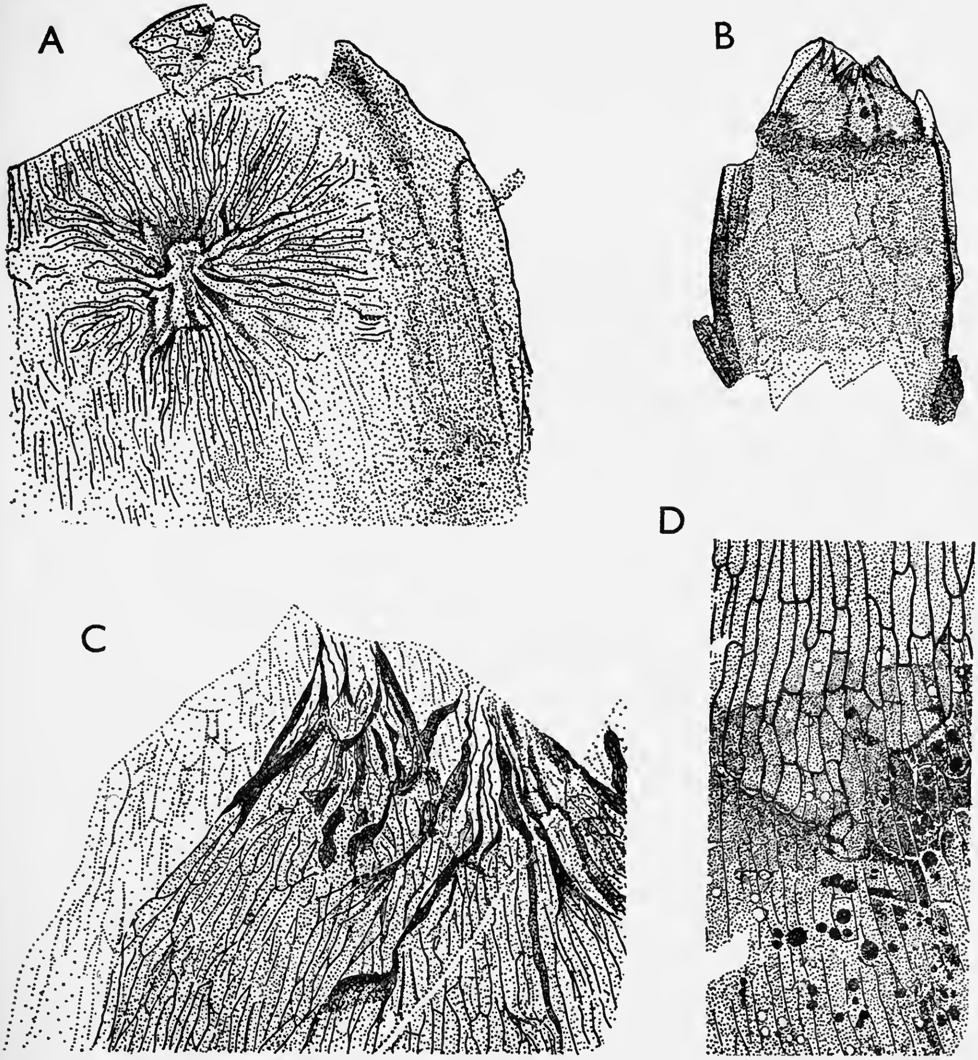

Fig 21. *Spermatites tetrapterus* n. sp. A, nucellar cap in top view showing radiating cell rows. V.34488. × 50. B, nucellus and inner cuticle of integument showing nucellar cap in side view. V.34489. × 25. C, upper part of B. There is a delicate cuticle outside the nucellus (inner lining of integument) and the apex of the nucellus forms processes. V.34489. × 125. D, part of B. The cells above belong to the nucellar cap and the dark spots occur at its junction with lower part of the nucellus. × 200.

grains are about 50 $\mu \times$ 30 μ. They are two-winged and show a body with transverse striations. One pollen grain which has a similar texture and shows no wings is 60 $\mu \times$ 40 μ, another is a smaller two-winged one measuring 35 $\mu \times$ 25 μ.

COMPARISON. Similar seeds have been described from Wankie, Rhodesia, by Walton (1929 : 11, pl. c, figs. 25, 26) but their fine details are unknown. These seeds show wing-like expansions which Walton regarded as formed by the angular inner tissue.

S. *tetrapterus* resembles S. *crystallinus* in its general organization but differs in being larger and in having surface ridges, S. *crystallinus* shows ridges only when laterally flattened and has a marginal tissue which is not present in S. *tetrapterus*. It has short surface cells while S. *tetrapterus* usually shows longitudinally elongated cells on the surface. S. *crystallinus* has an outer membrane showing short cells with crystalline imprints whereas the outer cuticle of S. *tetrapterus* usually shows elongated cells and no crystals.

III. SUMMARY

The paper describes details of the epidermal and cuticular structure of three new species of *Glossopteris* (*G. fibrosa*, *G. hispida*, *G. colpodes*) and a possible fourth (*Glossopteris* sp. A) from borehole cores in the Mhukuru Coalfield, Songea District Tanganyika. All the *Glossopteris* leaves, described here, agree in their haplocheilic stomata and in their guard cells having lignine lamellae of the Gymnosperm type. They range from mono- to amphicyclic but all have subsidiary cell papillae covering the stoma, palisade and spongy mesophyll cells and scalariform tracheids in veins. Fibres in vein meshes are found in *G. fibrosa* and *G. hispida*. *G. colpodes* is a wider-meshed form usually showing sinuous-walled epidermal cells on both the upper and the lower sides of the leaf. *G. hispida* is unique in having multicellular hairs on the lower surface of the leaf. The imperfectly known *Glossopteris* sp. A is rather like *G. fibrosa* but has no fibres in vein meshes. The species are compared with others of *Glossopteris* described by earlier authors.

A new genus *Rhabdotaenia* is made for the Indian leaf *Taeniopteris danaeoides* (Royle) and its fine structure is described. A rather similar leaf, *R. harkini*, is described from Mhukuru, Tanganyika. *Rhabdotaenia* shows haplocheilic stomata and differs from other taeniopterid haplocheilic leaves, e.g. *Doratophyllum* and *Bjuvea* (Florin, 1933) in having irregular subsidiary cells and rather exposed stomata with or without protecting subsidiary cell papillae.

Some rounded or lanceolate scale-leaves showing a scarious margin, an ill-defined midrib and anastomosing veins have been studied. They usually have short simple hairs on their convex side and occasionally fibres in vein meshes. The epidermal structure of the various forms is similar and resembles that of *G. fibrosa* of which they may be bud scales.

Fine details of some well-preserved African and Australian microsporangia, closely resembling Arber's " sporangium-like organs of *Glossopteris browniana* " are described. Some undehisced specimens were found to be full of two-winged spores. It was found that the African sporangia are borne terminally on branched

slender axes. Two discs bearing similar sporangia, from Newcastle, New South Wales, are also described; one of them has sporangia full of spores. The finding of undehisced specimens, still full of spores, finally proves these bodies to be sporangia.

Two types of compressed seeds, *Spermatites crystallinus* and *S. tetrapterus* were found in the cores. Their structure is described in detail. Both show gymnospermous pollination by two-winged spores. Both the sporangia and the seeds may belong to the same plants as the *Glossopteris* leaves abundant in this collection. Similar sporangia and seeds occur in *Glossopteris* bearing rocks at Ranigenj coalfield.

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PLATE 18

Glossopteris fibrosa n. sp.

FIG. 1. Epidermal pull showing a rather exposed stoma with lignine lamellae. V.34440*d*. × 400.

FIG. 2. Lower epidermis isolated with HF. The dark lignine lamellae of stomata are obvious. There are two folds both exposing the inner side so that the stomatal pits appear raised. V.34441. × 100.

FIG. 3. Upper epidermis showing pale cell walls and dark cell contents with granules of various sizes. V.34442. × 450.

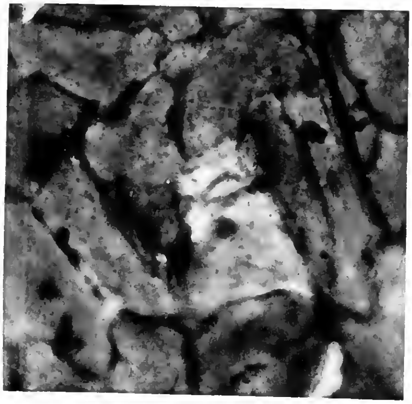
FIG. 4. Cuticle showing stoma. The polar and lateral lignine lamellae have dissolved by maceration. V.34443. × 400.

FIG. 5. Tracheids from the midrib. V.34440*d*. × 450.

Glossopteris hispida n. sp.

FIG. 6. Matrix in contact with the lower surface of leaf showing hairs when moistened with oil. Holotype V.34450. × 10.

FIG. 7. Pull showing lower epidermis and a fibre between two veins. A few spongy mesophyll cells (dark rectangles) remain. V.34450*a*. × 110.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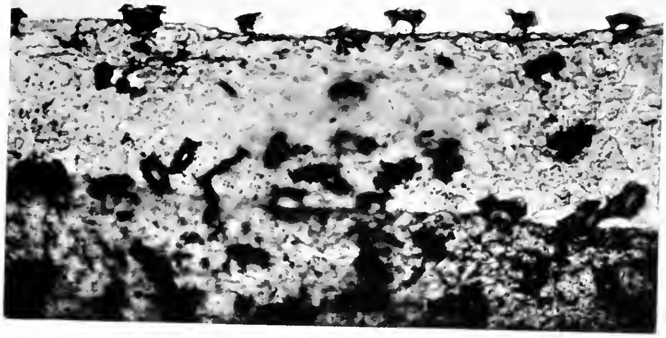
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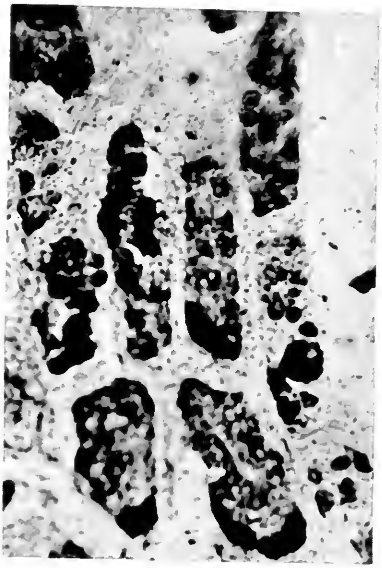
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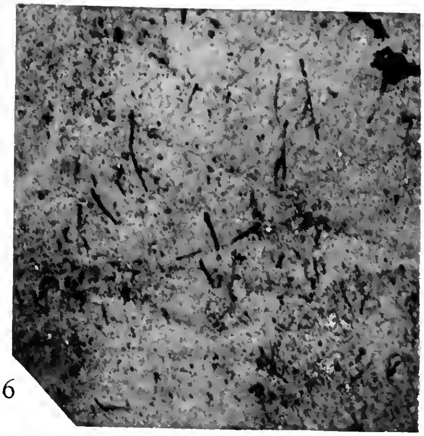
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7

GLOSSOPTERIS FIBROSA, G. HISPIDA

PLATE 19

Glossopteris fibrosa n. sp.

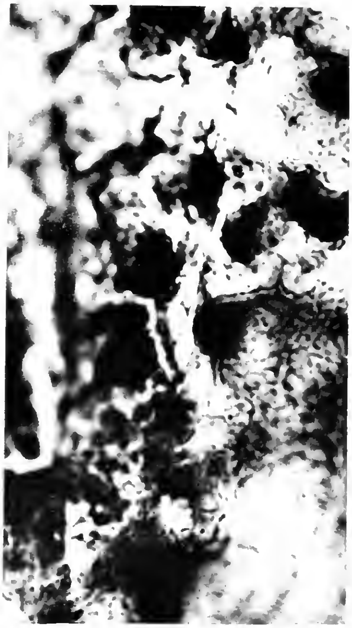
FIG. 1. Epidermal pull showing stomatal aperture protected by thickened subsidiary cell papillae. V.34449*a*. × 800.

Glossopteris colpodes n. sp.

FIG. 2. Epidermal pull showing stoma protected by thickened subsidiary cell papillae. V.34466*a*. × 800.

Glossopteris hispida n. sp.

FIG. 3. Epidermal pull showing stoma protected by subsidiary cell papillae. V.34450*a*. × 800.



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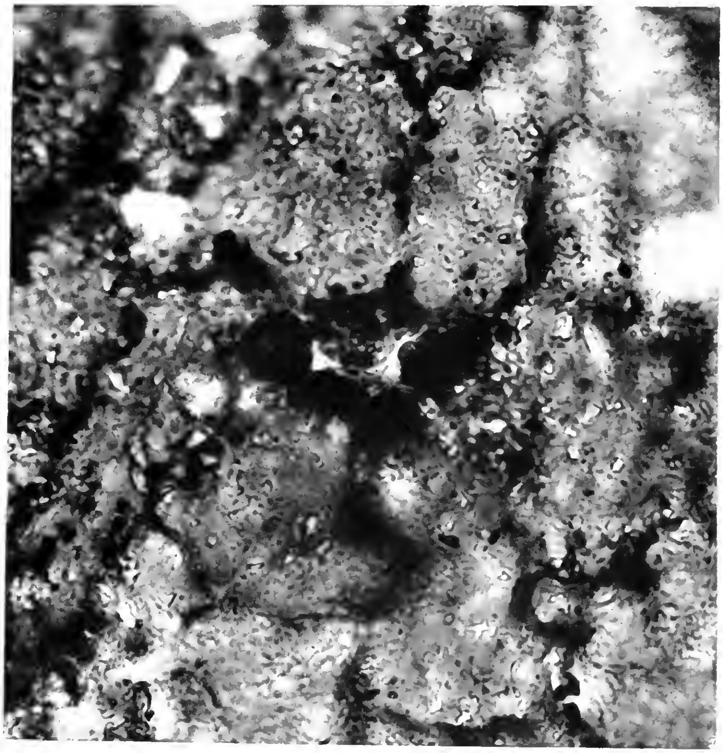

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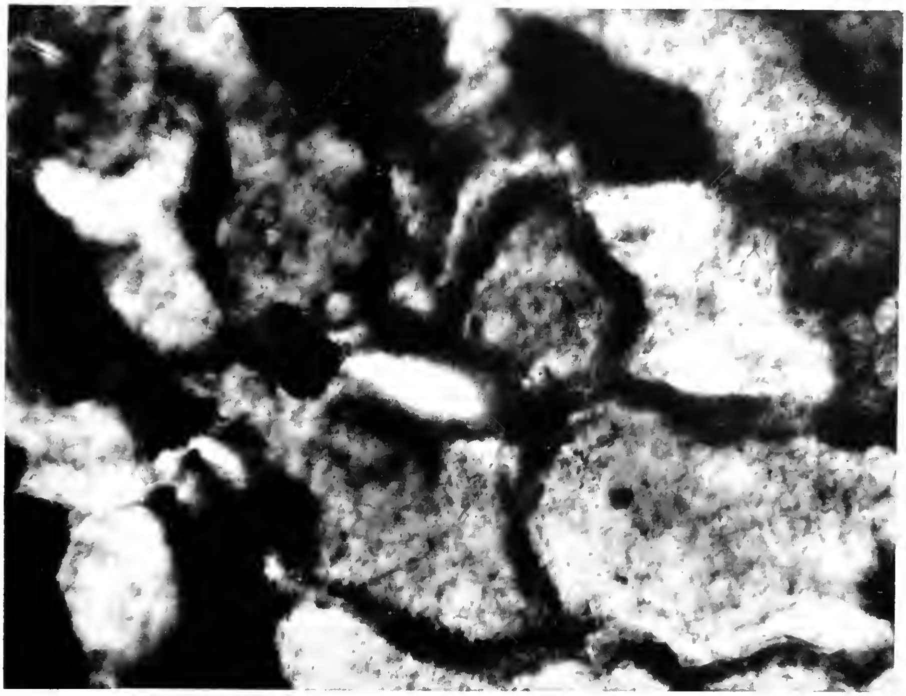

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GLOSSOPTERIS FIBROSA, G. COLPODES, G. HISPIDA

PLATE 20

Glossopteris hispida n. sp.

FIG. 1. Pull showing a one-celled hair base overlapping a number of epidermal cells. V.34450*a*. × 450.

FIG. 2. Pull showing a two-celled hair base overlapping epidermal cells. V.34450*a*. × 450.

Scale Leaves

FIG. 3. Scale leaf isolated from rock with HF. V.34453 (1). × 6.

FIG. 4. Scale leaf isolated from rock with HF. V.34453 (2). × 6.

Rhabdotaenia harkini n. sp.

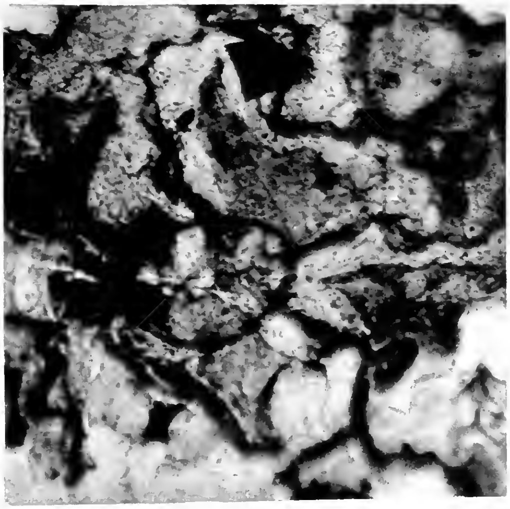
FIG. 5. Stoma protected by papillae of irregular subsidiary cells. V.34454*b*. × 400.

Spermatites crystallinus n. sp.

FIG. 6. Outer cuticle showing crystals of various forms. V. 34455. × 400.

Glossopteris hispida n. sp.

FIG. 7. Upper cuticle showing numerous small surface papillae. V.34451*b*. × 400.



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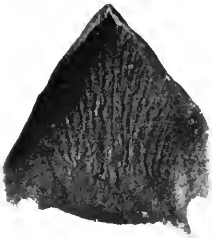

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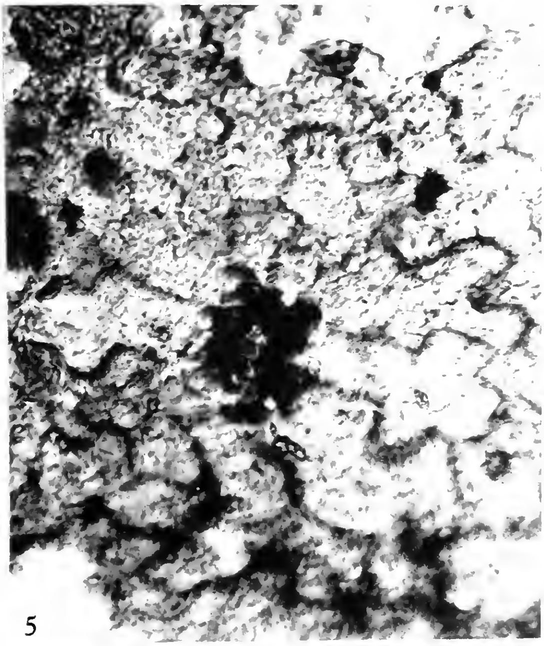

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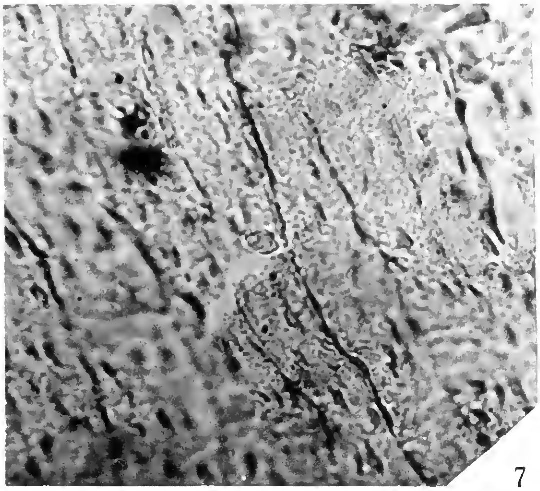


7

SPERMATITES, SCALE LEAVES, RHABDOTAENIA, GLOSSOPTERIS

PLATE 21

Sporangia

FIG. 1. Dehisced sporangium showing outer cuticle with elongated cells (near stalk) and inner cuticle with polygonal cells. Two-winged spores of varied size are seen inside the sporangium. V.34456. ×40.

FIG. 2. Sporangia borne terminally on branches of an axis. V. 34457. × 8.

FIG. 3. Dehisced sporangium showing gaps between the wall cells. V.34458. × 40.

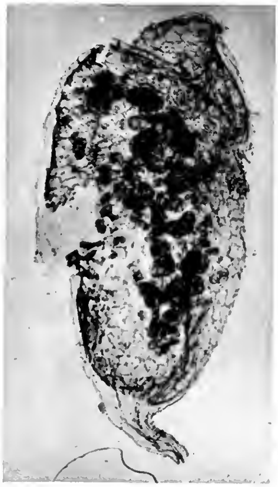
FIG. 4. Longitudinally flattened dehisced sporangium showing outer cuticle and a long stalk. V.34459. ×40.

FIG. 5. Undehisced sporangium full of spores. V.34459. × 40.

FIG. 6. Two closed sporangia borne terminally on forks of a stalk. V.34460. × 40.

FIG. 7. A disc showing attached sporangia flattened in various planes. V.24233. × 6.

Figs. 1–6 from Mhukuru Coalfield, Tanganyika.
Fig. 7 from Newcastle, New South Wales.



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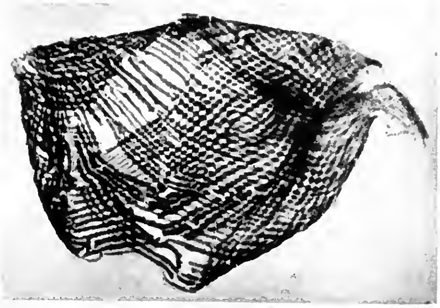

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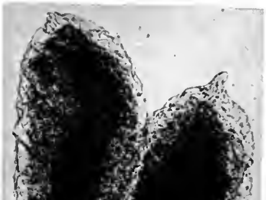

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SPORANGIA

LIDGETTONIA, A NEW TYPE OF FERTILE *GLOSSOPTERIS*

H. HAMSHAW THOMAS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
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LIDGETTONIA,
A NEW TYPE OF FERTILE *GLOSSOPTERIS*

BY

H. HAMSHAW THOMAS, F.R.S.

Pp. 177–189 ; *Pls.* 22–23 ; 2 *Text-figures*

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LIDGETTONIA, A NEW TYPE OF FERTILE *GLOSSOPTERIS*

By H. HAMSHAW THOMAS

SYNOPSIS

Reproductive organs of two kinds have already been described attached to leaves of *Glossopteris*. Cuticle studies suggest that this leaf is a form genus and that it was borne on plants of several different types. The present paper describes leaves of another species which are accompanied by fertile scale leaves bearing a number of delicate stalked cupules. The cupules are empty but the matrix around them contains the remains of a very large number of empty sporangia and of many small seeds. There was thus a third or perhaps a fourth genus of plants with leaves of the *Glossopteris* type.

INTRODUCTION

THE genus *Glossopteris* was instituted by Brongniart (1828) for leaves which were entire, more or less lanceolate, with a midrib and fine secondary veins which showed dichotomy and anastomosis. Two forms were mentioned as belonging to the new group, *G. browniana* from Australia and India, and *G. nilsoniana* from Hör in Sweden. Subsequently Brongniart added two further forms, *G. angustifolia* from India and *G. phillipsi* from Yorkshire. Thus at the outset *Glossopteris* was a form or artificial genus. The two European Mesozoic species were separated by Sternberg (1838) and placed in the genus *Sagenopteris*; they have proved to be leaflets of members of the Caytoniales. The position of the remainder was uncertain, but the study of their cuticular structure has shown that there are considerable differences in the epidermal cells of other species of *Glossopteris*. Zeiller (1896), Sahni (1923) and Harris (1932) described the differing cuticles of three species, and recently Srivastava (1956) has added considerably to our knowledge by descriptions of the cuticles of fourteen additional species. Surange & Srivastata (1956) have suggested that on this evidence six groups, possibly of generic rank, may be recognized. All the epidermal structures suggest that the leaves known as *Glossopteris* and *Gangamopteris* belonged to seed-bearing plants. Mrs. Plumstead (1952, 1956) has shown that this view is true for five species, and although the preservation of her material makes its interpretation very uncertain, it seems likely that the five species belong to two genera which she has named *Scutum* and *Lanceolatus*.

The paper which follows shows that another species with *Glossopteris* leaves, produced what must have been reproductive structures of a different type on small leaves of the form called by some previous authors scale leaves. These are quite distinct from *Scutum* and *Lanceolatus*, and merit the creation of a new genus. *Glossopteris* was thus a leaf type belonging to several unrelated genera. It is still a form genus and confusion is likely if it is used in the designation of a taxon of higher rank as has been recently suggested (Plumstead, 1956*a*).

The material. The specimens here described were obtained from a narrow bed of shale, 2–3 ft. thick, exposed in the sides and bed of a small stream on the estate of Mr. S. Thomson at Lidgetton, about 35 kilometres north-west of Pietermaritzburg, Natal, South Africa. This plant bed was originally discovered by Mr. A. D. O. Mogg, he kindly sent two large blocks to the author, who visited the locality in 1929* and made a collection of specimens, which have only recently been studied. The plant remains occur in fine-grained shale which varies in colour and character along the stream. In some places the rock is compact, dark in colour, and often nearly black. The plants are well preserved as black carbonaceous compactions, but are difficult to photograph because of the lack of contrast with the matrix (see Pl. 22, fig. 1). At other places the matrix is coarser and light grey in colour, the plant remains being less highly compressed. This again grades into fine-grained material of a pale buff colour, in which the plant substance has entirely disappeared, or is represented by ferruginous material lacking any trace of epidermal structure (Pl. 22, fig. 3).

The macroscopic remains of plants in the accessible parts of this bed were of two main types. A series of leaves of various sizes referable to the genus *Glossopteris*, and including a number of shorter forms without a midrib, of the type called scale leaves by previous authors. With these, towards the bottom of the bed, are parts of equisetalean plants, stems, pith-casts, branches and leaves. These may belong to the form called by Du Toit (1927 : 315) *Neocalamites carreri* Zeiller, but, from the more abundant material present in this collection, it is clear that the plant differed very considerably from the species described by Zeiller. In addition to these larger remains there are very large numbers of detached sporangia scattered in the matrix, and many isolated seeds of a uniform size and form.

Age of the specimens. The organic remains in the bed furnish no clear indications of its age, and there is a heavy cover of soil and vegetation in the area. According to the latest map published by the Geological Survey of South Africa the outcrop is of Ecca age in the Karroo System. The boundary between the Ecca and the Beaufort series is not far distant, and it is thus possible that the material is of Upper Ecca age. But there is little lithological difference between the rocks of the Ecca and those of the Beaufort series, as is stated by Du Toit, and it is also possible that the forms described are of Beaufort age. In any event they are appreciably younger than the fertile forms described by Mrs. Plumstead.

Genus *LIDGETTONIA* nov.

DIAGNOSIS. Sterile leaves of *Glossopteris* type, simple, lanceolate; strong tuberculate midrib almost to apex; veins numerous, close, ascending; forking and anastomosing; meshes narrow elongated, longer near midrib. Fertile leaves distinct, short, spathulate-lanceolate; midrib absent; veins spreading from base,

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* The author's thanks are due to the late Mr. J. A. Lidgett and to Mr. G. C. Lidgett who gave valuable assistance in the re-discovery and working of the bed.

forking and anastomosing ; meshes considerably larger than in sterile leaves ; lower (?) surface with two longitudinal rows of 4–6 small cupules on slender stalks, arising from petiole or basal portion of leaf ; cupules open campanulate or disc-like, finely striated, margins lobed.

Differences from comparable forms (*Scutum, Lanceolatus*) :

Several small cupules with slender stalks borne on small leaves differing from the sterile leaves in size, shape and venation, instead of a single, large, bifid cupular structure on a stout pedicel springing from the midrib or petiole of a leaf of normal size and venation and containing massive fertile structures.

TYPE SPECIES. *L. africana* n. sp.

Lidgettonia africana n. sp.

(Plates 22, 23 ; Text-figs. 1, 2)

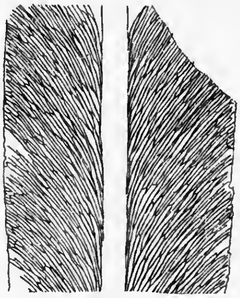
DIAGNOSIS. As for genus.

HOLOTYPE. Fertile leaf with remains of cupules on either side of the petiole. (Brit. Mus. N.H. No. V. 34633.)

DESCRIPTION. *Sterile leaves* : Most of the specimens are the remains of sterile leaves (Pl. 22, fig. 1). From their simple, lanceolate form, their well-developed midrib and their crowded anastomosing veins, they are clearly referable to the form genus *Glossopteris*. They vary considerably in size, their venation is uniform, but differs somewhat in appearance on the two sides of the leaf, and there is no reason to suppose that more than one species is represented. No complete leaf has been found, the longer pieces are about 15 cm. in length and 2·5–3 cm. broad in their widest part. The lamina tapers very gradually towards the base, where the petiole was 4–5 mm. broad. The length of the petiole is unknown, it is more than 2 cm. in some examples, but in no case is its base visible. Towards the apex the lamina tapers to a blunt tip. In the larger specimens the midrib is visible to within a short distance from the apex. Below it merges without marked change into the petiole. As it becomes broader it has a characteristic appearance due to the presence of small rounded projections, 0·3–0·5 mm. in diameter, probably indicating the presence of groups of hard cells in the original tissue. In addition, the well preserved specimens show a series of slender longitudinal ridges, probably due to lines of thicker epidermal or hypodermal cells.

The secondary veins are very numerous and crowded (Text-fig. 1). They leave the midrib at a very acute angle, and often run parallel to it at first for about 5 mm., then curving outwards they run steeply to the margin, diverging from the midrib at an angle of 30°–40°. Between the midrib and the margin they show frequent cross connections and they fork in an irregular way so that the number of veins reaching the margin is rather more than double the number which leave the midrib. Near the centre of the leaf the secondary veins are about 0·6 mm. apart, near the margin they are only 0·3–0·4 mm. distant. The anastomoses of the veins are either by small transverse veinlets, or by the fusion of veins which have come from dichotomies at a lower level. The areolae are elongated and fusiform, becoming shorter near the margin. In some hand specimens the anastomoses of the veins can only be seen clearly in the lower part of the leaf and near the midrib. In the rather rare cases where the lower surface of the leaf is seen the veins appear thicker and very close together. The strength of the veins probably rendered possible the appearance of the specimen represented in Text-fig. 1; here almost all of the tissue of the lamina had disappeared leaving the midrib and the veins clearly seen in the matrix, but the junction of the veins with the midrib was obscured in some places.

The surface of the upper side of well-preserved specimens shows, under the binocular microscope, fine ridges above the secondary veins; five such ridges are visible following the course of the larger veins, some of them branching off when the vein forks. Towards the margin of the leaf only one such ridge is seen. The outlines of the epidermal cells are frequently visible, these cells were elongated above the veins and rounded and isodiametric between the veins.



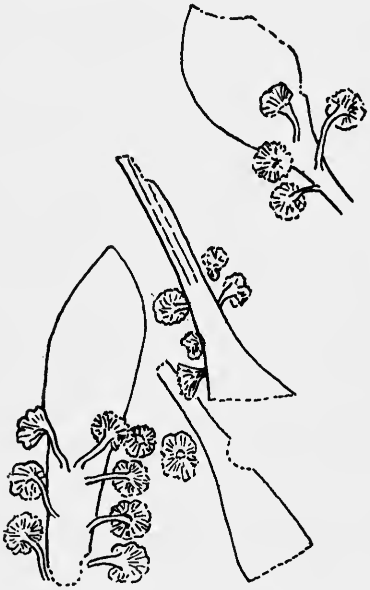
TEXT-FIG. 1.—Part of a sterile leaf showing the venation. Drawn from a photograph of a specimen in which only the midrib and the veins were preserved. Nat. size. (V.34639).

Although the preservation of some specimens appears very good it has proved impossible, as yet, to obtain cuticle preparations, evidently the cuticle was very thin and breaks into tiny fragments when stripped from the matrix.

Scale leaves. The leaves which have been described above are accompanied by a number of smaller leaves, 2–6 cm. long and 1–1·5 cm. broad. They often show a broad base and little or no trace of a midrib. Their veins are coarser, more distant and show frequent anastomoses. Such structures have been described by previous authors (see Arber 1905*a*) under the somewhat inappropriate name of scale-fronds. They probably were organs intermediate between the normal photosynthetic leaves and the fertile structures now to be described.

Fertile leaves. A large slab of grey shale, showing many compressed leaves, and very similar to the specimen shown in Pl. 22, fig. 1, contains the remains of four shorter leaves close together (Text-fig. 2). They appear to have been very thin and present little contrast with the matrix. All are incomplete but three of them are contracted at the base to form a petiole; they show anastomosing veins but no midrib. When examined in a strong beam of oblique light three of them were found to bear small lateral appendages springing from their basal portions. These structures are small campanulate bodies or peltate discs, 5–6 mm. in diameter, borne on slender stalks about 5 mm. long and 0·6 mm. wide. They sprang from the surface of the leaf and appear to have been produced in two rows, one on either side of the longitudinal axis of the leaf. Fine striations, probably due to elongated epidermal cells run from the stalks to the margins of the discs, which in the best preserved specimens are seen to have a number of small lobes. One of the four leaves in this group shows no appendages, but there are some small discs close to it which may have sprung from the surface embedded in the matrix.

None of these structures contains any sporangia or seeds, but it seems highly probably that they originally contained such reproductive organs. From a comparison with the pteridosperms they may be termed cupules.



TEXT-FIG. 2.—Group of fertile leaves, showing stalked cupules. Nat. size.

A second specimen (Pl. 23, fig. 4) shows a similar leaf preserved in a light grey shale, the plant tissue being less compressed and altered. The apical part of the lamina is not seen, at the top the lamina is 12 mm. broad, it tapers in a distance of 4 cm. to a petiole-like base, one and a half millimetres broad. In the expanded portion fine veins run upwards and outwards from the basal region, there is no midrib. As in the sterile leaves the epidermal cells above the veins were elongated while those in the meshes were isodiametric and rounded. The petiolar portion shows the remains of lateral appendages differing somewhat in appearance from those described above, probably owing to the different preservation. Their stalks are not clearly seen, they probably sprang from the lower side of the petiole. Parts of four cupules can be detected on one side and parts of three on the other margin of the petiole; most of them are laterally compressed and are somewhat hemispherical in outline. One example, 3 mm. in diameter, shows some of the marginal lobes. In two places parts of seeds, like those to be described later, are seen in contact with cupules; they may possibly have been extruded when the original structure became compressed in the matrix.

Another example shows a different type of preservation (Pl. 22, fig. 2). The plant substance is converted to structureless red matter. The lamina has a different shape, lacking the petiole-like base and the expanded upper portion; it is 3 cm. long, about 7 mm. broad at its widest part, and 5 mm. broad at the base. The remains of six or possibly of seven cupules are seen on one margin, with indications of two or three on the other margin. The stalks of several of them are seen on the surface of the lamina but their exact place of origin cannot be determined. Some of the cupules are conical in form, others appear as flattened discs. A well preserved seed is seen lying in contact with one of the cupules, but its position may have been accidental.

The form of the cupules is clearly shown in the specimen figured in Pl. 22, fig. 3. Here the plant remains are reddish impressions or moulds in a light coloured matrix, all the plant tissue has disappeared but the outlines of the original structures are very clearly seen. The specimen and its counterpart show the impressions of seven stalked cupular discs, which, from their positions, were probably attached to a fertile leaf embedded in the matrix and not visible. The stalks of four of them are more or less parallel and probably sprang from near one margin while three probably came from near the other margin. The stalks are 0·7 mm. broad, they seem to have expanded to form a somewhat thicker central portion of the cupule, about 3 mm. in diameter, surrounded by a thinner zone, 2 mm. wide, with a lobed margin. The surface of the outer zone shows a series of undulations associated with the lobes and the whole is traversed by a series of fine radial striations. The cupules were empty at the time of preservation, a seed is seen lying near to them. The same hand-specimen contains also the remains of a scale leaf which is shown in the lower part of Pl. 22, fig. 3. This is about 2 cm. long, narrow at the base but quickly broadening to a width of 1 cm. and then rapidly contracting. No cupules are seen attached to this leaf, but the remains of fragments of tissue and also surface irregularities suggest that it may also have been fertile.

The specimens described show that associated with leaves of typical *Glossopteris* form there were small (scale) leaves with a venation of the *Gangamopteris* type. These structures often bore on their lower (?) surface rows of small and delicate stalked cupular structures. It is very difficult to explain the presence of these cupules except on the hypothesis that they formed the place of origin of the reproductive structures of the plant. But there is at present no certain direct evidence that this was true.

Sporangium-like organs. Arber (1905, 1905*a*) described some characteristic structures from several localities in New South Wales which he designated sporangium-like structures. Almost identical structures are present in considerable numbers in the Lidgetton shales associated with the plants just described. Isolated examples occur abundantly, but they are also found in circular or elongated groups about 1 cm. in diameter (Pl. 23, figs. 5, 6). The individual structures have a very characteristic appearance, they are usually elliptical or ovoid in shape but sometimes appear to have had one side flattened or concave, others are fusiform (Pl. 23, fig. 7). They measure 1–1·5 mm. long and about 0·7 mm. broad. Well-preserved examples show a series of longitudinal anastomosing ridges, these appear to have been specially thickened cell walls which are more resistant than the rest of the wall substance to maceration. Some of the specimens described by Arber show a " neck-like prolongation " at one end, this was believed to be the part by which the sporangium was attached to the organ on which it was borne. No evidence of a similar prolongation has been found in the present specimens.

A number of these organs were removed from the rock and macerated in acid oxidizing liquid. They dissolved away completely when transferred to dilute ammonia leaving no trace of spores, but some of them contained a little of the matrix material. Either the sporangia were completely empty when preserved or the spores were not cutinized with material withstanding acid maceration. Several of the fusiform specimens (like those shown in Pl. 23, fig. 7) appear to have a longitudinal slit probably representing the line of dehiscence. Though these structures do not appear to contain spores the matrix contains large numbers of winged spores of different sizes which are seen when pieces of the rock are dissolved in hydrofluoric acid. Although there seems to be no proof that the structures in question were sporangia or that they had any connection with the plants described above, it seems difficult, in view of their large numbers, to regard them as unconnected. They do not resemble the sporangia of Equisetalean plants, and in each of the seven places where they have been found they are associated with *Glossopteris*. But it is possible that they were derived from some plant not represented by macroscopic remains in the present collection.

Isolated seeds. Mention has already been made of the presence of many isolated seeds in close proximity to the sterile and fertile leaves. A considerable number of these structures is present in the collection, and they are very uniform in size and shape (Pl. 22, figs. 2, 3 ; Pl. 23, fig. 5). They are almost circular in outline, and between 2 and 3 mm. in diameter, some of them are slightly flattened at their base. They show two distinct portions, a central elliptical part evidently composed of thick walled tissue, the sclerotesta, and a thinner peripheral part, or wing, which does not seem to extend round the base of the seed. In the centre the sclerotesta measures about 1·3 mm. across and the wing is about 0·8 mm. wide. Almost all the examples have the same shape, which seems to show that the seeds were originally flattened in form and that the rim round the sclerotesta had the form of a wing and was not due to the squashing of a soft sarcotesta during preservation. Had the original structures been spherical the appearance of the specimens would have varied somewhat. In some specimens (Pl. 22, fig. 2) there is a slight indentation in the wing at the apical end, in others the wing appears to extend beyond the apex of the sclerotesta and shows a projecting point. No clearly defined micropylar canal can be seen and there was no apical extension of the sclerotesta. No definite traces of vascular tissue can be seen but in well preserved specimens there may be concentric striations in the wing-like portion.

It would seem quite certain that these structures are the remains of seeds, and that their size is such that they may have grown inside the cupular structures described above. But the specimens in the present collection do not establish this suggestion, and much more material is needed.

COMPARISON WITH OTHER FORMS

A comparison of the sterile leaves from Lidgetton with those of the many species that have been described is somewhat difficult and is probably untrustworthy in the absence of cuticle preparations. In general form they resemble some of the specimens that have been described as *G. indica* but they must belong to a different type, probably to a distinct genus, because the fertile leaves are not at all similar to those described by Mrs. Plumstead (1956) and found to bear reproductive organs of the *Scutum* type.

They most closely resemble the specimens described and figured by Feistmantel (1881) as *G. communis*. These had an acute apex, a gradually tapering lamina at the base, closely crowded veins which run out to the margin at an acute angle, especially near the tip of the leaf. The midrib was similar in being relatively broad and distinct below but thinning out at the apex. Feistmantel noticed small rounded projections on the midrib and the petiole, which he said had not been found on any other species ; they are shown as rather smaller structures than those of the Lidgetton leaves.

Another comparable form is the species named by Srivastava (1956) *G. arberi*, but in this there is said to be not much difference in the size of the meshes at the midrib and the margin, while in the present specimens the difference in size is very noticeable.

It may be mentioned that the Lidgetton leaves are quite unlike the forms from the Molteno beds of the Upper Umkomaas, Natal, which the author described under the inapplicable name of *G. longicaulis* (Hamshaw Thomas, 1952).[1]

The specimens which have been described above as fertile leaves have little in common with the reproductive structures described by Mrs. Plumstead (1952, 1956) from the Middle Ecca at Vereeniging. Although, owing to their mode of preservation the morphological nature of these objects is still, in my view, uncertain, they were large structures borne on a stout pedicel which arose from the midrib of a normal foliage leaf. At the top of the pedicel was a cupule-like structure divided into two halves, and containing a massive cone-like structure composed of a number of closely packed bodies, probably containing seeds. The smallest specimen of *Scutum* was more than three times the size of any of the cupules here described. The only feature in common is that both were produced on foliar organs. In view of the essential differences between the structures now discovered and those formerly described, it seems desirable to make a new genus for their reception, in spite of the fact that so many of the details of their structure are unknown. The name of *Lidgettonia* is proposed for their designation.

It has already been mentioned that the sporangia seen at Lidgetton closely resemble

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[1] In transferring the plant which Du Toit (1927) had named *Sagenopteris longicaulis* to the form genus *Glossopteris*, the fact was overlooked that Feistmantel had previously used the name *longicaulis* for a different plant. Since the name was preoccupied it is proposed that the specimens from the Molteno Series of the Upper Umkomaas described and figured by Hamshaw Thomas (1952) should be named *Glossopteris verticillata* Thomas instead of *Glossopteris longicaulis* (Du Toit).

those described by Arber (1905) as sporangium-like organs. After the examination of a large number of these structures in the present collection there seems to be no reason for doubt that they are really the remains of sporangia. Our inability to find in them the remains of cutinized spores may be due to the unsuitability of our methods of treating the material or the spores may have been only lightly cutinized. It may be noticed that the specimens described by Arber were also associated with leaves of the normal type (*G. browniana*) and with " scale fronds ", they came from two localities in New South Wales. He also referred to the discovery by Zeiller (1896) of an example from the Transvaal among fronds and scale leaves of *Glossopteris*.

Arber drew attention to the similarity between his sporangia and those of the Recent cycad, *Stangeria*. He suggested the possible affinity of *Glossopteris* with the Pteridosperms. Recent work gives strong support to this view. It may therefore be noticed that the sporangia may be further compared with those of the pteridosperm *Pteruchus*, which occurs in the somewhat younger (Molteno) Beds of Natal. Both are alike in size and shape, though those of *Pteruchus* have a broad basal attachment. Both show longitudinal striations and a similar mode of dehiscence.

Similar sporangia were described by Seward (1908) from Zululand, by Lundquist (1919) from Brazil, and by Walkom (1928) from New South Wales, all associated with *Glossopteris* leaves but without evidence as to their place of origin. But Du Toit (1932) found in the Lower Beaufort beds of Natal examples of the same size and form in close association with small spathulate structures which he named *Eretmonia natalensis*. These were 15–35 mm. long with a narrow stalk and a spoon-shaped head; anastomosing veins were faintly visible in the head. I have recently examined these specimens by the kindness of Dr. Crompton, Director of the South African Museum. This material also shows a graded series of leaves referable to *Glossopteris*, the smallest being about 20 mm. long and 7 mm. broad with a rounded apex and a narrow lamina. The sporangia are only seen in the matrix near the Eretmonias, but there is no certain evidence of their attachment. Poorly preserved remains of seeds, comparable in size to those from Lidgetton, also are present.

It seems very probable that *Eretmonia* was a fertile structure from another plant with *Glossopteris* leaves, possibly *G. cordata* Feist. If this is so, *Lidgettonia* and *Eretmonia* may well be related, though they could scarcely be regarded as species of the same genus.

The isolated seeds described above are comparable in form to seeds found in other places associated with *Glossopteris* and *Gangamopteris*, but they differ by being smaller in size. Arber (1905*a*) described winged seeds from India, Australia and South Africa under the name *Cardiocarpus*, and Seward (1917) described somewhat similar forms from a number of places under the name *Samaropsis*. Of the examples described *Samaropsis seixasi* (White) from Brazil would seem to resemble the present forms most closely. It seems to have had a sclerotesta 8–10 mm. long and 5 mm. broad, with a wing which completely surrounded it. Another small seed from Tasmania was mentioned by Arber as having an oval sclerotesta, 5·5 mm.

long with traces of a narrow wing. Walkom (1921) found winged seeds associated with *Glossopteris* in a number of localities in Australia, which he called *Nummulospermum bowenense*. This was a larger structure in which the sclerotesta had a marked nucellar beak, and the sarcotesta, or wing extended all round the seed and was broader in the micropylar region.

Although such winged seeds are often found associated with *Glossopteris* we have no evidence of an original connection. Seeds of a somewhat similar form are known to have been produced by plants of the *Cordaites* type, and Cordaitalean forms often occurred in the Southern Hemisphere with *Glossopteris*. But it is far from certain all the winged forms that have been found were derived from plants allied to *Cordaites*. It seems likely that the seeds of structures like *Scutum* were set free and dispersed when ripe, but we do not yet know their individual form.

CONCLUSION

The collection of *Glossopteris* leaves and the structures associated with them that is here described, adds something to our knowledge of this puzzling form, but does little to elucidate the morphological and taxonomic problems relating to this widespread plant organ of Permian and Early Triassic times. It shows, however, that in addition to the types which bore strobilus-like aggregates of reproductive structures on stout pedicels springing from foliage leaves, there were other forms in which the foliage leaves were accompanied by smaller fertile leaves. In these reproduction was probably effected through the agency of structures produced in small and delicate cupules borne on stalks on the fertile leaves. While there is no direct and indisputable evidence as to the nature of the bodies borne in the cupules, there is considerable likelihood that the cupules contained groups of small elongated sporangia and that small seeds were borne in some of them; both these structures occur in considerable abundance in the matrix with the fertile leaves. Even if this suggestion as to the probable nature of the actual reproductive organs is rejected as unproven, it is clear that the plant remains at Lidgetton show certain fundamental differences from the older types found in the Middle Ecca rocks at Vereeniging. These differences support the view, based on the study of cuticles, that there were several different groups of plants with leaves whose form and venation has led to their inclusion in the form genus *Glossopteris*. This form of leaf may well have evolved by parallel or even convergent development.

The problems raised by this work can only be solved by the discovery of much well preserved material showing different stages in the growth of the structures which have been described. When the vast extent of the beds containing *Glossopteris* is remembered, the ultimate finding of such material does not seem improbable. But a very careful search will be necessary as it has proved very easy to overlook specimens like those described when collecting in the field.

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PLATE 22

Lidgettonia africana n.sp.

FIG. 1. Large block of dark grey shale from Lidgetton, containing well preserved remains of parts of sterile leaves. Groups of sporangia occur at the points marked by arrows, and some isolated seeds are present. × 1/3. (V.34637).

FIG. 2. Part of a fertile leaf in light buff shale. Remains of the stalked cupules are shown on the right hand side, and a seed is seen in contact with one of them. × 3. (V.34634.)

FIG. 3. Two series of impressions of stalked cupules are shown in the upper part of the figure, which are believed to have sprung from one fertile leaf, which is not seen. An isolated seed is in the centre of the figure, and a short " scale " leaf which may have been fertile is seen below. ×3. (V.34635.)

1

2

3

LIDGETTONIA AFRICANA

PLATE 23

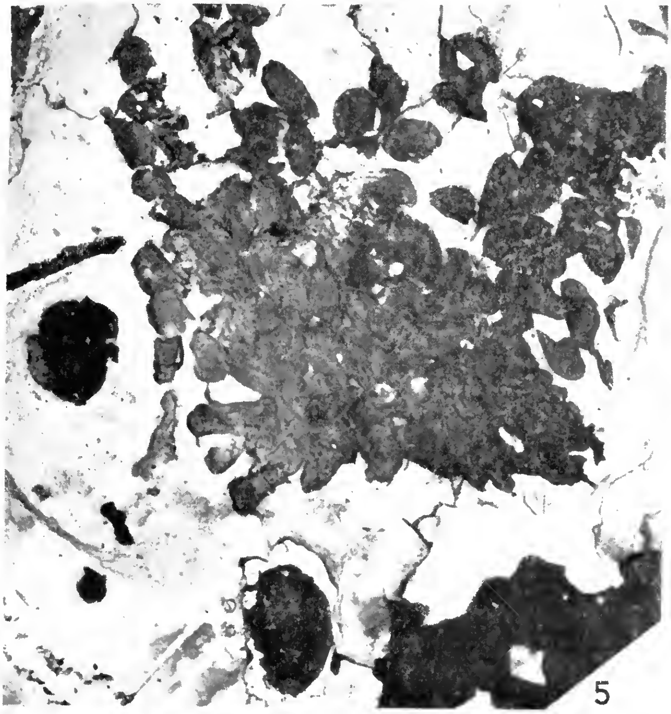
Lidgettonia africana n.sp.

Fig. 4. Holotype. Fertile leaf with some preserved remains of tissues. The remains of broken cupules are seen on either side of the petiole. × 2. (V.34633.)

Fig. 5. Large group of sporangia. Remains of two seeds are shown at the bottom and on the left hand side. × 6·5. (V.34636.)

Fig. 6. Group of well preserved sporangia. × 10. (V.34638.)

Fig. 7. Remains of two sporangia, which had probably dehisced before preservation. × 60. (V.34638.)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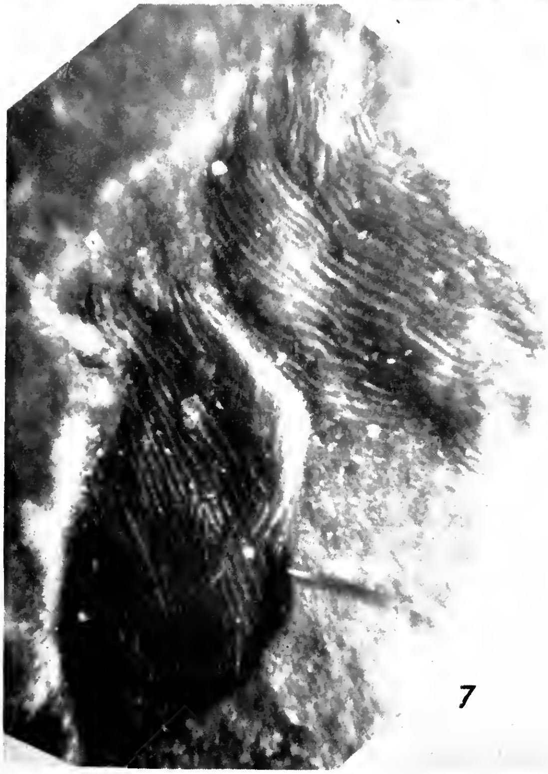
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LIDGETTONIA AFRICANA

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THE FAUNAL SUCCESSION IN THE CARADOC SERIES OF SOUTH SHROPSHIRE

W. T. DEAN

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THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 3 No. 6
LONDON : 1958

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THE FAUNAL SUCCESSION IN THE CARADOC SERIES OF SOUTH SHROPSHIRE

BY

WILLIAM THORNTON DEAN

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Pp. 191–231 ; *Plates* 24–26 ; *4 Text-figures*

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THE FAUNAL SUCCESSION IN THE CARADOC SERIES OF SOUTH SHROPSHIRE

By WILLIAM THORNTON DEAN

SYNOPSIS

The history of the subdivision of the Caradoc Series in the type area is traced from the time of Murchison to the present day. The faunally defined Stages proposed by Bancroft are examined and redefined, and their relationship to established lithological units discussed. A new interpretation of the correlation between shelly and graptolite faunas is suggested, with some notes on the possible extension of the scheme to other areas.

I. INTRODUCTION AND ACKNOWLEDGMENTS

THE name " Caradoc " as applied to the succession of Ordovician rocks in south-east Shropshire originated in 1839 when Murchison, in his great work *The Silurian System,* gave the name " Caradoc Sandstone " to the strata cropping out along the strip of country between the Wrekin in the north-east and Coston, near Clunbury, in the south-west. Stratigraphically the beds lay between the igneous rocks forming the Church Stretton Hills and the Wenlock Shales. The clearest section was said by Murchison (1839 : 216) to be found in the valley of the River Onny near Horderley, which may thus be taken as the " type " succession. Unfortunately the beds assigned by Murchison to his " Caradoc Sandstone " included also horizons now known to be Pre-Cambrian, Cambrian and Silurian in age, and the basal quartzites of the Lower Cambrian were thought to be Caradoc Sandstone which had been altered by the " igneous traps " of the Church Stretton range of hills.

It was not until 1854 that any detailed subdivision of the Caradoc Sandstone was attempted, when Salter & Aveline published their classic results. Perhaps the most important of these was the proving of the unconformity, displayed in the so-called " Onny Section ", between what they termed the *Trinucleus* Shales (topmost Caradoc) and the overlying Purple Shales (Upper Llandovery). They divided the " Caradoc Sandstone " into five parts as follows, the youngest at the top of the table :

5. *Trinucleus* Shales
4. Flagstones of Cheney Longville, etc.
3. Sandstones of Horderley and Chatwall
2. Hoar Edge Grits
1. Shales of Harnage and Shineton

They failed to differentiate between the Shineton Shales (Tremadoc) and the Harnage Shales (Caradoc), but the two were separated later by Callaway (1877 : 653) who placed the Harnage Shales in their correct position above the Hoar Edge Grits, and gave them the stratigraphical name by which they are now generally known. In addition Callaway (p. 654) named Salter & Aveline's subdivision No. 3 the Chatwall Sandstone.

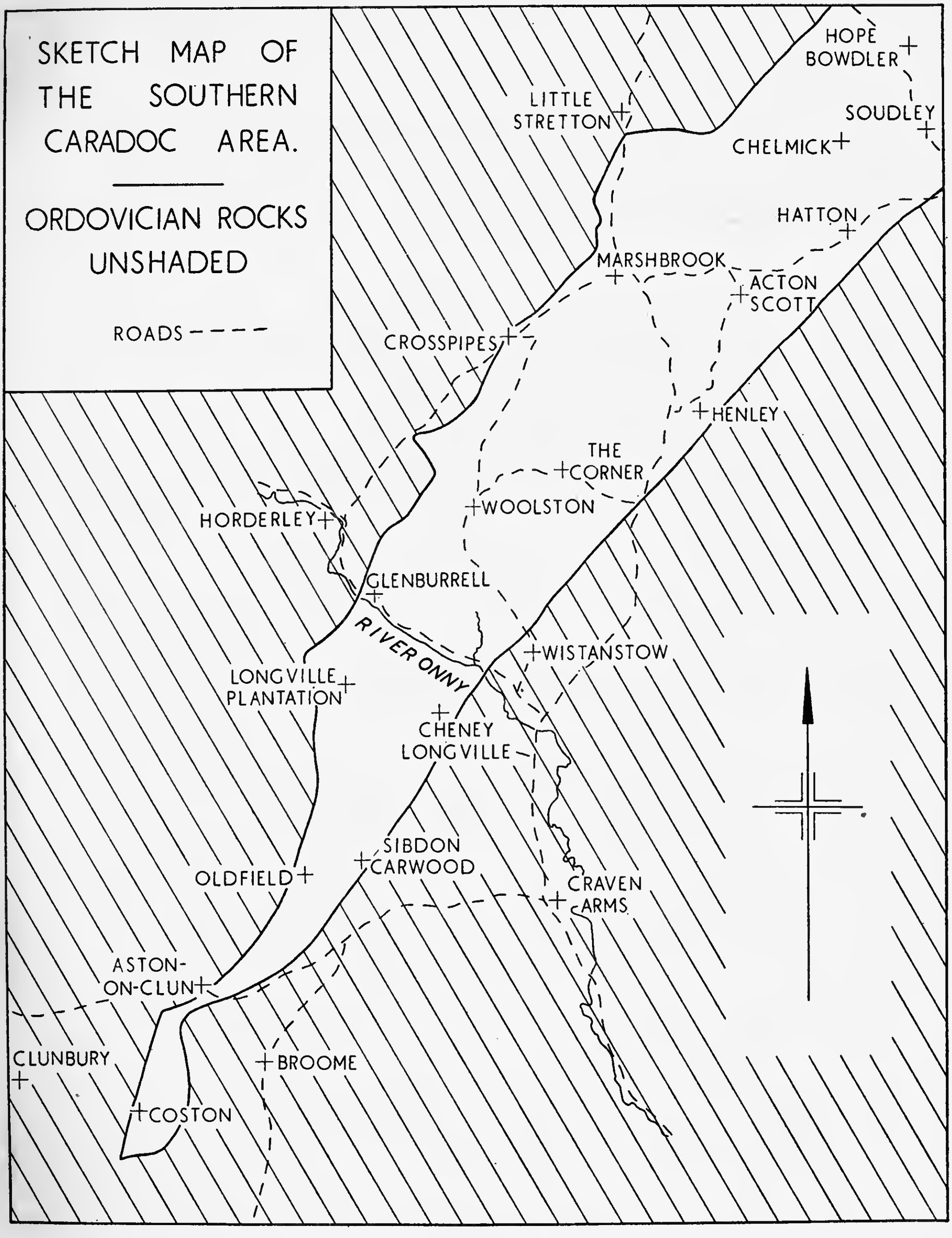
In 1884 the Shropshire geologist J. D. La Touche introduced the new names Horderley Sandstone, Cheney Longville Flags and Onny Shales, corresponding to Salter & Aveline's subdivisions 3, 4 and 5, and gave localities where the horizons might be examined. Ten years later Lapworth & Watts (1894 : 320) erected the name Acton Scott Beds for strata between the Cheney Longville Flags and the *Trinucleus* Shales.

No further modifications or additions were made to the succession until 1916 when Lapworth proposed the name "Caradoc Series" for the Ordovician strata concerned, and divided them into "Groups", each being named after a locality in south Shropshire. The Groups were subdivided further but Lapworth gave neither type localities for his subdivisions nor any information regarding their distinctive lithologies and faunas. Nevertheless the Geological Survey has attempted to use Lapworth's subdivisions (Pocock *et al.*, 1938 : 81–90), but these are in need of more precise definition and will be examined in the following pages.

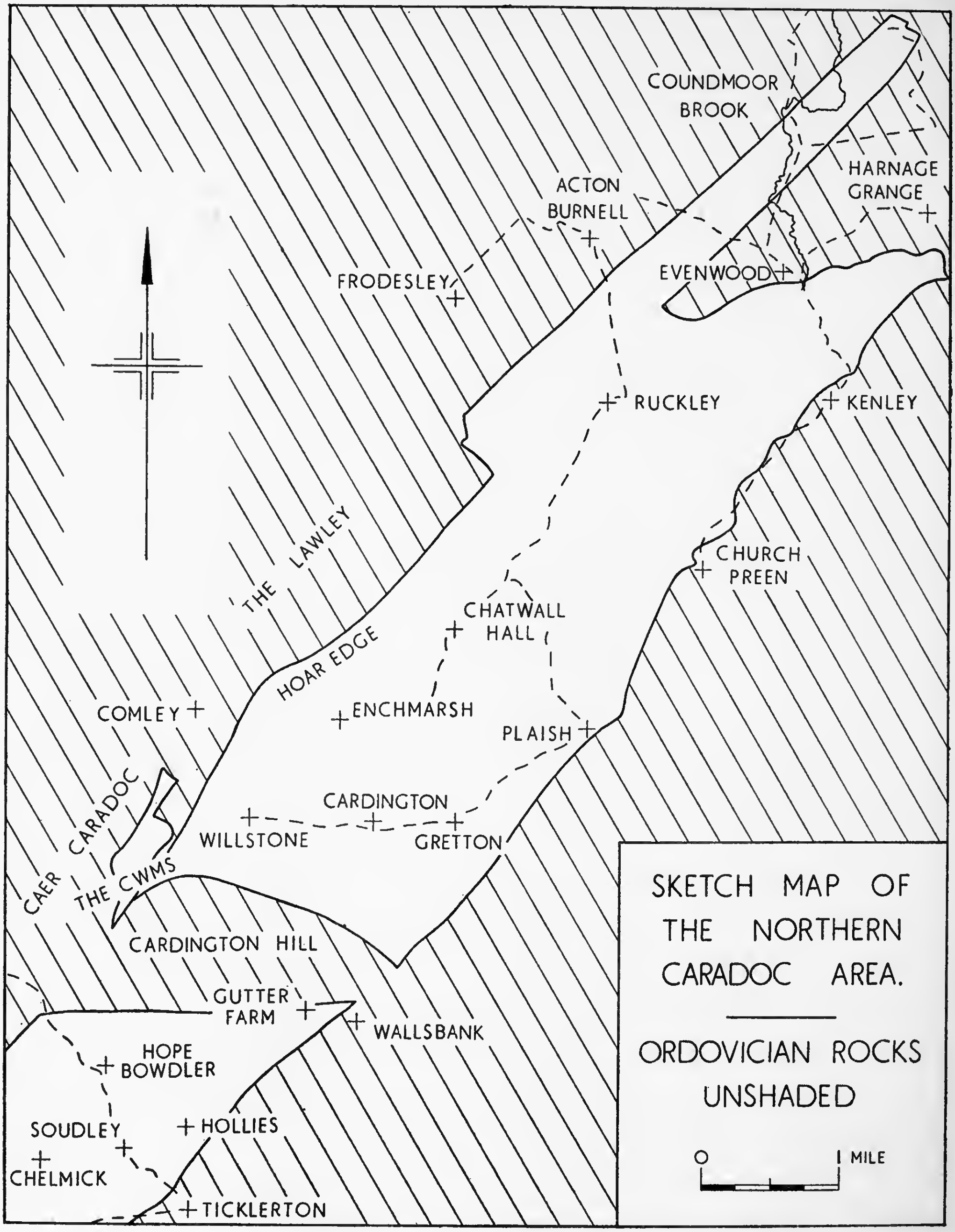
The most significant advance in our knowledge of Caradoc stratigraphy was made in 1929 when B. B. Bancroft published the first of a number of papers on the subdivision of the Series. All previous schemes of subdivision having been founded on lithology, Bancroft pioneered the splitting of the Caradoc succession into units defined by their contained faunas, in particular the brachiopods and trilobites. He erected the three Stages, Soudleyan, Longvillian and Marshbrookian (1929*a* : 33–35), but later listed seven Stages, Girvanian, Harnagian, Soudleyan, Longvillian, Marshbrookian, Actonian and Onnian in ascending order (1929*b* : table opposite p. 76). Four years later (1933) appeared a series of tables showing the distribution of the Stages Costonian to Onnian (the term Costonian not being defined, but replacing Girvanian), and listing both lithological divisions and zonal fossils. Many of the latter had not been described and were, therefore, *nomina nuda*. Additional data relating to Bancroft's Stages were published posthumously (1945) ; a correlation of the shelly and graptolitic faunas which was attempted is probably incorrect.

Much of Bancroft's earlier work did not receive the recognition it merited, due in part to the fact that many of his zonal indices had not, at that time, been described. In addition his results were marred by indiscriminate erection or suppression of subdivisions without sufficient description, and sometimes by inadequate diagnoses of critical fossils. Nevertheless, his pioneer work revolutionized research on the detailed stratigraphy of the Upper Ordovician strata in much the same way as did S. S. Buckman's on that of the Jurassic.

During recent work in south Shropshire Bancroft's major subdivisions, the Stages, of the Caradoc Series have been found to be applicable, though some emendation and redefinition are necessary in order to make the stratal classification more effective. The Stage will serve as a basis for the following account of the subdivisions, both large and small, of the Caradoc Series, and correlations with the graptolite zones will be re-examined. Correlation Tables and Plates of critical fossils are included.


SKETCH MAP OF THE SOUTHERN CARADOC AREA.
ORDOVICIAN ROCKS UNSHADED
ROADS
HOPE BOWDLER
LITTLE STRETTON
SOUDLEY
CHELMICK
HATTON
MARSHBROOK
ACTON SCOTT
CROSSPIPES
HENLEY
THE CORNER
WOOLSTON
HORDERLEY
GLENBURRELL
RIVER ONNY
WISTANSTOW
LONGVILLE PLANTATION
CHENEY LONGVILLE
SIBDON CARWOOD
OLDFIELD
CRAVEN ARMS
ASTON-ON-CLUN
CLUNBURY
BROOME
COSTON

Text-fig. 1.


COUNDMOOR BROOK
HARNAGE GRANGE
ACTON BURNELL
EVENWOOD
FRODESLEY
RUCKLEY
KENLEY
THE LAWLEY
CHURCH PREEN
CHATWALL HALL
HOAR EDGE
ENCHMARSH
PLAISH
COMLEY
CAER CARADOC
CARDINGTON
WILLSTONE
GRETTON
THE CWMS
CARDINGTON HILL
GUTTER FARM
WALLSBANK
HOPE BOWDLER
SOUDLEY
HOLLIES
CHELMICK
TICKLERTON
SKETCH MAP OF THE NORTHERN CARADOC AREA.
ORDOVICIAN ROCKS UNSHADED
0
1 MILE

Text-fig. 2.

The field-work upon which these results are founded was carried out from the University of Bristol during the tenure of a Post-Graduate Research Scholarship, for the award of which I wish to express my thanks to the Shell Petroleum Co. Ltd. Professor W. F. Whittard supervised the initial research, and I am also grateful to him for much useful discussion, and for reading and criticizing this manuscript.

II. THE STAGES OF THE CARADOC SERIES

(a) *Costonian Stage*

In the first instance, the strata constituting the Costonian were named the Girvanian Stage by Bancroft (1929*b* : 67, table opposite p. 76), and divided into five zones as follows :

5. *Horderleyella plicata*
4. *Harknessella subquadrata*
3. *Harknessella subplicata*
2. *Reedolithus subradiatus*
1. " *Orthis* " *confinis*

Of these, 1 and 2 were applied to the succession at Girvan, Ayrshire, 3 and 4 to the Cressage District, Shropshire, and 5 to the Horderley District, Shropshire. Such a composite succession, founded on faunal provinces so distinct as those of Girvan and south Shropshire, would appear to be unsafe ; it is not surprising that when next Bancroft (1933) published the succession comprising the Stage, and at the same time renamed the latter Costonian, he omitted the two lowest zones and retained only those three from Shropshire.

The name Costonian implies in itself the use of Coston, near Clunbury, as the type-locality, though Bancroft described it as being " typified by the grits of Horderley, Hoar Edge and Coston in the East Shropshire area " (1945 : 182). At Coston the succession is as follows :

	U.	*Costonia ultima* Beds *nom. nov.*
Coston Beds *nom. nov.*	M.	*Harknessella* Beds *nom. nov.*
	L.	Basal Conglomerates

The type-area for the three new stratigraphical terms in the above table is the general vicinity of Coston Farm, one mile east-south-east of Clunbury.

No fossils have yet been found in the Basal Conglomerates. The succeeding *Harknessella* Beds contain an abundant brachiopod fauna of *Harknessella vespertilio* (J. de C. Sowerby), *H. jonesi* Bancroft, *Dinorthis flabellulum* (J. de C. Sowerby) and *Heterorthis patera* (Davidson), occurring in lenticular shell-beds. The *Costonia ultima* Beds represent Bancroft's Zone of *Horderleyella plicata*, and consist of thickly-bedded sandstones throughout which the fossils are distributed more or less uniformly. *Horderleyella plicata* Bancroft occurs throughout, though not commonly, but has not yet been found in significant numbers outside the Coston-Horderley District, and may prove to be no more than a local species. *Costonia ultima* suffers from similar limitations to its distribution, but the genus is more widespread. The topmost Costonian beds between the Onny Valley and Brokenstones have also yielded *Lichas* (*s.l.*) sp. and *Salopia salteri* (Davidson) ; the latter is predominantly a Harnagian species and a few specimens only are known from the Costonian.

Although Bancroft's Correlation Tables of 1929 and 1933 showed no subdivision of the *H. plicata* Zone, in a later paper (1945 : 235, 244) he referred to two subzones within it, those of *Smeathenella strophomenoides* Bancroft and *Dinorthis robusta* Bancroft. The order of superposition of these two was not at that time stated, but later Bancroft described the former as being the younger (1949 : 297). The usefulness of such a subdivision is doubtful, at least outside the Coston District, because the subzonal brachiopods have now been found associated at Brokenstones Quarry, a few miles north of Coston. *Costonia ultima* is present in the Upper Coston Beds of both Coston and Brokenstones, and constitutes probably the most useful zonal index but only within those districts.

In the northern part of the Caradoc Area the detailed succession within the lower beds of the Caradoc Series can be summarized as follows :

3. Rhynchonellid Grits
2. Sandy limestones with *Harknessella subquadrata*
1. Sandy shales and limestones with *Harknessella subplicata*

The lowest strata, constituting Bancroft's *Harknessella subplicata* Zone, contain a fauna of few species which, in addition to the zonal brachiopod, includes *Reacalymene pusulosa* Shirley and *Rafinesquina*, the interbedded shale-bands having yielded *Nemagraptus gracilis* (Hall). Beds 1 to 3 were placed in the Costonian by Bancroft (1933) who supposed them all to be older than the *Horderleyella plicata* Zone of Coston and Horderley. This age-relationship is considered here to be incorrect ; Bancroft gave no explanation but he probably relied on the supposed equivalence of the strata with abundant *Harknessella* at Cressage and Coston, even though no species is common to both districts. Such a correlation, founded solely on large, shallow-water brachiopods apparently confined to marginal marine deposits, appears to be unreliable.

Near Harnage the trilobite fauna of the *H. subquadrata* Zone presents a picture quite different from that of the preceding *H. subplicata* Zone. *Decoroproetus* [*Proetidella* Bancroft], *Brongniartella*, *Eohomalonotus*, *Lichas* (*s.l.*) and *Costonia* sp. nov., of which the first two become more abundant in the basal Harnagian of the Onny Valley, are associated with *Reacalymene pusulosa*. The topmost beds of the so-called Hoar Edge Grits, that is those succeeding the *H. subquadrata* Zone and termed the Rhynchonellid Grits, are imperfectly exposed in the Harnage area, but at Stevenshill they contain, in addition to *Salopia salteri* and rhynchonellids, the diagnostic cryptolithid *Salterolithus*, and must be included in the Harnagian Stage, even though they immediately underlie the Harnage Shales (*s. s.*). There is no evidence whatsoever for the assertion that a considerable break exists between the Hoar Edge Grits and Harnage Shales of the Harnage area (Pocock *et al.*, 1938 : 86), and even the *H. subquadrata* Zone may best be regarded as showing signs of a transition towards the basal Harnagian, though the horizon must still be retained in the Costonian on account of the presence of *Costonia* and the absence of *Salterolithus* and *Reuscholithus*.

STAGE		CHARACTERISTIC TRILOBITE		CHARACTERISTIC BRACHIOPOD	LOCAL SUBDIVISION		MAX. THICK -NESS
ONNIAN	14	ONNIA SUPERBA		'RAFINESQUINA' HOLLI	ONNIA BEDS		50′
	13	ONNIA GRACILIS		ONNIELLA BRÖGGERI			60′
	12	ONNIA COBBOLDI		ONNIELLA INCONSTANS			40′
ACTONIAN	11	PLATYLICHAS LAXATUS		CRYPTOTHYRIS PARACYCLICA	ACTON SCOTT BEDS s.l.		190′
MARSHBROOKIAN	10	BROEGGEROLITHUS TRANSIENS	C	ONNIELLA REUSCHI	U	CHENEY LONGVILLE FLAGS	140′
			B	DALMANELLA UNGUIS			80′
			A	DALMANELLA WATTSI			75′
UPPER LONGVILLIAN	9	BROEGGEROLITHUS LONGICEPS	B	KJAERINA TYPA & DOLERORTHIS DUFTONENSIS	L		410′
			A	KJAERINA BIPARTITA	ALTERNATA LIMESTONE		65′
LOWER LONGVILLIAN	8	BROEGGEROLITHUS GLOBICEPS	C	BANCROFTINA TYPA	U	HORDERLEY SANDSTONE	150′
			B	DALMANELLA INDICA & D. LEPTA			
			A	DALMANELLA HORDERLEYENSIS	M		115′
SOUDLEYAN	7	BROEGGEROLITHUS SOUDLEYENSIS		REUSCHELLA HORDERLEYENSIS	L		280′
	6	BROEGGEROLITHUS BROEGGERI		SOUDLEYELLA AVELINEI	GLENBURRELL BEDS		140′
HARNAGIAN	5	ULRICHOLITHUS ULRICHI					
	4	SALTEROLITHUS CARACTACI			SMEATHEN WOOD BEDS		80′
	3	REUSCHOLITHUS REUSCHI & SALTEROLITHUS SMEATHENENSIS		SMEATHENELLA HARNAGENSIS & SALOPIA SALTERI			
COSTONIAN	2	COSTONIA ULTIMA		HORDERLEYELLA PLICATA	U	COSTON BEDS	35′+
	1	HARKNESSELLA - BEDS (TRILOBITES VERY RARE)		HARKNESSELLA VESPERTILIO & DINORTHIS FLABELLULUM	M		25′+
	BASAL CONGLOMERATES (NO FOSSILS)				L		45′+

TEXT-FIG. 3.—The Caradoc succession in the Onny Valley District.

It can thus be claimed, with some degree of certainty, that the *H. subquadrata* Zone of Cressage and Harnage is the equivalent of the *Costonia ultima* Beds (or *Horderleyella plicata* Zone) of Coston, at least in part. The *H. subplicata* Zone of Harnage may reasonably be equated with the *Harknessella* Beds of Coston. The strata containing abundant *Harknessella* would appear, then, to be diachronic, becoming progressively younger from south to north, and it is probable that the Basal Conglomerates of Coston may be the oldest members of the Caradoc Series in the whole Caradoc Area, and unrepresented in the Harnage District.

The so-called Hoar Edge Grits of the Cwms, east of Church Stretton, represent what is probably only a small portion of the Costonian succession, as trilobites found therein include *Decoroproetus* together with *Costonia* sp. nov. identical with that found in the *H. subquadrata* Zone of Harnage. The presence of *Salterolithus* in the same area indicates a Harnagian age for, probably, the uppermost part of the Hoar Edge Grits there.

(b) *Harnagian Stage*

The Harnagian was proposed by Bancroft (1929*b* : 67) and was said by him to extend from the summit of the Girvanian to the base of the Soudleyan. It was described merely as being characterized " by the *caractaci* group of *Cryptolithus s.l.*" (later *Salterolithus*). In the same paper (table opposite p. 76) he divided the Harnagian into four zones as given below, the two lower being described as occurring at Cound Brook (near Cressage) and Trilobite Dingle, Welshpool, and the two upper at Horderley and Trilobite Dingle.

Salterolithus caractaci
Salterolithus cf. *intermedius*
Reuscholithus reuschi
Salterolithus harnagensis

In a later work, however, Bancroft (1933) included only three zones in the Stage, the zonal trilobite of the topmost of these being at that time undescribed and, until 1949, unfigured :

Ulricholithus ulrichi
Salterolithus caractaci
Reuscholithus reuschi (misprinted as *Reuschella* [*sic*] *reuschi*)

It was in 1945 that Bancroft defined the type-locality of the Harnagian, stating it to be in the " Harnage Shales of Cound Brook, Cressage ", but he also defined the base as being marked by the appearance of *Reuscholithus* and *Salterolithus*.

Like those of the underlying Costonian, the strata assigned to the Harnagian Stage in south Shropshire are marked by changes in lithology along the strike, with their attendant variations in fauna. A further complication is introduced by Bancroft's fixing of the type-succession as the highly-faulted area of "Harnage Shales" in Cound Brook, near Evenwood, implying the inclusion of only the shale lithology at that locality. *Salterolithus* is described by Bancroft (1945 : 182) as being a genus especially characteristic of the Harnagian, and in the Evenwood District it first appears in sandstones immediately and conformably overlying others of definite Costonian age (see p. 198). It would seem advisable, therefore, to redefine the base of the Harnagian and to describe it as being marked by the appearance of the trilobite genera *Reuscholithus* and/or *Salterolithus*.

In the basal Harnage Shales of the Cound Brook section *Reuscholithus reuschi* Bancroft is abundant and occurs at, apparently, the same horizon as *Salterolithus harnagensis* Bancroft, both species inhabiting grey mudstones and, more rarely, sandy shales. Farther south, however, near the Onny Valley, *R. reuschi* is relatively uncommon, though attaining a larger size than at Cound Brook, and the basal horizon of the Harnagian is marked by an abundance of *Salterolithus smeathenensis* Bancroft and *Phacopidina harnagensis* Bancroft. *S. harnagensis* is not known from this area, and it is not surprising that Bancroft found it advisable to discard the *S. harnagensis* Zone in favour of using the single index *R. reuschi* for this particular horizon. As yet *Phacopidina harnagensis*, together with the uncommon accompanying form *Nieszkowskia stubblefieldi* Bancroft, has not been recovered from the Harnagian of Cound Brook, but *Primaspis* [*Acidaspis*] *harnagensis* (Bancroft) occurs there as well as near the Onny, together with rare *Decoroproetus* [*Proetidella*] *fearnsidesi* (Bancroft).

It has already been shown (p. 200) that the topmost part of the Hoar Edge Grits in The Cwms, east of Church Stretton, contains trilobites of Harnagian age, and on the nearby Hazler Hill basal Harnagian deposits form the infillings of the well-known neptunian dykes there. Details have been given of the fauna from these beds (Strachan *et al.*, 1948), but as long ago as 1929 Bancroft had stated that they were of the same age as his Zone of *Salterolithus harnagensis*, that is, basal Harnagian (1929*b* : 81). Apart from the large number of contained pebbles of Uriconian material, the lithology of the Hazler Harnagian beds is closely similar to that of the *R. reuschi* Zone in the Onny Valley, and the two may reasonably be equated. Certain differences exist, probably as the result of a shallower-water environment at Hazler, and the fauna there, while lacking most of the trilobites so abundant in the Onny Valley, includes the Baltic brachiopod genus *Vellamo*, a record new to Shropshire.

Bancroft's Zone of *Salterolithus caractaci* denotes an horizon stratigraphically higher than that of *Reuscholithus reuschi*. Although Murchison's syntypes were obtained from the Welshpool District, the zone was first established as a usable stratigraphical horizon in the vicinity of Glenburrell Farm, near Horderley (Bancroft, 1949 : 294). A large collection was obtained by Bancroft from the excavations that were dug here, and the material shows that there exists at this horizon in the Horderley District a large cryptolithid fauna consisting of one species, which seems best referred to *Salterolithus caractaci* (Murchison), though the latter has yet to be described adequately. Murchison's species has not been discovered in association with *R. reuschi* and its attendant fauna, and it seems advisable to retain the *S. caractaci* Zone as a separate unit. The state of preservation of the material from Bancroft's excavations is closely similar to that of the *R. reuschi* Zone in the Horderley District, and the *S. caractaci* Zone can be taken to represent the upper part of the yellow, blocky mudstones of Harnagian age which crop out at Smeathen Wood, just south of the Onny, and for which the name Smeathen Wood Beds *nom. nov.*

is here proposed. These comprise the strata in the Onny Valley belonging to the *Reuscholithus reuschi* and *Salterolithus caractaci* Zones, and the type-locality is the general area of Smeathen Farm, near Horderley.

The *S. caractaci* Zone formed the highest subdivision of the Harnagian as interpreted by Bancroft (1929*b*, table opposite p. 76), but in a later paper (1933) he introduced an overlying Zone of *Ulricholithus ulrichi*. Unfortunately the zonal trilobite was not then figured or described, and the name remained a *nomen nudum* until sixteen years later (Bancroft, 1949 : 295, pl. 9, fig. 14), although Bancroft had cited the species from Shropshire, Welshpool and North Wales (1933). He described Welshpool (1949 : 296) as being " the more important type locality " ; the text suggests that he had intended to formulate the species on a number of syntypes from Welshpool and from south Shropshire, but only an incomplete cephalon from Welshpool was figured by him ; this is the holotype (British Museum (Nat. Hist.) In. 42371). In the Caradoc Area the species is known from only two localities, both near Glenburrell Farm. Once again, a single cryptolithid species constitutes the whole trilobite fauna, and the writer accepts provisionally the existence of an *Ulricholithus ulrichi* Zone marking the horizon between the *S. caractaci* Zone and the base of the succeeding Soudleyan Stage, though the lateral distribution of the species in the remainder of the Caradoc Area has yet to be demonstrated. In order to do this, extensive excavations would be necessary as the strata, consisting of easily-weathered shales and mudstones, are almost invariably poorly exposed. Near Horderley they include the lower part of the Glenburrell Beds, comprising dark green mudstones and shales which are a continuation of the mudstone phase of sedimentation commenced in the Smeathen Wood Beds. The *Ulricholithus ulrichi* Zone is retained in the Harnagian because it contains no specimens of *Broeggerolithus*, the incoming of which genus indicates the base of the Soudleyan Stage.

Harnagian strata crop out elsewhere in the Caradoc Area, but the faunas are not so completely known as in the districts already mentioned. At the southern end of Ragleth Hill shales and limestones of Harnagian age rest unconformably on Western Longmyndian sandstones, but their exact zonal position is difficult to determine owing to the scanty numbers and poor preservation of the fossils.

Grey sandy shales exposed in the stream-section west of Wallsbank, on the south-eastern flank of Cardington Hill have yielded well-preserved specimens of *Reuscholithus reuschi*, and other, more fragmentary, material from the same neighbourhood suggests that at least one higher horizon may be present.

(c) *Soudleyan Stage*

The type-locality of the Soudleyan is not, as the name implies, at Soudley itself, but was defined by Bancroft (1945 : 182) as being " in the Onny Valley beginning in the Glenburrell Beds and terminating at the summit of the middle Horderley Sandstone ". The reason for this apparent anomaly is, no doubt, the superior series of exposures to be found throughout the Stage in the Onny Valley.

The name was first proposed by Bancroft (1929*a* : 33–34) to include " the highest beds of the Harnage Shale and the lower half of the Horderley Sandstone in Shropshire ". Faunally it was described as " corresponding to the upper part of the series with the *expansa* group of *Rafinesquina*, and especially characterized by a group of species of *Cryptolithus* in which the features of the *gibbifrons* group are modified or not fully developed ".

Later in the same year (Bancroft, 1929*b*, table opposite p. 76) the Soudleyan was listed in a table and divided into four zones as follows :

Dinorthis sp.
Reuschella horderleyensis
Cryptolithus sp.
Cryptolithus broeggeri

In 1933 Bancroft gave a rather more detailed succession for the Stage, dividing it into the following five zones :

Dinorthis multiplicata
Cliftonia persculpta
Broeggeria [*sic*] *soudleyensis* and *Reuschella*
Heterorthis retrorsistria, Broeggeria [*sic*]
Horderleyella and *Broeggeria* [*sic*]

The type-specimens of *D. multiplicata* Bancroft derived from near Glyn Ceiriog, where the species is relatively abundant and occurs with *Rafinesquina expansa.* It is not common in south Shropshire, and cannot be considered a satisfactory zonal fossil there. Of the other forms, *Cliftonia persculpta* is a *nomen nudum*, and Bancroft's genus *Broeggeria* has since been replaced by *Broeggerolithus* (Lamont, 1935 : 320). The two lowest zones were equated with part of what Bancroft termed the Glenburrell Beds, and the three highest with part of the Horderley Sandstone.

In the Onny Valley to the east of Horderley the series of mudstones already described under the Harnagian Stage continues upwards as far as the base of the Horderley Sandstone. The beds are well exposed in the sections behind and near Glenburrell farmhouse, which may thus be taken as the type-locality of the Glenburrell Beds. These consist of dark green mudstones, similar to those with *Ulricholithus ulrichi* at the top of the Harnagian. At Glenburrell they contain abundant *Broeggerolithus broeggeri* (Bancroft). The beds crop out in the bed of the Onny south-east of Glenburrell, and for a short distance to the south of the river. *B. broeggeri* is fairly common, and a good zonal index for the horizon ; it is accompanied by the characteristic brachiopod *Soudleyella* [*Onniella*] *avelinei* (Bancroft), with *Brongniartella* and a new, though uncommon, species of *Salterolithus.* When traced upwards in the Onny Valley the Glenburrell Beds become rather more arenaceous, and it is believed that these levels constitute Bancroft's Zone of " *Heterorthis retrorsistria, Broeggeria* " and, perhaps, correspond to the term " *Horderleyella* Beds " used by him in his description of *Horderleyella corrugata* but never defined (1945 : 238). The diagnostic species of cryptolithid is still *B. broeggeri*, and *Horderleyella corrugata* ranges upwards just into the lowest sandstones of the overlying Horderley Sandstone.

In turn the more arenaceous members of the Glenburrell Beds pass upwards into the lowest, flaggy strata of the Horderley Sandstone group, known to many geologists as the " *Glyptocrinus* Flags " on account of the abundance of the remains of the crinoid *Rhaphanocrinus* [*Glyptocrinus*] *basalis* (McCoy). In the Onny Valley these comprise greenish-brown, flaggy sandstones with lenticular shelly bands in which brachiopods, especially *Dinorthis*, *Sowerbyella*, *Rafinesquina expansa* and *Reuschella horderleyensis* Bancroft, predominate. Of the trilobites the most important is *Broeggerolithus soudleyensis* (Bancroft). Early forms of this species occur rarely in the *B. broeggeri* Zone (Bancroft, 1935 : 33), but *B. soudleyensis* occurs in abundance over most of the Caradoc Area in the zone to which it gives its name, and then disappears. The disappearance of this stock was only temporary, as related forms reappeared later, though not in large numbers, in the Alternata Limestone of the Upper Longvillian Substage (see p. 207).

As stated earlier, *Cliftonia persculpta* is a *nomen nudum*, and neither the *C. persculpta* Zone nor the *Dinorthis multiplicata* Zone of Bancroft has been found to be particularly valuable as a subdivision of the Soudleyan in south Shropshire. It is preferred here to make one *Broeggerolithus soudleyensis* Zone for the whole of the upper sandy portion of the Soudleyan in the Onny region, with *Reuschella horderleyensis* acting as a supplementary index (see table on p. 199). The *B. soudleyensis* Zone is considered to be broadly equivalent to the Lower Horderley Sandstone, the latter being used in a restricted sense, corresponding to the flaggy sandstones of the *Glyptocrinus* Flags of the Onny Valley. Bancroft used the term Lower Horderley Sandstone in a broader sense which is difficult to follow exactly in the field, including as it does both the flaggy beds and some of the overlying massive sandstones.

The most southerly outcrops of the Soudleyan in the Caradoc Area are found near Sibdon Carwood, west of Craven Arms, where quarries were opened in the " *Glyptocrinus* Flags ". These have yielded *Broeggerolithus soudleyensis*, *Soudleyella* and poorly-preserved graptolites. The Glenburrell Beds are not exposed in this area, but may be seen in the valley to the north-east of Hopesay Hill.

North of the Onny Valley, strata of Soudleyan age crop out near Brokenstones, but beyond this point they are cut out by faulting. They reappear near the southern end of Ragleth Hill, near Little Stretton, but only the upper arenaceous beds have been examined, the junction with the underlying Harnagian not being exposed. Similarly, near Soudley the lowest beds are not seen, but at Soudley Quarry the well-known purple and green sandstones are of Soudleyan age. These yielded the type specimens of *Broeggerolithus soudleyensis* and, as they are disconformably overlain by the Alternata Limestone (Upper Longvillian), the often used term " Soudley Sandstone " must be restricted to the upper part of the Soudleyan.

Palaeontological evidence suggests that the diachronism known from the earlier Caradoc strata is repeated in the Soudleyan, in the district north of the Cardington Hills. In the Onny Valley the lower zone of the Soudleyan, that of *B. broeggeri*, consists of dark green mudstones, followed by sandstones of the *Glyptocrinus* Flags (*B. soudleyensis* Zone). Both near Chatwall and The Cwms typical *Glyptocrinus* Flags are found to contain a form of *Broeggerolithus* close to *B. broeggeri* with *Rafinesquina expansa* and *Soudleyella* cf. *avelinei*. This fauna suggests an horizon somewhat earlier than that of the Zone of *B. soudleyensis*, a species not yet found in these beds.

(d) *Longvillian Stage*

The name was first employed by Bancroft (1929*a* : 34), who also termed it "*Kjaerina* Stage" and indicated that the lower and upper portions had distinct faunas; his description of the succession may be summarized as follows :

E.	Middle Longville Flags	
E2.	*Kjaerina geniculata* Beds or Zone	120 ft.
E1.	Laminated micaceous flagstones	165 ft.
D.	Lower Longville Flags	
D1.	*Heterorthis alternata* Beds (*Kjaerina bipartita* Zone)	110 ft.
C.	Upper Horderley Sandstone	
C7.	Green sandstones. *Wattsella* sp. D Super-zone	
C6.	Green and buff sandstones. *Wattsella* sp. C Zone	12 ft. +
C5.	Grey sandstone. *Kjaerina hedstroemi* Zone	Few ft.
C4.	Greenish and buff-grey sandstones. *Kjaerina intermedia* Zone	Few ft.
C3.	Grey sandstone. *Wattsella* sp. A Super-zone	*c.* 25 ft.
C2.	Green and purple sandstone	12 ft.
C1.	Buff sandstone. *Wattsella* sp. A Super-zone	18 ft.

Later in the same year Bancroft (1929*b*, table opposite p. 76) correlated some of these horizons with strata in North Wales, and divided the Longvillian into six "Zones and Super-zones" as follows :

Kjaerina geniculata Bancroft
Kjaerina bipartita (Salter)
Wattsella sp. D
Wattsella sp. C
Kjaerina hedstroemi Bancroft
Wattsella sp. A

Including as it did part of the Horderley Sandstone, together with the Alternata Limestone and the Lower Cheney Longville Flags, the Longvillian constituted a major and somewhat cumbersome subdivision of the Caradoc Series, and in a later work (1933) Bancroft found it convenient to subdivide the Stage into Lower and Upper Longvillian Substages. The dividing line was drawn at the base of the Alternata Limestone, and in the present account the two parts will be discussed separately.

Lower Longvillian Substage

When this subdivision was used by Bancroft for the first time, the previously lettered species of *Wattsella* were given names, though *nomina nuda*, and the following zones proposed :

Raymondella typa
Wattsella indica

Wattsella lepta
Wattsella horderleyensis and *Kjaerina*

The brachiopod faunas of the Caradoc Series in south Shropshire and part of North Wales were described by Bancroft in 1945. He did not recognize the fact that certain of the species, such as *Dalmanella horderleyensis*, *D. indica* and *Bancroftina typa*, had been described for the first time by Whittington (1938*a*, 1938*b*) who, although the names had first been used in manuscript by Bancroft, thus became their author.

In the present account it is recognized that a three-fold division of the Lower Longvillian can be established on the basis of the brachiopods as follows:

Bancroftina typa (Whittington)
Dalmanella indica Whittington and *D. lepta* (Bancroft)
Dalmanella horderleyensis (Whittington)

The beds with *Dalmanella horderleyensis* constitute the best-known strata of the Horderley Sandstone group, viz., the massive purple and green sandstones of Long Lane quarries, north-west of Craven Arms, and of the Onny Valley, east of Glenburrell Farm. The characteristic dalmanellid is abundant in lenticular limestone bands, with less common *Kjaerina jonesi* Bancroft and gastropods such as *Sinuites* and *Lophospira* cf. *gyrogonia* (McCoy). The overlying sandstones were divided into the separate zones of *Dalmanella lepta* and *D. indica* by Bancroft, but the evidence for the two distinct horizons is not altogether satisfactory and, for the present, it is proposed to group them together as one. The Shropshire syntype of *D. indica* came from Longville Plantation, whilst the type specimens of *D. lepta* were obtained from near the south bank of the River Onny, a mile or so to the north along the strike from Longville Plantation, and the division of the beds into two separate entities cannot be accepted as satisfactorily established. The succeeding beds are characterized by *Bancroftina typa* (Whittington), though *Kjaerina* also occurs in some numbers. A conspicuous feature of the fauna of the Lower Longvillian is the extraordinary abundance of *Sowerbyella soudleyensis* Jones, a form which occurs throughout the Substage and constitutes a large proportion of the lenticular limestones.

Tribolites are not uncommon in the Lower Longvillian, and include *Brongniartella*, *Eohomalonotus* (rare), *Phacopidina apiculata* (Salter) and *Reacalymene*. The most characteristic form is *Broeggerolithus globiceps* (Bancroft) which occurs throughout most of the Substage and is now taken as the zonal index. Bancroft recorded *Platylichas laxatus* from the highest strata with *Bancroftina typa*, but intensive searching has failed to substantiate this claim.

The sandstones with *Dalmanella horderleyensis* constitute the best-known building stone in the Onny Valley district, but at higher faunal horizons the beds become less suitable for building purposes, and are noticeably more flaggy, marking a transition to the overlying Upper Longvillian. Farther north, in the Soudley District, the latter beds rest upon sandstones of Soudleyan age, the whole of the Lower Longvillian being cut out by overstep.

Upper Longvillian Substage

In his first usage of the Substage Bancroft (1933) divided the beds into three brachiopod zones :

Kjaerina geniculata Bancroft
Raymondella gigantea—manuscript name
Kjaerina bipartita (Salter)

Of these, *Raymondella gigantea* is still an undescribed species and, hence, a *nomen nudum*. In practice it has been found most convenient to divide the Upper Longvillian into only two parts. The lower is represented by the Alternata Limestone, so-called from the abundance of *Heterorthis alternata* (J. de C. Sowerby), a species which forms lenticular limestones at this horizon throughout the Caradoc Area. The same brachiopod is known from higher horizons in south Shropshire and, for zonal purposes, Bancroft's practice of employing *Kjaerina bipartita* is preferred. Other brachiopods which appear to be restricted to this horizon are *Bancroftina robusta* (Bancroft) and *Marionites typa* (Bancroft), though not in such abundance.

The Alternata Limestone is not a single calcareous band, but consists of impersistent shelly lenses separated by dark green flaggy sandstones and siltstones. Passing upwards, the limestone lenses die out, and there is a transition to the rather monotonous series of green flaggy sandstones, known generally as the Lower Cheney Longville Flags. Fossils occur mainly on bedding-planes throughout the group ; *Kjaerina typa* Bancroft is abundant and is considered to be commoner than *K. geniculata*, the index-species chosen by Bancroft. Other brachiopods found in moderate abundance include *Dolerorthis duftonensis* (Reed) and a species of *Bancroftina* (possibly Bancroft's *Raymondella gigantea*), both of which occur throughout the beds with *Kjaerina typa*.

Trilobites are frequent in parts of the Upper Longvillian but only one form can be considered suitable as the zonal index. This is *Broeggerolithus longiceps* (Bancroft) a species which is more abundant in the flaggy siltstones separating the shelly lenses of the Alternata Limestone than in the lenses themselves. *B. longiceps* persists through the higher beds of the Upper Longvillian, but in reduced numbers. *Phacopidina apiculata* (Salter) is common in the Alternata Limestone, as is *Brongniartella bisulcata* (Salter), the *forma typica* of which appears for the first time at this horizon. *Chasmops* makes its first appearance in Shropshire in the higher beds with *Kjaerina typa*, and individuals of both this genus and of *B. bisulcata* often attain large sizes. An interesting feature of the trilobite fauna of the Upper Longvillian, at least in the Soudley District, is the reappearance of a form of *Broeggerolithus*, closely allied to *B. soudleyensis* (Bancroft), in which several pits of the outermost or E2 row on the fringe are missing in front of the glabella. Nothing like it is yet known between the Upper Soudleyan and the Upper Longvillian in south Shropshire, nor from any strata later than the Upper Longvillian. In the Llansantffraid-ym-mechain District of Montgomeryshire Whittington (1938*c* : 436, 451) records "*Cryptolithus soudleyensis*" from beds which are Lower and Upper Longvillian in age.

The Upper Longvillian follows the Lower Longvillian with apparent conformity in the Onny Valley, but farther north, at Soudley, it rests on the upper part of the Soudleyan. At Chatwall the Upper Longvillian may include at its base both conglomerates and sandstones which have been classified in the broad term of " Chatwall Sandstone " ; this problem is discussed later (see p. 216).

(e) *Marshbrookian Stage*

The Marshbrookian Stage was first adopted by Bancroft, who also gave the alternative name of *Kjerulfina* Stage, named after what he considered to be the typical brachiopod genus (1929*a* : 34). The lower limit was taken arbitrarily at the base of what he called the *Wattsella wattsi* Zone, owing to the fact that *Kjerulfina* appeared just below the summit of the Longvillian Stage. In the same paper (p. 39) he divided the Stage, which was described as being represented by the upper 130 ft. of the Cheney Longville Flags in east Shropshire, as follows :

F4. Transition Bed (*Kjerulfina polycyma* Zone)
F3. *Wattsella unguis* Beds (*W. unguis* Super-zone)
F2. *Heterorthina praeculta* Beds (*H. praeculta* Subzone)
F1. *Wattsella wattsi* Beds (*W. wattsi* Zone)

F2 was stated to be a subzone of F1, and, in another paper (1929*b*, table opposite p. 76), exactly the same subdivisions were again used. Bancroft claimed at first that the fauna of the Marshbrookian was unknown elsewhere, but subsequently (1933) he assigned strata in Westmorland, west Shropshire and North Wales to the Stage and proposed a subdivision into the following three zones :

Onniella reuschi
Wattsella unguis
Wattsella wattsi

Not until 1945 did Bancroft define the type-section of the Marshbrookian as being " through the highest beds of the Longville Flags as exhibited in the lane through Marsh Wood, half a mile south of Marshbrook Station ".

Although Bancroft appeared to attach most importance to the brachiopods as zone-fossils and used them in his first definition, in practice the fossil most characteristic of the Marshbrookian as a whole is *Broeggerolithus transiens* (Bancroft). This is not known from strata earlier than those lowest in the Marshbrookian, and extends throughout the Stage in moderate numbers. Further, with reference to the beds above the Marshbrookian, the absence of cryptolithids from the Actonian in Shropshire is conspicuous and helps to fix the boundary between the two Stages. The claim by Bancroft (1945 : 183) that *Broeggerolithus* disappears somewhat later than the base of the Actonian has not been substantiated in Shropshire, and may possibly refer to strata outside the county. Of Bancroft's zonal brachiopods, *Wattsella wattsi* Bancroft and *W. unguis* (J. de C. Sowerby), both of which are now referred to *Dalmanella*, appear to indicate successive horizons, but they have been found to overlap slightly, at least in the Marshbrook District. *Heterorthina praeculta*

Bancroft is characteristic of the lower series of beds, but as it occurs in small numbers throughout most of the strata containing *D. wattsi* its use as a subzonal fossil should be discontinued. The third index-brachiopod, *Onniella reuschi* Bancroft, appears to have some practical advantage, if not priority of publication, over *Kjerulfina polycyma* Bancroft as an horizon indicator, and is retained for the topmost brachiopod horizon of the Stage. Unless reasonably well-preserved, specimens of *K. polycyma* may be difficult to distinguish from *K. trigonalis* Bancroft, a species which is found only in the *Dalmanella unguis* Beds.

The type-section of the Marshbrookian, in Marsh Wood where the beds were once quarried, is now almost overgrown and detailed collecting is difficult. The topmost beds are not fully exposed, and probably the best continuous exposures through the Stage are those in the Onny Valley, north-north-east of Cheney Longville, where the lowest beds represent a transition from the underlying Upper Longvillian, and comprise brownish-green flaggy siltstones with numerous lenticular shelly bands. The latter are nearly always crowded with fossils, the most abundant of which are *Dalmanella wattsi* and *Tentaculites*, with *Broeggerolithus transiens*, *Brongniartella bisulcata* (Salter) and *Chasmops*. Individuals of the two last-named often attain a large size.

Both lithologically and faunally the succeeding beds resemble those already described, the only conspicuous difference being in the preponderance of *Dalmanella unguis* which, although it overlaps slightly with *D. wattsi*, replaces that species as the characteristic brachiopod. Rare and unusual trilobitic elements in the *D. unguis* Beds of Marshbrook are *Otarion* and *Encrinurus*, the only horizon from which they are known in the Caradoc of south Shropshire. The *D. wattsi* and *D. unguis* Beds exhibit little change in lithology along the strike, but to the north-east of Soudley the latter horizon includes some grey mudstones with abundant and conspicuous ochreous-weathering fossils, such as *D. unguis* and *B. transiens*.

The upper beds of the Cheney Longville Flags consist typically of greenish-yellow flaggy siltstones with lenticular fossil-bands. In the Onny Valley they are followed in the succession by beds of the Actonian Stage, at this, the type-locality, comprising grey mudstones from which cryptolithids are absent, and in which small lamellibranchs, gastropods and cephalopods are dominant. The junction of the two Stages is not usually exposed and there is some difficulty in mapping the precise line of demarcation. In the Onny the highest visible Marshbrookian beds are flaggy siltstones with *Kjerulfina polycyma*; a gap in the exposures supervenes before the Actonian mudstones are seen at Jack Slither. To the north, at Woolston, what may be slightly higher beds with *K. polycyma* are exposed, and there is a partial transition to a finer-grained mudstone lithology, some of the beds being grey as well as the more usual yellowish-brown. Though the complete transition is nowhere entirely exposed, the south-western portion of the track through Marsh Wood, near Marshbrook, affords a good opportunity for further study, even though partly overgrown. Flaggy siltstones, apparently the upper part of the *D. unguis* Beds, are followed by a thin band of mudstone containing abundant worm burrows. Next come mudstones resembling the Actonian beds of the Onny Valley, but containing a fauna which comprises both Marshbrookian and Actonian elements. It includes small lamellibranchs, orthoceratids, *Tropidodiscus acutus*, *Sinuites*, *Broeggerolithus*, *Brongniartella bisulcata*, *Harknessella* (*s.l.*), *Hedstroemina fragilis*, *Sowerbyella sericea* and dalmanellids. Slightly higher in the succession flaggy siltstones containing *K. polycyma* and *Primaspis* cf. *caractaci* are encountered.

The entry of new faunal elements seems to have been at least partly governed by the lithology, and the line between the Marshbrookian and Actonian in south Shropshire probably varied slightly from place to place, depending upon the conditions at any one point. In this instance the transitional beds described are considered to be best included in the Marshbrookian, primarily on account of their content of cryptolithids, which are not found in the Actonian of the Onny Valley. This description casts some doubt on the reliability of *Kjerulfina polycyma* as a zonal index ; it does not usually occur in a mudstone environment, at least in Shropshire, and appears to be restricted to the more arenaceous strata.

(f) *Actonian Stage*

The term Actonian was introduced first by Bancroft (1929*b*, table opposite p. 76) who, without giving definition or details, listed it in a stratigraphical table and subdivided it into two zones, a lower one of *Hedstroemina robusta*, and an upper one of *Resserella* (now *Cryptothyris*) *paracyclica*. The Stage was stated to be represented by part of the Acton Scott Beds of the Horderley District. Subsequently Bancroft again listed the Stage in a stratigraphical table (1933), but on this occasion used only the single brachiopod index of *Onniella grandis*, at that time an undescribed species. Strata in south Shropshire, Westmorland and various parts of North Wales were assigned to the Actonian.

It was not until twelve years later that Bancroft (1945 : 183) defined the base and top of the Actonian, and designated the section exposed in the Onny Valley " east of Burrells Coppice " as constituting the type-succession. His definition of the base as being " marked by the disappearance of *Kjerulfina* and *Tentaculites anglicus*, and the appearance of a large species of *Onniella* and *Colpomya* " is not found to be sufficiently precise in practice, and does not take into account any variation of fauna with environmental changes ; consequently, a detailed re-examination of the type-succession is necessary.

The only place in Shropshire where a reasonably exposed succession through the whole Actonian can be found is in the Onny Valley. Here it is possible, on the basis of their faunas, to divide the beds roughly into three parts as follows, though some difficulties arise when detailed correlation with other parts of the Caradoc Area is attempted.

(i) The lowest Actonian comprises yellow and grey mudstones, with occasional thin, nodular limestones, and shows a lithological transition from the topmost beds of the Marshbrookian. Particularly noticeable is the sudden absence of cryptolithids ; instead, the mudstones of the Onny District were invaded by considerable numbers of *Platylichas laxatus* (McCoy) and *Chasmops*, the latter usually considerably larger than those from earlier strata. *Kjerulfina* has not yet been found in the Actonian of the Onny, though *Hedstroemina* persists into the lowest beds, and the most abundant brachiopod is *Onniella depressa* Bancroft. After a long absence *Heterorthis alternata* (J. de C. Sowerby) returns to form a limestone band several inches thick. The gastropods *Holopea striatella* (J. de C. Sowerby) and *Sinuites* are often abundant, as are the corals *Favosites* and *Coenites*?, though there is no suggestion of reef-conditions having existed.

(ii) The strata of the middle Actonian are marked by a decline in the number of individuals of *Platylichas* and *Chasmops*, though these two genera are not altogether uncommon. They are joined by another phacopid genus *Calyptaulax*, previously unrecorded from Shropshire which, though not abundant, appears to be relatively restricted in its vertical range. *Primaspis* [*Acidaspis*] *caractaci* (Salter) is uncommon in this mudstone environment. Of the brachiopods *Onniella grandis* is not very abundant, but *Cryptothyris paracyclica* and *Reuschella semiglobata* Bancroft are moderately common. All three species appear to be characteristic, but *C. paracyclica* is here preferred to *O. grandis* as index-brachiopod. *Nicolella actoniae* (J. de C. Sowerby), abundant in some other districts of the Caradoc Area, is markedly uncommon in the vicinity of the Onny.

(iii) The faunas of the upper Actonian in the Onny Valley appear to be less prolific than those of the earlier beds, and diagnostic forms are less obvious, though the strata are less well exposed. *Platylichas* and *Chasmops* are very much less abundant, but they are accompanied by numerous *Remopleurides* sp. nov., a few individuals of which first appeared late in the middle Actonian. Of the brachiopods only *Sowerbyella* and *Onniella* are common, but *Dolerorthis*, *Chonetoidea* and *Sampo* (recorded in Shropshire for the first time) occur. *Onniella sinuata* Bancroft is known to be typical of an horizon fairly high in this upper third of the Actonian, but its overall distribution is not yet fully known.

Northwards from the Onny Valley the beds are covered by Drift as far as the neighbourhood of Acton Scott, where strata of Actonian age form the capping to the high ground on which the village is situated. The detailed succession here is much more difficult to follow, as well as being probably less complete, than in the Onny Valley, and it has not been possible to examine fully the lowest beds and their junction with the Marshbrookian. The valley running eastwards from Marshbrook Village exposes strata which are probably rather higher in the Actonian succession. They consist of yellowish-grey, sandy mudstones with a good fauna which includes *Platylichas*, *Primaspis caractaci*, *Remopleurides*, *Chonetoidea*, *Cryptothyris*, *Nicolella actoniae* and *Onniella grandis*, with common small gastropods and lamellibranchs. A reasonable correlation is with the lower part of the middle Actonian of the Onny Valley. The mudstones appear to pass upwards into more arenaceous beds, almost quartzitic sandstones in part, which are more resistant to erosion than the underlying mudstones, and which were once quarried extensively both at and near Acton Scott. The most conspicuous elements of the fauna are *Nicolella actoniae* and *Reuschella bilobata* (J. de C. Sowerby), associated with *Cryptothyris paracyclica* and *Leptaena*. Trilobites also occur and include *Platylichas*, *Chasmops*, *Primaspis caractaci* and *Gravicalymene*, with rare *Illaenus* and *Atractopyge*. Occasional bands of mudstone yield locally abundant ostracods, such as *Tetradella* and *Beyrichia*?. The assemblage suggests that the beds may be equated with part of the middle Actonian of the Onny

Valley. Higher horizons have not yet been confirmed, but this may be due to lack of exposures. The assemblage of *Platylichas*, *Illaenus*, *Atractopyge* and *Nicolella* is interesting in that it occurs at a much lower level in the Derfel Limestone (probably basal Harnagian) of the Bala District (Whittington & Williams, 1955).

In the vicinity of Hatton, north-east of Acton Scott, Actonian beds are exposed in the stream west of the village. The arenaceous strata of Acton Scott are not in evidence, and the succession consists almost entirely of grey mudstones with bands of impure limestone. The fauna is a prolific one, with *Platylichas*, *Chasmops*, *Reuschella bilobata* and *Onniella grandis* in abundance, suggesting a lower to middle Actonian age. The absence of higher beds is almost certainly due to the cover of Drift or to the unconformable Upper Llandovery.

In the banks of Ticklerton Brook, between Ticklerton and Soudley, soft grey mudstones occur below the basal Llandovery strata. Fossils are not abundant but include *Reuschella semiglobata*, and the beds are probably middle Actonian in age. The Marshbrookian/Actonian junction is not exposed in this section.

It has been stated in recent years that strata belonging to Lapworth's Acton Group do not occur to the north of the Cardington Hills (Pocock & Whitehead, 1948 : 51), but many years ago Salter & Aveline (1854 : 66) recorded them from the then well-known fossiliferous locality of Gretton, near Cardington, cited again by Cobbold (1900 : 55). Gretton Quarry, now unfortunately filled in, produced an enormous fauna which clearly indicates a middle Actonian age. The large number of forms found there include *Platylichas*, *Chasmops*, *Illaenus*, *Gravicalymene*, *Calyptaulax*, *Primaspis caractaci*, *Nicolella actoniae*, *Reuschella bilobata*, *Onniella grandis*, *Sampo*, *Cryptothyris paracyclica*, and abundant polyzoans and corals. The beds are soft, yellow, flaggy sandstones with shelly lenses. The underlying and overlying strata are insufficiently exposed for any detailed observations to be made.

(g) *Onnian Stage*

This, the most restricted areally of all the Stages of the Caradoc Series in south Shropshire, was introduced by Bancroft (1929*b*, table opposite p. 76) ; it was divided into three trilobite zones of *Onnia cobboldi*, *O. gracilis* and *O. superba* in ascending order, and stated to occur only in the Onny Valley. Later it was again listed in a tabular succession, but was correlated with strata in both south Shropshire and Westmorland (Bancroft, 1933). In 1945 Bancroft named the Onny Valley as the type-section and gave further details of the Stage (1945 : 183). The base of the Onnian was described as being marked by the appearance of the cryptolithid genus *Onnia*, and the summit by the disappearance of *Onnia* and the reappearance of *Tretaspis kjaeri*, the latter being said to have a limited distribution in the Actonian. *Tretaspis* is known from the Caradoc Series in Westmorland, but there is no evidence that it has been found in south Shropshire.

Examination of the Onnian within the Caradoc Area is hampered by the unconformable cover of Llandovery strata, as well as by extensive Drift deposits, and the only accessible succession is in the Onny Valley south of Wistanstow. In practice

Bancroft's definition of the base has proved convenient; the preceding Actonian contains no cryptolithids, and their sudden reappearance can be easily followed in the field. The three successive cryptolithid zones erected by Bancroft appear to be well established in the Onny region, but unfortunately their lateral development cannot be traced owing to paucity of exposures.

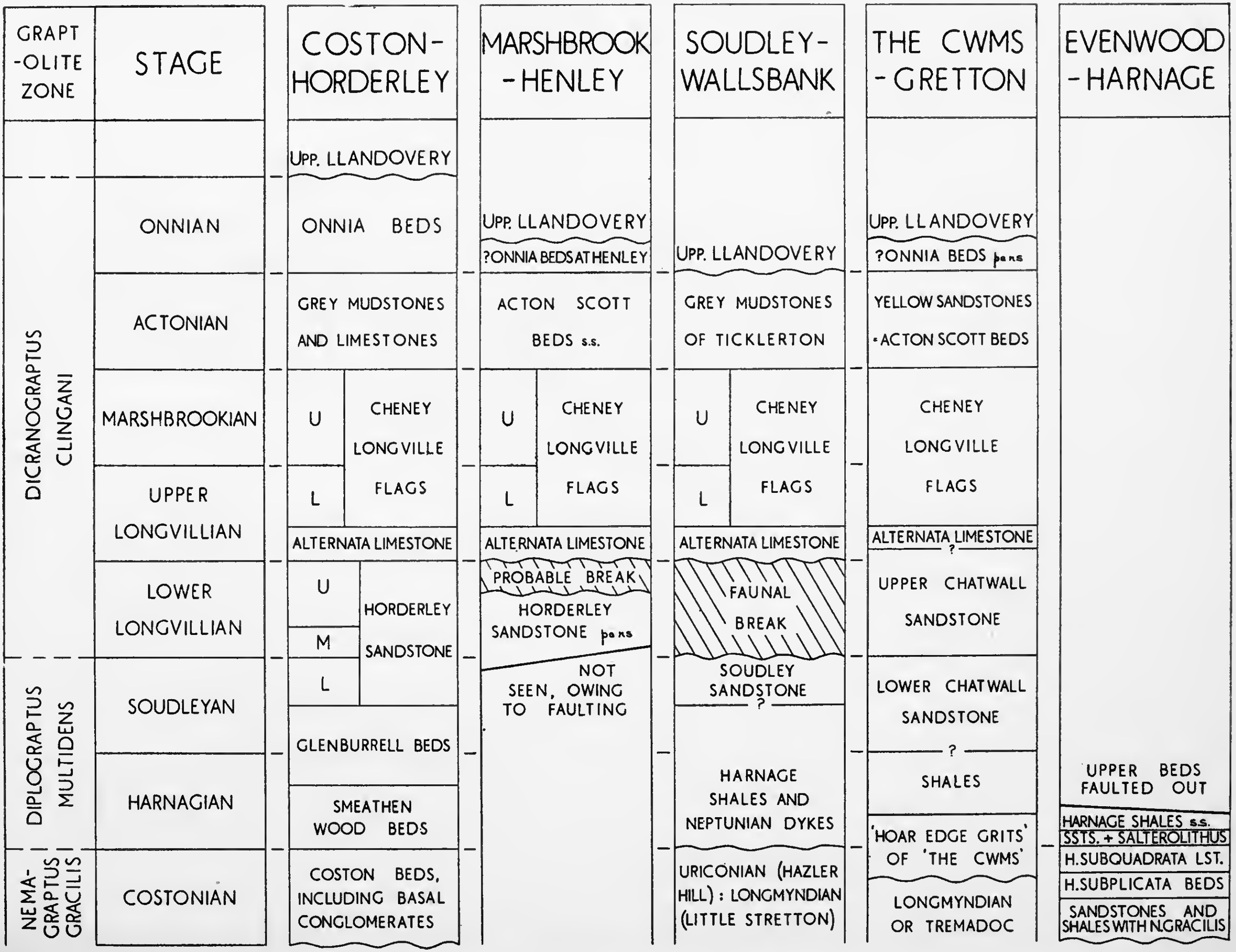
Lithologically the *Onnia cobboldi* Zone shows no obvious change from the Actonian, but the trilobite fauna differs markedly, although occasional Actonian elements remain. *Platylichas* and *Chasmops*, genera so abundant in parts of the Actonian, occur merely as occasional isolated individuals, and only the former genus has been recorded from the succeeding *Onnia gracilis* Zone. Similarly, illaenids like those of the Actonian are sometimes found. The occurrence of two specimens of *Gravicalymene* in the *O. gracilis* Zone is interesting because it is apparently the same form as is so abundant in some of the Actonian sandstones. The trilobite fauna of the topmost zone of *Onnia superba* is particularly rich in individuals of the zonal cryptolithid, but other forms include *Lonchodomas pennatus* (La Touche), *Raphiophorus edgelli* (Reed), *Remopleurides burmeisteri* Bancroft, *Triarthrus*, *Pseudosphaerexochus* and *Eobronteus*?, the last two being extremely rare. The brachiopod fauna of the two lower zones of the Onnian comprises mainly the genus *Onniella*. *O. inconstans* Bancroft in the *Onnia cobboldi* Zone is followed in the *Onnia gracilis* Zone by the related *Onniella broeggeri* Bancroft, accompanied by abundant small *Chonetoidea* and ostracods.

The strata of the *Onnia superba* Zone would appear to indicate quieter conditions of deposition, and whole trilobites are of frequent occurrence. Coincident with these conditions *Onniella* almost disappears, and the brachiopods usually found are *Chonetoidea* (like that in the Actonian), and the very small "*Rafinesquina*" *holli* (Davidson) which may be locally abundant.

The term Acton Scott Beds was used by Bancroft (1929*b*, table opposite p. 76; 1933) to include the Actonian and the two lower trilobite zones of the Onnian, leaving the *Onnia superba* Zone equivalent to the Onny Shales, which is apparently the same usage as that of La Touche (1884). As stated earlier, however, the Acton Scott Beds (*s. s.*) of the Acton Scott District include only part of the Actonian Stage. Furthermore, the sharp colour change between the yellow-weathering mudstones of the *Onnia superba* Zone at the well-known "Cliff Section", with their limonitic fossils, and the earlier Onnian strata is apparent rather than real, and all the rocks appear as grey mudstones when seen in fresh section. Accordingly, the strata belonging to the Onnian Stage in south Shropshire are here named *Onnia* Beds *nom. nov.*, with the Onny Valley between Cheney Longville and Wistanstow as type-locality.

III. LAPWORTH'S SUBDIVISIONS OF THE CARADOC SERIES

Lapworth (1916) published a series of vertical sections covering the Lower Palaeozoic rocks of Shropshire. He applied the name "Caradoc Series" to the Ordovician rocks forming the elongated outcrop in the Caer Caradoc-Wrekin District and subdivided them to give the following succession:



GRAPTOLITE ZONE	STAGE	COSTON-HORDERLEY	MARSHBROOK-HENLEY	SOUDLEY-WALLSBANK	THE CWMS-GRETTON	EVENWOOD-HARNAGE
		UPP. LLANDOVERY				
DICRANOGRAPTUS CLINGANI	ONNIAN	ONNIA BEDS	UPP. LLANDOVERY ?ONNIA BEDS AT HENLEY	UPP. LLANDOVERY	UPP. LLANDOVERY ?ONNIA BEDS pars	
	ACTONIAN	GREY MUDSTONES AND LIMESTONES	ACTON SCOTT BEDS s.s.	GREY MUDSTONES OF TICKLERTON	YELLOW SANDSTONES ACTON SCOTT BEDS	
	MARSHBROOKIAN	U CHENEY LONGVILLE FLAGS	U CHENEY LONGVILLE FLAGS	U CHENEY LONGVILLE FLAGS	CHENEY LONGVILLE FLAGS	
	UPPER LONGVILLIAN	L ALTERNATA LIMESTONE	L ALTERNATA LIMESTONE	L ALTERNATA LIMESTONE	ALTERNATA LIMESTONE ?	
	LOWER LONGVILLIAN	U M HORDERLEY SANDSTONE	PROBABLE BREAK HORDERLEY SANDSTONE pars	FAUNAL BREAK	UPPER CHATWALL SANDSTONE	
DIPLOGRAPTUS MULTIDENS	SOUDLEYAN	L GLENBURRELL BEDS	NOT SEEN, OWING TO FAULTING	SOUDLEY SANDSTONE ?	LOWER CHATWALL SANDSTONE ?	
	HARNAGIAN	SMEATHEN WOOD BEDS		HARNAGE SHALES AND NEPTUNIAN DYKES	SHALES 'HOAR EDGE GRITS' OF 'THE CWMS'	UPPER BEDS FAULTED OUT HARNAGE SHALES s.s. SSTS. + SALTEROLITHUS
NEMAGRAPTUS GRACILIS	COSTONIAN	COSTON BEDS, INCLUDING BASAL CONGLOMERATES		URICONIAN (HAZLER HILL): LONGMYNDIAN (LITTLE STRETTON)	LONGMYNDIAN OR TREMADOC	H.SUBQUADRATA LST. H.SUBPLICATA BEDS SANDSTONES AND SHALES WITH N.GRACILIS

TEXT-FIG. 4.—Correlation of the Caradoc Series in the Type Area.

Acton Group .	Upper *Trinucleus* Beds Acton Calcareous Beds
Longville Group .	Lower *Trinucleus* Shales Birrells Wood Flags Chelmick Flags and Shales
Chatwall Group .	Alternata Limestone Upper Chatwall Sandstone Lower Chatwall Sandstone (*Glyptocrinus* Flags)
Harnage Group .	Harnage Shales
Hoar Edge Group .	Transition Bed Upper Hoar Edge Sandstone Hoar Edge Limestone Lower Sandstone and Conglomerate

Lapworth supervised extensive collecting by the Geological Survey from horizons throughout the Series, but the results remained unpublished and the subdivisions listed above were never defined or described. Some use has been made of the terms (Watts, 1925 : 340 ; Pocock *et al.*, 1938 : 81–90) and it is necessary to re-assess them and ascertain their usefulness in the light of present-day knowledge.

Hoar Edge Group

No details having been given in addition to the table, it is difficult to fit the succession into the zonal sequence, but it has been pointed out (Pocock *et al.*, 1938 : 86) that the specimens of *Nemagraptus gracilis* identified from the Evenwood District came from beds containing *Harknessella subplicata* near the top of the Hoar Edge Group, which at that point is only about 100 ft. thick. These beds would, then, coincide at least approximately with Lapworth's Lower Sandstone and Conglomerate, the so-called *Harknessella subquadrata* Limestone above being equivalent to his Hoar Edge Limestone. It is possible, though not certain, that the Upper Hoar Edge Sandstone refers to the Rhynchonellid Grits, the latter, together with the "Transition Bed", being considered Harnagian in age. It is doubtful whether Lapworth's detailed succession can be applied successfully to the southern part of the Caradoc Area.

Harnage Group

As stated earlier, the strata referred to his "Transition Bed" by Lapworth are almost certainly those topmost portions of the Hoar Edge Grits in the Evenwood District which contain *Salterolithus* and are thus of Harnagian age.

The Harnage Shales of the type-area of Coundmoor Brook represent only the *Reuscholithus reuschi* Zone of the Harnagian, the higher zones being cut out by faulting. The Harnage Group, strictly interpreted, cannot therefore include more than the lowest trilobite Zone of the Harnagian. It does not constitute a good stratigraphical subdivision on faunal grounds and is probably best allowed to lapse.

Chatwall Group

The term "*Glyptocrinus* Flags" has already been referred to in the discussion of the Soudleyan Stage, and is considered to be almost exactly equivalent to the *Broeggerolithus soudleyensis* Zone in the Onny Valley, but farther north may include beds of a slightly earlier date. The term appears to be in more general use than that of "Lower Chatwall Sandstone".

In order to summarize the stratigraphical position of those strata known as the Upper Chatwall Sandstone, it is necessary to examine the succession in the type-area around Chatwall Hall, one-and-a-half miles north-north-east of Cardington. To the north-west of Chatwall Hall the *Glyptocrinus* Flags crop out and have been quarried, for example, 70 yards north-north-west of the Hall, where they consist of dark green flaggy sandstones with deeply-weathered shelly lenses containing abundant *Broeggerolithus* cf. *broeggeri*. These beds appear to pass upwards into more massive maroon and grey-green sandstones, such as those quarried just south-east of Chatwall Farm. From this quarry a narrow cutting has been made, leading south-eastwards to the adjacent crossroads, and at the eastern end of the cutting slightly higher beds have been extensively quarried. These two series of strata have generally been grouped together as the Chatwall Sandstone, and the intermediate beds exposed in the cutting have been described by Robertson (*in* Pocock *et al.*, 1938 : 88). The higher sandstone beds, or Upper Chatwall Sandstone, are followed in the succession by lenticular limestones of the Alternata Limestone series (Upper Longvillian), but there are certain features which make it difficult to accept them without question as being of pre-Upper Longvillian age. For example, the fauna includes *Heterorthis alternata* (J. de C. Sowerby) with abundant large *Sowerbyella sericea* and *Brongniartella bisulcata*, all of which are particularly abundant and characteristic in the lower part of the Upper Longvillian elsewhere in the Caradoc Area. Furthermore, the lithology of the Upper Chatwall Sandstone, comprising soft, yellow-weathering flaggy sandstones with shelly lenses, is quite different from that of the Lower Chatwall Sandstone, and is separated from it by thick bands of conglomerate which often contain abundant gastropods. The problem is not yet satisfactorily resolved, but it is possible that the Upper Chatwall Sandstone may eventually prove to be at least partly Upper Longvillian in age, forming what is virtually an arenaceous development of the basal beds of the Alternata Limestone. The exact horizon of the sandstones below the conglomerates is not yet known, but the possibility of the further extension of the stratigraphical break below the Upper Longvillian which is so apparent at Soudley cannot be excluded.

The Alternata Limestone was placed by Lapworth in his Chatwall Group, but on faunal grounds there can be no doubt that its place is with the Lower Cheney Longville Flags in the Upper Longvillian.

Longville Group

Lapworth's term "Chelmick Flags and Shales" presumably refers to the area of Chelmick, about one mile south-west of Hope Bowdler. The derivation of "Birrells Wood Flags" is less clear, as no such place exists on the present-day

Ordnance maps, but it is here suggested that the name may refer to what is now known as Burrells Coppice, by the south bank of the River Onny, rather less than half-a-mile north of Cheney Longville. It is probably true that the beds near Chelmick are fairly low in what generally are called the Lower Cheney Longville Flags, and those exposed at the eastern end of Burrells Coppice are certainly high in the same group. Owing to lack of good continuous exposures at both places it is difficult to correlate the two subdivisions exactly, and the most practical solution is to allow the two names to lapse, while retaining the term Lower Cheney Longville Flags. The latter has the great merit of possessing a definite type-locality, in the lane leading westwards from Cheney Longville, and the almost continuous section available there does not suggest that further lithological subdivision would be of any great value, though there are certain variations in the faunas.

The " Lower *Trinucleus* Shales " must be taken to represent the whole of what is now regarded as the Marshbrookian Stage, but for a number of reasons the name is highly unsuitable. The Marshbrookian, or Upper Cheney Longville Flags, consists almost entirely of massive and flaggy siltstones and mudstones. Cryptolithid trilobites occur throughout, but certainly not in numbers sufficient to give their name to the beds. Furthermore, no type-locality was ever cited, and the name is best rejected.

Acton Group

Though not defined as such, it is certain that Acton Scott must have been the intended type-locality of the " Acton Calcareous Beds ", which are thus at least approximately equivalent to the Acton Scott Beds (*s. s.*) discussed on p. 211. No type-locality was chosen for the Upper *Trinucleus* Beds, though one can claim that, by implication, they are equivalent to at least part of the Onnian Stage of the Onny Valley.

If the Acton Calcareous Beds and the Upper *Trinucleus* Beds are, in fact, equivalent to the Acton Scott Beds (*s. s.*) and part of the Onnian respectively, then, if they are used in their restricted sense, they cannot be exactly equivalent to the Actonian and Onnian Stages, as it has already been shown that the Acton Scott Beds (*s. s.*) probably represent only a part of the Actonian Stage.

IV. FAUNAL LISTS

Each of the species in the following lists is accompanied by a number, or numbers, followed by a letter, or letters. The former refers to the horizon as indicated in Text-fig. 3 ; the latter refers to the district, or districts, within the Caradoc Area, as listed below.

A.—Coston.
B.—Onny Valley.
C.—Brokenstones, near Horderley.
D.—Marshbrook.
E.—Acton Scott.
F.—Little Stretton.
G.—Soudley-Ticklerton.
H.—The Cwms, near Church Stretton.
K.—Evenwood—Harnage Grange.

Costonian Stage

Favosites fibrilla Smith	2 ; A, C, K
Polyzoans (various)	2 ; A, B, C, H, K
Cliftonia cf. *andersoni* Reed	1, 2 ; A, C, K
Dalmanella sp. (small)	2 ; A, C
Dinorthis flabellulum (J. de C. Sowerby)	1 ; A
D. aff. *flabellulum* (J. de C. Sowerby)	2 ; C, K
Dinorthis sp. A	1 ; A
Dinorthis sp. B	2 ; C
Dolerorthis sp.	2 ; A, C
Glyptorthis ? sp.	2 ; A
Harknessella jonesi Bancroft	1 ; A
H. subplicata Bancroft	1 ; K
H. subquadrata Bancroft	2 ; K
H. vespertilio (J. de C. Sowerby)	1 ; A
Harknessella sp.	2 ; C
Heterorthis patera (Davidson)	1 ; A : 2 ; C
Horderleyella plicata Bancroft	2 ; A, C
Leptaena sp.	2 ; A, C
Lingula cf. *ovata* McCoy	2 ; A
Orbiculoidea sp.	2 ; A
Rafinesquina cf. *complanata* (J. de C. Sowerby)	2 ; A, K
R. aff. *expansa* (J. de C. Sowerby)	1 ; A
Rafinesquina sp.	2 ; A, C
Rafinesquina sp. (? nov.)	2 ; K
Salopia salteri (Davidson)	2 ; C
Siphonotreta cf. *micula* McCoy	2 ; K
Smeathenella strophomenoides Bancroft	2 ; A, C
Sowerbyella sp.	1, 2 ; A, C, K
Cyclonema cf. *crebristria* (McCoy)	1, 2 ; K
Leseurilla balclatchiensis Longstaff	2 ; K
Liospira aequalis (Salter)	2 ; K
Rhaphistomina ? sp.	1 ; A
Hyolithes sp.	2 ; A, K
Ambonychia sp.	2 ; K
Ctenodonta cf. *varicosa* (Salter)	1, 2 ; K
" *Orthoceras* " sp. indet.	2 ; K
Asaphid indet.	1 ; A
Brongniartella aff. *bisulcata* (Salter)	2 ; K
Costonia ultima (Bancroft)	2 ; A, C
Costonia sp. nov.	2 ; H. K
Eohomalonotus sp.	2 ; K
Flexicalymene cf. *acantha* Bancroft	2 ; A, C
Flexicalymene sp.	1 ; A: 2 ; K
Metopolichas ? aff. *verrucosa* (Eichwald)	2 ; C, K
Reacalymene pusulosa Shirley	1, 2 ; K
Primitia simplex (Jones)	2 ; A, K
P. strangulata (Salter)	2 ; K
Tetradella scripta Harper	2 ; A, C, K ?

Harnagian Stage

Cystid plates	3 ; B, G, K
Crinoid ossicles	3, 4 ; B : 3 ; K
Lepidocoleus suecicus Moberg	3 ; B, G, K
Plumulites sp.	3 ; B, K
Turrilepas ? sp.	3 ; B
Polyzoans (various)	3 ; B, C, F, G, K
Chonetoidea ? sp.	4 ; B
Cliftonia cf. *andersoni* Reed	3 ; B, C
Dalmanella sp.	3 ; B
Dinorthis sp.	3 ; B, C, F, G
Dolerorthis sp.	3 ; B, G
Harknessella cf. *vespertilio* (J. de C. Sowerby)	3 ; B, G
Heterorthis aff. *patera* (Davidson)	3 ; B, C
Horderleyella sp.	3 ; B
Lingula sp.	3 ; B, K
Orbiculoidea sp.	3 ; B
Orthorhynchula sp.	3 ; B, G
Paterula cf. *albida* Reed	3 ; K
Rostricellula aff. *triangularis* Williams	3 ; B
Salopia salteri (Davidson)	3 ; B, C, F, G
Siphonotreta cf. *scotica* Davidson	3 ; B
Smeathenella harnagensis Bancroft	3 ; B, C, K ?
S. cf. *harnagensis* Bancroft	3 ; B
Sowerbyella aff. *sericea* (J. de C. Sowerby)	3 ; B, C, F, G, K
Vellamo sp.	3 ; G
Carinopsis cf. *gracilis* (Reed)	3 ; K
Cyrtolites sp.	3 ; B, K ?
Phragmolites sp.	3 ; B
Raphistoma sp.	3 ; K
Conularia (*s.l.*) sp.	3 ; B, K
Hyolithes sp.	3 ; B, K
Ctenodonta aff. *coarctata* (Phillips)	3 ; B, K
C. cf. *varicosa* Salter	3 ; B, G, K : 4 ; B
Modiolopsis ? aff. *postlineatus* McCoy	3 ; K
" *Orthoceras* " sp.	3 ; K
Basilicus marstoni (Salter)	3 ; B
Brongniartella sp.	3 ; B, K
Decoroproetus fearnsidesi (Bancroft)	3 ; B, K
D. cf. *fearnsidesi* (Bancroft)	3 ; F
Diacalymene ? *praecox* Bancroft	3 ; B, K
Flexicalymene acantha Bancroft	3 ; B, K
Flexicalymene sp.	3 ; B
Nieszkowskia stubblefieldi Bancroft	3 ; B
Parabasilicus powisi ? (Murchison)	3 ; B
Reuscholithus reuschi Bancroft	3 ; B, G, K
Salterolithus harnagensis Bancroft	3 ; K
S. aff. *harnagensis* Bancroft	3 ; G, H, K
S. smeathenensis Bancroft	3 ; B
S. caractaci (Murchison)	3 ; B, G ?
Primitia nana Jones & Holl	3 ; B, C, G, K
P. simplex (Jones)	3 ; B, G ?, K
Tetradella scripta Harper	3 ; B, C, F, G, K : 4 ; B, G ?
Ulrichia bicornis (Jones)	3 ; B, C, G, K

Soudleyan Stage

Favosites fibrilla Smith	6; H: 7; B, G
Crinoid ossicles	6; H: 7; B, G, H
Rhaphanocrinus basalis (McCoy)	6; H: 7; B, G. H
Cliftonia cf. *andersoni* Reed	6; B: 7; B, G, H
Craniops sp.	6; B: 7; B, H
Dinorthis aff. *flabellulum* (J. de C. Sowerby)	7; B, G
Heterorthis retrorsistria (McCoy)	6; B: 7; B, G, H
Horderleyella corrugata Bancroft	7; B
Leptaena sp.	6; B
Orbiculoidea sp. (small)	6; B
Rafinesquina expansa (J. de C. Sowerby)	7; B, G ?, H
Rafinesquina sp.	7; B
Reuschella horderleyensis Bancroft	7; B, G
Soudleyella avelinei (Bancroft)	6; B
Sowerbyella sp.	6; B, H: 7; B, H
Carinopsis cf. *gracilis* (Reed)	7; H
Cyclonema crebristria (McCoy)	7; B, H
Cyrtolites nodosus (Salter)	7; B
Sinuites bilobatus (J. de C. Sowerby)	7; B, H
S. soudleyensis Reed	7; H
Hyolithes sp.	7; H, K
Ctenodonta sp.	6; B: 7; H, K
Orthonota sp.	6; B: 7; H
" *Orthoceras* " sp.	6; B
Broeggerolithus broeggeri (Bancroft)	6; B, H ?
B. constrictus Bancroft	6; B
B. soudleyensis (Bancroft)	7; B, G, H
Broeggerolithus sp.	6; B
Brongniartella sp.	6; B, H
Calymenid indet.	6; B
Decoroproetus ? sp.	6; B, H: 7; B, H
Parabasilicus powisi (Murchison)	6; B: 7; B
Reacalymene cf. *pusulosa* Shirley	7; K
Salterolithus sp.	6; B
Primitia sp.	6; B
Tetradella scripta Harper	6; B
Climacograptus antiquus Hall var.	6; B
Orthograptus cf. *apiculatus* Elles & Wood	7; B

Longvillian Stage

(i) *Lower Longvillian Substage*

Favosites fibrilla Smith	8 a, b, c; B
Polyzoans (various)	8 a, b, c; B
Bancroftina typa (Whittington)	8 c; B
Cliftonia cf. *spiriferoides* (McCoy)	8 b; B
Dalmanella horderleyensis (Whittington)	8 a; B
D. indica Whittington	8 b; B
D. lepta (Bancroft)	8 b; B
Dinorthis sp.	8 b; B
Dolerorthis sp.	8 b; B
Kjaerina hedstroemi Bancroft	8 b; B

K. horderleyensis Bancroft	8 a; B
K. intermedia Bancroft	8 a; B
K. jonesi Bancroft	8 a; B
K. cf. *jonesi* Bancroft	8 c; B
cf. *K. richteri* Bancroft	8 c; B
Leptaena sp.	8 a, b; B
Lingula sp.	8 b, c; B
Orbiculoidea sp.	8 c; B
Rafinesquina sp.	8 c; B
Resserella canalis (J. de C. Sowerby)	8 a, b, c; B
Sowerbella soudleyensis Jones	8 a, b, c; B
Clathrospira ? sp.	8 a; B
Cyrtolites nodosus (Salter)	8 a, b; B
cf. *Liospira aequalis* (Salter)	8 a; B
Lophospira cf. *gyrogonia* (McCoy)	8 a; B
Murchisonia ? sp.	8 a, b; B
Sinuites anceps Reed	8 a; B
S. bilobatus (J. de C. Sowerby)	8 a; B
S. soudleyensis Reed	8 a, b; B
Ambonychia ? sp.	8 a; B
Ctenodonta sp.	8 a; B
Broeggerolithus globiceps (Bancroft)	8 a, b, c; B
Broeggerolithus sp.	8 b; B
Brongniartella bisulcata (Salter) var.	8 a, b; B
Eohomalonotus sp. (? nov.)	8 b; B
Phacopidina apiculata (Salter)	8 a, b, c; B, D
P. aff. *harnagensis* Bancroft	8 a; B
Parabasilicus powisi ? (Murchison)	8 a; B
Reacalymene sp. nov.	8 a, b; B, D

(ii) *Upper Longvillian Substage*

Favosites fibrilla Smith	9 a, b; B, G
Streptelasma ? sp. indet.	9 b; B
Lepidocoleus suecicus Moberg	9 b; B; G
Bancroftina robusta (Bancroft)	9 a; B
B. aff. *typa* (Whittington)	9 b; B
Dolerorthis duftonensis (Reed)	9 a, b; B, G
Harknessella (*s.l.*) sp.	9 b; B
Heterorthis alternata (J. de C. Sowerby)	9 a; B, D, G
Kjaerina bipartita (Salter)	9 a; B, G
K. geniculata Bancroft	9 b; B
K. typa Bancroft	9 b; B
Kjaerina sp.	9 b; B
Lingula sp.	9 a, b; B
Marionites typa (Bancroft)	9 a; B, G
Nicolella ? sp.	9 b; B
Orbiculoidea sp.	9 a; G
Philhedra drummuckensis Reed	9 a; G
Platystrophia sp.	9 b; B
Plectorthis ? cf. *plicatella* Reed	9 b; B
Rafinesquina sp.	9 b; B
Schizocrania sp.	9 a; G
Sowerbyella sericea (J. de C. Sowerby)	9 a, b; B, D, G

Strophomena grandis (J. de C. Sowerby)	9 a, b ; B, G
Trematis punctata (J. de C. Sowerby)	9 a ; B, G
Cyrtolites nodosus (Salter)	9 a ; G
Lophospira cf. *gyrogonia* (McCoy)	9 a ; G
Sinuites soudleyensis Reed	9 a ; G
Tentaculites cf. *scalaris* Schlotheim	9 a, b ; B, D, G
Ambonychia orbicularis (J. de C. Sowerby)	9 b ; B
Ctenodonta aff. *varicosa* Salter	9 a ; G
Pterinea sp.	9 a ; G
Asaphid indet.	9 a, b ; B
Broeggerolithus longiceps (Bancroft)	9 a, b ; B, C, G
B. aff. *soudleyensis* (Bancroft)	9 a ; G
Brongniartella bisulcata (Salter)	9 a, b ; B, D, G
Chasmops sp.	9 b ; B
Flexicalymene aff. *caractaci* (Salter)	9 b ; B
Phacopidina apiculata (Salter)	9 a, b ; B, G
P. cf. *apiculata* (Salter)	9 a ; G
Primitia sp.	9 a ; G
Tetradella cf. *scripta* Harper	9 a ; G

Marshbrookian Stage

Favosites fibrilla Smith	10 a, b, c ; B, D
Polyzoans (various)	10 a, b, c ; B, D
Craniops sp.	10 c ; B
Dalmanella multiplicata (Bancroft)	10 a ; B, D
D. unguis (J. de C. Sowerby)	10 b ; B, D
D. wattsi (Bancroft)	10 a ; B, D
Dolerorthis sp.	10 b ; D
Hedstroemina fragilis Bancroft	10 c ; B, D
H. parva Bancroft	10 b ; B
Heterorthina praeculta Bancroft	10 a, b ? ; B, D
Heterorthis alternata (J. de C. Sowerby)	10 c ; B
Kjaerina sp.	10 c ; B
Kjerulfina polycyma Bancroft	10 c ; B, D
K. trigonalis Bancroft	10 b ; B, D
K. cf. *trigonalis* Bancroft	10 a ; D
Lingula sp.	10 a ; D
Lingula sp. (large)	10 a ; D
Nicolella cf. *actoniae* (J. de C. Sowerby)	10 a, b, c ; D
Onniella reuschi Bancroft	10 c ; B, D
Plectorthis ? virgata Reed	10 a, b ; B
Reuschella aff. *bilobata* (J. de C. Sowerby)	10 c ; B, D
Schizocrania crassa (Salter *non* Hall)	10 a, b ; D
Strophomena grandis (J. de C. Sowerby)	10 a, b, c ; B, D
Cyrtolites nodosus (Salter)	10 b ; D
Sinuites sp.	10 c ; D
Tropidodiscus acutus (J. de C. Sowerby)	10 c ; D
Conularia (*s.l.*) sp.	10 b ; D
Hyolithes sp.	10 b ; D
Tentaculites cf. *scalaris* Schlotheim	10 a, b, c ; B, D, G
Ambonychia obliqua (J. de C. Sowerby)	10 b, c ; D
A. orbicularis (J. de C. Sowerby)	10 a, b, c ; D
Ctenodonta sp.	10 c ; D

Broeggerolithus transiens (Bancroft)	10 a, b, c ; B, D, G
B. cf. *transiens* (Bancroft)	10 c ; B, D
Brongniartella bisculata (Salter)	10 a, b, c ; B, D
Chasmops sp.	10 a, b, c ; B, D
Encrinurus sp.	10 b ; D
Flexicalymene caractaci (Salter)	10 b, c ; B, D
F. trigonoceps Bancroft	10 a, b, c ; B, D
Flexicalymene sp.	10 a, b ; D
Lichas (*s.l.*) sp. indet.	10 b ; D
Otarion sp.	10 b ; D, G
Phacopidina apiculata (Salter)	10 a, b ? ; B, D
Primaspis caractaci (Salter)	10 c ; D, G ?
Proetus (*s.l.*) sp.	10 b ; G
Tetradella cf. *scripta* Harper	10 b, c ; D, G

Actonian Stage

Coenites ? sp.	11 ; B, E, J
Favosites fibrilla Smith	11 ; B, E, J
Lepidocoleus suecicus Moberg	11 ; B
Polyzoans (various)	11 ; B, E, G, J
Chonetoidea sp.	11 ; B, E, J
Cryptothyris paracyclica (Bancroft)	11 ; B, E, J
Dolerorthis sp.	11 ; B
Heterorthis alternata (J. de C. Sowerby)	11 ; B
Kjaerina sp.	11 ; B, J
Leptaena sp.	11 ; B, E, J
Lingula cf. *attenuata* (J. de C. Sowerby)	11 ; B
Lingula sp.	11 ; B
Nicolella actoniae (J. de C. Sowerby)	11 ; B, E, J
Onniella aspasia Bancroft	11 ; B, E
O. depressa Bancroft	11 ; B
O. grandis Bancroft	11 ; B, G, J
O. sinuata Bancroft	11 ; B
Orbiculoidea cf. *perrugata* (McCoy)	11 ; B, J
Platystrophia sp.	11 ; J
Rafinesquina sp.	11 ; B, E
Reuschella bilobata (J. de C. Sowerby)	11 ; E, J
R. semiglobata Bancroft	11 ; B, E ?, G
Sampo sp.	11 ; B, J
Sowerbyella aff. *sericea* (J. de C. Sowerby)	11 ; B, E, J
Strophomena grandis (J. de C. Sowerby)	11 ; E
Trematis punctata (J. de C. Sowerby)	11 ; B
Triplesia sp.	11 ; J
Archinacella cf. *oblongata* (Portlock)	11 ; B
cf. *Clathrospira trochiformis* (Portlock)	11 ; B
Cyrtolites nodosus (Salter)	11 ; B
Ecculiomphalus sp.	11 ; B
Holopea striatella (J. de C. Sowerby)	11 ; B, J
Sinuites bilobatus (J. de C. Sowerby)	11 ; B
S. pseudocompressus Reed	11 ; B
Tropidodiscus acutus (J. de Sowerby)	11 ; B
Metaconularia cf. *sowerbyi* (de Verneuil)	11 ; J
M. vesicularis (Slater)	11 ; B, E, J

Hyolithes sp.	11 ; B
" *Orthoceras* " sp.	11 ; B, G
Ctenodonta varicosa Salter	11 ; E, G
Modiolopsis cf. *modiolaris* (Conrad)	11 ; B, E
Orthonota cf. *subcylindrica* (McCoy)	11 ; B
Orthonota sp. (large)	11 ; E
cf. " *Pectunculus* " *ambiguus* Portlock	11 ; B
Pterinea sp.	11 ; B, E
Calyptaulax sp.	11 ; B, J
Chasmops sp.	11 ; B, E, J
Flexicalymene cf. *caractaci* (Salter)	11 ; E
F. laticeps Bancroft	11 ; B, E
F. salteri Bancroft	11 ; B ?, E
Gravicalymene sp.	11 ; E, J
Illaenus sp.	11 ; B, E, J
Lonchodomas pennatus (La Touche)	11 ; B, G
Platylichas laxatus (McCoy)	11 ; B, E, G, J
Primaspis caractaci (Salter)	11 ; B, E, J
Raphiophorus edgelli (Reed)	11 ; B
Remopleurides sp. nov.	11 ; B, E
Beyrichia ? sp.	11 ; E
Primitia sp.	11 ; B, E
Tetradella cf. *scripta* Harper	11 ; E
Diplograptus sp.	11 ; B
Orthograptus of *truncatus* Lapworth group	11 ; B

Onnian Stage

Chonetoidea sp.	12, 13, 14 ; B
Onniella broeggeri Bancroft	13 ; B
O. inconstans Bancroft	12 ; B
Onniella sp.	14 ; B
Orbiculoidea cf. *perrugata* (McCoy)	14 ; B
" *Rafinesquina* " *holli* (Davidson)	14 ; B
Sowerbyella sp.	12 ; B
Raphistomina ? sp.	14 ; B
Sinuites pseudocompressus Reed	12, 13 ; B
Sinuites sp.	14 ; B
Tropidodiscus acutus (J. de C. Sowerby)	12, 13 ; B
Metaconularia cf. *vesicularis* (Slater)	14 ; B
Ceratotheca ? cf. *subuncta* Reed	13 ; B
Colpomya sp.	12 ; B
Ctenodonta sp.	13 ; B
Orthodesma sp.	13 ; B
cf. " *Pullastra* " *speciosa* McCoy	13 ; B
Orthonota cf. *subcylindrica* (McCoy)	13 ; B
" *Cyrtoceras* " sp.	14 ; B
" *Orthoceras* " sp.	14 ; B
Eobronteus ? sp.	14 ; B
Flexicalymene onniensis Shirley	13, 14 ; B
F. aff. *onniensis* Shirley	12 ; B
Gravicalymene sp.	13 ; B
Illaenus sp.	12, 13, 14 ; B
Lonchodomas pennatus (La Touche)	12, 13, 14 ; B

Onnia cobboldi (Bancroft)	12 ; B
O. gracilis (Bancroft)	13 ; B
O. superba (Bancroft)	14 ; B
Platylichas laxatus (McCoy)	12 ; B
Pseudosphaerexochus sp. indet.	14 ; B
Raphiophorus edgelli (Reed)	12, 13, 14 ; B
Remopleurides burmeisteri Bancroft	13, 14 ; B
Triarthrus sp.	14 ; B
Climacograptus sp.	13 ; B
Orthograptus cf. *apiculatus* Elles & Wood	14 ; B

V. THE CARADOC/LLANDOVERY JUNCTION

The Caradoc and Llandovery strata of south Shropshire are separated by a profound stratigraphical break, the importance of which was not, at first, fully realized. Murchison claimed that the succession in the Onny Valley continued unbroken from the " Caradoc Sandstone " to the Wenlock Shales, and it was left to Salter & Aveline (1854 : 70) to demonstrate the angular break below the Purple Shales (called by them, *Pentamerus* Beds) at the now classic " Cliff Section " in the north bank of the River Onny, one mile south-west of Wistanstow ; this has been described in detail by Whittard (1927 : 749). At different points along the outcrop Llandovery beds rest on different horizons within the Caradoc Series, and in the present account it is convenient to list these from the north to the south of the Caradoc Area.

The succession employed by the Geological Survey for the Llandovery strata (Robertson *in* Pocock *et al.*, 1938 : 106) is as follows :

3. Hughley Shales
2. *Pentamerus* Beds
1. Kenley Grit

Beds 1 and 2 are only local names, and it may be an advantage in the present discussion to follow Whittard (1927 : 738) in adopting stratigraphical terms which are of more general application, such as :

c. Purple Shales
b. *Pentamerus* Beds
a. Arenaceous Beds

The most northerly point of the Caradoc/Llandovery junction is to be found to the south-east of Harnage Grange, about seven-and-a-half miles south-east of Shrewsbury. Here the Arenaceous Beds rest on Costonian strata, successively higher horizons being transgressed as Church Preen is approached, to the south-west of Kenley, where the Upper Longvillian is overlain. Near Plaish, and at Gretton near Cardington, it is unlikely that the Caradoc outcrop includes any horizon higher than the Actonian Stage.

The continuity of the Caradoc outcrop is broken by the Uriconian of Cardington Hill, to the south-south-east of which the *Pentamerus* Beds rest on strata low in the Caradoc sequence, though possibly no lower than Harnagian. The actual contact is obscured by Drift. Farther south-westwards, about two-fifths of a mile east-north-east of Hollies Farm, the highest Caradoc strata are flaggy Marshbrookian siltstones with abundant *Dalmanella unguis* and *Broeggerolithus transiens.* In Ticklerton Brook, and probably also at Hatton, one mile farther south-west, *Pentamerus* Beds overlie mudstones of Actonian age.

As stated earlier, the highest Caradoc beds seen in the Acton Scott District are the Acton Scott Beds (*s. s.*), probably equivalent to the middle part of the Actonian. There is, however, some distance between their outcrop and the conjectured base of the *Pentamerus* Beds; the possibility that a small outcrop of Onnian exists immediately south-east of Acton Scott cannot be ignored, and some support is derived from Salter & Aveline's record of " *Trinucleus* Shales " (? Onnian) at Henley, one mile to the south-south-west. These are not now exposed, and the solid geology here is much obscured by extensive Drift deposits.

Tracing the lower limit of the Llandovery south-westwards, at the River Onny the Purple Shales have overlapped the *Pentamerus* Beds to lie unconformably on the *Onnia superba* Zone of the Onnian. South-west from the Onny the Purple Shales transgress successively lower Caradoc horizons but, as has been shown by Whittard (1927, pl. 57), they are in turn quickly overstepped by the Wenlock Shales. Near Sibdon Carwood these rest on strata of Longvillian age.

Professor Whittard informs me that a boring made in search of water at Aston-on-Clun some years ago proved the presence there of Wenlock Shales. These are not exposed at the surface, but are presumed to overstep the Costonian near the village and rest on Pre-Cambrian rocks (Western Longmyndian). The inlier of Costonian rocks at Coston is bounded on the west by the Church Stretton Fault, and on the east by, presumably, unconformable Wenlock Shales, though these are covered by alluvium of the Clun Valley.

VI. CORRELATION OF THE SHELLY AND GRAPTOLITIC FAUNAS

A great deal of attention has been paid to the problem of fitting the shelly succession of the Caradoc Series into the graptolite-zones, but no attempt has yet proved entirely successful or satisfactory. The graptolite-zones were established in the Lower Hartfell Shales of southern Scotland as follows:

Pleurograptus linearis
Dicranograptus clingani
Climacograptus wilsoni
Climacograptus peltifer
Nemagraptus gracilis

More recently it has been shown by Jaanusson & Strachan (1953 : 695) that the same succession cannot be used satisfactorily for both Scotland and Wales, and that the *C. peltifer* and *C. wilsoni* Zones of the Southern Uplands are replaced by a single Zone of *Diplograptus multidens* in the Welsh area. The succession of graptolite-zones which must be applied to the Caradoc Area is then:

Pleurograptus linearis
Dicranograptus clingani
Diplograptus multidens
Nemagraptus gracilis

The presence of the *N. gracilis* Zone was recognized some years ago when Stubblefield found the zonal graptolite in strata, loosely termed Hoar Edge Grits, which may be referred to the Costonian (1930 : 87). In view of the small thickness of these beds the presence of the whole of the *N. gracilis* Zone is improbable, and the Costonian, even in the thickest development at Coston, may represent only part of the Zone.

One of the fundamental differences in correlation between past works and the present paper lies in the interpretation of the vertical extent of the *D. multidens* Zone. In the Shrewsbury District Memoir (Pocock *et al.*, 1938 : 82) the whole of the Caradoc Series from the base of the Harnage Shales up to, and including, the Cheney Longville Flags was assigned to the *D. clingani* Zone. This correlation made necessary the acceptance of a large stratigraphical break between the Hoar Edge Grits and the Harnage Shales, and the missing *D. multidens* Zone was thought to be represented by Lapworth's so-called " Transition Bed ". In view of the evidence put forward earlier in this paper against the existence of a large break at the base of the Harnage Shales, it is essential to re-examine the foundations upon which the Geological Survey's argument rests.

The graptolite-species recorded from the Harnage Shales of the Evenwood District (Pocock *et al.*, 1938 : 250) are listed below, together with their vertical range according to Elles & Wood (1913 : 516–525) :

	N. gracilis Zone	*D. multidens* Zone	*D. clingani* Zone	*P. linearis* Zone
Climacograptus cf. *brevis* Elles & Wood	×	×	—	—
C. caudatus Lapworth	—	—	$\times^{c}$	—
C. minimus Carruthers	—	—	×	×
Dendrograptus sp.	—	—	—	—
Dictyonema cf. *fluitans* Bulman	—	×	—	—
Diplograptus multidens Elles & Wood var. *compactus* Elles & Wood	—	×	$\times^{r}$	—
Orthograptus calcaratus (Lapworth) var. *vulgatus* Elles & Wood	—	$\times^{c}$	×	—
O. truncatus Lapworth	—	—	$\times^{c}$	×
O. truncatus var. *intermedius* Elles & Wood	—	$\times^{c}$	×	—
O. truncatus var. *pauperatus* Elles & Wood	—	×	×	×

It can thus be seen that, rather than proving conclusively the *D. clingani* Zone age of the beds, the assemblage suggests at least the possibility of their belonging to the *D. multidens* Zone. According to Stubblefield (*in* Pocock *et al.*, 1938 : 87) the three species which enabled both the Harnage and Chatwall Groups to be referred to the *D. clingani* Zone were *C. minimus*, *O. truncatus* and *O. truncatus* var. *intermedius*. Recorded occurrences of *Climacograptus minimus* suggest this species is more characteristic of the *D. clingani* Zone but, on the other hand, *Orthograptus truncatus* var. *intermedius* is common only in the *D. multidens* Zone. *O. truncatus* itself has often been regarded as characteristic of the *D. clingani* Zone, but nowadays it is known to range from the *D. multidens* Zone upwards into the Ashgillian, with consequent reduction in its value as a zonal index. A factor strongly in support of the *D. multidens* Zone age of the Harnage Shales is that both *O. truncatus* and *O. truncatus intermedius* are found with *D. multidens* and other characteristic forms in the Caradoc mudstones and shales of the Pontesford outcrop, only a few miles west of the Harnage Grange District (Pocock *et al.*, 1938 : 91–92).

Of the other graptolites from the Harnage Shales, *Climacograptus brevis* is confined to the *N. gracilis* and *D. multidens* Zones, and the *Dictyonema* is close to *D. fluitans* from the Aldress Shales of west Shropshire, now known to belong to the *D. multidens* Zone (Whittard, 1955 : 5).

The available evidence for the age of the Harnage Shales thus tends towards assigning them to the *D. multidens*, and not to the *D. clingani*, Zone. Confirmation of this came when Bulman (1948 : 227) discovered *D. multidens* itself in the Harnage Shales of Coundmoor Brook, the type-locality of the Harnagian Stage. The exact place from which the species was collected is unknown but, as the upper beds of the Harnagian are faulted-out at Coundmoor Brook, it may reasonably be assumed that the specimen came from the *Reuscholithus reuschi* Zone. No graptolitic evidence is yet available from the topmost beds of the Hoar Edge Grits, which have yielded *Salterolithus* ; whether the junction between the *N. gracilis* and *D. multidens* Zones should be placed at the extreme base of the Harnagian as now defined (see p. 11) or slightly higher is not clear but, as the thickness of strata concerned is small, the possible error involved is correspondingly slight.

The base of the *D. multidens* Zone having been more or less satisfactorily established, there remains the problem of defining the upper limit of the zone. Apart from the Harnage Shales of the Harnage District, none of the horizons within the Caradoc Series of the type-area has yielded an abundant graptolitic fauna. A few specimens from the Glenburrell Beds of the Onny Valley have been identified by Dr. Isles Strachan as *Climacograptus antiquus* Hall var., and are considered by him to indicate an age earlier than the *D. clingani* Zone. The Caradoc shales of the Pontesford District (Pocock *et al.*, 1938 : 90) belong to the *D. multidens* Zone although they contain, in addition to the zonal graptolite, such forms as *Orthograptus truncatus* and *O. truncatus intermedius*, which were considered to indicate the *D. clingani* Zone when found in the Harnage Shales a few miles to the south-west. Re-examination of the trilobite assemblage at Pontesford shows that it includes the genera *Brongniartella*, *Salterolithus* and *Broeggerolithus*, indicating a Lower Soudleyan age, and the strata containing them can thus be correlated with the upper part of the Glenburrell Beds of the Onny Valley, an horizon which they also resemble lithologically.

Additional graptolitic material from the upper part of the Soudleyan in the Onny Valley has been identified by Dr. Strachan as *Orthograptus* cf. *apiculatus* Elles & Wood, and is probably indicative of a pre-*clingani* Zone age. The material is, however, scanty owing to the arenaceous lithology.

The *D. multidens* Zone therefore should apparently include at least the lower half of the Soudleyan and possibly the whole of that Stage. The massive sandstones of the Lower Longvillian Substage have not yet yielded any graptolites, and their inclusion in the *D. multidens* Zone is uncertain. For the present a provisional line of demarcation between the *D. multidens* and *D. clingani* Zones is drawn between the Soudleyan and Lower Longvillian, though a more convenient level might be at the base of the Upper Longvillian, as this would coincide with a known faunal break within the Caradoc Series in parts of the Caradoc Area. Further graptolitic material will probably enable the margin of error to be reduced considerably, but many difficulties are encountered when most of the strata involved are shallow-water sandstones.

The remaining problem concerns the zonal position of the upper beds of the Series, that is to say, the Actonian and Onnian Stages. The topmost Caradoc strata of the Onny Valley, presumably the *Onnia superba* Zone of the Onnian, were said by Wade (1911 : 445) to contain *Orthograptus truncatus* var. *socialis* Lapworth in abundance, and he accordingly assigned them to the Ashgillian. Bancroft (1933) equated the Actonian with the *Pleurograptus linearis* Zone ; no reasons for this were given, but he may have been influenced by Wade's view that at least part of the Onnian belonged to the Ashgillian. Whittard (1952 : 162) has drawn attention to the conflicting statements made by Bancroft at various times regarding the correlation of the shelly and graptolitic faunas ; these may be summarized as follows. The upper Stages of the series Costonian to Onnian include the *P. linearis* Zone and part or all of the succeeding Zone of *Dicellograptus complanatus*, the basal zone of the Ashgillian in its usually accepted sense (Bancroft, 1945 : 181). The Onnian was said to be succeeded in Westmorland by, first, the Pusgillian Stage, and then the Ashgillian, the latter apparently being used in a restricted sense, though few details were given. In the same paper Bancroft (p. 183) described the Actonian as including "the earliest deposits with *Tretaspis kjaeri*, *Phillipsinella* and other typical Upper Bala fossils", but on a later page (p. 186) caused considerable confusion by claiming that, at Girvan, "the Actonian and Onnian are represented in the series of grey flags with fossiliferous limestones underlying the Zone of *Dicellograptus complanatus* (Pusgillian)". It is thus difficult to see exactly what were Bancroft's views, but his work shows a definite tendency to include in the Ashgillian the Pusgillian Stage and, perhaps also, the Onnian.

During extensive collecting from the upper strata of the Onny Valley Wade's claim that they contain *Orthograptus truncatus* var. *socialis* in abundance has not been substantiated ; indeed, well-preserved graptolites are exceedingly rare in both the Actonian and Onnian. In view of this the shelly faunas, in particular the trilobites, afford the most promising means of assessing the position of the highest Caradoc beds. The assemblage in the Actonian includes *Platylichas*, *Chasmops*, calymenids and raphiophorids, and closely resembles that of the 4bδ Étage, or Upper *Chasmops* Limestone, in southern Norway, an horizon known to belong to the *D. clingani* Zone. As described earlier in this paper, the Onnian follows the Actonian conformably and the faunas of the lower portion include some Actonian elements, so that it would be difficult to claim a much later age for the Onnian. Supporting data comes from the trilobite fauna, including *Triarthrus* and raphiophorids, which resembles one described by Thorslund (1940) from the *D. clingani*

Zone of southern Sweden. A few fairly well-preserved graptolites have been obtained from the Actonian of the Onny, which Dr. Strachan has identified as *Orthograptus* of the *truncatus* group, and *Diplograptus* (*s. s.*) sp. He considers that the last-named cannot be later than the *D. clingani* Zone, and in view of the evidence of the shelly faunas outlined above, the youngest strata of the Caradoc Series in the type-section are concluded to be no later than the *D. clingani* Zone. There is no acceptable evidence for the existence of the *Pleurograptus linearis* or *Dicellograptus complanatus* Zones in the Ordovician of south Shropshire.

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EXPLANATION OF PLATES

All specimens in the British Museum (Natural History) except Pl. 26, fig. 5, which is in the Geological Survey and Museum (GSM.).

Photographs by J. V. Brown and C. Horton

PLATE 24

Harknessella vespertilio (J. de C. Sowerby)

Costonian Stage: CostonFarm, east of Clunbury.

FIG. 1. Internal mould of dorsal valve. BB.24051. × 1¼.

Dinorthis flabellulum (J. de C. Sowerby)

Costonian Stage: Coston Farm, east of Clunbury.

FIG. 2. Internal mould of dorsal valve. BB.24049. × 1.

Horderleyella plicata Bancroft

Costonian Stage: disused quarry 500 ft. south of Coston Farm.

FIG. 3. Internal mould of ventral valve. BB.10343. × 1½.
FIG. 4. Internal mould of dorsal valve. BB.10344. × 1½.

Smeathenella harnagensis Bancroft

Harnagian Stage: southern end of Smeathen Wood, near Horderley.

FIG. 5. Internal mould of ventral valve. BB.9149. × 1.
FIG. 6. Internal mould of dorsal valve. BB.9281. × 1.

Salopia salteri (Davidson)

Harnagian Stage: southern end of Smeathen Wood, near Horderley.

FIG. 7. Internal mould of dorsal valve. BB.24277. × 1½.
FIG. 8. Internal mould of ventral valve. BB.24278. × 1½.

Soudleyella avelinei (Bancroft)

Soudleyan Stage: north-eastern corner of Smeathen Wood, near Horderley.

FIG. 9. Internal mould of dorsal valve. BB.10326. × 2.

Reuschella horderleyensis Bancroft

Soudleyan Stage: near Glenburrell Farm, south-east of Horderley.

FIG. 10. Internal mould of dorsal valve. BB.9129. × 1.
FIG. 11. Internal mould of ventral valve. BB.9134. × 1.

Dalmanella horderleyensis (Whittington)

Lower Longvillian substage: Long Lane quarry, north-west of Craven Arms.

FIG. 12. Internal mould of ventral valve. BB.10316. × 1½.
FIG. 13. Internal mould of dorsal valve. BB.10315. × 1½.

Dalmanella indica Whittington

Lower Longvillian substage: Longville Plantation, near Cheney Longville.

FIG. 14. Internal mould of dorsal valve. BB.10325. × 1½.

Dalmanella lepta (Bancroft)

Lower Longvillian substage: Rookery Wood, near Horderley.

FIG. 15. Internal mould of dorsal valve. BB.10318. × 1½.
FIG. 16. Internal mould of ventral valve. BB.10319. × 1½

Bancroftina typa (Whittington)

Lower Longvillian substage: New House quarry, south-east of Horderley.

FIG. 17. Internal mould of ventral valve. BB.10304. × 1½.
FIG. 18. Internal mould of dorsal valve. BB.10309. × 1½.

Kjaerina bipartita (Salter)

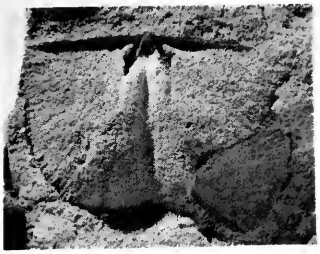
Upper Longvillian substage: Longville Lane, west of Cheney Longville.

FIG. 19. Internal mould of ventral valve. BB.10453. × 1.

Kjaerina typa Bancroft

Upper Longvillian substage: eastern end of Burrells Coppice, south-east of Horderley.

FIG. 20. Internal mould of ventral valve. BB.14383. × 1.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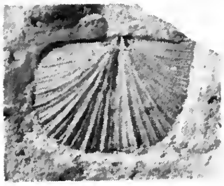
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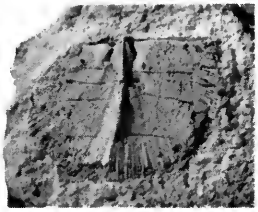
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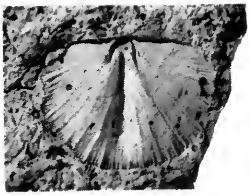
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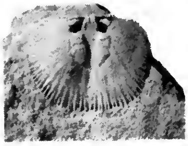
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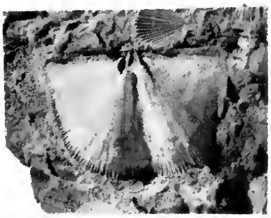
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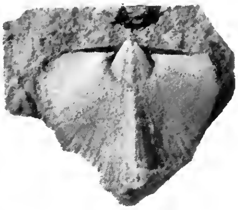
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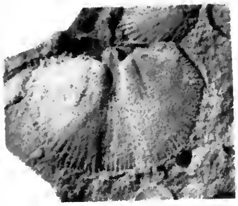
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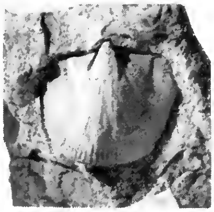
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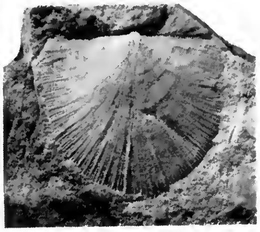
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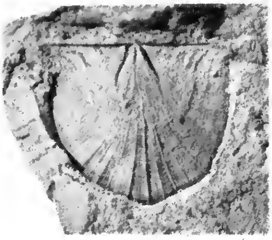
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ZONAL BRACHIOPODS OF THE CARADOC SERIES

PLATE 25

Dolerorthis duftonensis (Reed)

Upper Longvillian substage: eastern end of Burrells Coppice, south-east of Horderley.

FIG. 1. Internal mould of dorsal valve. BB.24050. × 1¼.

Dalmanella wattsi (Bancroft)

Marshbrookian Stage: Marsh Wood quarry, south of Marshbrook.

FIG. 2. Internal moulds of ventral valves. BB.9127. × 1.
FIG. 3. Internal mould of dorsal valve and external mould of ventral valve. BB.10341. × 1¼.

Dalmanella unguis (J. de C. Sowerby)

Marshbrookian Stage: Marsh Wood quarry, south of Marshbrook.

FIG. 4. Gutta-percha cast from external mould of ventral and dorsal valves. BB.10337. × 1¼.

Onniella reuschi Bancroft

Marshbrookian Stage: Woolston, north of Wistanstow.

FIG. 5. Internal mould of dorsal valve. BB.10233. × 1½.
FIG. 6. External mould of dorsal valve. BB.10256. × 1½.

Cryptothyris paracyclica (Bancroft)

Actonian Stage: south bank of River Onny, north of Cheney Longville.

FIG. 7. Internal mould of dorsal valve. BB.24172. × 2.

Onniella inconstans Bancroft

Onnian Stage: north bank of River Onny, south-west of Wistanstow.

FIG. 8. Dorsal aspect. BB.10258. × 1¾.
FIG. 9. Ventral aspect. Same specimen as Fig. 8. × 1¾.

Onniella broeggeri Bancroft

Onnian Stage: north bank of River Onny, south-west of Wistanstow.

FIG. 10. Dorsal aspect. BB.24052. × 2½.
FIG. 11. Ventral aspect. Same specimen as Fig. 10. × 2½.

" *Rafinesquina* " *holli* (Davidson)

Onnian Stage: " Cliff Section " in north bank of River Onny, south-west of Wistanstow.

FIG. 12. Various isolated valves. B.13641. × 3.


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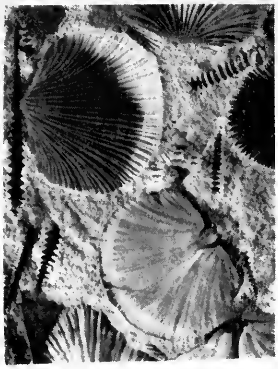
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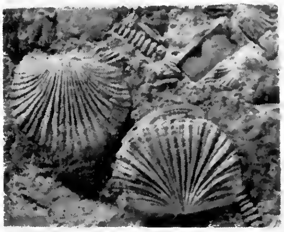
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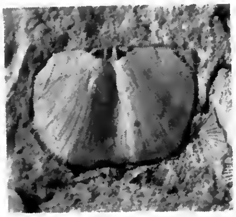
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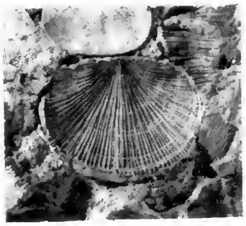
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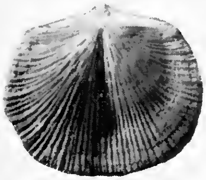
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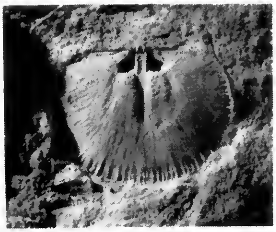
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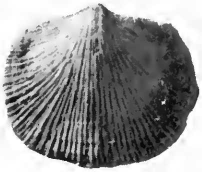
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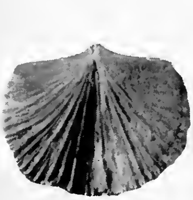
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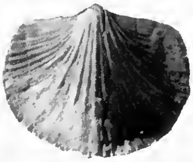
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ZONAL BRACHIOPODS OF THE CARADOC SERIES.

PLATE 26

Costonia ultima (Bancroft)

Costonian Stage: disused quarry 500 ft. south of Coston Farm.

Fig. 1. Latex cast from external mould of incomplete cranidium. In.48942. × 2.
Fig. 2. Latex cast from external mould of incomplete cranidium. In.48941. × 2.

Reuscholithus reuschi Bancroft

Harnagian Stage: southern end of Smeathen Wood, near Horderley.

Fig. 3. Internal mould. In.42080. × 1½.

Salterolithus smeathenensis Bancroft

Harnagian Stage: southern end of Smeathen Wood, near Horderley.

Fig. 4. Internal mould. In.49560. × 1½.

Salterolithus caractaci (Murchison)

Harnagian Stage: Welshpool, Montgomeryshire.

Fig. 5. Internal mould. GSM.6829. × 1.

Ulricholithus ulrichi (Bancroft)

Harnagian Stage: Middle House Dingle, near Welshpool, Montgomeryshire.

Fig. 6. Gutt-percha cast from external mould. In.42371. × 1¾.

Broeggerolithus broeggeri (Bancroft)

Soudleyan Stage: north-eastern corner of Smeathen Wood, near Horderley.

Fig. 7. Internal mould. In.42077. × 2.

Broeggerolithus soudleyensis (Bancroft)

Soudleyan Stage: Soudley Pool quarry, south-east of Hope Bowdler.

Fig. 8. Internal mould. In.49314. × 2.

Broeggerolithus globiceps (Bancroft)

Lower Longvillian substage: Rookery Wood, near Horderley.

Fig. 9. Internal mould. In.42076. × 2.

Broeggerolithus longiceps (Bancroft)

Upper Longvillian substage: south-west of Marshbrook.

Fig. 10. Internal mould. In.42073. × 1½.

Broeggerolithus transiens (Bancroft)

Marshbrookian Stage: Marsh Wood quarry, south of Marshbrook.

Fig. 11. Internal mould. In.49026. × 1¼.

Platylichas laxatus (McCoy)

Actonian Stage: south bank of River Onny, north of Cheney Longville.

Fig. 12. Test intact. In 46445. × 1.

Actonian Stage: Gretton quarry, east of Cardington.

Fig. 13. Latex cast from external mould. In.49558. × 1.

Onnia cobboldi (Bancroft)

Onnian Stage: south bank of River Onny, north-north-east of Cheney Longville.

Fig. 14. Testate specimen. In.42071. × 1½.

Onnia gracilis (Bancroft)

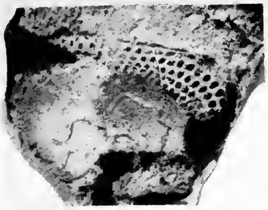
Onnian Stage: north bank of River Onny, north-east of Cheney Longville.

Fig. 15. Testate specimen. In.42074. × 2.

Onnia superba (Bancroft)

Onnian Stage: "Cliff Section", in north bank of River Onny, south-west of Wistanstow.

Fig. 16. Internal mould. In.49031. × 1½.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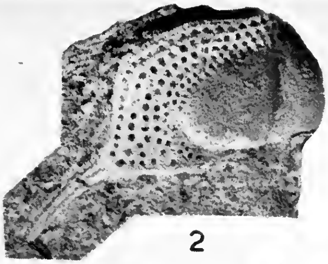
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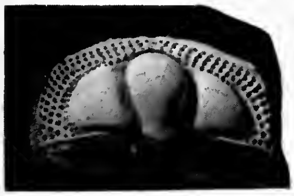
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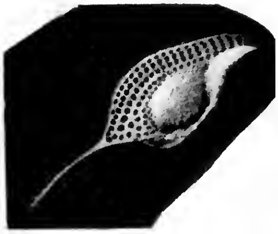
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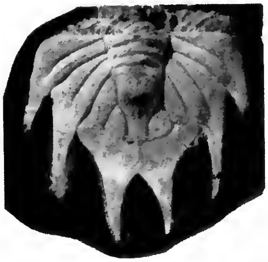
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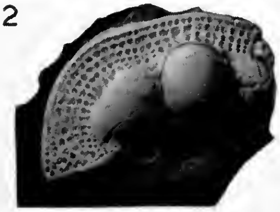
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ZONAL TRILOBITES OF THE CARADOC SERIES.

A NEW LABYRINTHODONT (*PARACYCLOTOSAURUS*) FROM THE UPPER TRIAS OF NEW SOUTH WALES

D. M. S. WATSON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 3 No. 7
LONDON: 1958

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A NEW LABYRINTHODONT (*PARACYCLOTOSAURUS*) FROM THE UPPER TRIAS OF NEW SOUTH WALES

BY

DAVID MEREDITH SEARES WATSON, F.R.S.
Trustee of the British Museum

Pp. 233–263 ; *Pls.* 27–31 ; 16 *Text-figures*

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A NEW LABYRINTHODONT (*PARACYCLOTOSAURUS*) FROM THE UPPER TRIAS OF NEW SOUTH WALES

By D. M. S. WATSON

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I INTRODUCTION

THE Namurian rocks of New South Wales containing characteristic plants found also in Scotland, are succeeded by a great series of beds with a total thickness of 14,000 feet. The upper part—some 3,500 feet of this—forms the Hawkesbury Series, whose lowest element, the Narrabeen Beds, may perhaps be held to include the fish fauna from Gosford, described by Woodward (1890) and revised by Wade (1940). In the middle of the succeeding Hawkesbury Sandstone is the very rich fish fauna of Brookvale, described by Wade (1935), and that of the Wianamatta shales (which rest on the Hawkesbury Sandstone) of St. Peter's near Sydney, described by Woodward (1908) and revised by Wade (1941). The St. Peter's fish occur in shales, and the ironstone nodules in them, worked in a series of brick pits near Sydney. They were collected by Mr. B. Dunstan of the Geological Survey of New South Wales.

In one of these pits, about 1910, Mr. Dunstan found fragments of an enormous ironstone nodule which by most careful search he was able to reconstruct completely. The nodule contained a complete labyrinthodont skeleton which I saw in July 1914. It was immediately obvious that the animal was closely related to *Cyclotosaurus*, then known only by specimens from the lower part of the Upper Trias of Germany. This gave a well fixed correlation for at least one point in the Hawkesbury Series, the only one, indeed, in the whole succession of rocks set out above. It was therefore desirable that the position of "*Cyclotosaurus*" as a descendant of "*Capitosaurus*" should be established, and the time range through which it lived should be determined. This I undertook to do, and Sir Edgeworth David, after whom the species is named, arranged for the British Museum (Natural History) to acquire the specimen.

MATERIAL. The nodule (B.M.N.H. R.6000), some 9 feet (2·75 metres) long, is split roughly into dorsal and ventral halves, each composed of more than fifty blocks, some of which weigh nearly a hundredweight. The matrix is an extremely hard and brittle ironstone, quite impossible to work. As the bone was largely rotten, and much of it already lost, Mr. F. O. Barlow of the Museum staff removed all the remains of bone, even from the deepest fissures in the blocks. Many of the blocks are very heavy and irregular in shape, and it was impossible to place them together, run in a flexible casting medium, and so draw out complete casts of individual bones. In practice the cavities in a block and its counterpart had to be cast separately in glue. From the glue impression a waste mould was prepared from which, in turn, a plaster positive was made. This was then trimmed until it fitted accurately the cast of the same bone similarly prepared from the counterpart. The two parts were then fitted together and cast in a jelly mould which yielded perfect replicas that for all practical purposes are as good as the original bones. Details of the braincase, however, can only be determined by supplementing them with flexible plastic casts. Barlow's work covered many years, and I do not know of any other man who could have done it; it was a technical triumph.

The articulated skeleton is complete, but the skull and lower jaws are distorted in a remarkable way. The mode of attachment of the head to the vertebral column is very difficult to determine, and some bones were broken and misplaced, evidently before burial. The fractures all lie in the same region, that of the hinder part of the head, lower jaws, and interclavicle. The skull, seen from above, is asymmetrical, the orbits evidently misplaced to the right. In direct dorsal view the lateral border of the right orbit lies 7 cm. from the margin of the skull at the front of the squamosal, the corresponding measurement on the left side being 11·5 cm. On the right side the outer surface is smoothly rounded from the mid-line at the parieto-dermosupraoccipital suture to the lower border of the quadratojugal. On the left the surface is concave and broken by a crack which has a displacement of a centimetre. This distortion extends forward to the anterior end, but scarcely affects the triangle of bone between the pineal foramen and the occipital border. On the palate the parasphenoid is broken at the ends of the sphenethmoid, the right pterygoid is crossed obliquely by a crack running backward from the hinder end of the right palatal vacuity, and the two occipital condyles are forced into contact. The left lower jaw seems to be undistorted, but the right is crushed down just in front of the opening through which the temporal muscles passed into it, so that its depth was decreased, its width increased, and the jaw as a whole bent upward and inward. These distortions agree with those of the palate. The interclavicle is crossed obliquely by a crack, matching those on the palate and skull roof, which posteriorly, on the left side, has a displacement of nearly one centimetre.

These breaks, and the displacements which result from them, lie almost entirely in the region behind the eyes, and can only reasonably be interpreted as the results of a single heavy blow, for it broke three horizontal sheets of bone—the skull roof, palate and interclavicle—each almost two centimetres thick. All these bones were surrounded and widely separated by soft tissues. Furthermore it appears from the results that such a blow must have been delivered by a massive cylindrical body, such as a tree trunk from the bank, falling across the animal; the body afterwards being washed into the bottom of the lake.

II. SYSTEMATIC DESCRIPTION OF *PARACYCLOTOSAURUS DAVIDI* gen. et sp. nov.

Braincase. The braincase is almost completely underlain by the hinder part of the parasphenoid, which except for a short border between the exoccipitals, has continuous sutural attachments to them and to the pterygoids, the details being obscure. The ventral surface of the parasphenoid posteriorly bears a very low transverse ridge, behind which its surface is depressed, a condition associated with the attachment of recti capitis muscles. The greater part of its area is, however, shallowly concave, continuous with that of the pterygoid attached to it, whose surface turns down laterally. The whole directly supported the skin of the roof of the mouth. At the hinder margin of the palatal vacuity, where the pterygo-parasphenoid suture ends, the bone narrows, the narrowest point of the " processus cultriformis ", some 10 cm. in front, being only 19 mm. wide, with a cylindroid surface and a shallow groove—presumably occupied in life by a cartilaginous septum—on its upper surface. It then continues forward, widening and having a flat lower surface, until it is overlapped by the vomers, and ends by rising up above the junction of these bones.

Each exoccipital bears a large hemispheroidal condyle covered by cartilage during life to an extent shown by a projecting ridge, which marks the end of the dense bony sheet that coated its outer surface. Viewed as a pair it is evident that the condyles allowed dorso-ventral motion of the head, perhaps through a large arc, and inhibited any horizontal movement. The lateral surface of the condyle passes forward and outward to a suture with the pterygoid, forming a thick rounded flange, the floor of the tympanic cavity. Above the inner part of the condyle a thin flange passes horizontally inward above the space occupied by the persistently cartilaginous basioccipital. Its upper surface forms the floor of the brain cavity and laterally curves upwards and then slightly inwards to form the side walls of the brain cavity. A foramen in the lateral grove leads into a canal passing through the bone, which opens on the posterior surface of the exoccipital just above the condyle. It transmitted a XIIth nerve. Damage obscures the exit of the vagus. The upper part of the exoccipital is continuous with the descending process of the dermosupraoccipital and of the tabular. These are massive bones separated by a triangular post-temporal vacuity.

It is natural to suppose that, as in all earlier capitosaurs, there should be an abruptly truncated projecting process, mesial to the junction of the dermosupraoccipital and exoccipital, which supported a cartilaginous supraoccipital. On the left side the surface of the two bones is perfectly shown and there is no trace of the process, but the sculpturing seems to show that the surface abutted on to a supraoccipital cartilage. Dorsally there remains a space on the under surface of the dermosupraoccipitals, partially subdivided into three by low ridges, which was clearly open and perhaps occupied by blood vessels above a supraoccipital. This unusual arrangement seems to be well established here.

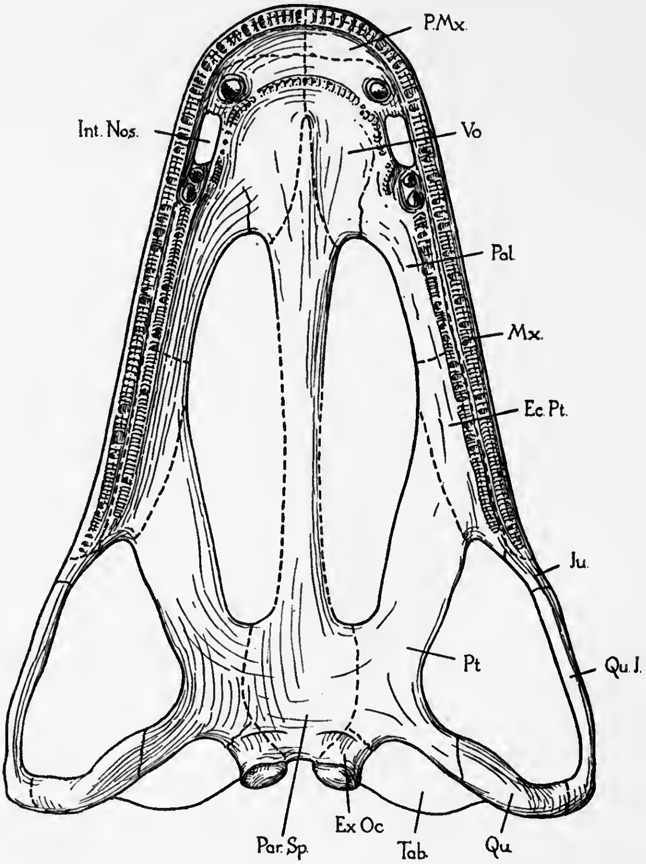

FIG. 1. *Paracyclotosaurus davidi* gen. et sp. nov. The palate. × 1/6. (For explanation of lettering see p. 263.)

The position of the supraoccipital and paroccipital can only be inferred as there is no trace of ossification in them. A small shapeless ossification, high up in the proötic, is attached to the summit of the pre-tympanic flange of the left pterygoid. On its inner side, at the hinder edge, is a narrow groove forming a quadrant of a circle. Presumably it housed the anterior vertical semicircular canal.

Fortunately the stapes is in position on the right side, giving some indication of the relations between the proötic, paroccipital and exoccipital. The cartilaginous paroccipital must have been a small mass, meeting the proötic above the fenestra, lying in contact above with the exoccipital, and separated from it below by the vagus. Primitively the paroccipital reached the occipital process of the tabular. In the present specimen that process passes downward and inward as a thick sheet of bone, which meets and fuses with the corresponding process of the dermosupraoccipital and the exoccipital, the sutures being invisible.

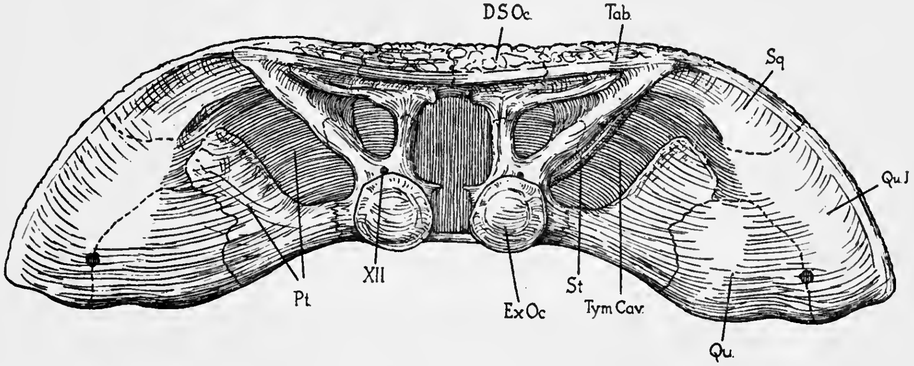

FIG. 2. *Paracyclotosaurus davidi*. The occiput. × 1/4.

The basisphenoid is entirely unossified. The impression of its lower surface on the parasphenoid, however, is easily interpreted by comparison with *Eryops*, and with a remarkable specimen of *Rhinesuchus* (B.118, D. M. S. W. Coll.). The key feature is the deep groove running transversely, housing a thickening of the lateral part of the basisphenoid, which extends into a pit excavated mainly in the mesial border of the pterygoid, and is roofed by the foot of the epipterygoid; this is the basipterygoid process. The groove is supported behind by a deep flange which extends outward, increasing in depth as it does so, to end on the border of the fenestra ovalis, where the accessory process of the stapes is attached to it.

In front of the proötic the floor and side walls of the braincase are entirely unossified, but the epipterygoids which lie immediately lateral to it (and are in part modelled on the Gasserian ganglion) are well preserved. They are described later, with the quadrate and pterygoid.

The anterior part of the brain was set within a massive bony sphenethmoid. This is a single structure, lying in the grooved upper surface of the processus cultriformis of the parasphenoid, and reaching the dermal roof of the skull between, and in front of, the eyes. It has the following measurements: length about 11 cm., depth (including the parasphenoid) posteriorly 6·5 cm., and anteriorly 7·5 cm., maximum width at the upper edge 3·6 cm. posteriorly and 5·3 cm. anteriorly (all figures being approximations). The brain cavity within, measured on a natural cast, is posteriorly 2·6 cm. deep and 2·0 cm. wide. This cavity was divided into two independent canals (for olfactory lobes?) 7·0 cm. in front of the hinder end. There is no trace of any further ossification of the braincase, and no evidence about the olfactory capsules.

The ossifications in the palatoquadrate cartilage are well shown, and as they are attached to the braincase through the intermediary of the pterygoid, it is convenient to begin by describing this bone. The pterygoid is attached by a long suture to the lateral border of the parasphenoid and the front of the exoccipital. The attachment is by interlocking surfaces about 2·5 cm. thick, and about 15 cm. long. From the attachment the bone stretches outward, turning downward as it does so, the palate between the subtemporal fossae being concave and cylindrical. The palatal ramus turns forwards and outward to meet the narrow strip of palate lateral to the palatal vacuity, the suture being unseen. The quadrate ramus, which is well shown (Text-figs. 3, 4), is essentially a sheet of bone that rises abruptly from the flat lower part attached by suture to the parasphenoid. It has a rounded edge admesially, which rises immediately above the deep ridge on the parasphenoid limiting the basipterygoid process behind, to extend upward and end some distance below the skull roof. The proötic is attached to this edge. From this mesial border the paraotic flange of the pterygoid rising to the skull roof, passes outward swinging round a conical surface until it sweeps backward and outward to pass to the quadrate. There it ends, the two bones meeting in a thick abutment, rather than in a deep overlap. On its hinder surface (Text-fig. 2) the quadrate ramus of the pterygoid is divided into two areas; the mesial (the anterior wall of the tympanic cavity) is a hollow cone, truncated below where the pterygoid and exoccipital meet, rising until it reaches the anterior border of the hole in the skull roof which housed the tympanic membrane. Laterally the pterygoid forms a triangular area that is attached to, but rises above, the quadrate. The summit of this area is sculptured for some other attachment, presumably that of a lateral wall of the tympanic chamber.

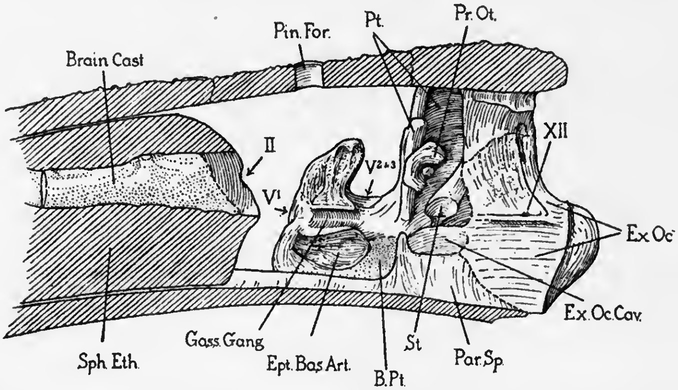

FIG. 3. *Paracyclotosaurus davidi.* Reconstruction of longitudinal section through the braincase along the middle line. × 1/3. The "brain" in the sphenethmoid is a drawing of a natural cast of the cavity.

There are two ossifications in the palatoquadrate cartilage, which apparently persisted between them. The posterior, the quadrate, is a massive bone whose very wide lower surface is entirely occupied by the condyle for the articulation of the lower jaw. Above this the bone rises as a solid sheet (22 mm. thick above the thickened articular lower part) surrounded by the pterygoid, squamosal and quadratojugal, which together hold it in place. The attachment to the pterygoid is almost edge to edge, rather than the extensive overlap usual in labyrinthodonts. Ventrally, just above and mesial to the condylar surface, the quadrate ends in a narrow surface from which a cartilaginous strip 5 mm. thick extended forward, lying in a groove in the pterygoid, until it met an abrupt face on the hinder and lower border of the epipterygoid.

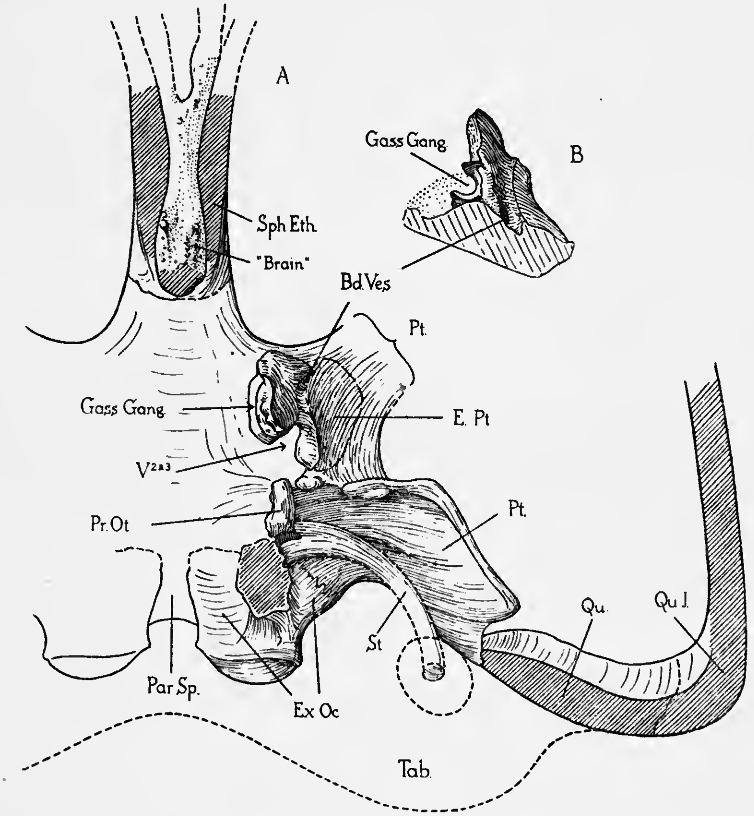

FIG. 4. *Paracyclotosaurus davidi*. A, the braincase and the parts in relation to it seen from above, with the dermal skull roof removed, and the right quadrate and quadratojugal cut at a lower level. B, the left epipterygoid viewed directly from in front. The drawing represents an actual glue cast from the original cavity. × 1/3.

The epipterygoid is well ossified, and elaborate (Text-figs. 3, 4). Its base rests on the upper surface of the pterygoid, where that bone passes forward and outward behind the palatal vacuity, and was continued by cartilage back to the quadrate, and perhaps a little forward and outward. On the inner surface the bone has a projecting boss abruptly truncated where it was attached to the side of the cartilaginous basis cranii. Above this level the inner surface of the bone is crossed horizontally by a deep groove, bounded above and below by shallow but projecting flanges. In this the Gasserian ganglion lay, the ophthalmic branch of that nerve passing outward and forward in front, and the maxillary and mandibular branches outward and upward over a rounded border above the pterygoid. Above this groove the bone extends upward until it ends, its admedian surface evidently embedded in a thick cartilaginous side wall of the braincase (between the proötic and the sphenethmoid). On the outer surface the bone has a deep notch separating the attachment to the pterygoid from the lower end of a special admedian process extending downward and a little forward laterally to the basisphenoid cartilage, and

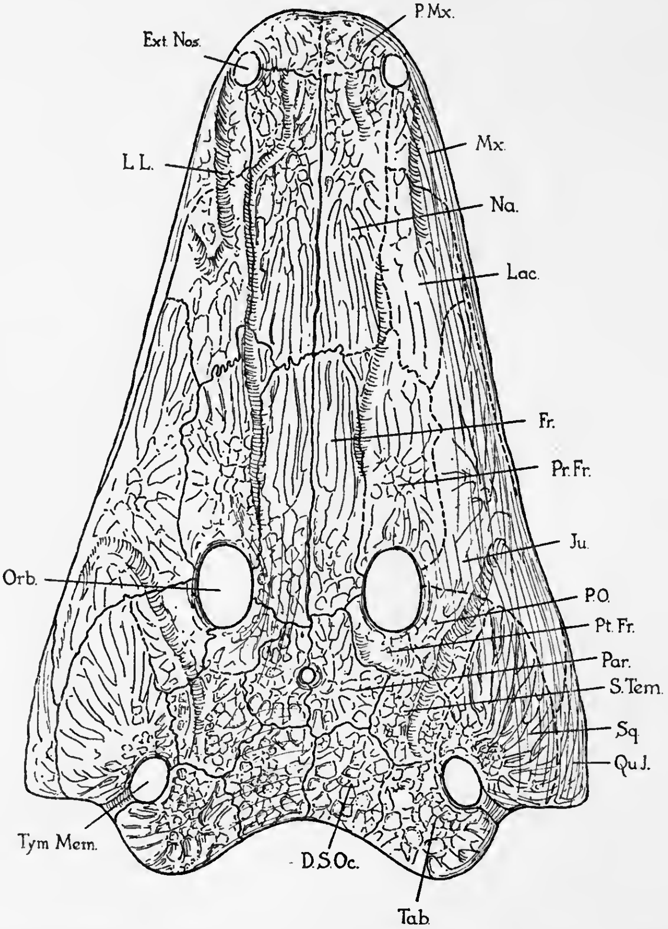

FIG. 5. *Paracyclotosaurus davidi.* The skull viewed from above, with its distortion corrected. × 1/6.

perhaps also to the parasphenoid. This notch must have been converted into a foramen by the parasphenoid or pterygoid, and no doubt transmitted a blood vessel.

The remainder of the skull consists of a series of membrane bones, attached to one another by interdigitating sutures which are not often seen. The whole outer surface is covered with bone except for orbits, nostrils, the pineal foramen, and the completely enclosed openings in which lay the tympanic membranes. The dermal bone coating the head is massive, about 2 cm. thick, and the individual bones of which it is composed were so tightly attached to one another by interlocking sutures that they withstood the blow from which the animal presumably died. In the cast actual sutures are seldom visible, but in most places the distribution of the pitted and grooved ornament determines their direction rather precisely. The general skull pattern differs very little from that found in other capitosaurs; the only striking peculiarity is the closure of the otic notch by a fusion behind it of the outer end of the tabular with a special shelf passing backward from the hinder border of the squamosal in front. The tabular is an unusually large bone, forming a wide upper surface behind the tympanic space. It is nearly as long from back to front as the dermosupra-occipital.

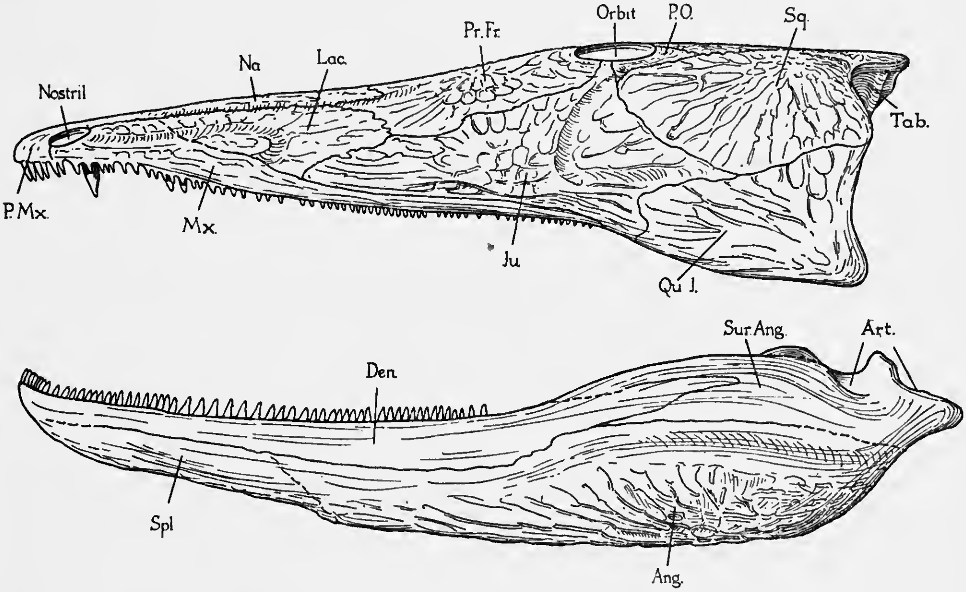

FIG. 6. *Paracyclotosaurus davidi.* Skull and lower jaw seen from the left. × 1/6.

Palate. The palate has the normal pattern of an advanced labyrinthodont. The quadrate condyles, though ventral to the occipital condyles, lie essentially in the same transverse plane, so that the quadrate ramus of the pterygoid is short and unusually laterally directed. The sub-temporal opening through which the jaw-closing muscles passed down to the lower jaw is large, but not unusually so;

and the flange formed by the ectopterygoid and pterygoid, which in labyrinthodonts is usually applied to the inner surface of the lower jaw, is vestigial. It is impossible to determine the sutures between the pterygoid, ectopterygoid and palatine; but it is evident that the three bones form the outer border of the large palatal vacuity, their respective parts being indeterminable. The pterygoid is toothless. The palatine bears an alternative pair of large teeth, about 2·6 cm. high, immediately behind the internal nostrils, set as always in a common recess. A similar tooth seems to be shown on the vomer. Behind these "tusks" is a single series of teeth set close to the maxillary suture of the palatine and ectopterygoid bones, numbering in all 56 to 60. The series is essentially uniform, teeth being shed and replaced occasionally. An individual tooth is attached to the bone on the bottom of a very shallow depression. It is a triangular structure, flattened antero-posteriorly, attached to the bone by a base rather more than twice as wide across the jaw as it is long. The outer side is rounded and convex in profile, the inner a little concave, the point (where it might be expected to meet the teeth of the lower jaw) is also rounded and smooth. The tooth is as high as it is wide at its base, and separated from its neighbours by about its own thickness, the height being uniformly 9 or 10 mm. only. The elongated, narrow internal nostril, whose inner border is probably largely made by the vomer, is bordered by a row of similar but much smaller teeth which ends posteriorly at a short set of some six or seven very small conical teeth mesial of the first palatine tusk. The maxilla bears a close-set series of teeth, which decrease somewhat in size backwards. These teeth agree in structure with those of the palate, from which they are separated only by a very narrow wedge-shaped continuous groove. In all probability the series continued round the premaxilla.

The teeth of the lower jaws, carried entirely by the dentaries, are slightly enlarged copies of those in the upper jaws. They bite within the maxillary row and laterally to the palatal row.

The only large teeth—those on the palatines and vomers—are about an inch high, little higher than the marginal teeth, and were evidently unsuitable for the capture of any big animal, into whose body they could not penetrate far enough to kill. Further consideration of the animal's diet is left until after the description of the whole skeleton.

Lower jaw. The lower jaw is well preserved and has a normal labyrinthodont structure. The articular is fused with the surrounding bones, and is articulated with the quadrate, so that no complete description can be given. This articulation is extremely wide, fitting the quadrate condyle and rising mesially as a powerful process to articulate with the front face of the inner end of the quadrate condyle. The bone has an analogous process rising behind the outer condyle, to form the hinder border of a deep cylindroid notch, which assures accurate closure of the mouth. Behind this a massive conical retroarticular process projects directly backward for about 8 cm. behind the axis of the articulation. The surangular, fused with the articular, projects forward, bounding the 19 cm. long suprameckelian vacuity through which the masticatory muscles pass down into the hollow jaw. A prearticular bone, attached to the inner side of the articular, stretches forward parallel to the surangular forming the inner border of the muscle opening, which is closed at the front by the third coronoid, a narrow bone wedged in between the dentary and the prearticular. There is a series of apparently three coronoids attached to the inner surface of the dentary, widely exposed above the splenial and postsplenial bones. Their upper border may lie free above the shelf of the dentary to which they are attached ; none bears any teeth, though they bound and held in place the strip of gum from which dentary teeth arose.

Jaw musculature. The nature of the ornament on the outer surface of the lower jaw makes it certain that the masticatory muscles can have had only an infinitesimal, if any, attachment to the outer surface. The flat upper surface of the surangular, which stretches forward from immediately in front of the articular surface, seems unlikely to have given attachment to a muscle. Its character and width are similar throughout its length, and a muscle attached immediately in front of the condyle could have very little value. It probably represents the limit of the cheek, lateral to the masticatory muscles. These would arise from the skull roof and pterygoid, passing downward and inward, through the opening between the surangular and prearticular, to the cavity of the jaw, and probably extending forward past the large inner fenestra to an insertion on the inner surface. A muscle arising from the skull roof, at the attachment of the pterygoid to it, and passing down to the upper surface of the surangular at its mid-length, would be only some 10 cm. long, and perhaps placed about the same distance from the articulation ; a range of shortening by a quarter of its length would allow the mouth to open only about 15 cm. at the front of the jaw. An attachment to the point within the cavity of the jaw immediately below would double the depth of the opening, and an extension forward to the front of the internal mandibular vacuity might well double it again, the palate then being nearly at right angles to the jaw. The relative position of the occipital and quadrate condyles shows that if the lower jaw rested on the ground, as must often have been the case, it would be moved forward as the mouth was opened by raising the skull.

Vertebral column. The vertebral column is articulated from head to tail, and in general is undisplaced. In *Mastodonsaurus* (which is not remote from the Capitosaurs) the 1st vertebra is a continuous structure whose anterior face bears a pair of articular facets for the occipital condyles, below and between which a canal for the notochord opens. This passes obliquely through the bone, and opens behind, a little below the neural canal. There is a small fused neural arch, and no rib facet. No such structure can be found in this specimen. The blow which the body suffered on the left side of the head disarticulated that structure, so that the occipital condyle lies some 6 or 7 cm. to the right of the mid-line of the first two recognizable elements. Of these the anterior, which is perhaps the intercentrum of the 1st vertebra, differs from all others throughout the column. The rest are crescentic—half rings surrounding a large notochordal space—their upper ends narrowing and eventually becoming rounded. The 2nd intercentrum is peculiar only in that it is divided into right and left halves meeting below the notochord by extensive flat surfaces. The 1st intercentrum is also paired, and the left element (which alone is known) lies nearly in articulation with the corresponding bone of the 2nd, differing from this (like the corresponding bone of *Eryops*) by the absence of an upstanding process lateral to the notochord. Its anterior face does not show any definite cup for articulation with the rounded condyle. A left half of a neural arch, though found behind and above the left half of the 2nd intercentrum, probably belongs to the 3rd intercentrum, which has none associated with it. It corresponds generally with those found further back in the column, having similar cartilage-covered facets for articulation with pleurocentra, a short transverse process truncated by a rib facet, and a peculiarly small anterior zygapophysis with a rounded articular surface. Thus we have to find neural arches for vertebrae 1 and 2, and the right half of 3. Lying dorsal to and on the right of the two anterior intercentra are six strange bones, forming a dorsal series of two, a ventral of three, and still further down a fragment which may be a rib head. These bones should be determinable as the missing neural arches, but I am unable to identify them.

From this point backward the vertebral column is continuous, and the ribs attached to it are identifiable. There is a systematic change in structure from front to back. Such vertebrae as nos. 5, 6 and 13 (see Text-fig. 7) have a large semicylindrical intercentrum whose upper border has a semicircular notch for the notochord, on either side of which the bone was rounded and presumably capped with cartilage. In side view the bone is somewhat wedge-shaped, its mid-ventral border being widest, and the lateral surface is recessed between out-turned ridges. Toward the summit, near the hinder edge, is a large shallow concavity, offset from the outer surface, for the capitulum of the rib. The neural arch, apparently composed of paired elements in many parts of the column, has a short neural spine rising above the posterior zygapophyses and ending abruptly. Its anterior face turns forward to form anterior zygapophyses, below which lie the two sides of the neural canal, a relatively large cylindrical space. The lower surface of the neural arch is cut out to form the roof of the neural canal, on each side of which it bears a nearly rectangular facet for articulation with the cartilaginous pleurocentrum. Laterally to this facet lies a transverse process of varied length whose outer end is abruptly truncated by a rib facet.

Observation shows that mid-ventrally the intercentra met one another with a minimum of ligament between them, so that a measured length of 20·5 cm. is occupied by six intercentra—with individual lengths mid-ventrally of 3·4 cm., 2·9 cm. and 3·1 cm. in three directly measurable cases. The more anterior intercentra are massive structures nearly as high as they are wide, with a cylindroid ventral surface. No. 13 is perhaps the extreme of this condition ; its intercentrum is wide and high, 3·6 cm. in length, and remains massive almost up to the extreme dorsal points which carry the outwardly and backwardly directed shallowly concave articulations of the ribs. By no. 21 the intercentrum, still 3·5 cm. long, has become very shallow, about 3·6 cm. in contrast with 5·5 cm. in no. 13. No. 27 has an intercentrum 3·9 cm. long, 7 cm. in maximum width (compared with 9·2 cm. in no. 13). The intercentrum has a flatly cylindrical lower surface and almost straight, vertical, lateral surfaces, with large rib facets placed posteriorly and extending very nearly to its summit. The transverse process is short, extending only 2 or 3 mm. on the ventral surface beyond the intercentrum. No. 28, the sacral, does not show the intercentrum, but its neural arch differs in the depth and massiveness of its transverse process. In nos. 32 and 33 the neural arches are fused on the left side, all trace of zygapophyses having vanished, but on the right the neural spines are not continuous, and the anterior zygapophysis of no. 33 is well shown. The intercentra are very square cut, with an essentially flat ventral surface, and a large facet for the rib head filling the hinder part of the lateral surface. There is a very small, short, down-turned transverse process, and the rib is articulated by two heads. The positions of the completely cartilaginous pleurocentra are well shown.

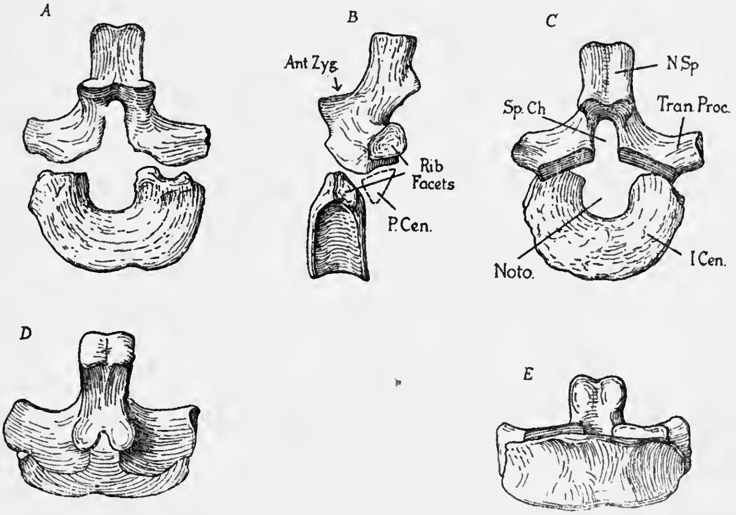

FIG. 7. *Paracyclotosaurus davidi.* Vertebra No. 13. A, from in front. B, left side. C, behind. D, from above. E, below. × 1/4.

These conditions continue down the tail, haemapophyses appearing at no. 36. Here the intercentrum is little more than a quadrangular sheet of bone, a little hollowed above, bearing a large downward and slightly backwardly directed chevron below and with a rib facet on the posterior end of its lateral border. The neural arch has a well-defined neural canal, lateral to which it extends out to a thickened and rounded end, which is presumably the upper part of the rib facet. Pre- and post-zygapophyses are well formed, with their articular faces at little more than right angles to one another.

Ribs. Ribs are in position from the first vertebra until they cease at the 36th. The first one is seen from below on the left side. It appears to be single headed, and is 7·6 cm. long. Proximally it is a thin, nearly vertical, bony sheet, but distally a peculiar ridge runs from its anterior surface making the bone about 2 cm. in maximum thickness. It extends outward practically horizontally. The upper end of the second rib is more than 3 cm. deep, and had a cartilaginous head which articulated with the appropriate facet on the intercentrum and the unknown neural arch. The bone is wide proximally, then becomes nearly circular in section, but widens distally, foreshadowing the conditions in those which follow. The ribs belonging to vertebrae 3, 4 and 5 are remarkable (cf. Pl. 29), for they are attached to the flat outer ends of the transverse processes, bone to bone, with little space remaining for cartilage between them. But the capitular part of the wide upper end of the rib fails to meet the facet on the intercentrum, to which it was attached in life, by about two centimetres, obviously a measure of the thickness of the cartilaginous capitulum. The rib then stretches out laterally and backward at about 45° to the mid-line. The ribs attached to vertebrae 3, 4, 5 and 6 are peculiar because their distal parts are widened so that they overlap one another and provide a large base of attachment to the muscles, the serrati anteriores, passing to the scapula. This widening is abrupt; the slender shaft of the rib, distal to a dorsal ridge it bears, is roughly circular in section, and later rapidly widens to become at least 8 cm. across, the lower border being inturned as a flange. Ribs, 3, 4 and 5 thus combine to form a firm, powerful, flat surface some 8 × 20 cm. for the attachment of the scapula. From the seventh or eighth vertebra backward the ribs are essentially straight, simple, bony rods. Both sacral ribs are preserved, supplementing one another so that the complete structure is shown. The head, whose confluent faces carried a single cartilage cap which articulated with the transverse process and intercentrum of the sacral vertebra, is 6·2 cm. deep, with a maximum thickness of 2 cm., so that its attachment to the vertebral column is powerful. The bone rapidly narrows, and at 7 cm. from the attachment is only about 2 cm. thick. It then widens, its anterior surface being hollowed out so that it ends in two separated processes which must have met and been attached to the inner surface of the ilium a little below its upper border. The area of such contact is very small, the attachment being presumably reinforced by ligaments, as it presumably was in *Eryops* and certainly was in embolomerous amphibia. It seems clear that there is only a single sacral. The anterior caudal vertebrae still carry two-headed ribs.

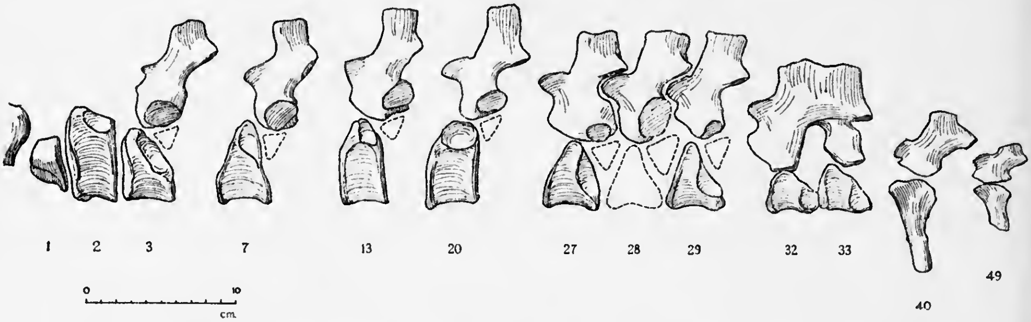

FIG. 8. *Paracyclotosaurus davidi*. Occipital condyle and selected vertebrae numbered below 1, 2, etc. No. 28 is the sacrum; note large rib facet. Nos. 32 and 33 are abnormal in the continuity of their neural arches on this side. × 1/5.

The vertebral column is thus largely cartilaginous, but with well-formed zygapophyseal articulations and rib attachments. It was evidently capable of lateral movement though it is improbable that this would be through any extensive arc—except in the tail which curves round abruptly at nearly a right angle. Flexure in a dorso-ventral direction was probably very restricted.

Shoulder girdle. The primary shoulder girdle is most easily discussed after the membrane bones which carry it have been described. The interclavicle is a sheet of bone a little longer than wide; the anterior end stretches forward as a narrow process and the middle strip may have been visible on the lower surface between the clavicles. The bone otherwise is rhomboidal with its three other corners rounded. Its visceral surface is shallowly concave a little in front of the mid-point, and quite posteriorly there is a small, shallow, but well-marked depression which is somewhat asymmetrical, opening backward to the left of the mid-line and presumably supporting the heart. The ventral surface is very largely covered by the usual pitted and ridged " ornament ", which extends to the borders of the bone in its posterior third, but ends abruptly laterally where the ventral surface has a sudden step dorsally for a centimetre or more, forming a recess into which the lower end of the clavicle fitted.

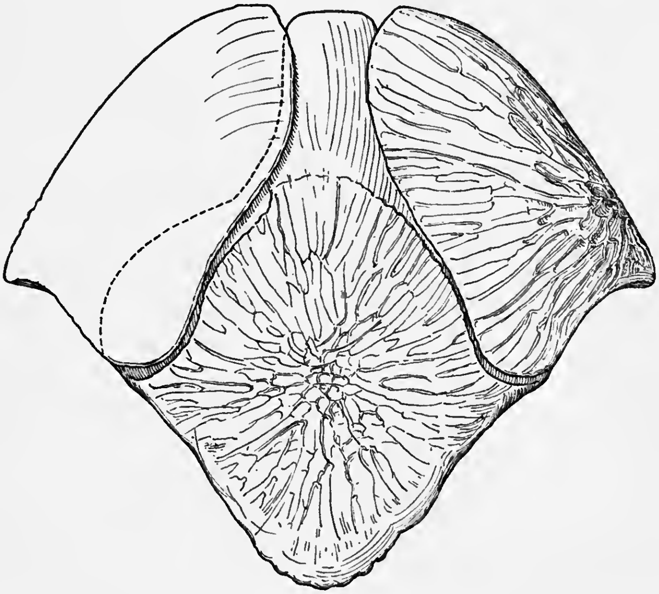

FIG. 9. *Paracyclotosaurus davidi.* Interclavicle and clavicles in articulation, from below. × 1/6.

The clavicles are almost completely preserved and undistorted. They fit the recesses in the interclavicle sufficiently well to make the whole structure certain; it is possible that they met anteriorly below the interclavicle.

The dorsal process of the clavicle is formed by an upturning of the lateral border of the bone, so that its outer surface lies at about 60° to the upper surface of the clavicle, or some 55° to the ground. This dorsal process is firmly attached to the ventral part of the bone by a base about 13 cm. long and (at its maximum) 3·5 cm. thick. The process is about 14 cm. high and 12 cm. antero-posteriorly; its upper border slopes down a little in front, and the outer surface below it is excavated into a pocket, about 4 cm. deep, across its whole width, presumably for a musculus cleido-mastoideus. Below it the anterior part of the lateral surface is recessed on a definite oblique line.

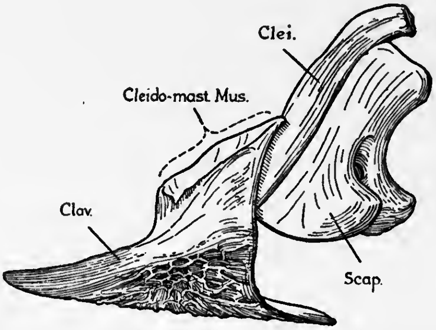

FIG. 10. *Paracyclotosaurus davidi.* Left clavicle in articulation with the cleithrum and scapula. × 1/6.

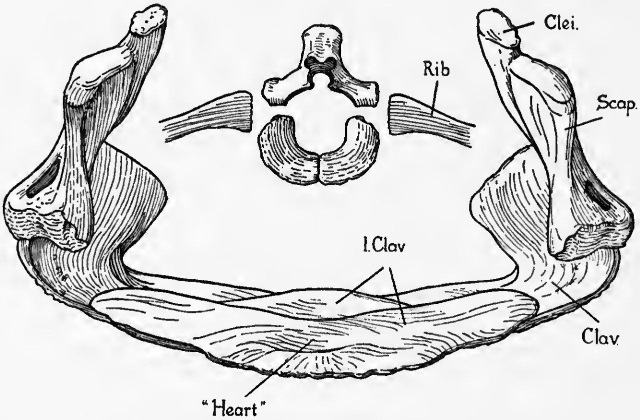

FIG. 11. *Paracyclotosaurus davidi.* The shoulder girdle in position with respect to the vertebral column and ribs, viewed from behind. × 1/6. (The intercentra and ribs belong to the second vertebra, the neural arch, to the third.) The figure shows the inclination of the dorsal processes of the clavicles towards one another as they pass forward and upward, so that the structure may lie between the hinder ends of the lower jaws. The modelling of the upper surface of the interclavicle to support the heart and other structures is shown.

The left cleithrum remains firmly attached to the scapula. It is a massive rod (4 cm. by 3 cm. in section at mid-height) which, beginning at a " blunt point " at the lower end of the scapula, rises to overhang the upper end of that bone by some 4 cm. The overhang slopes backward as a partial cap to a cartilage. The anterior face of the lowest 9 cm. of the bone is shallowly concave, and articulated with the hinder border of the dorsal process of the clavicle. Thus the position of the scapula is known with certainty, and that of the glenoid cavity can be inferred with accuracy.

The shoulder girdle thus built up is placed so far forward that the anterior parts of the clavicles and interclavicle lie directly below the braincase, the ascending ramus of the clavicle lying well within, but close up to, the hinder border of the cheek. The glenoid cavity for the humerus is about 18 cm. behind the quadrate.

The scapula is so small an ossification in the large cartilaginous scapulo-coracoid that nothing of the glenoid cavity is preserved, though the great thickening of the bone, below and behind, to more than 7 cm., shows its position. There is a large supraglenoid foramen passing forward and downward above the glenoid cavity. The position of the bones in the matrix, evidently still in articulation, gives a measure of the thickness of the cartilaginous caps to long bones, and to the glenoid cavity of the scapula; it seems to be usually about one centimetre.

The humerus may be interpreted as a reduction of that of *Eryops*, differing in being much less completely ossified, in having the rugged muscle attachments of that animal reduced to very small proportions, and in presenting only the merest indication—by a small out-turning of the surface—of the huge hemispherical knob which in *Eryops* gave attachment to the radius. The limb has become a paddle, not a leg capable of supporting more than half the animal's weight in air. In fact all the limb bones of this animal greatly resemble those of *Trimerorhachis*.

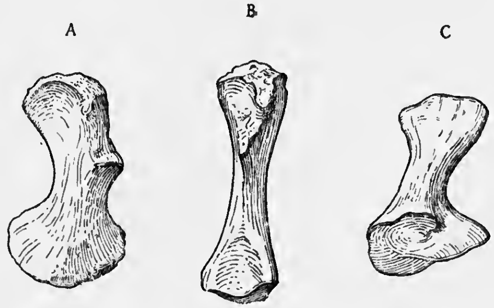

FIG. 12. *Paracyclotosaurus davidi*. A, the right humerus from below. B, the left femur from below. C, the left ilium, lateral aspect. All × 1/6.

The radius and ulna, about 8 cm. long, have widened extremities, once cartilage covered; and the sum of their widths distally is about 8 cm., the presumed width of the entirely cartilaginous carpus, which is apparently about 5 cm. long and 8·5 cm. wide, judging from the widths of the heads of the five metacarpals. The middle metacarpal supports a finger with three phalanges whose total length is just under 8 cm. The first digit has a short, very massive, metacarpal which is followed by two phalanges, of which the second has a rounded and widened end, and a ligament attachment well marked on its palmar surface. The metacarpals do not overlap one another. The phalangeal formula is 2, 2, 3, 3, 2.

Pelvis. The pelvis is remarkable because it is much wider between the iliac crests than it is between the acetabula. The ischium was evidently narrow, though all its borders, except the lateral, were extended by cartilage. The pubis is largely represented by an impression through a layer of skin and is a relatively large sheet containing some ossification, the width across the pair much exceeding that across the ischia (Pl. 30). The wide expansion of the pubis, presenting the greatest possible contrast to that of *Eryops*, illustrates the general flattening and widening of the body found in the Triassic labyrinthodonts. It gives some indication that the tail was sharply marked off from the body by its much smaller width.

The femur is longer and thicker in the shaft than that of *Eryops* with which it was compared. The head bore a large cartilaginous cap; the lower end, abruptly truncated but continued in cartilage, seems to have carried two condylar knobs. The massive shaft has a low crest running along its lower surface, ending proximally at a ventral process, the homologue of the meeting point of the three great ridges of the femur of *Eryops*. This bears a series of well-marked muscle (or ligament) insertions. The tibia, relatively massive, is incompletely known. No trace of the fibula is preserved. The tarsus is unossified, but there remain a series of rather scattered metatarsals and some phalanges. These merely show that the foot greatly resembled the hand in both size and structure.

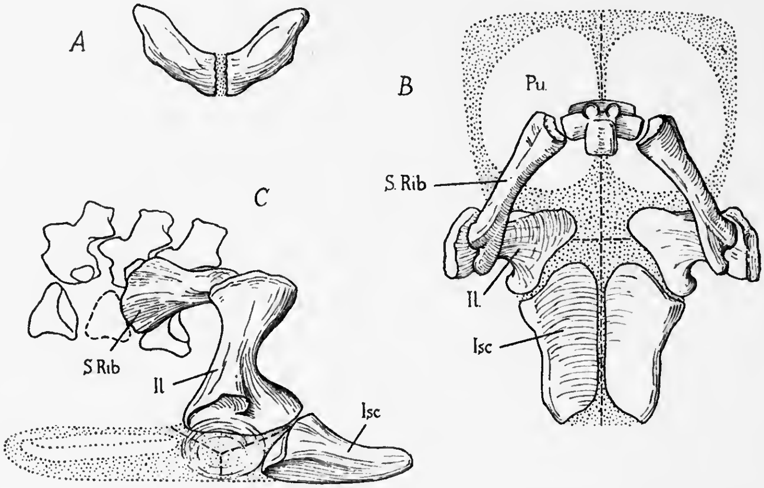

FIG. 13. *Paracyclotosaurus davidi*. Restoration of the pelvis. × 1/6. Cartilage is restored in the dotted areas, and the meeting of the three bones in the acetabulum is conventional. A, the ischia from in front; B, the pelvis from above. C, the pelvis from the left side.

Skin. The animal's skin is largely preserved as an impression, over part of the dorsal surface of the body, and of the ventral surface especially in the pelvic region. Block 14, dorsal surface (Pl. 31), lies from 15 to 30 cm. to the left of the mid-line opposite vertebrae 23–25. It bears an impression of the skin in an area where it has been rucked up in a manner which suggests that it was flexible, although it contained closely set, bony scales. These are irregularly oval in plan, ranging from 3·5 × 5 mm. to 9 × 6 mm. in size, devoid of definite ornament and set quite irregularly, but not in contact with one another. Their thickness cannot be measured, but appears to be less than 1 mm. They are calcareous, and presumably bony. An area of 50 square cm. contains more than one hundred scales.

A plastic cast of the ventral surface below the pelvis shows a clearly recognizable area of skin about 20 cm. square (cf. Pl. 30). Posteriorly a strip of skin with a torn anterior edge stretches across from the upper end of a femur on to a misplaced ischium. It then spans a gap until it is supported by another flat bone (presumably the other ischium), and then passes over another gap, where it is shown as an unsupported sheet some 3 mm. thick that continues over the ventral surface of a pubis, cracked by some accident with the cracks showing through the skin. It continues on to the other (misplaced) pubis. It is puckered in a convincing manner where the torn edge rests on the ischium. There is no suggestion that this ventral skin contains any bony scales, but it has a delicate surface sculpture of small pits which are clearly recognizable.

Such preservation of large areas and thicknesses of skin is remarkable, but it is paralleled by an ichthyosaur skull (No. R.509, D. M. S. W. Coll.) from the *planicostatus* zone between Lyme Regis and Charmouth. Here the skin is about 2 mm. thick, and in part it retains its cellular structure (Whitear, 1956).

III. BODY SHAPE AND MODE OF LIFE

The mode of life of the labyrinthodont described above should be discoverable, in part, from its unusually completely known structure. The small distortion of the head can easily be allowed for, and the complete preservation of skull and jaws makes its shape certain; its length is 60 cm. The right hinder corner of the head is essentially undistorted and shows that the skull at its point of greatest depth is almost exactly as high as the lower jaw. Similarly the lower jaw symphysis is the same height as the skull above it. Thus, at its point of greatest height, the head was essentially of oval section, 22 cm. high and 44 cm. wide. The nostril, orbit and tympanic membrane are all directed upward. Whether the eye could be projected upward above the head to give a horizontal view, as in the frog, is impossible to determine, but it may have been so.

The first rib is short, but the second, which is in undisturbed position, implies a body width of at least 35 cm., 10 cm. behind the condyles. The shoulder girdle is a rigid structure, the membrane bones lying in, or immediately below, the skin having a maximum width of 44 cm. at a point a little behind the lower jaws. The clavicles are upturned so that they incline inward, their minimum width of 23 cm. lying between the lower jaws, the interclavicle projecting along the throat below the skull for 15 cm. The maximum width of the body at the shoulder may well have been 53 cm. The forelegs, in a position of rest, would give a total width between the middle fingers of the forwardly directed hands of 87 cm. The distance of the sacral vertebra behind the skull is 115 cm. The body thus has a minimum height of 16 cm., and a width of more than 20 cm. The tail is about 50 cm. long, and is probably flattened laterally. The total length is approximately 225 cm.

The weight could be estimated by making a number of assumptions, but has little meaning in an aquatic animal. Roughly the creature is larger than a man in bulk and presumably in weight, but it may well have had no weight when submerged, depending on the size of the inflated lungs. On land it could no doubt walk to some extent, making a track little less than a yard wide, with a stride of perhaps 20 cm. As the individual prints of the well-preserved forefoot would be about 100 square centimetres, the track would consist of two strips of forefoot prints, with similar hindfoot tracks just within them, and with a wide streak of body impressions. In water it is probable that little but the ends of the fingers and toes would make impressions, the body streak probably not being seen It seems probable that the short tail could have had some use in swimming, though inadequate for rapid movement.

The animal's food may be considered here. It has a feeble dentition ; the only teeth which could be driven into the body of an animal seized in the mouth are those on the vomers and palatines, and these stand very little above the maxillary teeth, a close-set row lacking points of any kind. It is very likely that the creature caught its food as the living Giant Salamander is said to do—by waiting until the prey came near, then quickly opening its enormous mouth and swallowing it. The most probable food would be small fishes, up to some 15 cm. long, which swam in shoals. Fishes of such dimensions in the form of *Promecosomina,* a holostean, are those most abundantly found with the labyrinthodont.

How the animal breathed is uncertain. Had it done so as *Megalobatrachus* perhaps does, by moving the floor of the mouth by muscles attached to the hyoid and branchial arches, some of these elements would probably have been ossified, and none is. The ribs surround, at least, the upper part of the body, and articulate with the vertebral column by a wide and essentially two-headed upper end, attached obliquely to the column. They could presumably have been used in an essentially mammalian manner for breathing, though the rigidity of the shoulder girdle must have restricted rib movement there. But as the animal was probably as slow moving as a Giant Salamander, and the rate of its oxygen consumption very low, the buccal epithelium may have provided an efficient point of introduction of oxygen into the body, for the skin of the ventral surface is thick, and the skin as a whole was perhaps unlikely to be an important respiratory surface. It is difficult to imagine any such individual moving far, and impossible to imagine it traversing any very different environment.

IV. SYSTEMATIC POSITION

In 1914, when I first saw this animal as an impression, I referred it to the genus *Cyclotosaurus* on the grounds that its skull was in general structure like that of any capitosaur, and the otic notch closed by contact of the tabular and squamosal laterally. At that time the only known cyclotosaur was still the type species " *Mastodonsaurus robustus* ", given the new generic name *Cyclotosaurus* by E. Fraas in 1889 ; Smith Woodward's little English form (*C. stantonensis*) was at that time referred to *Capitosaurus.* Since then new discoveries have increased the number of species of *Cyclotosaurus* to ten[1], and added a new genus, *Rhadalognathus* Welles (1947), with a

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[1] Two other "species" have been referred to this genus without reason.

FIG. 14. *Paracyclotosaurus davidi.* Reconstruction of the skeleton in a walking pose. Total length approximately 225 cm.

similarly enclosed tympanic membrane. It is therefore necessary to examine each of these animals to distinguish which can rightly be referred to the genus.

The type species of *Cyclotosaurus, C. robustus* (Meyer & Plieninger) from the Schliffsandstein of the Lower Keuper, was described by Quenstedt (1850) and later by Fraas (1889). It is a large form with a triangular skull 53 cm. long in the mid-line with nearly straight sides except for the rounding off of the snout. The width posteriorly is about 43 cm. and the height at the occiput 5·1 cm. The skull is thus extremely flattened, though there is no reason to doubt that its real shape is preserved. Several skulls are known of similar proportions. There are large tusks on the vomers and palatines. The lower jaw has a maximum depth of 12 cm. at the articulation.

Cyclotosaurus posthumus Fraas (1913), from the Stubensandstein of the Upper Keuper, has a skull 53 cm. long and 42 cm. in maximum width, almost precisely the same as that of *C. robustus.* The height in the mid-line at the occiput is 6·3 cm. again similar to *C. robustus,* but the face is narrower, its lateral borders are concave, and the occiput lacks the deep concavity of the border found in *C. robustus.* There are large tusks on the vomers and palatines, and the dentition in general resembles that of *C. robustus.* It may well be placed in the same genus.

Cyclotosaurus mordax Fraas (1913), also from the Stubensandstein, was founded on a skull broken off about 2 cm. behind the orbits. The skull is flat and differs from *C. robustus* in having its interorbital width proportionally greater and its suborbital width less than in that form. It is also much shorter in relation to its width as judged from the palate. It differs from *C. posthumus* similarly, but may well be placed in the same genus.

Cyclotosaurus papilio Wepfer (1923), from the top of the Muschelkalk, is based on a fragmentary skull, clearly "*Cyclotosaurus*" by the complete enclosure of the tympanic membrane. The structural details are incomprehensible. It is thus not certainly determinable.

Cyclotosaurus ebrachensis Kuhn (1932), from the Middle Keuper of Oberfranken, was described from a complete skull about half the size of *C. robustus.* The general outline resembles that of *C. robustus,* but the orbits and tympanic membranes are relatively more widely set, no doubt a scale effect. The greatest width is 23 cm. and the height 3·2 cm., relatively more than in *C. robustus* and less than in *C. mordax.* It is evidently a member of the genus *Cyclotosaurus.*

Cyclotosaurus hemprichi Kuhn (1942), from the Upper Keuper (?Rhaetic) of Halberstadt, is an admirably preserved but, in part, scattered skull, excellently described. The skull is approximately 62·5 cm. long, 46 cm. wide, and the height (dorsal surface to quadrate condyle) is 11·4 cm. The depth of the occiput distinguishes this skull from all those listed above, and cannot be explained by growth, for it is little greater in size than the type species.

Cyclotosaurus stantonensis (A. S. Woodward) (1904), from Stanton, Staffordshire. Skull length 20·5 cm., width 15·3 cm., maximum height 4·2 cm. The depth of the occiput as a fraction of skull width agrees with *C. hemprichi* and differs from that of the type species. The skull is remarkable because the sutural connection of the exoccipital and pterygoid is short, whilst the quadrate ramus of the pterygoid has a well-developed post-tympanic flange, known in "*Capitosaurus*" (= *Parotosaurus*) but not in any other "*Cyclotosaurus*" (cf. Sushkin, 1927 : 273, 285).

"*Cyclotosaurus randalli*" Welles (1947), from the Moenkopi formation of Arizona, is founded on fragments including one showing a "closed otic notch" and part of a basis cranii. This species differs greatly, in the relations of the exoccipital, parasphenoid and pterygoid to one another, from any of the forms listed above and is evidently not closely related to them.

Rhadalognathus boweni Welles (1947) is founded on a very slender labyrinthodont lower jaw, impossible of comparison with those of capitosaurs. It is held by Welles, on the basis of associated fragments, to have had a closed otic notch. As reconstructed by Welles, the skull is unlike that of any of the cyclotosaurs mentioned above.

"*Cyclotosaurus spitzbergensis*" Wiman (1915) is an indeterminable fragment.

"*Labyrinthodon pachygnathus*" Owen (1842, pl. 46, figs. 6, 7) was recognized by Welles as being an English *Cyclotosaurus*.

Comparison of general proportions shows that the skull of the St. Peter's labyrinthodont differs from *C. robustus* (the type species of the genus), *C. posthumus*, *C. ebrachensis* and, presumably, *C. mordax*, in being much deeper in proportion to its length and width. In this matter it agrees closely with *C. hemprichi* and *C. stantonensis*.

C. stantonensis differs very greatly in the persistence in it of the post-tympanic flange of the pterygoid found in "*Capitosaurus*" (= *Parotosaurus*) and in the proportions of the tympanic cavity so far as it can be inferred. It retains more of the structure and proportions of this region in *Parotosaurus*, and appears to be a "primitive" form, not necessarily closely related to other cyclotosaurs and I therefore establish for it a new genus, ***Procyclotosaurus.***

C. hemprichi, however, very much resembles the Australian animal. It differs in the shape of the tympanic membrane, which is "triangular" in contrast to circular. But in the structure of the occiput (apart from the presence of a well-marked shelf on the exoccipital for the supraoccipital cartilage) the two are very alike; the relation of the exoccipital to the pterygoid (Kuhn, 1942, pl. 1, fig. 1*b*), the structures shown in his pl. 1, fig. 3, and the structure of the quadrate-pterygoid region (pl. 3, fig. 1*b*) are extremely similar in the two animals.

The resemblances and differences set out above imply that the "*Cyclotosaur*" condition of total enclosure of the otic membrane by contact of the tabular and squamosal lateral to it has arisen more than once, and hence cannot by itself characterize a genus.

Thus *Cyclotosaurus*, founded on *C. robustus*, may include *C. posthumus* Fraas, *C. mordax* Fraas and *C. ebrachensis* Kuhn.

The species with deep skulls—the Australian skeleton which is the subject of this paper, and *C. hemprichi*—differ noticeably from the true cyclotosaurs. That these differences are significant is shown by the remarkable fact that their peculiarities occur in three magnificent skulls from the Middle Trias of East Africa in Mr. Parrington's collection (Field no. 48, Mkongoleko, Stockley's B.9. "Upper Bone Bed" (2 specimens); Field No. 135, Gingama, Stockley's B.26. "Upper Bone Bed") which might well be their ancestors, but not the ancestors of the typical flat-headed *Cyclotosaurus*. There are accordingly two distinct lines.

Thus the St. Peter's labyrinthodont is made the type of a new genus and species, ***Paracyclotosaurus davidi***, and with it is placed *C. hemprichi* of the extreme Upper Keuper of North Germany.

That the St. Peter's labyrinthodont and *Paracyclotosaurus hemprichi* belong to the same genus and one manifestly distinct, by its ancestry, from true *Cyclotosaurus* is of stratigraphical significance, for *P. hemprichi* comes from the " oberen Knollen Mergel " at Halberstadt, at the extreme top of the Trias, or perhaps even in the Rhaetic. Nothing in the structure of the St. Peter's animal is inconsistent with such a late age, but nevertheless it might be somewhat older, that is, earlier in the Upper Trias.

V. DESCRIPTION OF *SUBCYCLOTOSAURUS BROOKVALENSIS* gen. et sp. nov.

Parrington's East African animals, in so far as the dorsal surface of their skull is concerned, resemble a small " Parotosaur " skull from the Brookvale clays of the Hawkesbury Sandstone, shown in Text-fig. 15. This specimen is the mould of a skull broken so that the right border is lost, and very slightly distorted by pressure so that the orbits are no longer quite symmetrical. The proportions of the skull resemble those of most others of *Parotosaurus* and *Cyclotosaurus*, the preorbital length being 66% of the total mid-line length, the extremes amongst parotosaurs being 61% in the small *Cyclotosaurus ebrachensis*, and 71% in *Parotosaurus helgolandicus*. The skull is characterized by the small tabular without any trace of a " horn ", but with a round lappet that approaches the squamosal flange lateral to the tympanic membrane, failing to meet it by about its own width. The occiput between the otic notches is proportionately wide, a reflection of the small size of the skull. The skull is otherwise of normal *Parotosaurus* structure, but has a small internasal vacuity between the dorsal processes of the premaxillae. Lateral lines are often shown as continuous grooves with well-defined borders. A deep groove on the maxilla begins immediately behind and lateral to the nostril and passes straight back to the lachrymal, on which bone it turns outward and forward and ends abruptly. Another groove appears to begin on the maxilla, immediately lateral to that described above. It passes back just above the insertion of the teeth for the full length of the bone. The supraorbital groove begins abruptly on the dorsal surface of the premaxilla, immediately passes on to the nasal, and extends back on that bone close to its suture with the lachrymal, it then comes on to the prefrontal, passing on to the frontal where that bone enters the orbital border. Then as a well-defined groove it surrounds the hinder part of the orbit, turns vertically on to the jugal, and then backward to cross the point where jugal, quadratojugal and squamosal meet, continuing over the squamosal to pass back on to the body. There is a canal, really a series of pits, crossing the supratemporal. For this skull, whose characters are shown in the figure, I propose the new genus ***Subcyclotosaurus*** and the trivial name ***brookvalensis.***

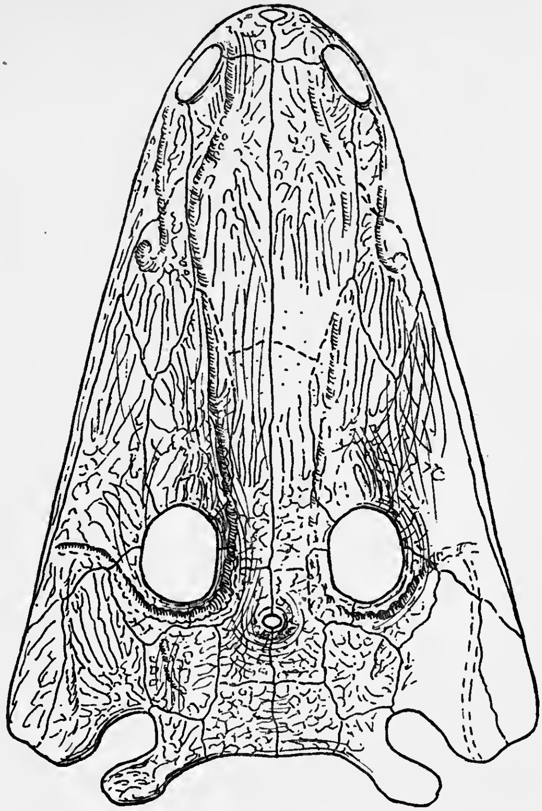

FIG. 15. The skull of *Subcyclotosaurus brookvalensis* gen. et sp. nov. × 3/4. The missing narrow strip on the right is restored from the left side, and the distortion corrected. The short tabular processes approaching but not meeting the squamosal are characteristic. [R. T. Wade Coll., Australian Museum, Sydney].

VI. ASSOCIATED BRACHYOPID

Some time after the discovery of *Paracyclotosaurus* Mr. Dunstan found another large piece of ironstone in the St. Peter's quarries which retained impressions of characteristic labyrinthodont bones. A flexible cast from this mould shows part of the dorsal surface of a skull, sometimes from both surfaces, and the upper surface of an incompletely preserved left pterygoid. So far as the material goes it is excellently preserved, but as the skull was partly disarticulated before burial, the bones displaced, and only the hinder part—not including an orbit—available, it is difficult to determine its systematic position with any assurance.

Text-fig. 16 represents the bones of the upper surface of the head as they lie, with the upper surface of the pterygoid. The mesial part of the skull table was clearly flat, but toward the outer end of the dermosupraoccipital it turns a little downward, so extending to the end of the tabular. The hinder border is there carried by the squamosal, continuing in the same direction until it rather suddenly turns vertically and descends, presumably to meet a quadratojugal. The well-preserved left dermosupraoccipital has a thickness of nearly 2 cm. on its hinder surface, which continues on to the tabular, where it is no longer seen. The tabular, shorter from back to front than the dermosupraoccipital, is wide, ending in a point laterally, presumably housed in a small groove in the hinder border of the squamosal, which continues laterally to it, so that there can be no trace of an otic notch. The supratemporal, which is cracked across and the two parts separated by about a centimetre, is completely shown as a relatively large bone surrounded by the dermosupraoccipital, tabular, squamosal, postorbital and presumably also by the missing postfrontal. The bone is crossed obliquely by an unusually wide and deep lateral line groove, which ends abruptly before reaching the parietal border of the bone. The postorbital, lying lateral to the supratemporal and attached to it by visible suture, bears a continuation of the wide lateral line groove, and has long sutures with the supratemporal and squamosal, and with what is presumably the jugal. The squamosal is firmly attached by suture to the jugal, postorbital and supratemporal, its lateral border for the quadratojugal implying an unusual mode of attachment. No recognizable piece of the orbital margin remains, but immediately in front and on the left side of the parietal is a wide spread of scarcely ornamented bone, which toward the middle line is attached to a small area of well-ornamented bone, probably a frontal: these are obviously misplaced with respect to the rest of the skull.

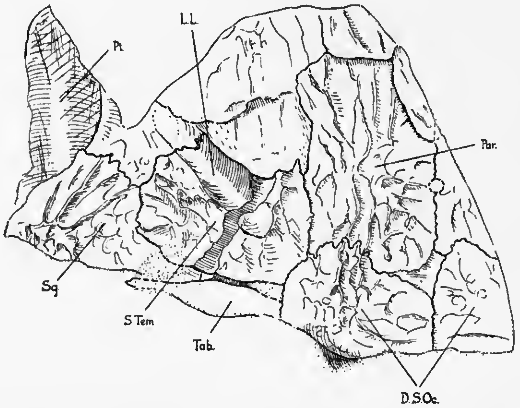

FIG. 16. Fragment of associated Brachyopid skull, drawn from a plastic cast from a block of ironstone from the Wianamatta Shales of St. Peters. × 1/3.

There can be no doubt that this skull belonged to a Brachyopid, but it is scarcely determinable generically, and is left unnamed.

VII. ACKNOWLEDGMENTS

The foregoing paper is a long delayed fulfilment of a promise made very many years ago to Sir T. W. Edgeworth David. The development of the specimen, so skilfully carried out by the late Mr. F. O. Barlow, required many years of patient work using the laborious methods then available, and the intervention of two wars much increased the delay in finishing the task of preparation.

I can only express my gratitude to these two men, and to the original discoverer Mr. B. Dunstan. I also owe thanks to Professor Medawar for the hospitality of the Zoology Department of University College, London, and to the Royal Society for enabling Miss J. Townend, who is responsible for all drawings which illustrate the paper, to work with me, and also to Mr. W. Brackenbury for the photographs on Pls. 29–31.

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VIII. KEY TO ABBREVIATIONS IN TEXT-FIGURES

Ang., angular.
Ant. Zyg., anterior zygapophysis.
Art., articular.

B. Pt., space formerly occupied by the cartilaginous basipterygoid process.
Bd. Ves., foramen for a blood vessel.

Clav., clavicle.
Clei., cleithrum.
Cleido-mast. Mus., cleido-mastoid muscle insertion.

D. S. Oc., dermosupraoccipital.
Den., dentary.

E. Pt., epiterygoid.
Ec. Pt., ectopterygoid.
Ept. Bas. Art., facet on epiterygoid which articulates with the basis cranii.
Ex. Oc., exoccipital.
Ex. Oc. Cav., cavity in the exoccipital.
Ext. Nos., external nostril.

Fem., femur.
Fr., frontal.

Gass. Gang., groove in the epipterygoid for the Gasserian ganglion.

I. Cen., intercentrum.
I. Clav., interclavicle.
Il., ilium.
Int. Nos., internal nostril.
Isc., ischium.

Ju., jugal.

L. L., lateral line groove.
Lac., lachrymal.

Mx., maxilla.

N. Sp., neural spine.
Na., nasal.
Noto., space for notochord.

Orb., orbit.

P. Cen., pleurocentrum.
P. Mx., premaxilla.
P.O., postorbital.
Pal., palatine.
Par., parietal.
Par. Sp., parasphenoid.
Pin. For., pineal foramen.
Pr. Fr., prefrontal.
Pr. Ot., proötic.
Pt., pterygoid.
Pt. Fr., postfrontal.
Pu., pubis.

Qu., quadrate.
Qu. J., quadratojugal.

S. Rib., sacral rib.
S. Tem., supratemporal.
Scap., scapula.
Sp. Ch., spinal chord.
Sph. Eth., sphenethmoid.
Spl., splenial.
Sq., squamosal.
St., stapes.
Sur. Ang., surangular.

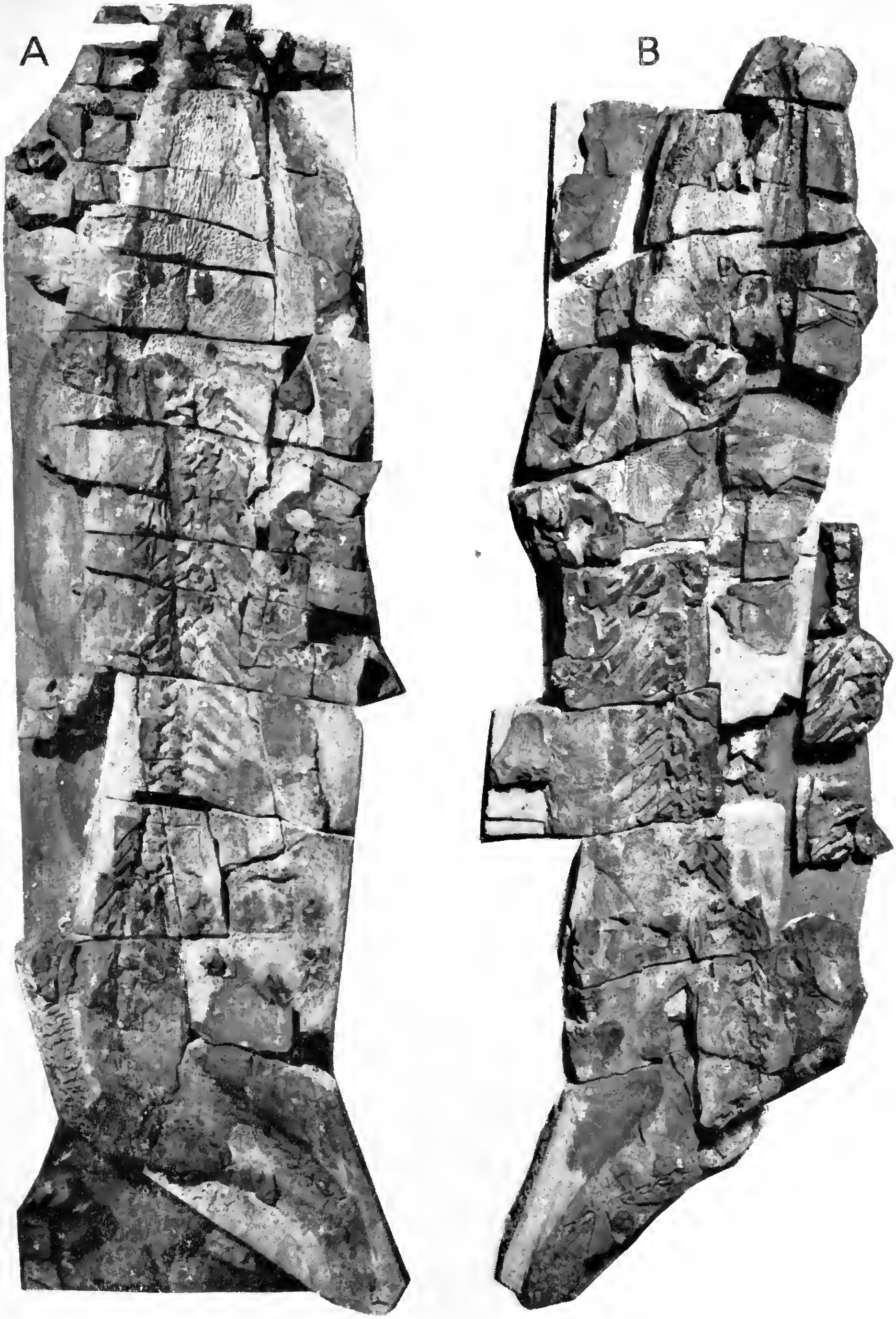
Tab., tabular.
Tran. Proc., transverse process.
Tym. Cav., tympanic cavity.
Tym. Mem., tympanic membrane.

Vo., vomer.
II, notch in sphenethmoid probably for optic nerve.
V^1, ophthalmic branch of N. trigeminus.
V^2 & ^{3}, maxillary and mandibular branches of N. trigeminus.
XII, foramen for nerve XII.

PLATE 27

Paracyclotosaurus davidi

Photographs taken before 1914 by Mr. B. Dunstan showing how the many blocks of ironstone in which the 9-foot skeleton is preserved were fitted together by him, so that one group, A, has the impression of the upper surface of the whole animal, whilst B shows its lower surface. The loose blocks to the right fit between the two main groups, showing vertebrae and ribs.



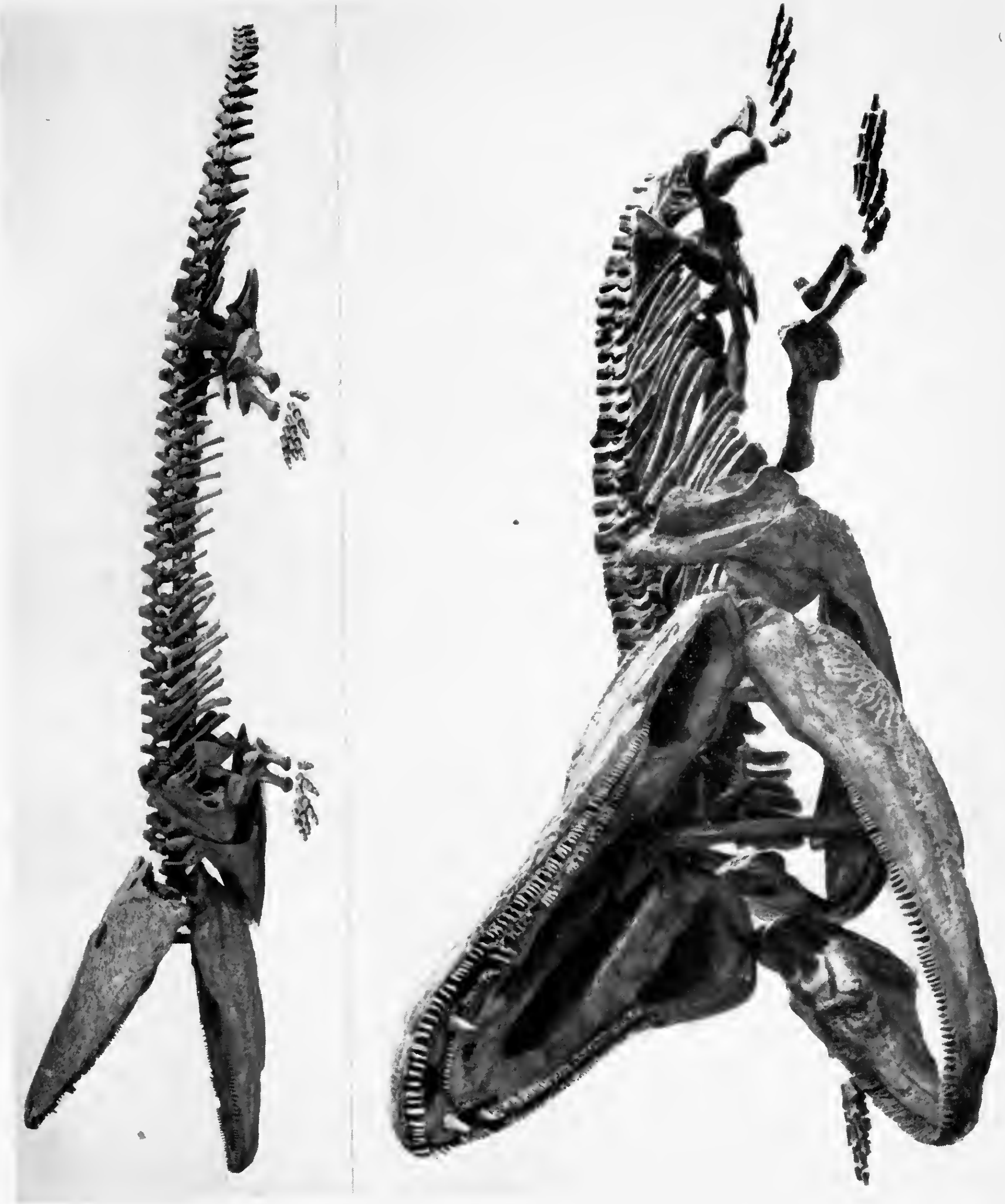
Paracyclotosaurus davidi.

PLATE 28

Paracyclotosaurus davidi

Upper: Left lateral view of the mounted skeleton, approximately 9 feet (2·75 m.) long.

Lower: Three-quarter front view of the left side of the mounted skeleton to show the open mouth and the character of the teeth. The animal could certainly have opened its mouth even more widely.



Paracyclotosaurus davidi.

PLATE 29

Paracyclotosaurus davidi

Photograph of a cast showing vertebrae 6–10 and the left ribs belonging to them, together with the distal part of ribs 4 and 5 and the upper ends of the cleithrum and scapula.

The cast was made by Mr. F. O. Barlow to show how the skeleton looked before the individual bones were disarticulated. × $\frac{1}{2}$ approx.

Paracyclotosaurus davidi.

PLATE 30

Paracyclotosaurus davidi

Plastic cast from a block showing (top, left and right) the ventral surface of the two pubes, and (bottom, left and centre) the two ischia somewhat displaced.

Skin covers the whole structure except for a rent across the middle, where (centre) a surface of ischium can be seen. A loose flap of skin crosses the left side of the tear. On the right side the head of the left femur can be seen displaced posteriorly. × $\frac{1}{2}$ approx.

Paracyclotosaurus davidi.

PLATE 31

Paracyclotosaurus davidi

Block No. 14 with skin of the dorsal surface with its included bony scales, from the region 25 cm. left of the mid-line a little in front of the sacrum. × ½.

Paracyclotosauras davidi.

AN EARLY PLEISTOCENE MAMMALIAN FAUNA FROM BETHLEHEM

D. A. HOOIJER

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AN EARLY PLEISTOCENE MAMMALIAN FAUNA FROM BETHLEHEM

BY

D. A. HOOIJER

(Rijksmuseum van Natuurlijke Historie, Leiden)

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AN EARLY PLEISTOCENE MAMMALIAN FAUNA FROM BETHLEHEM

By D. A. HOOIJER

SYNOPSIS

The fossil mammalian fauna from Bethlehem contains characteristically Villafranchian forms such as *Archidiskodon* cf. *planifrons* and *Leptobos*. It further comprises at least five species known from Villafranchian sites in Eurasia. As at Villarroya (Spain) and at Tatrot (India), which are likewise Villafranchian assemblages, there is *Hipparion* but no *Equus*. However, the Bethlehem fauna differs from those of the Eurasian Villafranchian in the presence of *Giraffa* cf. *camelopardalis* and in the absence of Cervidae; this puts an African " stamp " upon the Bethlehem fauna, as may have been expected *a priori* from its geographical position.

THE fossil mammalian remains described in the present paper were found at the highest point of Bethlehem, Israel, 790 m. above sea-level. The first bones were accidentally found by the owner of a garden digging for water; in 1934 Miss D. M. A. Bate drew attention to this discovery (Bate, 1934). In 1935 and 1936 under the auspices of the Department of Antiquities, Palestine, the Wellcome Archaeological Research Expedition to the Near East, with Miss Bate as palaeontologist and Miss E. W. Gardner as geologist, undertook the excavation of the bone-bearing beds of Bethlehem. Work was continued in 1937 through the support of the trustees of Sir Henry Wellcome and Sir Robert Mond. Finally, in 1940 the excavation was completed by Dr. M. Stekelis of the Hebrew University, Jerusalem. The geology and archaeology of the site was described by Miss Gardner, and Miss Bate contributed a discussion of the fossil vertebrate fauna (Gardner & Bate, 1937). In this paper Miss Bate, after a preliminary examination of the fossils, concluded that the Bethlehem fauna " is not later than Early Pleistocene, using this term palaeontologically as indicating the time of arrival of true *Bos*, *Elephas*, and *Equus* . . . Further, it is claimed for this fauna that it will provide a faunistic link for this period between Asia and East Africa . . . ". The following mammals were listed:

Felis sp. (size of *Panthera leo*)
Hippopotamus sp.
Bos sp.
Antelope.
Giraffoid.
Hipparion sp.
Rhinoceros cf. *etruscus*
Stegodon sp.
Elephas sp.
Small carnivore.

In a subsequent note, dealing with the results of the 1940 excavation reported upon by Dr. Stekelis, Miss Bate added " *Equus* sp. (? *Hipparion*) " (Bate, 1941).

The fossil collections obtained at Bethlehem were sent to the British Museum (Natural History) for study and description by Miss Bate, whose death in 1951 prevented completion of this phase of her Palestinian work, to which she had devoted so much of her time and energy.

In the summer of 1956 I had the opportunity of examining the Bethlehem collection at the British Museum (Natural History), and Dr. E. I. White, Keeper of the Department of Palaeontology, most kindly consented to send the material selected for further examination on loan to me in Leiden. I am much indebted to Dr. White for facilitating my study of this interesting fauna. To Dr. A. T. Hopwood I owe valuable information and kind advice. Mr. A. J. Sutcliffe was very helpful in arranging the shipment of the collection. The photographs were taken by Mr. H. F. Roman of the Rijksmuseum van Natuurlijke Historie at Leiden, with the exception of those of Pl. 32, which were made at the British Museum (Natural History). All this is here gratefully acknowledged.

The results of my study are given in the present paper. The material is preserved in the Department of Palaeontology of the British Museum (Natural History); registration numbers are given in each case. Unless otherwise stated, the measurements recorded in the present work are in mm.

CARNIVORA

CANIDAE

Nyctereutes megamastoides (Pomel)

(Pl. 34, fig. 7)

In her second note on the Bethlehem fossils Miss Bate (Gardner & Bate, 1937) mentioned a small carnivore, " but its remains are extremely fragile and have not yet been extracted from the matrix ". When I received the collection the small carnivore remains had been treated with preservative, and removed from the matrix. It is evident that both the teeth and the bones were broken before removal from the deposit ; a number of teeth and some vertebrae are partially embedded in plaster, apparently because otherwise they could not be preserved.

Although the carnivore remains are in a bad state of preservation their specific identity is certain : they belong to *Nyctereutes megamastoides* (Pomel), a species characterized by its small teeth ; the large size of M^1 relative to P^4 ; the slightly reduced M^2 ; the high and laterally compressed lower premolars with a concave posterior slope of the protoconid which bears an accessory cusp only in P_4 ; the elongated M_2 ; and the oval-shaped M_3. The mandibular ramus is quite slender, and, above all, characterized by the peculiar development of the subangular process or lobe ; this character cannot be observed in the Bethlehem material. There are two portions of the left mandibular ramus (M 18521), one with P_{3-4}, and the other with M_{2-3}, and also parts of the coronoid and the condyloid processes, apparently of the same individual. The upper dentition is represented by a left canine (M 18516), P^{3-4} sin. and M^{1-2} sin. (much worn down) (M 18512), and a P^4 dext. (M 18521). Post-cranial remains (M 18521) comprise several cervical vertebrae including a partial epistropheus, proximal and distal portions of a right humerus, the proximal ends of a left radius and ulna, the head of a right femur, a left astragalus and calcaneum, and a great many fragments of the shafts of the long bones, of metapodials, foot bones, and phalanges. In Table I the measurements of the Bethlehem teeth are compared with those of *Nyctereutes megamastoides* from Perrier (Boule, 1889) and from Villarroya (Villalta, 1952 : 42). There is no significant difference between the Bethlehem teeth and those of the Villafranchian of Europe.

TABLE I.—*Measurements of* Nyctereutes megamastoides

	Bethlehem	Perrier	Villarroya
P^3, length	8·5	8	—
width	3·1	3	—
P^4, length	12·7	13	—
width	5·6	6	—
M^1, length	10·2	10·5	—
width	*c.* 12	11·5	—
M^2, length	7·1	7	—
width	—	9	—
P_3, length	7·8	7·3	7–8
width	3·0	2·5	2–3
P_4, length	9·6	9	7–9·5
width	4·0	3	3–3·5
M_2, length	8·2	8·5	7–9·5
width	5·6	5	5–6
M_3, length	4·4	4·5	—
width	3·8	3·5	—
Height of ramus between P_2 and P_4	12·5	13	—
Maximum width	6·5	6	—

Besides Perrier (Les Etouaires and Roccaneyra : Bout & Azzaroli, 1952) and Villarroya, other Villafranchian localities that yield *Nyctereutes megamastoides* are the Val d'Arno, Sénèze, and Saint Vallier (Viret, 1954). The remains described as *Canis* (*Nyctereutes*) *sinensis* Schlosser from the Villafranchian of Nihowan, China (Teilhard de Chardin & Piveteau, 1930 : 88, pl. 17, figs. 1–3, pl. 18, figs. 2–3), and from the Middle Pleistocene of Choukoutien (Pei, 1934 : 23, pl. 3, figs. 1, 2, 4–6, 8, 10 ; pl. 4, figs. 1–3) appear to be at most subspecifically distinct from *Nyctereutes megamastoides.* As related by Pei (1934 : 31), the Chinese *Nyctereutes* has been traced back to the Middle Pliocene ; the Villafranchian remains are, on the average, a little larger than those from the Middle Pleistocene, and the Upper Pleistocene remains (Pei, 1940 : 15) as well as the protohistoric remains of Anyang (Teilhard de Chardin & Young, 1936 : 7) are as small as, and have been referred to the Recent *Nyctereutes procyonoides* (Gray), the " raccoon-dog " of Eastern Siberia, Japan, China, and Northern Indo-China. In view of this fossil record it is probable that *Nyctereutes megamastoides* arose in China, and should be considered a Villafranchian immigrant to Europe. The remains in the Bethlehem collection indicate that *Nyctereutes megamastoides*, in its east-west migration at the beginning of the Pleistocene, spread also to the Eastern Mediterranean region. There are no records of the species from Africa.

FELIDAE

Homotherium (?) sp.

(Pl. 34, figs. 1, 2)

A large machairodontine is represented in the Bethlehem collection by a left M_1 (M 18511), incomplete in front as well as behind. The top of the paraconid is missing. The powerful anterior root (below the paraconid) is for the most part preserved; the posterior root is broken off. Although the development of the metaconid and of the talonid cannot be studied in the present incomplete specimen, the wide concave area between the paraconid and the protoconid blades internally, and the mode of wear of the crown are machairodontine. The greatest length of the crown must have been over 30 mm.; the greatest width is 14·1 mm. These figures suggest a form similar in size to *Homotherium crenatidens* Fabrini from Perrier (length of M_1, 32 mm.: Teilhard de Chardin & Piveteau, 1930: 116, footnote), a Villafranchian species also known from Sénèze, the Val d'Arno, Chagny, Villarroya, and Saint Vallier (Schaub, 1944; Viret, 1954, table opposite p. 184). Kretzoi (1954 : 250), whose *Epimachairodus* is a synonym of *Homotherium* Fabrini (Simpson, 1945 : 121; Arambourg, 1947 : 438; Viret, 1954: 78), records remains probably referable to *H. crenatidens* from the Villafranchian site of Kisláng in Hungary.

According to Schaub (1934), part of the material described as *Machairodus nihowanensis* by Teilhard de Chardin & Piveteau (1930, pl. 22, fig. 2) does not seem to be specifically distinct from *H. crenatidens* from the Villafranchian of Europe. This Early Pleistocene form from Nihowan is succeeded in the Middle Pleistocene by *Homotherium ultimum* (Teilhard de Chardin) from Choukoutien, the lower carnassial of which measures 32 by 12 mm. (Teilhard de Chardin & Pei, 1941 : 40).

Homotherium (?) sp. from Bethlehem is too incompletely known to allow of a definite identification. Similar large machairodontines are recorded from the Villafranchian of East and South Africa (Arambourg, 1947 : 438; Ewer, 1955 : 612). Whether the affinities of the Bethlehem form lie with the Eurasian or with the African species cannot be decided until better specimens are available.

PROBOSCIDEA

ELEPHANTIDAE

Archidiskodon cf. ***planifrons*** (Falconer & Cautley)

(Pl. 32; Pl. 34; figs. 3, 4; Pl. 35, figs. 1, 2)

A mandible without the ascending rami, collected by Dr. M. Stekelis in 1940 (M 18582, Pl. 32, figs. 1, 2), is one of the most diagnostic specimens found. Like several of the others, this specimen is crushed, indicating the pressure to which the bone-bearing beds were formerly subjected. The right horizontal ramus has been pressed on from above and laterally, but the left ramus is only slightly distorted. The last molars are *in situ* on both sides; the M_3 dext. is fractured between the 4th and 5th plates from the front, and the two portions are displaced along the fracture, but M_3 sin. is undamaged. What remains of the ascending rami shows that their anterior borders are on a level with the 6th plates of M_3.

The symphysis is obliquely prolonged downward, forming a projection or " beak " just as in the mandible of *Archidiskodon planifrons* from the Siwalik Hills figured by Falconer & Cautley (1845, pl. 8, fig. 2*a*). This is a very characteristic feature of the species in question ; it is also present in the mandibles from Sénèze and from Chagny (Mayet & Roman, 1923 : 81, fig. 13). In the Bethlehem mandible as well as in the Siwalik specimen, which I have studied in the British Museum (Natural History) (regd. 36736), the beak is not complete ; in the French specimens the length of the beak is about equal to the height of the ramus below M_3. The portion preserved in the Bethlehem mandible is about 7 cm. long ; it has a height of 7–8 cm., and is about 4 cm. wide, just as in the Siwalik specimen referred to above. Because of the presence of this anterior downward projection of the symphysis the lower border of the ramus is concavo-convex from before backward, the convexity beginning approximately at the level of the anterior border of M_3. Presumably part of the M_2 was still in place at the time of the animal's death, but is now lost. The height of the ramus below the middle of M_3 is 15 cm., equal to the greatest width, measurements that correspond well with those of the mandible of *A. planifrons* figured by Falconer & Cautley (1845, pl. 8, fig. 2) as well as with those of an unfigured mandible of the same species in the British Museum (M 3090). There are two mental foramina on each side, a large one at the middle of the height of the outer surface of the ramus, on a level with the posterior border of the symphysis, and a smaller one about 5 cm. below and anterior to the former. In the unfigured mandible of *A. planifrons* from the Siwaliks the number and position of the foramina is the same ; in the figured mandible the larger of the mental foramina is duplicated on the right side but single on the left, and the distance between this and the smaller foramen is 6·5 cm. On either side of the depressed anterior surface of the beak a ridge runs upward to the alveolar edge ; the upper portion of this ridge is badly damaged in the Bethlehem mandible, but its lower part forms an angle of about 120° with the occlusal surface of the molar as in the two Siwalik specimens.

So far as the state of preservation of the Bethlehem mandible permits one to form an opinion, there is nothing to distinguish it from the mandible of *Archidiskodon planifrons* from the Upper Siwaliks.

The same is true of the molar, M_3. In the Bethlehem mandible M_3 is worn to and including the 6th plate from the front, and there are ten plates in all, besides the talonids. The greatest length of the crown, in a straight line from the middle of the anterior border to the heel, is 290 mm.; the greatest width, at the 2nd plate from the front, is 93 mm., cement included, and 84 mm. exclusive of cement. The height of the foremost unworn plate, plate 7, is 94 mm.; the slightly worn 6th plate has the same height and, therefore, must have been somewhat higher when unworn. In height it cannot have exceeded 100 mm., however, for the dentine cores of the conelets do not show yet, and the enamel thickness of the plates is about 6 mm. The cement coat is heavy ; even the sides of the plates are completely covered.

The enamel figure of the anterior talonid is confluent with that of the first plate ; only a labial enamel fold remains to indicate the boundary between the two. Plate 1 has a postero-median enamel projection that makes contact with a similar projection on the anterior surface of plate 2. Plates 2 and 3 are worn to single enamel figures, with median anterior and posterior expansions blocking up the valleys in between, which are open on either side, the antero-posterior width of the valleys being equal to that of the plates. The enamel is 6 mm. thick, and is slightly crimped.

Passing backward along the crown, the enamel expansions of the plate figures become less marked. In plate 3 the enamel border forms an almost entire loop, just to the labial side of the median line of the crown, with a diameter of 13 mm. and projecting 8 mm. posteriorly. The posterior expansion of plate 4 projects only 5 mm. beyond the surface. The width of the enamel figure of plate 4 is only 70 mm., whereas the greatest width of the same plate, including cement, is the same as that of plate 2, 93 mm. The enamel figure of plate 4 is constricted on either side of the median expansion, forming a transversely elongated enamel figure on either side of the central, antero-posteriorly extended figure. Of the lateral figures that on the lingual side is longer. In the right M_3 plate 4 is slightly less worn than that in the left, and the three enamel figures are distinctly separate.

In plate 5 the grooves between the conelets are still visible. There appear to be four conelets, the second from the labial side being more extended antero-posteriorly than either of the others. It is this conelet that forms the central expansion of the more worn plates in front. In plate 5 the two central conelets together measure 26 mm. transversely, the total width of the four enamel conelets being 63 mm. The greatest (basal) width of this plate, cement included, is again 93 mm. Plate 6 has the four conelets just touched by wear, the two in the centre occupying a width of 26 mm., as in plate 5. In plate 7 the conelets are still covered up with cement; evidently this plate had not erupted at the time of death.

From plate 7 backward the plates begin to diminish in width as well as in height; the basal widths cannot be measured as the base of the crown is not fully exposed, but the heights decrease from 88 mm. in plate 8 to 80 mm. in plate 9, then to 70 mm. in plate 10, the terminal full plate. The talonid is barely 50 mm. high with a width of about 35 mm., and is completely covered with cement. Because of the outward curvature of the hinder end of the molar the talonid is rather obliquely placed: it is in the same antero-posterior line as the labial ends of the foremost plate-figures.

The laminar frequency of the molar, that is, the number of plates per 10 cm. of antero-posterior length, varies somewhat with the place in which it is taken. The laminar frequency is just under 4 in the middle of the occlusal surface, the distance from the middle of the valley between plates 1 and 2 to the middle of the valley between plates 5 and 6 (covering four plates and four cement intervals) being 106 mm. When taken at the base lingually, which is exposed from the 4th plate backward in the left M_3, the laminar frequency is distinctly lower, not only because of the curvature of the long axis of the crown with the convexity inward, but also because of the rootward divergence of the plates, characteristic of lower molars. The laminar frequency is only 3 at the base lingually; at the labial alveolar margin it is 4.

The low plate formula (× 10 ×), the low laminar frequency (3–4), the height of the crown that hardly exceeds the greatest width (height-width index (plate height-width indices cannot be given) just over 100) the presence of median looped expansions of the enamel figures of the moderately worn plates, the great thickness of the enamel (6 mm.), and the abundance of cement, are characters that leave no doubt as to the specific identity of the Bethlehem elephant : it belongs to the most primitive archidiskodont stage exemplified by *Archidiskodon planifrons* of the Upper Siwaliks of India. In the characters of the mandible, notably in the downturned anterior end of the symphysis, the present Bethlehem specimen agrees perfectly with those from the Siwaliks and from certain Villafranchian sites in Europe.

A number of isolated molars and molar fragments in the Bethlehem collection are described below.

A right upper second molar collected in 1940 (M 18523, Pl. 34, figs. 3, 4) is only slightly damaged. The molar carries nine plates, five of which are worn, as well as the damaged anterior and posterior talons. The roots are preserved for the most part. The crown as a whole is slightly curved : the lingual surface is concave from before backward, and the labial surface is convex antero-posteriorly. The base of the crown is concave antero-posteriorly towards the roots. The total length of the crown is 262 mm.

The enamel figures of the anterior worn plates show the characteristic median expansions (just to the lingual side of the median line), the posterior loop of the 2nd and the anterior loop of the 3rd plates almost make a contact across the valley, which is filled with cement. The enamel thickness is 5–6 mm. Plate 5 has four conelets, the second from the lingual side being the largest. The remaining plates are fully embedded in cement, as well as the incomplete and very small terminal plate, the talon. Measurements are given in Table II.

TABLE II.—*Measurements of* M^2 *dext. of* A. *cf.* planifrons (*M* 18523)

	No. of plate									
	1	2	3	4	5	6	7	8	9	Talon
Width . . .	—	102	103	100	100	100	97	83	55	*c.* 30
Height . . .	—	—	—	—	—	84	81	74	*c.* 58	—
Height-width index .	—	—	—	—	—	84	84	89	*c.* 105	—

As shown by the height-width indices of the unworn plates, the plates are either lower or slightly higher than wide. The laminar frequency of the present specimen varies from 3 (in the middle of the worn surface) to $3\frac{1}{2}$ (at the base lingually). There is one powerful anterior root supporting the first two plates, a very large single root supporting the posterior five plates, and three intermediate roots, two labial and one lingual. The apical portions of these roots are broken off ; the portions preserved are as long as the height of the (unworn) crown.

In the Upper Siwalik *A. planifrons* the number of plates in M^2 varies from eight to nine. The length of the crown of the Bethlehem M^2 (262 mm.) is greater than that of any M^2 of *A. planifrons* from the Siwalik Hills as recorded by Falconer and by Osborn (see Osborn, 1942 : 949, 954 : 191–221 mm.), but this is not a matter of great moment, for an unquestionable M_2 of *A. planifrons* from the Punjab (Hooijer, 1955 : 99–101) is 261 mm. long against 178–204 mm. in Falconer's and Osborn's series of

Siwalik M_2, which tends to show that upper second molars of the size of the Bethlehem specimen occur in the Upper Siwalik *A. planifrons* also.

A left upper second molar (M 18524) is unworn (Pl. 35, figs. 1, 2). There are eight plates, plus the talons. Much of the enamel along the base of the crown is gone: the lingual edges of plates 1, 2, 7, and 8, and the external conelets and edges of plates 3 to 7, inclusive, are missing. However, it is mostly only the enamel coat that is lost, and the enamel thickness, wherever exposed in the present specimen, is 6 mm. Therefore, it is possible to give the basal widths of most of the plates by taking the actual width, and adding to it 6 mm. for the missing enamel layer. Cement is heavily developed; it covers up the conelets and the edges of all but the hindmost three plates. The conelets of plates 4 and 5 are destroyed, and the full height of these plates cannot be measured.

TABLE III.—*Measurements of M^2 sin. of* A. *cf.* planifrons (*M* 18524)

	No. of plate								Talon
	1	2	3	4	5	6	7	8	
Width	93	100	105	—	105	103	95	71 .	50
Height	69	74	70	—	—	70	65	54 .	33
Height-width index .	74	74	67	—	—	68	68	76 .	66

The number of conelets in the anterior plates is difficult to see because of the cement cover. There is a slight dislocation in the median line of plates 1–3, the labial portions being placed slightly more forward than those on the lingual side. Plate 6 bears five conelets, the two on the labial side are broken off. In plate 7 the number of conelets is likewise five, but in plate 8 there are four conelets only. The talon consists of three cones, and a very small accessory cone on the lingual side.

The length of this M^2 sin. is 242 mm., less than that of the M^2 dext. recorded above. The number of plates is also less (eight instead of nine), but the laminar frequency is the same in both specimens, viz., 3 to $3\frac{1}{2}$. The characteristic median expansions do not show because all the plates are unworn. It will be seen from Table III that the full height of the plates is only two-thirds to three-fourths the basal width (exclusive of cement), which indicates that the M^2 sin. is lower-crowned than the M^2 dext.

The anterior root is divided in the middle, and is preserved for a few centimetres only; the main root is broken off almost entirely, and the junction between the two is on a level with that between the 3rd and 4th plates of the crown.

Another specimen with unworn plates is the hinder end of an M^3 dext. (M 18527). It is broken off anteriorly through the 7th plate from behind, and is much corroded. The enamel is lost along the lingual edges of the plates, exposing the dentine cores. A large portion of the labial surface is covered with plaster. The enamel of the conelets of the plates is broken. Of the roots nothing is preserved. However, allowing for an enamel thickness of 5 mm. it is possible to estimate the widths at base of all the plates, and the height measurements of all but the last two plates and the talon, which are so much damaged that their height cannot be measured. The laminar frequency is 4.

TABLE IV.—*Measurements of* M^3 *dext. of* A. *cf.* planifrons (*M* 18527)

	No. of plate from behind							
	VII	VI	V	IV	III	II	I	Talon
Width	107	95	88	84	75	70	55	*c.* 25
Height	88	80	75	69	65	—	—	—
Height-width index	82	84	85	82	87	—	—	—

Table IV shows that the unworn plates are less high than wide ; this is also true of the unworn M^2 sin. from Bethlehem.

A portion of a molar consisting of seven fragments (M 18561) contains parts of two unworn, and two worn plates. The width and height of one of the unworn plates (the enamel thickness is 6 mm.) can be determined as 95 mm., and 85 mm., respectively, giving a height-width index of 89, the maximum figure for this index found in the molars described above. The present specimen is broken through the median line of the crown, and clearly shows the V-shaped valleys between the plates, open down to the bottom as is characteristic of archidiskodonts. The laminar frequency of the present fragment is 3½. Its serial position cannot be determined with certainty, but because of the relatively great basal width and low laminar frequency it presumably formed part of a penultimate or a last molar.

A fragment of a molar, probably of the same specimen as the last (M 18525), comprises part of an unworn plate 84 mm. high but of unknown basal width. There are at least five conelets to this plate, the grooves between which remain distinct rootward to over one-half the height of the crown.

Two last lower molars, one right and one left, evidently of the same individual (M 18528 and M 18529) are very much worn down. Their anterior portions are missing ; the left M_3 still comprises seven plates, the right, five only . The anterior plates have their dentine surfaces coalesced as the valleys between them are partially or entirely worn out. The laminar frequency of the occlusal surface is 3½. The enamel is very thick : 5–6 mm. The plate figures of the last four plates are irregularly expanded in the centre ; their lingual portions are placed more forward than the labial, and the enamel bands make contact in the median line of the crown. The greatest width of the crown (at the 5th plate from behind) is *c.* 100 mm., exclusive of cement which is well developed all round the crown. At the 2nd plate from behind the width is 85 mm., and at the talonid, 40 mm. There are accessory enamel cusps labially of the talonid and of the last plate as well as at the lingual entrances to the valleys. Height measurements cannot be given as even the talonids are worn. The main posterior root supports at least six plates and is of great length, the depth of the root below the talonid is 15 cm. at least.

There remain a number of molars, most of them very much worn down, that are either too incomplete or too much damaged for anything of value to be deduced from them. It is evident, however, that they belong to the same primitive archidiskodont elephant as the better-preserved specimens above described ; their enamel is very thick, the laminar frequency is low, the valleys are V-shaped, and the roots are very long. Two much worn molars, evidently of the lower jaw as their occlusal surfaces are concave from before backward (M 18557, M 18560) display these characters very clearly. The laminar frequency is approximately 4; the long roots are distinctly recurved backward. M 18557 seems to have had seven plates only, and presumably represents M_1 sin. The roots indicate that the length of the crown probably did not exceed 165 mm. Width measurements cannot be given. The median expansions of the enamel figures show well in a posterior fragment of another lower molar (M 18554) the root of which is 13 cm. long as preserved. A much worn crown fragment without the roots (M 18538) holds four plates in 10 cm. of length; the same laminar frequency obtains in a fragment of an upper molar (M 18526) that is interesting because it has had small stones pressed down on the plates with such force that these have been partially broken, and the crown surfaces deflected from their normal position. The following specimens are too fragmentary for their position to be determined: nos. M 18530, M 18531, M 18539, M 18540, M 18541, M 18543, M 18544, M 18551, M 18559.

As mentioned above the most complete and first described specimen of the Bethlehem elephant, viz., the mandible obtained during the 1940 season (M 18582) is indistinguishable from *Archidiskodon planifrons* from the Upper Siwaliks of India. However, in the isolated and (partially or entirely) unworn molars we observe a character in which it appears to differ from the Siwalik *A. planifrons.*

All the relevant data on the molars of the Upper Siwalik *A. planifrons* described and figured by Falconer and by Osborn are contained in two tables by Osborn (1942 : 949, 954). Upper Siwalik specimens of *A. planifrons* collected by Eug. Dubois in the Punjab, and now in the Leiden Museum, including a fine skull closely resembling the British Museum specimen (Falconer & Cautley, 1845, pls. 9, 10), have been described by the author (Hooijer, 1955 : 96–100). The material of *A. planifrons* obtained by the Yale North India Expedition of 1932 (Hooijer, 1955 : 100–102; 1956) includes the geologically oldest specimen yet obtained, viz., a portion of M^3 collected near the base of the Tatrot zone first recorded by Lewis (1937 : 198), basal Upper Siwaliks and basal Pleistocene. This specimen (Hooijer, 1956) cannot be distinguished from other M^3 of *A. planifrons* (the bulk of the material is presumably from the Pinjor zone overlying the Tatrot zone), and the plates are higher than wide (height-width indices 110–124). The M^3 *in situ* in the British Museum skull of *A. planifrons* has a height-width index of 115. An M^3 from the Punjab in the Leiden Museum (Hooijer, 1955 : 102, 103) has five unworn plates very nearly as high as wide, the height-width indices varying from 97 to 105.

As can be seen from the tables by Osborn (1942 : 949, 954) the height of the molars of *A. planifrons* as given by Falconer and by Osborn is either greater or much less than the width of the same specimens. Fortunately, most of the specimens have been figured, and from the figures it is evident that where the height exceeds the width the crown has unworn plates, e.g., M^3: Falconer & Cautley, 1845, pl. 10 (width 89 mm., height 102 mm., index 115); M^1: Falconer & Cautley, 1845, pl. 6, fig. 5 (width 69 mm., height 77 mm., index 112); M_3: Falconer & Cautley, 1845, pl. 12, fig. 13 (width 91 mm., height 114 mm., index 125); pl. 12, fig. 12 (width 89 mm., height 102 mm., index 115), Osborn, 1942, fig. 842 (width 101 mm., height 124 mm., index 123); fig. 835 (width 109 mm., height 114 mm., index 105). On the other hand, in those molars where the height is less than the width, the height has been taken at a worn plate, e.g., M^3 : Falconer & Cautley, 1846, pl. 14, fig. 8 (width 89 mm., height 63 mm.), Osborn, 1942, fig. 834 (width 100 mm., height *c.* 88 mm.) ; M^1 : Osborn, 1942, fig. 833 (width 94 mm., height *c.* 66 mm.) ; fig. 832 (width 80 mm., height 65 mm.) ; fig. 831 (width 90 mm., height 67 mm.) ; M_3 : Falconer & Cautley, 1845, pl. 11, fig. 5 (width 105 mm., height 89 mm.), Falconer & Cautley, 1846, pl. 18A, fig. 1 (width 104 mm., height 81 mm.) ; pl. 14, fig. 9 (width 89 mm., height 77 mm.), Osborn, 1942, fig. 855 (width 80 mm., height 53 mm.) ; fig. 839 (width 78 mm., height 45 mm.) ; M_1 : Osborn, 1942, fig. 838 (width 80 mm., height 45 mm.).

The examples given above will suffice to show that the unworn molar crowns of *A. planifrons* from the Upper Siwaliks are either about as high as wide, or higher than wide. In those specimens where the height is less than the width (see above) it is clear from the figures that the height recorded is not the height of the unworn plate, and height-width indices based on these figures are meaningless. They are only indicative of the degree of wear shown by the molars in question, and should be excluded from comparison.

Among the *Archidiskodon* molars from Bethlehem, only the third molars in the mandible M 18582 have a height-width index of just over 100 ; in the remaining specimens the plates are neither fully nor even nearly as high as wide, the highest height-width index found being 89, the lowest (talons excluded) being 67.

It is therefore evident that the Bethlehem *Archidiskodon* does not belong to the species *A. planifrons* as known from the Upper Siwaliks (Tatrot and Pinjor zones) of India. The mandible is within the variation limits of the Siwalik specimens, but the unworn plates of the upper molars (two M^2 and one M^3) show that the Bethlehem *Archidiskodon* is more primitive than *A. planifrons* in the height of the unworn crown being less than the basal width.

Certain primitive archidiskodont molars from the Vaal river gravels in the Transvaal, South Africa, have been described by Osborn (1934, 1942 : 983–988) as *A. subplanifrons*, and *A. proplanifrons*, respectively. Although the Vaal river specimens are claimed by Osborn to be much more primitive than the most primitive molars thus far discovered in the Siwaliks (*A. planifrons*) the point is somewhat difficult to make as none of the South African molars is unworn. The holotype of *A. subplanifrons*, an M_3 dext. (Osborn, 1934, fig. 1 ; 1942 : 987, fig. 874) is worn to and including the hind talonid, and is broken off in front through the 5th plate from behind. The laminar frequency is 4, the enamel thickness, 4 mm. The valleys are V-shaped in longitudinal section, and the enamel figures of the 3rd and 4th plates from behind have median anterior and posterior expansions. In all these characters the specimen resembles the Siwalik *A. planifrons*, and as neither the plate formula nor the exact height of the crown can be determined it would seem unjustified to create a new species for the inclusion of this specimen. The estimated height of the plates is given by Osborn as 53–63 mm.

The holotype of *A. proplanifrons* Osborn (1934 : 10, fig. 2 ; 1942 : 986, fig. 873) is an M^3 dext. with all the plates and the hind talon worn ; it is broken off in front of the 5th plate from behind. The laminar frequency is 3, the thickness of the enamel is 5 mm. Again, there is no way of telling the full number of plates or the height of the unworn crown ; Osborn gives the height of the last plate as 55 mm.; the basal width of the same plate (measured from the figure) is 66 mm. These measurements are intermediate between those of the last plates in the two second upper molars from Bethlehem recorded above (height *c.* 58 mm., and 54 mm., respectively, and width 55 mm. and 71 mm. respectively), and the resulting height-width index is also intermediate : 83 in *A. proplanifrons,* and *c.* 105, and 76, in the two Bethlehem specimens. However, in the Bethlehem molars the height increases to 84 mm., and 74 mm., respectively, in the more anteriorly placed plates, and Osborn's reconstruction of the type of *A. proplanifrons,* in which all the plates are shown of the same height as the last, is extremely improbable. The last plate is always lower than the others. Osborn further compares the M^3 of *A. proplanifrons* with an M_3 of *A. planifrons* (Amer. Mus. 19965 ; Osborn, 1934, fig. 4 ; 1942, figs. 840, 876) all the plates of which are worn but boldly reconstructed in longitudinal section to a height of about 55 mm. This reconstruction, again, is very improbable, for in the unworn M_3 of *A. planifrons* the crown height is seen to rise to 124 mm. (Amer. Mus. 19951 ; Osborn, 1942, figs. 842, 845, and 855). Osborn (1934 : 9; 1942 : 986) says that the worn M_3 of *A. planifrons* is " the most primitive stage found in the large series of the *Archidiskodon planifrons* molars collected by Barnum Brown in the Upper Pliocene Pinjor horizon of the Siwaliks, India ", but it has a laminar frequency of 4½, whereas the partially unworn M_3, thrice figured by Osborn, has a laminar frequency of 3½–4½, and another (Amer. Mus. 19952 ; Osborn, 1942, fig. 835) is only 3½–4, which brings *A. planifrons* within the range of laminar frequencies of the South African and Bethlehem types (3–4).

As stated by Dietrich (1942 : 79) and by Cooke (1947 : 455) *A. subplanifrons* and *A. proplanifrons* are conspecific. In my opinion there is no proof at present that they can be specifically distinguished from the Upper Siwalik *A. planifrons* proper, a point that cannot be settled until unworn, entire molars have been found in the same deposits from which the types of *A. subplanifrons* and *A. proplanifrons* were obtained. In revising the South African " species " of *Archidiskodon,* Cooke (1947 : 507) placed *A. subplanifrons* (including *A. proplanifrons*) in group I : " Archidiskodonts (with broad crowns and thick enamel). A : Low Crowned (less than 75 mm.) ", thereby accepting Osborn's low estimates of the crown heights. It seems to me that such a group for the South African types is invalid prior to the discovery of molars with unworn full plates.

Archidiskodon exoptatus Dietrich (1942 : 72) from the Lower Pleistocene of the Southern Serengeti in Tanganyika, East Africa, is very close to the Upper Siwalik *A. planifrons* ; the unworn full plates of the molars are higher than wide. The molars from Kanam and Laetolil, East Africa, described by MacInnes (1942 : 86) as *Archidiskodon planifrons nyanzae,* are all worn ; their laminar frequency is about 3½. None of the molars described by Dietrich (1942) as *A. exoptatus* has a laminar frequency of less than 4.

The North African *Elephas africanavus* Arambourg (1952), found in the Villafranchian (Lower Pleistocene) of Ichkeul, Tunisia, has molar crowns that are either very slightly lower, or higher than wide (height-width index of type M_3, 97 ; of M^1, 110), which is within the limits of the Upper Siwalik *A. planifrons* (97–125, see above). The laminar frequency is 3½ to 4½, the enamel thickness, 4–5 mm. These specimens also appear to be indistinguishable from those of *A. planifrons.*

Archidiskodon planifrons has also been recorded from Villafranchian sites in Europe

(Osborn, 1942 : 961–969 ; Hooijer, 1953) ; the most primitive specimens have laminar frequencies of $3\frac{1}{2}$–4, and their crowns are not higher than wide. It should, however, be realized that these specimens might equally well represent primitive variants of *Archidiskodon meridionalis* (Nesti) ; the molars of these two species grade imperceptibly into one another, without a break to indicate a convenient boundary line between low-crowned *A. planifrons* and higher-crowned *A. meridionalis*.

At the end of this brief survey of primitive Eurasian and African archidiskodonts, let us reconsider the *Archidiskodon* from Bethlehem. It is apparently identical with *A. planifrons* in mandibular characters, but has upper molars that are lower than wide in the unworn state. There are no counterparts of such molars among the known material of the Upper Siwalik *A. planifrons* ; even the geologically oldest specimen, viz., the M^3 from the base of the Tatrot zone (Hooijer, 1956), has unworn plates higher than wide. The East and North African archidiskodonts mentioned above agree with *A. planifrons* in relative crown height, and so do the most primitive archidiskodonts from the Villafranchian of Europe. The crucial question is whether the South African *A.* " *subplanifrons* " really has lower molar crowns than the Upper Siwalik species ; this is still unknown. The Bethlehem elephant appears to represent a somewhat less advanced evolutionary stage than *A. planifrons* proper, and should perhaps be sub-specifically distinguished. As long as the " *subplanifrons* " problem has not been solved it would seem best to place the Bethlehem elephant on record as *Archidiskodon* cf. *planifrons*.

A large portion of an elephant's tusk, length almost 170 cm. (M 18584), diameter 13 cm. proximally, is so much distorted that the amount of curvature is uncertain. The tusk, however, appears to have been nearly straight as far as preserved. There are also a number of vertebrae and limb bones of the Bethlehem elephant, but except for an atlas they are in a very bad state of preservation. The measurements of the atlas are given in Table V.

TABLE V.—*Measurements, in centimetres, of Atlas of* Archidiskodon *cf.* planifrons *M* 18579)

Total height	26
Facies articularis cranialis, vertical	15
transverse	*c.* 9
Antero-posterior diam. of corpus	9·5
Height of foramen vertebrale	13·5
Least width of *idem*	*c.* 6
Foramen transversarium, diameter	3
Foramen for first cranial nerve, diameter	1·5

The height of the atlas of the *A. planifrons* skeleton from Chagny-Bellecroix is 27 cm. (Mayet & Roman, 1923 : 82).

The following approximate measurements have been taken from a poorly preserved radius: length *c.* 80 cm., greatest proximal width *c.* 11 cm., and greatest distal width *c.* 16 cm.

The measurements of a left femur (M 18583) are, length from head to media condyle *c.* 112 cm., greatest proximal diameter over head and great trochanter *c.* 33 cm., least width of shaft *c.* 14 cm, greatest distal width *c.* 24 cm.

In the skeleton of *A. planifrons* from Chagny-Bellecroix (Mayet & Roman, 1923 84) the femur measures 133 cm. from head to medial condyle.

In a portion of the pelvis from Bethlehem (M 18585) the diameter of the acetabulum is 21 cm.

A right and a left patella, evidently of the same individual (M 18535 and M 18588), agree in the following dimensions : Height 17·5 cm., width, 13 cm., greatest antero-posterior diameter, 9 cm.

The reference of the tusk and post-cranial material to *A.* cf. *planifrons* is provisional but it is probable that these specimens belong to the same species as the mandible and the molars described above because there is no evidence of the presence of more than one species of elephant in the Bethlehem fauna.

PERISSODACTYLA

EQUIDAE

Hipparion sp.

(Pl. 35, figs. 3–6)

An isolated right lower last molar (M 18518, Pl. 35, figs. 3–4) gives evidence of the presence of *Hipparion* in the Bethlehem fauna. The tooth is in the germ stage and lacks the cement coating ; the height of the crown unfortunately cannot be determined. However, several slightly worn M_3 of *Hipparion gracile* (Kaup) from the Pontian of Pikermi in the British Museum (Natural History) agree with the Bethlehem M_3 in every visible detail of their structure. The sharp vertical groove between metaconid and metastylid is a character common to *Hipparion* and the zebras, but *Equus stenonis*, the smallest zebrine horse of the Villafranchian, has an M_3 larger than the Bethlehem tooth (see Major, 1877–80, pl.7, figs. 21, 30, 31). The Bethlehem M_3 has a length of 25 mm. and a greatest width of 9·5 mm., exclusive of cement. A Pikermi specimen measures 25·5 mm. antero-posteriorly near the top, and 26·5 mm. near the base of the crown (also exclusive of cement), and the greatest transverse diameter of the crown is 11·5 mm., some cement included.

In *Hipparion antelopinum* (Falconer & Cautley) M_3 measures 28 by 12·5 mm.; in *H. theobaldi* (Lydekker) M_3 measures 30 by 13 mm. (Colbert, 1935 : 148). These are Middle Siwalik species, but an isolated M_3 dext. of *Hipparion* from the Tatrot zone, basal Upper Siwaliks, exhibited in the British Museum (Natural History) is very similar : length 29 mm., and width, 11·5 mm., inclusive of cement. *Hipparion* also occurs in the Pinjor zone of the Upper Siwaliks (Pilgrim, 1938 : 447, 449 ; 1944 : 32) where it is associated with *Equus* ; the latter genus is absent from the underlying but likewise Villafranchian Tatrot zone (Hooijer & Colbert, 1951).

Hipparion is known to occur in several European Villafranchian faunas, such as those of Roccaneyra near Perrier, France (Stehlin, 1904, 1929 ; Bout & Azzaroli, 1952 : 39), of Villarroya, Spain (Villalta, 1952 : 107), and of Kisláng, Hungary (Kretzoi, 1954 : 251). Of these faunas only that of Villarroya lacks *Equus*, but, as remarked by Viret (1954 : 182) there is no reason to consider Villarroya any older than the Villafranchian faunas with *Equus*. The last lower molar of the Roccaneyra and Kisláng hipparions is unknown ; three specimens of the Villarroya *Hipparion crusafonti* Villalta measure 26·2 to 29·9 mm. in length, and 10·1 to 11·5 mm. in width, cement included (Villalta, 1952 : 119).

Although the crown height of the Bethlehem M_3 cannot be measured exactly it seems improbable that it belongs to the very hypsodont hipparion (*Stylohipparion*) which occurs in the Villafranchian of North and East Africa (Arambourg, 1947, 1949 ; Dietrich, 1942) in association with *Equus*.

There is a second specimen in the Bethlehem collection referable to *Hipparion*, viz., the distal portion of a small metapodial (M 18576, Pl. 35, figs. 5, 6). This specimen seems to represent the lateral metacarpal or metatarsal, either II sin. or IV dext. The total length of the fragment is only 4 cm. The shaft is much compressed transversely : the surface facing the large median metapodial is flat, the abaxial surface convex. The anterior edge is more marked than the posterior, which is rounded. The distal extremity, somewhat curved backward on the line of the shaft, likewise is much flattened transversely, and consists of a single condyle with a fossa on either side. The fossa on the abaxial surface is marked, and surmounted by a weak tubercle. The distal antero-posterior diameter is 17 mm., the distal condyle width only 8 mm. The shaft is 7 mm. transversely, and diminishes in antero-posterior diameters from 15 mm. just above the distal condyle to 11 mm. at a point only 2 cm. higher up, where the bone is broken off.

The present metapodial fragment closely resembles the fourth metatarsal of *Hipparion* sp. from Roccaneyra figured by Stehlin (1929, fig. 2B), a cast of which has been figured as ? *Hipparion crusafonti* by Villalta (1952 : pl. 23). Whether the specimen from Bethlehem belongs to the fore or to the hind foot, and whether it is the outer or inner lateral metapodial cannot be made out. Determination of its exact position must await the discovery of more complete material, but this fragment provides definite proof of the presence of a three-toed horse in the Bethlehem fauna.

RHINOCEROTIDAE

Dicerorhinus etruscus (Falconer)

(Pl. 33, fig. 5)

In the Bethlehem collection there is an almost entire skull (M 18542, Pl. 33, fig. 5) which unfortunately is crushed to a considerable extent. All the parts are firmly cemented with plaster, evidently in the positions in which they were found. A fragment of the palate with P^{3-4} sin. lies upside down in the right lateral nasal notch, a partially exposed tooth (? P^2 sin.) is seen in the right temporal fossa, and a portion of distinct bone, possibly of the mandible, projects upward through the left temporal fossa. The ventral surface of the skull is concealed by a thick mass of cement. The left zygomatic arch is missing, and the right is broken.

The occipital portion of the skull is rather well preserved, but somewhat distorted; the right maxillary and the zygomatic process of the jugal are displaced outward and upward, and are almost in the plane of the dorsal surface of the skull. The right upper tooth series is more or less in place but comprises only P^3–M^2, the anterior premolar (P^2) and the third molar being lost.

The dorsal surface of the skull shows numerous cracks and fractures, and the shape of the dorsal profile, therefore, cannot be relied upon. The nasals (incomplete on the left side) show a slight rugosity for a horn, and there is no trace of a nasal septum on their ventral surface; the skull, therefore, is probably that of a female (cf. Thenius, 1955). The rugosity for the second, frontal horn is likewise slight, and hardly raised; behind it the skull surface is slightly concave antero-posteriorly, and gently rises into the nuchal crest, which overhangs the occiput. The infra-orbital foramen is just behind the nasal notch, which ends posteriorly on a level with the anterior border of P^4. The anterior border of the orbit is above the anterior portion of M^2. The post-tympanic process has united with the post-glenoid process below the sub-aural channel.

In all these structural characters the skull closely resembles those of *Dicerorhinus etruscus* figured by Falconer (1868, pl. 26), Schroeder (1903, pl. 1, figs. 1, 1*a*), and Schaub (1944, fig. 1), except for the absence of the nasal septum, which apparently is confined to males (Thenius, 1955 : 11–14). The greatest length of the Bethlehem skull, from nuchal crest to tip of nasals, is about 68 cm. the greatest length of the Florence Museum skull figured by Falconer (1868) as well as by Schroeder (1903, pl. 1, figs. 2, 2*a*) is slightly less, 64 cm. The length from the anterior border of the right orbit to tip of nasals is about 34 cm. in the Bethlehem skull, against about 32 cm. in the Florence Museum skull. The height of the nuchal crest, right side, from lower surface of condyle, is 15·5 cm. against 16·5 cm. in the Florence Museum skull. The greatest width of the frontals (right half only) is 11·5 cm. in both skulls (Falconer, 1868 : 358). These figures tend to show that the Bethlehem skull agrees well with that of *D. etruscus* in size; further measurements cannot be given because of the crushing of the specimen.

The dentition of the present specimen is badly preserved; all the internal borders of the crowns are incomplete, and the external surfaces broken and distorted. It is, therefore, impossible to measure the crowns exactly. However, there is little or no crown cement, the anterior cingulum is prominent and slightly inclined upward, there is a horizontal lingual cingulum (P^3 sin.), and a high and wide entrance to the medisinus; all characters pointing to *D. etruscus* (Falconer, 1868 : 354–368; Dawkins, 1868; Wüst, 1901 : 273; Schroeder, 1903; Bernsen, 1927; Vialli, 1956). In all the premolars and molars present the crochet is rather large, and united to the crista so as to cut off a medifossette; this is an individual peculiarity that is apparently rare in *D. etruscus*, although in many of the specimens figured by the above cited authors there are traces of cristae beside the large crochets (Falconer 1868, pl. 29; Dawkins, 1868, pl. 8; Wüst, 1901, pl. 4, figs. 2, 4, 7, 8; Schroeder, 1903, pl. 4; Bernsen, 1927, pls. 1, 2; Vialli, 1956, pl. 1, fig. 5). Small cristae are also seen in the complete upper dentition of *D. etruscus* figured by Tuccimei (1891, pl. 11).

In the collection there is also a fragment of the maxillary with the right P^3–M^2

(M 18563, M 18570). The two premolars have broken off at their bases, but the anterior portion of the ectoloph of P^4 dext. is preserved (M 18577). Of M^1 a small posterior portion, with the laterally compressed post-sinus, only remains. M^2 is the best preserved tooth, lacking, however, the hinder portion. The anterior cingulum is only slightly inclined upward toward the external side, the crown is low, and does not show any cement, there is an inner cingulum forming a knob at the wide entrance to the medisinus, and the crochet is large. There is also a very weak crista, which would, however, never unite with the crochet. The antero-transverse diameter of the crown base of M^2 is 59 mm.

Nos. M 18563, M 18572, and M 18577 comprise a number of fragments, some of which may well have formed part of the dentition just mentioned.

An isolated M^1 or M^2 sin. (M 18562), partially restored with plaster, has all the characters distinctive of *D. etruscus* enumerated above. There is no crista, but a small antecrochet. The lingual cingulum is stronger than that in M 18563.

A left (?) M^1 (M 18564), found in 1935, is very incomplete but shows the characteristic inner cingulum.

A broken and distorted portion of the left ramus of the mandible with part of M_3 *in situ* (M 18558) is of the 1940 season. Portions of lower molars are further contained in specimens M 18574 and M 18514.

Dicerorhinus etruscus (Falconer), to which the Bethlehem rhinoceros may be confidently referred, is characteristically a Villafranchian type widely spread in Europe (see, e.g., Viret, 1954, table opposite p. 184).

ARTIODACTYLA

SUIDAE

***Sus* cf. *strozzii* Meneghini**

(Pl. 33, fig. 1 ; Pl. 34, fig. 8)

In the Bethlehem collection there are two specimens that belong to a suid very close to or identical with *Sus strozzii* Meneghini, a species thus far known from the Villafranchian of Italy, France (Sénèze), and the Netherlands (Tegelen) only. The first of these (M 18515) is a fragment of the right mandibular ramus with the second premolar (P_2) unerupted. The crown measures 12·8 mm. antero-posteriorly. In a mandible from Tegelen described by Schreuder (1945 : 188) P_2 measures 13·0 by 7·0 mm. The Bethlehem specimen also displays part of the alveolus of the canine ; the internal upper angle of the alveolus is approximately a right angle, which shows it to have lodged a canine of the *verrucosus* type (Azzaroli, 1954 : 44, fig. 2). The width of the upper surface of the alveolus is over 10 mm. as far as preserved, and this surface is perfectly straight and the canine thus agrees with those of male individuals of *Sus strozzii* (Azzaroli, 1954 : 63, fig. 7). The second specimen (M 18520) is a left upper incisor, probably I^2 sin., rather worn. The length and width of the crown are 14 mm. and 6·5 mm, respectively. A left second upper incisor is *in situ* in a skull of *Sus strozzii* from the Val d'Arno figured by Azzaroli (1954 : pl. 10, fig. 4*a*), but its measurements have not been given. The upper incisors of the Tegelen *Sus strozzii* are unknown as yet, and in the sub-adult Sénèze specimen (Schaub, 1944 : 276, fig. 3 ; Azzaroli, 1954 : pl. 15, fig. 4*b*) they are missing.

The existence of *Sus* cf. *strozzii*, at any rate of a large suid with a *verrucosus*-like lower canine, at Bethlehem is interesting in view of the fact that *Sus strozzii* of the Val d'Arno, Sénèze, and Tegelen is generally accepted to be an invading form from Asia. There is no fossil species of *Sus* known from Asia that meets all the conditions ancestral to *Sus strozzii*, however, and both Schaub (1944 : 277) and Azzaroli (1954) derive *Sus strozzii* from *Sus minor* Depéret of the Pliocene of Roussillon.

GIRAFFIDAE

Giraffa cf. ***camelopardalis*** (L.)

(Pl. 34, figs. 5, 6)

A small fragment of a molar, the distal portion of a metapodial and a crushed distal condyle of another metapodial give evidence of the presence of a giraffe in the Bethlehem fauna.

The molar fragment (M 18517, Pl. 34, figs. 5, 6) is part of the external surface of a left upper molar, probably M^3. It comprises the portion just behind the prominent median rib of the antero-external cusp (paracone) backward to and including the weak median rib of the postero-external cusp (metacone). The preserved portion of the paracone slopes inward, and abuts against the metacone with a small but distinct, hook-shaped, outward turn. Between the paracone and the anterior style of the metacone there is an outer valley, 2 mm. wide and about 4 mm. deep, that extends rootward to 7 mm. from the crown base. The anterior style of the metacone is very prominent, and marked off behind by a sharp fold that likewise extends rootward to 7 mm. from the border of the enamel. It is worn down to a height of 13 mm. from the crown base ; the highest points of the paracone in front, and of the metacone behind it are 16 mm. high from the crown base, as worn. The median external rib of the metacone is weakly developed, and is more inclined inward than the paracone. The enamel is rugose. Internally, the molar fragment is broken off vertically just along the high and narrow pulp cavities of the external cusps.

I have compared the present fossil fragment with a number of dentitions of the Recent giraffe, and found the closest resemblance with the external portion of the left M^3. Doubtless there is much individual variation in the development of the anterior style of the metacone, which is very strongly marked in some, and only slight in others. The closest approach to the condition seen in the fossil is in two specimens (Leiden Museum, 7085 and 4216), in which the anterior metacone style is distinctly marked off behind by a groove, and as prominent laterally as that in the fossil, although not quite so thick (3–4 instead of 5–6 mm.). The valley just anterior to it is a little wider in the Recent specimens than in the fossil, and the basal cingulum in the Recent specimens is a trifle less high (5–6 mm. instead of 7 mm.). However, had more Recent dentitions been available it is quite probable that the condition observed in the fossil would be seen to fall within the limits of individual variation in the Recent giraffe. It is important to note that the fossil specimen does not appear to be larger than the Recent; the distance between the apices of the external surfaces of para- and metacone is about 14 mm. in the fossil as well as in the Recent molars.

The next specimen referable to a giraffe is the distal portion of a metatarsal (M 18508, found in 1934. It has largely been restored with plaster. The dorsal surface has a shallow vascular groove, as in the metatarsals of the Recent giraffe, but the foramen perforating the shaft distally does not show. The volar surface is restored with plaster for a height of 3–4 cm. above the condyles, but more proximally shows a weak median ridge, emerging about 6 cm. above the condyles, and flattening out at about 11 cm. above the condyles, at which level the bone is broken off. At this point the volar surface is still slightly convex transversely. In Recent metatarsals of *Giraffa camelopardalis* there is exactly the same condition, the posterior median longitudinal groove that extends along most of the length of the shaft fades away some 12–15 cm. above the distal condyles, to be replaced distally by a weak median ridge. The greatest distal width of the fossil metatarsal is about 85 mm. (85–90 mm. in three Recent metatarsals), and the greatest dorso-volar diameter of the condyles in the fossil specimen is 54 mm. (54–55 mm. in the Recent). The distal condyle width is greater in the fossil than in the Recent metatarsals (about 84 mm. as opposed to 78–80 mm.), but the condyles are slightly less closely approximated in the fossil, which is apparently due to a slight fault in the reconstruction. The condyles are shaped exactly as those in the Recent specimens used for comparison.

The last specimen (M 18507) is an isolated distal condyle of a metapodial, broken, and with the abaxial part displaced upward relative to the axial portion. Exact measurements cannot be given, but the specimen seems to be slightly larger than the corresponding part of the metatarsal, and, therefore, may have formed part of a metacarpal instead.

The remains described above differ slightly, if at all, from the Recent giraffe, and may be identified as *Giraffa* cf. *camelopardalis* (L.). This species has never been recorded in the fossil state from Europe, but remains apparently indistinguishable from the living species of *Giraffa* have been recorded from Villafranchian deposits in East and South Africa (Dietrich, 1942 : 112; Arambourg, 1947 : 375; Cooke & Wells, 1947). The presence of this form sets a decidedly African stamp upon the Bethlehem fauna.

BOVIDAE

Leptobos sp. nov.?

(Pl. 33, fig. 4)

A right horn core (M 18522) broken off approximately at the base, and without the tip, must be referred to *Leptobos*. The core is slightly compressed vertically at the base, and is curved backward and outward in a gentle curve; the distal half is curved upward. In the basal portion there are distinct longitudinal grooves along the posterior upper and the anterior lower surfaces; these grooves indicate a slight anti-clockwise torsion. They flatten out toward the middle of the length except for one along the lower surface anteriorly that continues to about 10 cm. from the broken distal end. Another, along the lower surface posteriorly, originates only in the middle of the length, and flattens out some 15 cm. from the broken end. Apart from these grooves the distal portion is smooth.

The length of the horn core from base to broken end is 65 cm. along the outer curve; it describes about one-fourth of a circle. The basal diameters are about 94 mm. horizontally, and 86 mm. vertically; these diameters have diminished to 76 mm., both ways, at the middle of the length. At the broken distal end the core still measures 48 mm. in diameter, and remains perfectly round in cross section.

The present specimen, although incomplete, resembles the horn core of *Leptobos stenometopon* (Rütimeyer, 1867, pl. 1, figs. 3, 4; 1878, pl. 7, fig. 3; Merla, 1949, pl. 8, fig. 1 *a*, *c*) except in size: the horn core of the latter species is only two-thirds as long as the incomplete Bethlehem specimen (Table VI). The Bethlehem horn core differs from the other European Villafranchian species of *Leptobos*, viz., *L. etruscus* (Falconer) and *L. vallisarni* Merla, in having the convexity backward and inward instead of outward (Merla, 1949: 71, fig. 2). The horn cores of the two last-mentioned species, moreover, are shorter than the Bethlehem specimen. In *Leptobos falconeri* Rütimeyer of the Pinjor zone of the Upper Siwaliks the complete horn core is unknown; the American Museum specimen restored by Pilgrim (1937: 816, 817), although it has the convexity backward and inward just as in the Bethlehem specimen, is less curved than either the Bethlehem core or that of *L. stenometopon*.

TABLE VI.—*Measurements of Horn Core of* Leptobos *species*

	Bethlehem	*stenometopon*	*etruscus*	*vallisarni*	*falconeri*
Length along outer curve	650+	420	500	330	*c.* 590
Basal diameters	94×86	72×58	79×73	88×77	85×77
Idem, middle of length	76×76	56×46	50×50	75×62	—
Idem, 7 cm. from tip	(48)	35×32	32×34	45×40	—

The Bethlehem core undoubtedly represents a species of *Leptobos*, but does not seem to be identical with any of the European species[1] (Merla, 1949) or with the Upper Siwalik *L. falconeri* (Table VI). There are further specimens of *Leptobos* in the Bethlehem collection, viz., a horn core fragment about 71 by 66 mm. in diameters (M 18556), a broken distal condyle of a metapodial (M 18552), a proximal sesamoid (M 18567), and, finally, two fragments of what appear to be upper premolars (M 18519) but these specimens are of no use for comparative purposes. To indicate the possibility that the Bethlehem *Leptobos* eventually may prove to be a new species it is recorded provisionally as *Leptobos* sp. nov.?

Gazellospira torticornis (Aymard)

(Pl. 33, figs. 2, 3)

The collection contains four mandibular rami, six isolated molars and molar fragments, as well as the distal epiphysis of a right radius and a second phalanx that belong to an antelope. The upper dentition is badly represented: two very

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[1] *Leptobos* is the only bovine in the Villafranchian of Europe (Pilgrim, 1938: 451, 466; 1944: 29).

incomplete upper molars (M 18548, and one fragment M 18519) do not show any diagnostic characters. The lower dentition, however, is very characteristic.

A left horizontal ramus of the mandible (M 18536) has the full permanent dentition P_2–M_3 (Pl. 33, fig. 3). The ramus is fractured below and in front of the premolars, and the fractures are filled with matrix, leaving a diastema between P_4 and M_1, while P_2 is displaced backward and outward. The teeth are undamaged except for P_2, which lacks part of the anterior border of the crown. P_2 is simply built ; its external surface is about as wide as high, and shows a single cusp and a very weak posterior fold. The internal surface is not exposed. P_3 has an inner cusp, two anterior and two posterior wings. The anterior valley is open internally, but the inner cusp is united to the posterior wing, the posterior outer fold is stronger, and the external surface is higher than wide. P_4 has a closed internal wall ; there is a small but marked anterior internal fold, while the posterior lobe is marked off by a deep external fold. The molars are characterized by weak internal ribs, strong anterior folds both internally and on the external side, and the apparent absence of basal pillars. The crowns are hypsodont and rather narrow ; M_{1-2} possess a postero-internal fold, M_3 has a laterally compressed third lobe.

A right ramus of the mandible (M 18534) lacks the two anterior premolars, and the third lobe of M_3 ; the ramus is broken and also distorted at M_1. In the closed internal wall and marked external fold P_4 resembles that of the preceding ramus closely. The molars likewise agree with those of the foregoing specimen in the presence of strong anterior folds, internally as well as externally, and in their weakly ribbed internal surfaces. Basal pillars are not exposed either.

M 18533 is a younger specimen than the foregoing rami ; the milk molars DM_{2-4} are still in place, and M_3 just appears above the alveolar margin. DM_2 and DM_3 resemble their successors in the permanent dentition in crown structure but are narrower and more elongated ; DM_4 is three-lobed ; the cingulum forms a knob at the base of the groove separating the second and third lobe externally. As in the molars, there is a postero-internal fold. The molars show the anterior folds very distinctly ; the internal ribs are more marked apically than those in the more worn molars of M 18536 and M 18534, but become less distinct toward the base. The antero-posterior diameter of the crown diminishes rootward so that the length of an unworn or slightly worn molar is greater than that of a much worn specimen. The hypsodont character of the molars is shown by a fragment of the left mandibular ramus (M 18532) with M_3 unerupted ; the height of the slightly worn M_2 in this specimen is not less than 30 mm. by a transverse diameter of the crown of only 8·5 mm.; the antero-posterior diameter of the crown is 19·5 mm. apically.

An isolated right M_1 (M 18546), moderately worn, and a right M_3 (M 18545), the second and third lobes of which are incomplete, possess the characteristic anterior folds and weak ribs of the preceding specimens. In these specimens the base is exposed, and there are cingular knobs at the external grooves between the lobes basally. The transverse diameters of the crowns slightly increase rootward, while the antero-posterior diameters decrease from the apex toward the base of the crown. Finally, a much worn M_3 sin. (M 18537) shows that the third lobe is shorter antero-posteriorly at base than the second lobe, and much compressed laterally. There is no basal knob in the groove between the second and third lobes, but there is a regular basal pillar between the first and second lobes externally. The folds at the anterior end of the crown are very marked on both sides. In M$_1$ the postero-internal fold is also marked.

TABLE VII.—*Measurements of* Gazellospira torticornis

	M18533	M18534	M18536	M18546 M18532 M18545	Pilgrim & Schaub, 1939
DM$_2$, ant. post.	7·5	—	—	—	8·2
transv.	3·9	—	—	—	—
DM$_3$, ant. post.	11·1	—	—	—	10·5
transv.	5·5	—	—	—	—
DM$_4$, ant. post.	17·8	—	—	—	19
transv.	8·1	—	—	—	—
Length DM$_{2-4}$	37·5	—	—	—	36
P$_2$, ant. post.	—	—	*c.*9	—	9·5–10
transv.	—	—	—	—	—
P$_3$, ant. post.	—	—	10·8	—	14
transv.	—	—	7·0	—	—
P$_4$, ant. post.	—	13·0	13·0	—	*c.*16
transv.	—	7·7	7·8	—	—
Length P$_{2-4}$	—	32	—	—	37
M$_1$, ant. post.	—	16·5	15·9	17·9	—
transv.	9·3	9·9	9·1	9·0	—
M$_2$, ant. post.	20·0	19·0	18·7	19·5	—
transv.	9·0	9·6	9·5	8·5	—
M$_3$, ant. post.	—	—	22·8	—	—
transv.	—	8·7	7·9	10·2	—
Length M$_{1-3}$	—	—	58	—	61·5–72
Height of ramus below M$_1$	24	27	26	—	24
Idem, below P$_2$	—	23	—	—	21

Although nothing of the skull or of the horn cores is preserved, the lower dentition of the Bethlehem antelope leaves no doubt as to its specific position : it clearly belongs to *Gazellospira torticornis* (Aymard) as described by Pilgrim & Schaub (1939). There is such a close resemblance between the Bethlehem specimens and those from the Villafranchian of Roccaneyra, La Loubière de Pardines, and Sénèze described and figured by Pilgrim & Schaub (1939), not only in structural details but also in size (Table VII), that their conspecificity is rendered certain. The ascending ramus of the Bethlehem mandibles is not preserved, but the anterior end is more complete than in the specimens figured by Pilgrim & Schaub ; the distance between P$_2$ and the mental foramen is 30 mm. both in M 18534 and in M 18533, and the height of the ramus half way between, 15 mm.

With the aid of Pilgrim & Schaub's monograph it has also been possible to identify a few limb bones in the Bethlehem collection : the distal epiphysis of a right radius (M 18510) agrees perfectly with that of *Gazellospira* from Roccaneyra (Pilgrim & Schaub, 1939, pl. 3, fig. 20), and differs from that of deer in the same points mentioned (p. 15) : the lunar and scaphoid facets are wider, the former almost reaches the ulna, and extends more distally, the latter is less convex antero-posteriorly, etc. The greatest distal width cannot be measured in the Bethlehem specimen, but that of the distal articular surface is 35 mm. as in a Sénèze specimen (p. 19). There is also a second phalanx (M 18575), damaged proximally, the length of which is 30 mm. and the proximal width, 15 mm., as in a *Gazellospira* phalanx II from Sénèze (Pilgrim & Schaub, 1939 : 20, pl. 3, fig. 6. lower figs.).

Gazellospira torticornis is a characteristically Villafranchian species known from France, Italy, and Spain (Villarroya : Schaub, 1944 : 280). Its occurrence at Bethlehem is of interest as according to Pilgrim & Schaub (1939 : 29) the species may be considered to be an immigrant from Asia.

AGE AND COMPOSITION OF THE BETHLEHEM FAUNA

The faunal list of the mammals from Bethlehem resulting from the present study is as follows :

Nyctereutes megamastoides (Pomel).
Homotherium (?) sp.
Archidiskodon cf. *planifrons* (Falconer & Cautley).
Hipparion sp.
Dicerorhinus etruscus (Falconer).
Sus cf. *strozzii* Meneghini.
Giraffa cf. *camelopardalis* (L.).
Leptobos sp. nov.?
Gazellospira torticornis (Aymard).

This faunal assemblage as a whole leaves no doubt as to the age of the bone-bearing beds of Bethlehem. It is a characteristic Villafranchian fauna, and there is general agreement nowadays among palaeomammalogists that the Villafranchian should be assigned to the basal Pleistocene. Thus, Miss Bate's preliminary statement of the age of the Bethlehem fauna is borne out by the present study.

When the list given above is compared with Miss Bate's provisional list of 1937 given in the introduction to the present paper certain discrepancies will be observed. I have found no evidence of the presence of *Hippopotamus* in the Bethlehem fauna, and none of *Stegodon* either. It is suggested that Miss Bate's record of the hippopotamus is based on a deceptive fragment of an *Archidiskodon* molar, in which the median looped expansions of the plates, at a certain stage of wear of the crown, may resemble the trefoil pattern of the cusps in a *Hippopotamus* molar. There is such a misleading fragment in the Bethlehem collection (M 18543). Likewise, it would seem evident that Miss Bate's record of *Stegodon* in reality is based on an *Archidiskodon* molar. The Bethlehem *Archidiskodon* cf. *planifrons* is an exceptionally low-crowned form, and such forms may be easily mistaken for stegodonts. On the other hand, I have been able to add one faunal element, viz., *Sus* cf. *strozzii*. This form is poorly represented in the collection, and the two small fragments must have been overlooked in the provisional study of the Bethlehem fauna.

We know nothing as yet of the so-called microfauna, the small mammals such as insectivores, bats and rodents. The condition in which the small carnivore (*Nyctereutes megamastoides*) was found, however, is an indication that the small animals would have been unable to withstand the conditions of the bone-bearing deposit.

On comparing the Bethlehem fauna as we now know it with well-known European

Villafranchian faunas such as those of Perrier, Sénèze, and Saint-Vallier (Schaub, 1944; Viret, 1954) we notice two important differences: the Bethlehem fauna lacks Cervidae, and contains *Giraffa*. In the absence of cervids and the presence of the giraffe the Bethlehem fauna agrees with those from the Villafranchian of East and South Africa (Arambourg, 1947). The Bethlehem fauna, however, differs from the East and South African faunas of the same age in the presence of *Nyctereutes*, *Dicerorhinus*, and *Gazellospira*, which are characteristic of the Villafranchian of Europe.

Therefore, the Bethlehem fauna is predominantly European, or rather Eurasiatic in character, with an African stamp upon it, as, in fact, might have been expected *a priori* from its geographic position.

As such, the Bethlehem fauna provides a faunistic link for the Villafranchian between the continents to the north and that to the south. It is one of those rare Villafranchian faunas such as that of the Tatrot zone of the Upper Siwaliks and that of Villarroya in Spain in which *Hipparion* lingers on and from which *Equus* is absent. Its *Archidiskodon* would appear to be more primitive even than that of the Tatrot (Hooijer, 1956), but the faunal assemblage of Bethlehem is as characteristically Villafranchian as any, and adds materially to our knowledge of the distribution of the sites over the Old World that give evidence of the great mammalian migration that occurred, we believe, at the beginning of the Pleistocene.

The so-called industry of the Bethlehem bone-bearing beds (see Gardner & Bate, 1937) has been re-examined by Dr. J. Desmond Clark who concluded that all the flaking has the characteristics of a natural origin. His report will be published later.

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PLATE 32

Archidiskodon cf. *planifrons* (Falconer & Cautley)

FIG. 1. Mandible, right view. × 2/11. M 18582. Bethlehem.
FIG. 2. Same, top view. × 2/11.

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2

PLATE 33

Sus cf. *strozzii* Meneghini

FIG. 1. Fragment of right ramus of the mandible with P_2 and alveolus of C, outer view. × $1\frac{1}{3}$. M 18515. Bethlehem.

Gazellospira torticornis (Aymard)

FIG. 2. Left ramus of the mandible with P_2–M_3, inner view. × $\frac{3}{5}$. M 18536. Bethlehem.

FIG. 3. Same, outer view. × $\frac{3}{5}$.

Leptobos sp. nov. ?

FIG. 4. Right horn core, anterior view. × 2/9. M 18522. Bethlehem.

Dicerorhinus etruscus (Falconer)

FIG. 5. Skull (crushed), right view. × $\frac{1}{6}$. M 18542. Bethlehem.

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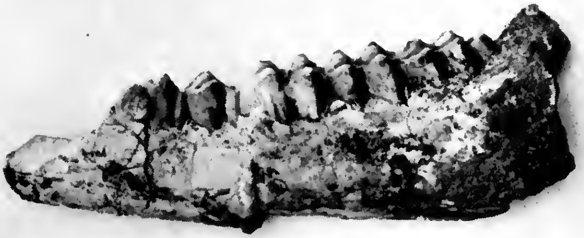

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PLATE 34

Homotherium (?) sp.

FIG. 1. Left lower carnassial (M_1), outer view. × 1⅓. M 18511. Bethlehem.
FIG. 2. Same, crown view. × 1⅓.

Archidiskodon cf. *planifrons* (Falconer & Cautley)

FIG. 3. M^2 dext., crown view. × 5/11. M 18523. Bethlehem.
FIG. 4. Same, inner view. × 5/11.

Giraffa cf. *camelopardalis* (L.)

FIG. 5. External fragment of left upper M, crown view. × 1⅓. M 18517. Bethlehem.
FIG. 6. Same, outer view. × 1⅓.

Nyctereutes megamastoides (Pomel)

FIG. 7. Fragment of left ramus of the mandible with P_{3-4}, outer view. × 1⅓. M 18521. Bethlehem.

Sus cf. *strozzii* Meneghini

FIG. 8. Left upper I, inner view. × 1⅓. M. 18520. Bethlehem.


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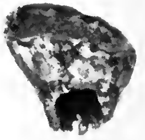
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PLATE 35

Archidiskodon cf. *planifrons* (Falconer & Cautley)

FIG. 1. M^2 sin., crown view. × 5/11. M 18524. Bethlehem.
FIG. 2. Same, inner view. × 5/11.

Hipparion sp.

FIG. 3. M_3 dext., crown view. × $1\frac{1}{3}$. M 18518. Bethlehem.
FIG. 4. Same, external view. × $1\frac{1}{3}$.
FIG. 5. Distal portion of metapodial II sin. or IV dext., abaxial view. × $1\frac{1}{3}$. M 18576. Bethlehem.
FIG. 6. Same, front view. × $1\frac{1}{3}$.


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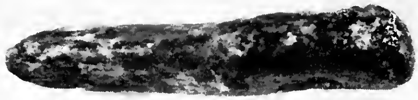
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THE UPPER PERMIAN FLORA OF ENGLAND

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BY

HILDA M. M. STONELEY

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THE UPPER PERMIAN FLORA OF ENGLAND

By HILDA M. M. STONELEY

SYNOPSIS

The paper brings together existing information relating to the scanty flora of the Upper Permian beds of northern England. Of the 24 fossil plant species described, the majority are also known from the German Zechstein, but there are new species of the algal genera *Piaea* and *Calathella*, a new cycadophyte provisionally included in *Pseudoctenis*, and a representative of *Hiltonia*, recently described as a new genus elsewhere. Other plant remains not referable to Zechstein species closely recall *Cordaites aequalis* (Göppert) and *Psygmophyllum cuneifolium* (Kutorga), both well-known Russian Permian species ; these records, however, need confirmation from more adequate material. The cuticle structure of several species is described. Leaf fragments with preserved cuticles of distinctive types show that further species are represented in the English Upper Permian, but the material is too imperfect for description. Certain non-vegetable structures previously regarded as fossil plant remains are also discussed.

I. INTRODUCTION

In England beds of established Upper Permian (Thuringian) age have two main outcrops, one east of the Pennines, extending from the south of Northumberland to near Nottingham, and the other west of the Pennines. There are also small outcrops still further west. These beds lie unconformably on Upper Carboniferous rocks which are not the latest known in this country. Rocks of intermediate age succeed the Coal Measures conformably in Warwickshire, Staffordshire and some adjacent areas. Some must unquestionably be included in the Upper Carboniferous, but the youngest, a series of red marls, sandstones and breccias known as the Enville or Corley Group, have been assigned by some writers to the Lower Permian (Autunian). They have yielded a scanty flora of which it is hoped to give an account elsewhere. No plant-bearing beds thought to be of Middle Permian (Saxonian) age occur in this country.

The Upper Permian rocks contain a flora which has hitherto been little investigated and is the subject of the present paper. Identifiable specimens are, however, very limited in number and are largely from localities no longer available for collecting. An attempt has, therefore, been made to locate and examine all such specimens found in the past. Material was collected personally, mainly at Hilton and Kimberley, where plant remains still abound but are mostly ill-preserved. The writer thanks the authorities of the following institutions for access to and the loan of specimens :

British Museum (Natural History)[1]; Geological Survey[2], Royal Scottish, Hancock (Newcastle-upon-Tyne), Yorkshire, Manchester, Carlisle, Dorman Memorial (Middlesbrough), Sunderland, Warwick, Wollaton Hall (Nottingham), and Birmingham City Museums; Geological Departments of Birmingham, Nottingham, and Leeds Universities, King's College, Newcastle-upon-Tyne, and University College, Galway (where W. King's collection is deposited). Dr. C. T. Trechmann kindly lent specimens, since presented to the British Museum (Natural History), from his own collection, and Professor R. Kräusel sent for comparison type specimens of German Upper Permian algae belonging to the Senckenberg Museum. The writer also wishes to acknowledge most helpful advice given her by Professor R. Florin and Dr. Britta Lundblad during a visit to Stockholm, and by Professor T. M. Harris. The investigation, undertaken at the suggestion of the late Mr. W. N. Edwards, was carried out with the aid of a grant from the Department of Scientific and Industrial Research in the Sedgwick Museum, Cambridge, to the authorities of which the writer tenders her thanks.

2. HISTORY OF PREVIOUS WORK ON THE ENGLISH UPPER PERMIAN FLORA

The first record of the occurrence of plant remains in English Upper Permian beds was by Sedgwick (1829 : 76, 77, 120), who mentioned the discovery of impressions of " ferns " in the Marl Slate of Middridge, S. of Bishop Auckland, during the construction of the railway. This locality long continued to yield fossil plants, including the best found in the Permian of this country. Lindley & Hutton (1837 : 123, pl. 195) described only one Permian species, *Voltzia phillipsii* [= *Ullmania frumentaria* (Schloth.)], from Whitley, Northumberland. King (1850) included descriptions and figures of the plant species *Caulerpa* ? *selaginoides* (Brongniart) [= *Ullmannia frumentaria*], *Neuropteris huttoniana*, and *Polysiphonia* ? *sternbergiana*, from Durham, and of *Chondrus binneyi* (an inorganic structure) from red Permian marls near Manchester. This work also included a brief description of that important organism (possibly an alga) of the Upper Magnesian Limestone, *Filograna* ? *permiana*, tentatively referred to a worm genus.

For many years Kirkby and Howse were the most active students of Durham Permian fossils. Among Kirkby's papers was an important one (1867) on the Marl Slate and Lower Magnesian Limestone with records of several fossil plants, but a more important list of Permian plants was included in Howse's (1890) catalogue of the fossils in the Museum at Newcastle (now the Hancock Museum). From the Marl Slate were recorded, besides *Ullmannia selaginoides*, two other well-known German Upper Permian species, *U. bronni* Göppert and *Zonarites digitatus* (Brongniart), a specifically unidentified *Calamites*, and two supposedly new species given the *nomina nuda Taeniopteris duffiana* and *Ctenis permiana*. From the Upper Magnesian Limestone were recorded *U. selaginoides* and a supposedly new species of *Calamites* which had been first mentioned by Kirkby (1864) and was assigned the *nomen nudum C. wakei*. The algal species *Chondrites virgatus* Münster was recorded from several horizons, but Howse seems to have confused under this name both King's

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[1] Abbreviated to 'B.M.N.H.' in the systematic descriptions.

[2] The abbreviation ' G.S.M. ' is used for the Geological Survey Museum in the systematic descriptions.

Polysiphonia ? sternbergiana and his *Filograna ? permiana*. Since 1890 little attention has been paid to the Permian plants of Durham, with the exception of *Filograna ? permiana*, which has lately attracted notice as an index fossil of the Upper Magnesian Limestone (Trechmann, 1925, 1942, 1952; Dunham, 1948).

The few records of plant remains from the Permian outcrop between Co. Durham and Nottingham are mentioned on p. 299. Wilson (1876) first recorded their presence in beds exposed in the railway cuttings between Kimberley and Cinderhill, and stated (1881 : 122) that Carruthers had pronounced them to " disclose a flora known on the Continent ". Neither in these nor in later references (Gibson & others, 1908 : 104; Lamplugh & Gibson, 1910 : 67; Smith, 1913 : 215) to the presence of fossil plants in the Kimberley Marl Slates is a single specific identification cited.

Borings in Nottinghamshire and Yorkshire passing through Permian rocks east of the outcrop have brought to light a number of plant remains, hitherto almost uninvestigated. An exception is a well-preserved cone-scale of *Pseudovoltzia liebeana* (Geinitz), the structure of which was described in detail by Walton (1929).

It was not until 1862 that Harkness (p. 215) recorded the discovery of the now well-known plant beds at Hilton Beck, near Appleby, Westmorland. As identified by the palaeobotanist Heer, they included " ferns referable to *Neuropteris* and *Sphenopteris* ", among them a species close to *S. erosa* (Morris), of the Russian Permian; remains " allied to *Weissites* (Göppert) ", as figured by Geinitz from the German Zechstein; a form " having the aspect of *Caulerpites selaginoides* (Sternb.) "; and " detached leaves, resembling *Cupressites Ullmanni* Brongn." Two years later Murchison & Harkness (1864 : 154) published a more satisfactory list of Hilton plants, this time determined by Etheridge. The species mentioned are *Sphenopteris naumanni* Gutbier, *S. dichotoma* Althaus, *Alethopteris goepperti* Naum., *Ullmannia selaginoides*, *U. bronnii*, *Odontopteris* ? sp., *Sphenopteris* ? sp., and *Cardiocarpon triangulare* Gein. To these records Goodchild (1889) added *Walchia piniformis* (Schloth.) and *Noeggerathia cuneifolia* Geinitz, but the first may be dismissed as incorrect as the species in question belongs to the Lower Permian, while the second may also be ignored as Geinitz himself had already withdrawn this species as based on generically indeterminate remains. Brockbank (1892) described a visit to Hilton and published three plates of unnamed and mostly indeterminate plant remains. Later authors who have mentioned the Hilton plants have merely quoted Etheridge's identifications.

Ill-preserved plant remains found by Roeder in the Upper Permian Manchester Marls were submitted to Geinitz for identification (Geinitz, 1889, 1890; Roeder, 1890, 1890*a*, 1890*b*). The species identified were *Voltzia liebeana* Geinitz, ? *Ullmannia selaginoides* (Brongn.), and *Filograna permiana* King, together with two non-vegetable structures (*Guilielmites permianus* and *Spongillopsis dyadica*) which Geinitz had previously described from the German Permian and regarded as plant remains. In the present paper doubt is cast on the reliability of the plant determinations on account of the poorness of the material. Records of plant remains from borings in Permian rocks in SW. Cumberland are referred to on p. 303.

It is uncertain if the Permian rocks found in Devon, Shropshire, Ayrshire, northern Scotland, Ulster, and certain other areas include beds of Thuringian age, and so far they have yielded no plant remains.

3. NOTES ON THE PLANT LOCALITIES, WITH SPECIES FOUND AT EACH

(a) *Eastern Outcrop, Localities Enumerated from North to South*

Cullercoats Bay (Trechmann, 1931 : 247 ; Hickling & others, 1948 : 6). The Marl Slate, with fish and plant remains, formerly cropped out on the foreshore 50 yards from the tip of the promontory, but it has been almost entirely removed by collectors. It has yielded :

Paracalamites kutorgai (Geinitz)
Annularia ? sp.
Ullmannia frumentaria (Schlotheim)
Unidentifiable fossil wood, including large branches

Whitley. At this locality, near Cullercoats, was formerly a quarry exposing Yellow Sands overlain by Marl Slate and Lower Magnesian Limestone. It yielded the type specimen of *Voltzia phillipsi* L. & H. (= *Ullmannia frumentaria*).

Westoe, South Shields. Here was a quarry in Lower Magnesian Limestone mentioned by Kirkby (1867*a* : 188). Bedding planes were covered with *Algites sternbergianus* (King).

Fulwell Hill Quarries (Kirkby, 1864 : 345 ; Woolacott, 1912, section facing p. 260). On the north side of Sunderland and famous for concretionary structures. Here the Upper Magnesian Limestone yielded plant remains (now lost) consisting, according to Kirkby, of a stem of *Calamites*, *Ullmannia selaginoides* (= *U. frumentaria*), and a large, reed-like plant. These were a unique occurrence at this horizon.

Fulwell Water Works. A specimen of *Paracalamites kutorgai* (Geinitz) came from this locality. There is no published record of the beds that were exposed there.

Claxheugh (Kirkby, 1867 : 197 ; Woolacott, 1898 : 14 ; 1903 : 211 ; 1912, figs. 3, 4, facing p. 256). A river bluff 2 miles west of Sunderland, now in a shipbuilding yard and inaccessible. There was formerly an interesting section exposing Permian beds ranging from Yellow Sands to Middle Limestone. Specimens of *Ullmannia frumentaria* are from the Marl Slate.

Thrislington Gap (King, 1850 : xii). A railway cutting about 1 mile N. of Ferryhill Station, exposing Coal Measure Sandstone, Marl Slate and Lower Magnesian Limestone. The type locality of *Mixoneura huttoniana* (King).

Ferryhill (Calvert, 1884 : 73). Railway cuttings near the one mentioned last. From them come :

Ullmannia frumentaria (Schlotheim)
Pseudovoltzia liebeana (Geinitz)

Cornforth. Presumably from the old quarries near the village King recorded " *Caulerpa selaginoides* " (= *Ullmannia frumentaria*).

Raisby Hill Quarry (Hickling, 1931). Two miles E. of Cornforth and just north of the railway. This large quarry, 1 mile long, affords the best section of the lower beds of the Magnesian Limestone now to be seen in Durham. The Marl Slate, thickly developed at the western end, yielded the large branch of *Ullmannia bronni* Göppert represented in Pl. 38, figs. 1*a*, *b*.

Brusselton. A farm S. of Bishop Auckland with quarries near-by. Cited by King as a locality for " *Caulerpa selaginoides* " and " *Neuropteris* " *huttoniana.*

East Thickley Quarry (Trechmann, 1921). Adjoining Shildon railway station and exposing Coal Measure Sandstone, Marl Slate, and Lower Limestone. Recorded as the type locality of *Algites sternbergianus* (King), which probably came from the Lower Limestone. From the Marl Slate of this quarry come :

Ullmannia frumentaria (Schlotheim)
Pseudovoltzia liebeana (Geinitz)
Hiltonia rivuli Stoneley

Middridge (Sedgwick, 1829 : 76 ; Hancock & Howse, 1870 : 356 ; Trechmann, 1921 : 538). Quarries adjoining the railway E. of Shildon Station and S. of Middridge village formerly showed Coal Measure Sandstone succeeded by Marl Slate and Lower Limestone, but only unfossiliferous Lower Limestone is now visible. The Marl Slate at this locality was the source of the best Permian plants yet found in England. Species identified by the writer are :

Algites virgatus (*Münster*)
Taeniopteris eckhardti Kurtze
? *Psygmophyllum cuneifolium* (Kutorga)
Sphenobaiera digitata (Brongniart)
Pseudoctenis middridgensis sp. nov.
Ullmannia bronni Göppert
Ullmannia frumentaria (Schlotheim)
? *Pseudovoltzia liebeana* (Geinitz)
Hiltonia rivuli Stoneley

Glass Houghton, NW. of Pontefract, Yorks. Wilson (1881 : 122) recorded plant remains from beds underlying Lower Magnesian Limestone in sandpits at this locality. No specimens have been traced.

Glapwell, Derbyshire. Five miles NW. of Mansfield, Notts. In the Geological Survey Museum are obscure leaf impressions resembling *Ullmannia bronni* Göppert and other remains said to have come from Permian beds here.

Fackley Hill, near Skegby, Notts. (Aveline, 1861 : 5 ; Lamplugh, *in* Gibson & Wedd, 1913 : 80). The locality of leaf impressions here identified as cf. *Cordaites aequalis* (Göppert), a unique record for this country. The specimens occur as impressions in yellowish limestone.

Fulwood Top, near Sutton-in-Ashfield, Notts. About 2 miles due S. of the last locality. Aveline (1861 : 6) recorded fossil wood from sandstones representing Lower Magnesian Limestone here.

Kimberley, near Nottingham (Wilson, 1876 ; 1881, pl. 7 ; Smith, 1913, pl. 38*a* ; Carr, 1913, pl. 14*b*). Two parallel railway cuttings extending eastwards from Kimberley Station for about a mile expose Upper Coal Measure Sandstone overlain by the lower beds of the Magnesian Limestone series, with a breccia at the base. The plant-bearing Marl Slates (about 30 ft. thick) have been exposed in the more northerly cutting by a recent landslip, and the writer was able to collect from and make a detailed measurement of the section. The following plant remains have been identified from Kimberley :

Callipteris martinsi (Kurtze)
Pseudovoltzia liebeana (Geinitz)
Hiltonia rivuli Stoneley
Strobilites bronni Solms-Laubach
Samaropsis triangularis (Geinitz)

Cinderhill. A colliery 2 miles on the Nottingham side of Kimberley. A temporary exposure here some years ago enabled Dr. H. S. Holden to collect fossil plants, now in the British Museum (Natural History), from the Marl Slate. They include isolated leaves of *Ullmannia bronni* Göppert and *U. frumentaria* (Schlotheim).

(b) *Borings and Colliery Shafts in S. Yorkshire, Lincolnshire and Nottinghamshire*

Ulleskelf Nurseries Boring (Edwards, Mitchell & Whitehead, 1950 : 81). About 8 miles NW. of Selby, Yorks. The Upper Magnesian Limestone yielded *Tubulites permianus* (King) and structures resembling *Chondrus binneyi* King.

Wressell Boring (Edwards, 1951 : 263). About 7 miles E. of Selby, Yorks. At depth 1,982 ft. the Lower Magnesian Limestone yielded a fragment of a shoot of *Pseudovoltzia liebeana* (Geinitz).

Bentley Colliery No. 2 Shaft (Edwards, 1951 : 127). Plant-bearing specimens from the Lower Marl, in the Wollaton Hall Museum, contain *Ullmannia bronni* Göppert, an unidentified fructification, and fossil wood.

Sutton Boring (Edwards, 1951 : 247). Two miles NNE. of East Retford, Notts. The Lower Marl, at depth 1,085 ft., is rich in plant remains, including the following :

Callipteris martinsi (Kurtze)
Ullmannia sp.
Pseudovoltzia liebeana (Geinitz)
Hiltonia rivuli Stoneley

West Drayton Boring. Four miles S. of East Retford. Lower Limestone at depth 1,073 ft. yielded an indeterminate conifer fragment recorded as *Pinnularia capillacea* L. & H. (Edwards, 1951 : 101).

Haughton Hall Boring. Five miles S. of East Retford. Lower Marl at depth 111 ft. yielded well-preserved leaves of *Hiltonia rivuli* Stoneley, recorded as *Cordaites* sp. by Edwards (1951 : 99).

Doddington Boring (Edwards, 1951 : 162). About 6 miles W. of Lincoln. Lower Limestone or Lower Marl (unseparated in record of boring) yielded the following :

Callipteris martinsi (Kurtze), depth 2,320 ft.
Ullmannia bronni Göppert, depths 2,300, 2,303, 2,310 ft.
Ullmannia frumentaria (Schlotheim) ?, depth 2,327 ft.
Hiltonia rivuli Stoneley, depths 2,310, 2,330 ft.

Markham Moor Boring. About 6 miles S. of East Retford. Plant remains occurred through a range of 248 ft. of Permian beds, as follows :

Piaea anglica sp. nov., depth 1,140 ft.
Piaea sp., depth 1,105 ft.
Calathella dictyonemoides sp. nov., depth 1,056 ft.
Ullmannia frumentaria (Schlotheim), depth 1,055 ft.
Ullmannia sp., depths 1,046 ft., 1,047 ft.
Pseudovoltzia liebeana (Geinitz), depth 1,105 ft.
Hiltonia rivuli Stoneley, depth 1,294 ft.

Thoresby Colliery Shaft. About 7 miles NE. of Mansfield, Notts. *Ullmannia frumentaria* (Schlotheim), depth unrecorded.

Wellow Boring (Edwards, 1951 : 259). About 14 miles S. of East Retford. *Ullmannia bronni* Göppert from Lower Marl or Lower Limestone at an unrecorded depth.

Farnsfield Boring (Edwards, 1951 : 167). About 9 miles W. of Newark. Cuticle preparations made by Professor R. Florin from bulk-macerated material from Lower Limestone yielded, besides several new cuticle types, the following :

Ullmannia sp.
Hiltonia rivuli Stoneley

Calverton Colliery Shaft. About 5 miles NNE. of Nottingham. Material labelled " Marl Slates 134–152 yards " has yielded the following :

Callipteris martinsi (Kurtze)
Ullmannia bronni Göppert

Lowdham (*or Cliff Mill*) *Boring* (Edwards, 1951 : 201). About 7 miles ENE. of Nottingham. Unidentifiable plant remains were found in Middle Marl at depth 688 ft. and in Lower Marl at depth 782 ft.

Bulcote Boring (Edwards, 1951 : 140). Six miles ENE. of Nottingham. Lower Marl at depth 711 ft., 1 ft. above the Basal Breccia, yielded the interesting fossil, *Conites* sp. (p. 329).

(c) *Eden Valley* (*Westmorland and SE. Cumberland*)

Hilton Beck. The chief exposure of Hilton Plant Beds is in a low cliff near the southern bank of Hilton Beck at a spot called Ash Bank, about ½ mile W. of Hilton village and close to the road to Appleby. The strata are also exposed along the stream course, and in the northern bank, just above the Penrith Sandstone, was found a bed full of well-preserved leaves, study of which gave the clue to the existence of the genus *Hiltonia.* The plant beds consist of sandstones, which frequently are current-bedded and have ripple-marked surfaces, and of shales, often finely laminated and highly micaceous. No fossils other than plant remains were found during several days' collecting. The list from this locality is :

Callipteris martinsi (Kurtze)
Sphenopteris bipinnata (Münster)
Schützia ? sp.
Sphenobaiera digitata (Brongniart)
Ullmannia bronni Göppert

Ullmannia frumentaria (Schlotheim)
Pseudovoltzia liebeana (Geinitz)
Hiltonia rivuli Stoneley
Strobilites bronni Solms-Laubach
Strobilites ludwigi (Weigelt)

Murchison & Harkness (1864 : 154) recorded the seed *Cardiocarpon* (now *Samaropsis*) *triangularis* Geinitz from Hilton, but the specimen recorded (Geological Survey Museum) is not that species and may not be a seed. The writer has collected small cordate seeds at Hilton.

Belah Brook (Eccles, 1871 : 34). Plant beds occur in the section exposed along this stream between Belah Bridge, Brough Sowerby, and Robridding. They consist of grey micaceous shale rich in plant remains which, however, are even more ill-preserved than those at Hilton. The following species are represented in material collected at Belah Brook in August 1957 :

Callipteris martinsi (Kurtze)
Ullmannia bronni (Göppert)
Ullmannia frumentaria (Schlotheim)
Pseudovoltzia liebeana (Geinitz)
Hiltonia rivuli Stoneley
Strobilites bronni Solms-Laubach

Birkshead Gypsum Mine, Marton Moor. Three and a half miles N. of Appleby. Plant remains are associated with the gypsum and may be seen in the roof of the mine. The following species were collected in August 1957 :

Callipteris martinsi (Kurtze)
Pseudovoltzia liebeana (Geinitz)
Hiltonia rivuli Stoneley

Opencast Gypsum Mine (*Thos. M'Ghie & Sons*), 1 *mile E. of Kirkby Thore.* Situated 4¼ miles NNW. of Appleby. About 5 ft. of plant beds occur just above " gypsum bed B " of Hollingworth, and have yielded *Hiltonia rivuli* Stoneley.

Acorn Bank Gypsum Pit (Russell, *in* Dakyns, Tiddeman & Goodchild, 1897 : 81). Situated NNE. of Temple Sowerby. Penrith Sandstone is overlain by 20 ft. of massive gypsum, and this by shale with ill-preserved plants. From the gypsum itself came the remarkable specimen of *Callipteris martinsi* (Kurtze) illustrated in Text-fig. 5*d* (p. 313).

Little Salkeld. Five and three-quarter miles NE. of Penrith. A few specimens from Hilton Plant Beds at this locality are in the Carlisle Museum. They include leaves of the following :

Ullmannia bronni Göppert.
Ullmannia frumentaria (Schlotheim)
Hiltonia rivuli Stoneley

(d) *Manchester District*

Fallowfield (Roeder, 1892). A railway cutting 3¼ miles S. of the centre of Manchester.

From the red marl at this locality Geinitz (1889, 1890) identified *Voltzia liebeana* Geinitz and *Guilielmites permianus* Geinitz, and, from limestone bands, *Filograna permiana* King. Specimens in the Manchester Museum labelled as the first species are now indeterminate, *Guilielmites* is an inorganic structure, and the identification of the last species is uncertain. The best specimen seen from here is a red marl impression of a small shoot with broad, linguiform leaves recalling those of *Hiltonia rivuli* Stoneley.

(e) *South-West Cumberland and Furness*

Old Layriggs Borehole, Kirksanton (Smith, 1919 : 17). Obscure plant remains were found in sandy shale between depths 227 ft. and 243 ft.

Haverigg Haws Borehole, near Kirksanton (Dunham & Rose, 1949 : 20). Dark grey shales at depth 1,675 ft. overlying Lower Brockram yielded plant remains recorded as *Ullmannia bronni*, but actually *Callipteris martinsi* (Kurtze).

Davy Street Boring, Barrow (Dunham & Rose, 1949 : 21). Plant remains, not traced, occurred in grey shale between depths 2,786 ft. and 2,790 ft.

4. STRATIGRAPHICAL AND GEOGRAPHICAL DISTRIBUTION OF THE PLANTS DESCRIBED

The following are lists of the fossil plant species from (*a*) the Marl Slate or approximately equivalent beds near the base of the Magnesian Limestone Series in eastern England (either along the outcrop or in borings) from the south of Northumberland to near Nottingham ; (*b*) higher Permian beds in the same area ; (*c*) the Hilton Plant Beds. Plant remains from the Manchester Marls and from Furness and SW. Cumberland are too scanty to be considered here.

Marl Slate or Approximately Equivalent Beds in Eastern Area

Algites virgatus (Münster)
Paracalamites kutorgai (Geinitz)
Annularia ? sp.
Callipteris martinsi (Kurtze)
Mixoneura sp. (*huttoniana* (King))
Taeniopteris eckardti Kurtze
? *Psygmophyllum cuneifolium* (Kutorga)
Conites sp.
Sphenobaiera digitata (Brongniart)
Cordaites aequalis (Göppert)
Pseudoctenis middridgensis sp. nov.
Ullmannia bronni Göppert
Ullmannia frumentaria (Schlotheim)
Hiltonia rivuli Stoneley
Pseudovoltzia liebeana (Geinitz)
Strobilites bronni Solms-Laubach
Samaropsis triangularis (Geinitz)

Higher Beds in Eastern Area

Piaea anglica sp. nov. Horizon not yet certain.
Calathella dictyonemoides sp. nov. Ditto.
Algites sternbergianus (King). Lower Limestone.
Tubulites permianus (King). Upper Limestone.
Paracalamites kutorgai (Geinitz). Upper Limestone.
Ullmannia frumentaria (Schlotheim). Upper Limestone.

Hilton Plant Beds

Callipteris martinsi (Kurtze)
Sphenopteris bipinnata (Münster)
Schützia ? sp.
Sphenobaiera digitata (Brongniart)
Ullmannia bronni Göppert
Ullmannia frumentaria (Schlotheim)
Hiltonia rivuli Stoneley
Pseudovoltzia liebeana (Geinitz)
Strobilites bronni Solms-Laubach
Strobilites ludwigi (Weigelt)

5. FLORAL EVIDENCE ON CORRELATION OF ENGLISH UPPER PERMIAN ROCKS

The marine Upper Permian beds of England were probably laid down in the same sea as the German Zechstein. The following are the subdivisions of the latter formation in Thuringia :

Oberer Zechstein
  Obere Letten
  Plattendolomit
  Untere Letten
Mittlerer Zechstein
  Hauptdolomit
Unterer Zechstein
  Zechsteinkalk
  Kupferschiefer
  Zechsteinkonglomerat

The palaeontological investigation of these deposits has been much more thorough than in the case of the English Permian beds, but the number of fossil plant species known to occur in them is not great. The majority have been found only in the Kupferschiefer, but a few species range upwards. Fossil plants are not infrequent in the Upper Zechstein, although apparently they are not common in the intermediate beds. The following is a list of species which have been described from the Kupferschiefer, omitting synonyms and Weigelt's two species of the unsatisfactory genus *Archaeopodocarpus*, which appear to have been founded mainly on specimens of *Ullmannia frumentaria*.

List of Fossil Plants of the German Kupferschiefer

Algites virgatus (Münster)
Paracalamites kutorgai (Geinitz)
Sphenopteris geinitzi Göppert
Sphenopteris bipinnata (Münster)
Sphenopteris kukukiana Gothan & Nagalhard
Sphenopteris gibbelsi Gothan & Nagalhard
Sphenopteris gothani Weigelt
Sphenopteris densifolia Weigelt
Sphenopteris röpkei Weigelt
Sphenopteris gillitzeri Weigelt
Odontopteris goepperti Weiss
Callipteris martinsi (Kurtze)
Taeniopteris eckardti Kurtze
Sphenobaiera digitata (Brongniart)
Cordaites pangerti Weigelt
Ullmannia bronni Göppert
Ullmannia frumentaria (Schlotheim)
Ullmannia orobiformis (Schlotheim) (doubtful species)
Pseudovoltzia liebeana (Geinitz)
Strobilites bronni Solms-Laubach
Strobilites ludwigi (Weigelt)
Strobilites major Weigelt
Strobilites elongatus Weigelt
Strobilites minor Weigelt
Strobilites dentatus Weigelt
Samaropsis triangularis (Geinitz)
Cyclocarpon eiselianum Geinitz
Carpolithes rotherianus Geinitz

The following is a list of fossil plants recorded from the Upper Zechstein. The chief localities are in Hesse (including the deposits at Frankenberg from which *Ullmannia bronni* was first described) and Saxony (Schuster, 1933).

List of Fossil Plants of the Upper Zechstein

Sphaerococcites dyadiccus Sterzel
Piaea punctata Florin. Obere Letten.
Piaea gigantea Florin. Obere Letten.
Calathella kräuseli Florin. Obere Letten.
Algites virgatus (Münster)
Tubulites permianus (King). Plattendolomit.
Sphenopteris sterzeli Schuster. Plattendolomit.
Sphenopteris sp. I, Schuster. Obere Letten.
Callipteris martinsi (Kurtze)

Taeniopteris eckardti Kurtze. Untere Letten.
Ullmannia bronni Göppert. Untere Letten and Plattendolomit.
Ullmannia frumentaria (Schlotheim). Untere Letten, Plattendolomit and Obere Letten.
Pseudovoltzia liebeana (Geinitz). Plattendolomit and Obere Letten.
Strobilites bronni Solms-Laubach
Cyclocarpus spongioides Geinitz
Rhabdocarpus klockeanus Geinitz. Plattendolomit.

The possibility must not be overlooked that deposition of the basal member of the Upper Permian series in the eastern counties of England may have been diachronous, as Sherlock and others have suggested. The view is here taken, however, that any time that may have elapsed between the incoming of marine conditions at different localities was not great in comparison with the duration of Upper Permian time, so that species found at all the localities may be considered together. The great majority of the plants in the first of the foregoing lists have, moreover, been found in the Marl Slate at the same Durham locality, Middridge.

It has always been considered that the Marl Slate should be correlated with the German Kupferschiefer. Their stratigraphical positions are similar, separated as they are from the base of the Upper Permian succession only by a basal breccia or by sands, and they are similarly rich in fossil fishes and plant remains. The flora of the Marl Slate supports this conclusion, for several species are common to this formation and to the Kupferschiefer. The stratigraphical importance of some of these species is, however, limited, for the ranges of *Callipteris martinsi*, *Taeniopteris eckardti*, *Ullmannia bronni*, *U. frumentaria* and *Pseudovoltzia liebeana* extend to the Upper Zechstein, while *Paracalamites kutorgai*, although not recorded from the Upper Zechstein in Germany, occurs in England in the Upper Magnesian Limestone, if (as is probable) an untraced "*Calamites*" recorded by Kirkby belonged to this species. *Sphenobaiera digitata* and the seed *Samaropsis triangularis*, both common to the Kupferschiefer and the Marl Slate, have not, however, been found in the Upper Zechstein.

Of great interest, however, is the occurrence in the Marl Slate of certain species not known from the Kupferschiefer or any other horizon in Germany. Two of these, *Hiltonia rivuli* (abundant in England) and *Pseudoctenis middridgensis*, are new, while *Mixoneura huttoniana*, known only by isolated leaves, was described long ago by King (1850). An important discovery is that of specimens possibly belonging to *Psygmophyllum cuneifolium*, previously known only from the Permian of the Urals. A leaf which seems to belong to the well-known species *Cordaites aequalis*, from Central Asia, Pechoraland, and Siberia, and barely distinguishable from the widespread Gondwana species *Noeggerathiopsis hislopi*, comes from near the base of the Upper Permian at a locality in Nottinghamshire which deserves further investigation.

The re-appearance of *Ullmannia* in the Upper Magnesian Limestone of Durham is in agreement with our knowledge of its range in the German Zechstein. The most important fossil plants found at horizons above the Marl Slate in the English beds are, however, the algae. *Tubulites permianus* (hitherto called *Filograna permiana* in England) is an index fossil of the Upper Magnesian Limestone throughout Durham, Yorkshire and Nottinghamshire, and occurs in similar abundance in Germany in the Plattendolomit, confirming the correlation of the English and German beds. In Germany the algal genera *Piaea* and *Calathella* have been found only in the Obere Letten of the Upper Zechstein. The beds in the Nottinghamshire borehole in which they occur, although not assigned to their exact stratigraphical positions, are well above the base of the Upper Permian.

Earlier workers considered that the Hilton Plant Beds should be correlated with the Marl Slate and with the Kupferschiefer, but Trotter & Hollingworth (1932 : 124) put forward the view that they are the equivalent of the Middle Permian Marl of Durham. This conclusion was based on a comparison of the lithological succession in the two areas, the fossil plants being considered useless for correlation. While several plant species range throughout the Zechstein, three found at Hilton (*Sphenopteris bipinnata*, *Sphenobaiera digitata* and *Strobilites ludwigi*) have been recorded only from the Kupferschiefer in Germany, and so support the earlier view as to the age of the Hilton beds. *Hiltonia rivuli*, moreover, is common to the Hilton beds and the Marl Slate and is not known from later beds east of the Pennines.

6. SYSTEMATIC DESCRIPTIONS

THALLOPHYTA

ALGAE

Genus ***PIAEA*** Florin, 1929

Piaea anglica sp. nov.

(Pl. 36, fig. 3)

Diagnosis. A *Piaea* with axes unbranched in their upper parts; axes about 1 mm. wide, bearing whorls of filaments at intervals of about 0·25 mm.; filaments about 10 in a whorl, up to 2 mm. long, and mostly arising at an angle of about 60°.

Occurrence and material. Magnesian Limestone Series, Markham Moor borehole, Notts. (p. 300); types (G.S.M. no. 76607) from depth 1,140 ft.; a single specimen from depth 1,105 ft.

Description. There are about 30 axes lying mostly parallel on a bedding plane in a core; those shown in the figure are typical. The length of the longest fragment is 5 cm. None is branched; the lower parts, however, are not seen, being broken or outside the core. Two axes show in places transverse rows of dots thought to have been bases of the lateral filaments; the number (about 4) visible in each row suggests that there were about 10 in a complete whorl. The substance is carbonaceous and there is no evidence of original calcification.

Comparison. Professor R. Kräusel kindly sent me the original specimens of *Piaea punctata* Florin (1929) from the Zechstein. Though very similar to the English specimens, they have narrower axes, shorter filaments and more conspicuous filament scars, and they branch freely.

Genus *CALATHELLA* Florin, 1929

Calathella dictyonemoides sp. nov.

(Pl. 36, fig. 4; Text-figs. 1, 2)

Diagnosis. A *Calathella* with longitudinal strands, 0·2–0·3 mm. wide, connected by transverse strands of the same width to form meshes mostly rectangular and about 0·5 mm. long and 0·2–0·3 mm. wide.

Occurrence and material. Magnesian Limestone Series, Markham Moor borehole, Notts. (p. 300); core with several specimens (G.S.M. no. 76608) from depth 1,056 ft.

Description. The figures show all that can be seen of two typical specimens. With them is associated a second type of structure (Text-fig. 2) which may be a different part of the same plant. It consists of a group of axes diverging fan-wise from a point. These axes vary in width, the majority between 0·1 and 0·2 mm., and some are narrowest near the base. They are often curved and occasionally fork, but are not joined by cross-connections.

Fig. 1. *Calathella dictyonemoides* sp. nov. Magnesian Limestone Series; depth 1,056 ft., Markham Moor borehole. Geological Survey, no. 76608. × 5.

Comparison. The original specimens of *C. kräuseli* Florin from the Zechstein bear at their apices what seem to be basket-shaped bodies composed of anastomosing strands. These bodies somewhat resemble the English specimens but have narrower strands. At the apex of one specimen of *C. kräuseli* is a bunch of narrow, irregularly spreading filaments like those arising from the lower parts of axes in that species. The

Fig. 2. *Calathella dictyonemoides* sp. nov. Rectangular mesh (at top) and associated structures. Magnesian Limestone Series; depth 1,056 ft., Markham Moor borehole. Geological Survey, no. 76608. × 2·5.

brush-like structures in the material now described may similarly have been terminal on some axes.

The new specific name recalls the graptolite *Dictyonema* for which the present specimens were originally mistaken.

Genus **ALGITES** Seward, 1894

Algites virgatus (Münster)

(Text-fig. 3)

1842 *Chondrites virgatus* Münster, p. 102, pl. 15, fig. 18.
1862 *Chondrites virgatus* Münst.: Geinitz, p. 132, pl. 24, fig. 5.

English occurrence and material. Marl Slate, Middridge, Durham; one specimen (Hancock Museum).

Description. The figure shows all the features that can be seen. The distal ends of some axes seem to bear plume-like structures, but no details are visible.

Comparison. The holotype from the Kupferschiefer is in the Palaeontological Department of the British Museum (no. 46674). It much resembles the English specimen, and the axes, some of which seem to branch, bear some sort of rounded body at the apex; these bodies are, however, smaller than the "plumes" of the English specimen.

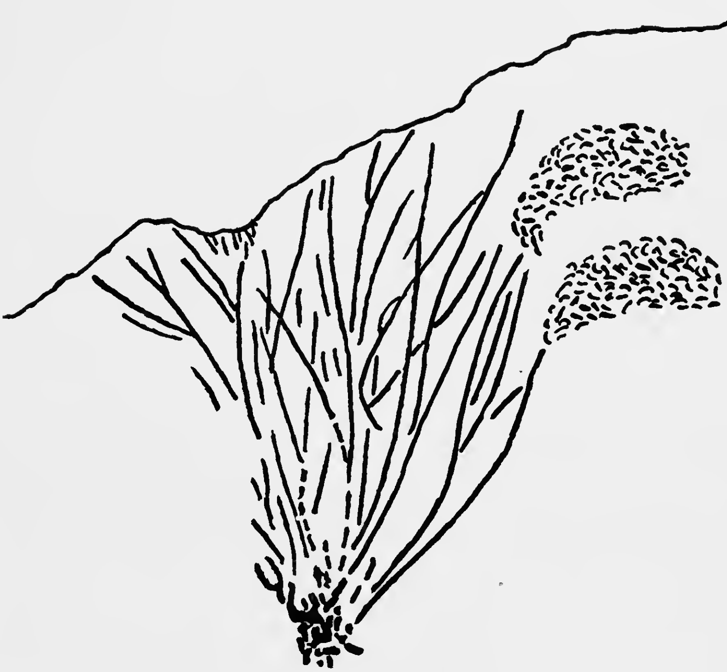

Fig. 3. *Algites virgatus* (Münster). Marl Slate, Middridge. Hancock Museum. × 2.

It is clear from the recent paper by Simpson (1957) that the generic name *Chondrites*

Sternberg should not be used for true algal structures. It is here replaced by *Algites* Seward.

Algites sternbergianus (King)

(Pl. 36, figs. 1, 2, 5)

1850 *Polysiphonia* (?) *Sternbergiana* King, p. 3, pl. 1, fig. 2.
1867*a* *Chondrites virgatus* Münster : Kirkby, pp. 192, 197.
1890 *Chondrites virgatus* Münster : Howse, pp. 244, 248.

Occurrence and material. Lower Magnesian Limestone of Westoe, South Shields ; numerous specimens in the Hancock, Geological Survey, and Manchester Museums. Also recorded (as *C. virgatus*) from Claxheugh. The holotype (not traced) was stated by King to be from the Marl Slate of Thickley, but was probably from the Lower Magnesian Limestone.

Description. The specimens are axes up to 1 mm. wide and 8 cm. long, straight or curved but not branched. Some are naked but others are clothed with irregular fine filaments up to 1 cm. long, and some bear a brush of these filaments at their distal end. No scars of filaments can be seen on the naked axes.

Remarks. These specimens are too imperfectly characterized to be placed in a more definite genus such as *Calathella*. It is to be noted that Geinitz (1858 : 6 ; 1862 : 132) thought this species inseparable from *A. virgatus*, and in this he was followed by Kirkby, Howse, and others. To me they seem different.

Genus ***TUBULITES*** Bein, 1932

Tubulites permianus (King)

(Pl. 36, figs. 6–9)

1850 *Filograna* (?) *Permiana* King, p. 56.
1861 *Filograna Permiana* King : Geinitz, p. 41.
1932 " Stäbchenkalk ", Prager, p. 358, pl. 9, figs. 1–3.
1932 *Tubulites articulatus* Bein, p. 798, pl. 27, figs. 3, 4.
1934 *Tubulites articulatus* Bein : Naumann, p. 194, pl. 13*a*, fig. 1.
1942 *Filograna* (?) *permiana* King : Trechmann, p. 317.
1948 *Filograna permiana* King : Dunham, p. 220, pl. 10, fig. 3.
1952 *Filograna permiana* King : Trechmann, p. 307.

Occurrence and material. Upper Magnesian Limestone throughout Durham and Yorkshire. Localities of specimens studied are Blackhall Rocks, 5 miles N. of Hartlepool (material from here includes King's types, University College, Galway, nos. 130, 131) ; shore at Easington, Durham (B.M.N.H., C. T. Trechmann Colln.) ; Low Park Farm, Yorks. ; east of Hepworth Wood, Yorks. ; near Toulson Lodge, Yorks.; and near Cross Newton, Doncaster (last four, G.S.M.). Borehole material is from depth 4,240 ft., Eskdale, near Whitby (G.S.M.) ; also recorded from depth 638 ft., Sutton borehole, Notts. (Edwards, 1951 : 102). Very doubtful specimens (Manchester Mus. nos. L.706, L.12336) from the Manchester Marls of Strangeways and Fallowfield, near Manchester, have also been examined ; they were the basis of records by Geinitz (1890 : 548) and Roeder (1892 : 15).

Description. The broken calcareous tubes from Easington shown in Pl. 36, fig. 7, are typical of this abundant organism; they are 0·5 mm. wide and up to 7 mm. long. No carbon is present in them and there is no fine sculpture of any kind. Specimens were examined in thin section, but the original structure was not clear on account of metasomatic changes. The calcareous wall of the tube is usually 30–40 μ thick and in one case an inner tube 100 μ thick was observed. In no instance are the tubes arranged like strings of beads. Specimens from the Eskdale borehole are a little wider (0·75 mm.). The length of the longest single tube seen from any locality was about 2 cm.

Some specimens from Blackhall Rocks (Pl. 36, fig. 6) are only 0·3 mm. wide and may occur in bundles, sometimes as many as 24 side by side; one bundle of 5 can be traced for 2 cm. There is a suggestion that certain of these groups may arise by the branching of one tube. It is not certain that all the specimens mentioned are specifically identical.

Discussion. King gave no figure of this organism, which he referred with doubt to a genus of living worms, *Filograna*, and his description was too brief to distinguish it. His type specimens (kindly lent to me by Professor J. Mitchell) are too eroded to be worth figuring here, but show that the species has been correctly identified by modern authors. Kirkby (1861 : 309), however, who gave a description of this organism, seems not to have known of King's name for it, while Howse (1890), in a list, doubtfully placed *Filograna permiana* as a synonym of *Chondrites virgatus*. Trechmann (1925), who revived the name *F. permiana*, called attention to the importance of the organism as a characteristic fossil of the Upper Magnesian Limestone, and considered it an alga because he occasionally saw one tube branching out of another. None of the specimens I have seen, however, shows this feature unmistakably.

In 1932 Prager gave the name " Stäbchenkalk " to an Upper Zechstein limestone full of tubes 1 mm. wide and up to 8 mm. long. In the same year Bein gave reasons for considering them algal and assigned to them the new name *Tubulites articulatus* in ignorance of the earlier name for English specimens. Bein (1932) and Naumann (1934) noted the frequent presence of an inner tube inside the outer one.

PTERIDOPHYTA

EQUISETALES

Genus ***PARACALAMITES*** Zalessky (1927) 1932

This generic name was first published in Zalessky's Atlas (1927) without a diagnosis. The species there figured were *Paracalamites decoratus* (Eichwald), *P. kutorgae* (Geinitz), and *P. striatus* (Schmalhausen), all of which had been originally described under *Calamites*. The name was subsequently published (Zalessky, 1932 : 112) in a paper on Upper Palaeozoic plants from Siberia, and the new species *Paracalamites sibiricus* was described at the same time. Even in this paper no formal generic diagnosis was given, but a few remarks were made on the reasons for founding a new genus, and seem just sufficient to validate it with *P. sibiricus* as the type species.

It was explained that the casts of the pith-cavities of *Calamites*-like stems and rhizomes found in the Permian have the ridges of successive internodal segments in alignment instead of alternating in position and interdigitating at the nodes, as in true *Calamites*. In this respect they resemble the Lower Carboniferous genus *Asterocalamites*. Knowledge of their foliage, Zalessky thought, might eventually establish their identity with either *Phyllotheca*, *Schizoneura*, or *Lobatannularia*, but for the time being it seemed advisable to refer them to a new genus, *Paracalamites*. The foliage of one of these Permian species has, however, been described by Weigelt (1928 : 470, pl. 10, fig. 1), who founded a new species *Asterocalamites mansfeldicus* on specimens from the German Kupferschiefer. The characters of *Paracalamites*, in so far as they are known, may now be summarized as follows.

Stems and the casts of their pith-cavities with numerous narrow longitudinal ridges which are in alignment along successive internodal segments. Leaves lanceolate, not joined, arranged as star-shaped verticils on slender foliage shoots which arise in pairs and opposed at each node, and are directed upwards at an angle of about 45° ; number of leaves in each verticil small.

The genus resembles *Asterocalamites* in the alignment of the internodal ridges, but differs in the form of its leaves, which are not filiform and repeatedly forked.

Paracalamites kutorgai (Geinitz) Zalessky

(Pl. 37, fig. 1)

1880 *Calamites Kutorgai* Geinitz, p. 14, pl. 6, fig. 1.
1887 *Calamites Kutorgae* Geinitz : Schmalhausen, p. 33, pl. 1, figs. 7–17.
1927 *Paracalamites Kutorgae* (Geinitz) Zalessky, p. 36, pl. 1, fig. 1 ; pl. 44, figs. 3, 7.
1928 *Asterocalamites mansfeldicus* Weigelt, p. 470, pl. 10, figs. 1–4, 7–14.
1930 *Asterophyllites* (*Neocalamites*) *mansfeldicus* (Weigelt) Weigelt, p. 649.

Occurrence and material. Marl Slate of Fulwell Water Works, near Sunderland (one specimen) and of Cullercoats (two specimens), Hancock Museum.

Description. All three specimens are flattened stem fragments in shale. One specimen is 25 cm. long and 17 cm. wide and shows three nodes with internodes 45 mm. long. One node is shown enlarged in Pl. 37, fig. 1. The ribs on one internode are in alignment with those on the next. Another specimen is 25 mm. wide and shows internodes about 50 mm., 25 mm., 35 mm., and 25 mm. in length.

Discussion. Stems such as these agree with those of Lower Carboniferous *Asterocalamites*, but they match specimens from the German Kupferschiefer identifiable as *Paracalamites kutorgai*. It may be noted that Kirkby (1864) recorded " *Calamites arenaceus* ?" from the Upper Magnesian Limestone of Fulwell Hill, and that the specimen was catalogued by Howse (1890) under the name *Calamites wakei*. The specimen, which has not been traced, may have belonged to *P. kutorgai*.

Genus ***ANNULARIA*** Sternberg, 1821

Annularia ? sp.

(Text-fig. 4)

Occurrence and material. Marl Slate of Cullercoats, two specimens (Hancock Museum).

Description. Each specimen shows a whorl of what are taken to be 11 very small leaves, not more than 3 mm. long, round a circular space representing the node. No midrib is, however, visible in these " leaves ". They occur in the same bed as *Paracalamites kutorgai* but differ in number and shape from the leaves of that species as described by Weigelt (1928).

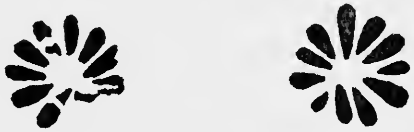

FIG. 4. *Annularia* ? sp. Marl Slate, Cullercoats. Hancock Museum. × 2.

PTERIDOSPERMAE

Genus ***CALLIPTERIS*** Brongniart, 1849

Callipteris martinsi (Kurtze) Zeiller

(Pl. 37, figs. 2, 5 ; Text-figs. 5, 6)

1839 *Alethopterin* (*sic*) *Martinsii* Germar MS.: Kurtze, p. 34, pl. 3, fig. 2.
1907 *Callipteris Martinsi* (Germar) : Gothan, pp. 1–4, figs. 1, 2. (See this for full synonymy.)
1928 *Callipteris Martinsi* (Germar) : Weigelt, p. 457, pl. 2, figs. 14, 15, 26 ; pl.7 ; pl. 35, figs. 7, 14, 21, 22, 26.

OCCURRENCE AND MATERIAL. Marl Slate of Kimberley, Watnall, and Cinderhill, near Nottingham ; several specimens (B.M.N.H.). Lower Marl of Magnesian Limestone Series, Doddington borehole (p. 300), depth 2,320 ft.; fragment (G.S.M.). Hilton

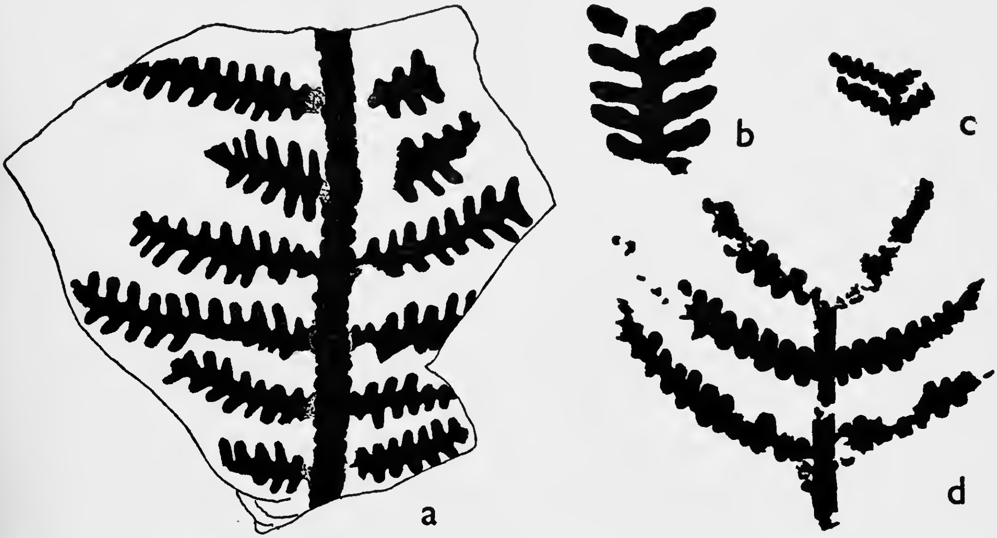

FIG. 5. *Callipteris martinsi* (Kurtze) Zeiller. (*a*), Marl Slate, Kimberley. British Museum (Natural History), no. V.5963*a* ; (*b*), Marl Slate, Kimberley. British Museum (Natural History), no. V.5963*b* ; (*c*), Hilton Plant Beds, Hilton. British Museum (Natural History), no. V.5975 ; (*d*), Main gypsum horizon, Acorn Bank quarry, near Temple Sowerby. Private collection. All × 1.

Plant Beds, Hilton and Belah Brook; several small shoots (B.M.N.H. and G.S.M.). Gypsum of Acorn Bank quarry, near Temple Sowerby (Text-fig. 5*d*, private coll.) and of Birkshead Mine (B.M.N.H.). Kirksanton Beds, Haverigg Haws borehole (p. 303); one fragment (G.S.M. no. TW 3846). Fragments were also identified in bulk-macerated cores from the borings at Sutton (p. 300), depth 1,085 ft., Lowdham (p. 301), depth 688 ft., and Farnsfield (p. 301); also from the Calverton Colliery shaft (p. 301).

Description. The best English specimens are from Kimberley; the largest is shown in Text-fig. 5*a*. The rachis has transverse ridges which may represent the pinnules known to be borne directly on it in German specimens, and the pinna rachises have similar but smaller ridges. Another Kimberley specimen (Pl. 37, fig. 5) has scars of unknown origin at some pinna bases; a previous worker who labelled this specimen regarded these as seed scars, but they may be the remains of pinnules; seeds of *C. martinsi* are unknown. Text-fig. 5*b* represents a specimen from the same locality in which the pinnules are lobed and relatively large. A few specimens from

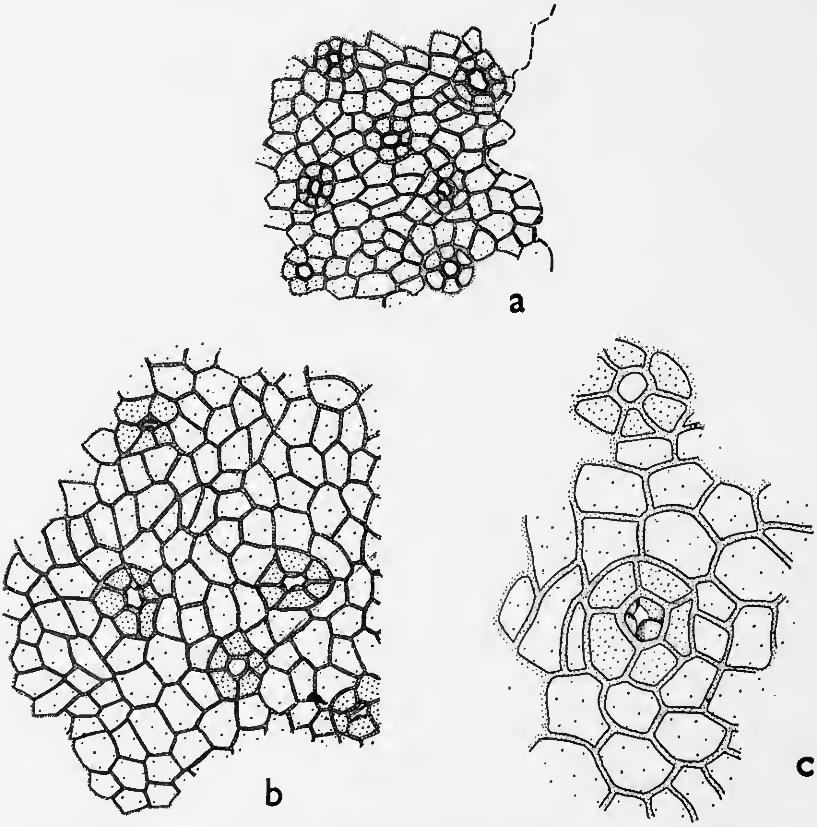

Fig. 6. *Callipteris martinsi* (Kurtze) Zeiller. Cuticle. (*a*), Marl Slate, Cinderhill. British Museum (Natural History), no. V.26971. × 110; (*b*), Marl Slate, Kimberley. British Museum (Natural History), no. V.35114. × 150; (*c*), Hilton Plant Beds, Hilton. British Museum (Natural History), no. V.35115. × 270.

this locality show a midrib and lateral veins. Small fragments with deeply lobed pinnules (Text-fig. 5*c*) are common at Hilton Beck and were recorded by Murchison & Harkness (1864) as *Alethopteris goepperti* (Münster), a synonym of *C. martinsi*. The specimen shown in Text-fig. 5*d* is remarkable for its preservation in gypsum.

CUTICLE. Preparations were made from several specimens from Kimberley, Watnall, Cinderhill, and Hilton Beck. Text-fig. 6 and Pl. 37, fig. 2, show the cuticular structure. The ordinary epidermal cells of both cuticles are polygonal and do not show a median papilla, but the subsidiary cells often have a prominent papilla over the stomatal pit. The subsidiary cells number either five or six, the latter number appearing to be more usual on deeply lobed pinnules. The stomata are rare on one face of the leaf and frequent on the other.

REMARKS. Although there are slight differences in their form, I consider that the numerous English fragments all belong to one species, as they have the same general type of cuticular structure. All of these forms can be matched (macroscopically) with German specimens included in *C. martinsi*, and they are, therefore, identified with that species. It is, however, surprising that there is a striking difference between their cuticle and that of an Upper Zechstein specimen figured by Gothan & Nagalhard (1922) and of another from the same locality, Frankenberg, figured by Florin (1931), which I examined in Stockholm ; for in the German specimens the epidermal cells have a clearly marked dark spot, representing a thickening of the cuticle. It may be that the presence of a papilla on epidermal cells is inconstant in *C. martinsi*, but it is also possible that some forms from the Zechstein once thought distinct species but now included in *C. martinsi* are, after all, distinct. Hence, the English specimens cannot be satisfactorily identified until the cuticles of many more German specimens have been studied.

Genus ***SPHENOPTERIS*** Brongniart, 1822

Sphenopteris bipinnata (Münster) Geinitz

(Pl. 37, fig. 6 ; Text-fig. 7)

1842 *Caulerpites bipinnatus* Münster, p. 102, pl. 14, fig. 3.
1846 *Sphenopteris dichotoma* Althaus, p. 30, pl. 4, fig. 1.
1928 *Sphenopteris dichotoma* Althaus : Weigelt, p. 448, pl. 8, figs. 3, 4.

FIG. 7. *Sphenopteris bipinnata* (Münster) Geinitz. Hilton Plant Beds, Hilton. British Museum (Natural History), no. V.35117. × 1·5.

Occurrence and material. Hilton Plant Beds, Hilton Beck; several fragments (B.M.N.H. and G.S.M.).

Description. In some of the fragments the leaves show their veins excellently, but in others the form alone is visible as the veins are not preserved in the coaly substance. Some small fragments resemble *S. patens* (Althaus), which Geinitz (1848) and Schenk (1864) but not some later authors have considered synonymous with *S. bipinnata*. No cuticle is preserved in the specimens examined.

Genus ***MIXONEURA*** Weiss, 1869

Mixoneura sp.

(Pl. 37, fig. 4)

1850 *Neuropteris Huttoniana* King, p. 6, pl. 1, fig. 4.

Occurrence and material. Marl Slate of Thrislington Gap, Durham. The type is preserved in University College, Galway. It is the only specimen seen, although King also recorded the species from Middridge, Brusselton, and East Thickley.

Remarks. The type specimen shows four pinnules on a single small piece of rock. This may have been broken and re-assembled and it is impossible to say how close they were originally. One pinnule is shown in Pl. 37, fig. 4; others seem to have been slightly broader or slightly longer. No further details are visible.

These fragments much resemble *Mixoneura neuropteroides* (Göppert), from the Lower Permian of Germany; it is interesting that no *Mixoneura* is known to occur in the German Upper Permian.

Genus ***TAENIOPTERIS*** Brongniart, 1828

Taeniopteris eckardti Kurtze

(Pl. 37, figs. 3*a*, *b*)

1839 *Taeniopteris Eckardti* Germar MS., Kurtze, p. 34, pl. 3, fig. 1.
1851 *Taeniopteris Eckhardi* Germar: Ettingshausen, p. 99, pl. 13, figs. 2, 3.
1890 *Taeniopteris duffiana* Howse, p. 248 (*nom. nud.*).
1928 *Taeniopteris Eckardti* Germar: Weigelt, p. 461, pl. 2, fig. 21; pl. 9, figs. 7–18.
1930 *Taeniopteris eckardti* Germar: Weigelt, p. 647, figs. 13–16.
1933 *Taeniopteris eckardti* Germar: Schuster, p. 85, fig. 5; pl. 7, fig. 8.

Occurrence and material. Marl Slate of Middridge, Durham; one specimen (Hancock Museum).

Description. The figures show the only English specimen, catalogued by Howse as *T. duffiana*. Its veins, clearly seen, are all parallel, forming an angle of 60° with the midrib, and number 8–9 to the centimetre. Its cuticle is not preserved. It agrees with *T. eckardti* from the Upper Permian of Germany.

Genus ***PSYGMOPHYLLUM*** Schimper, 1870

? ***Psygmophyllum cuneifolium*** (Kutorga) Schimper

(Pl. 40, figs. 14, 15; Text-figs. 8, 9)

1838 *Sphenopteris cuneifolia* Kutorga, p. 32, pl. 7, fig. 3.
1927 *Psygmophyllum cuneifolium* (Kutorga): Zalessky, pl. 8, figs. 3, 4; pl. 9, figs. 2, 3; pl. 12, fig. 1; pl. 14, fig. 5; pl. 16, fig. 6; pl. 32, fig. 6; pl. 33, fig. 8; pl. 37, fig. 6.
1927 *Sphenopteris incerta* (Fischer): Zalessky, p. 40, pl. 11, fig. 2.
1937 *Psygmophyllum cuneifolium* (Kutorga): Zalessky, p. 64, text-fig. 27.

Occurrence and material. Marl Slate of Middridge, two specimens (B.M.N.H.).

Description. Satisfactory photographic illustration of the specimens is not possible as they are dirt-stained and the leaf substance, once complete, has peeled off in places. The form of the leaves, as shown in Text-figs. 8*a*, *b*, can, however, be made out. One

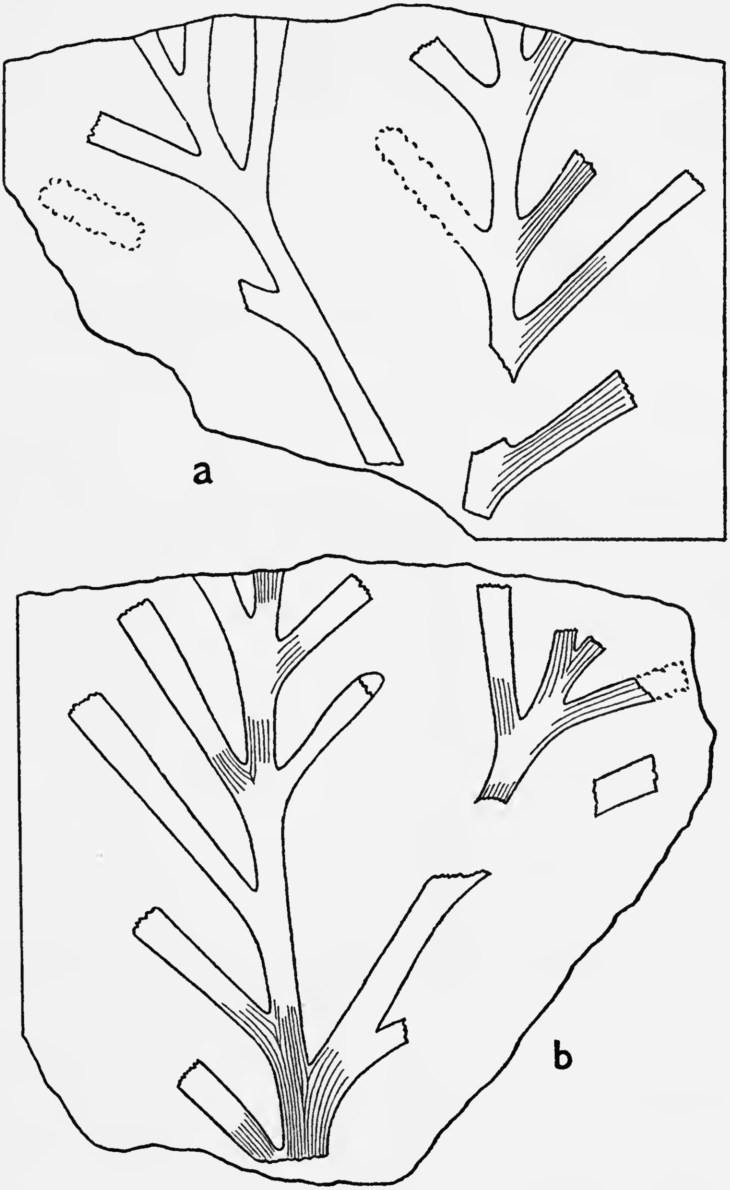

Fig. 8. ? *Psygmophyllum cuneifolium* (Kutorga) Schimper. Some remaining irregular patches of leaf substance are not indicated. Marl Slate, Middridge. British Museum (Natural History), nos. V.35131, V.35132. × 1.

clearly shows forking of the leaf below and perhaps the beginning of a repeated forking at the apex. The other specimen indicates probable forking below (where broken away). Where the cuticle has disappeared the veins are visible as parallel longitudinal strands on the impressions of both rachis and pinnae.

Cuticle. The preparations were fragile and broke into small pieces. It was impossible to distinguish the two sides, but different kinds of epidermis were recognized along the veins and between them. Along strips assumed to be the veins the cells mostly form elongated polygons. Between the veins they are either isodiametric polygons, or polygons elongated in various directions often with one or more walls curved. At intervals on both types of epidermis are round scars most of which probably represent unicellular trichome bases although some are stomata. Six or more subsidiary cells form an imperfect ring round a circular pore in which the guard cell aperture is occasionally visible.

Discussion. These specimens resemble the one from the same locality (but apparently not from the same bed) described below (p. 321) as *Pseudoctenis middridgensis*. Unfortunately comparison of the cuticular structure is impossible as only very poor preparations are obtainable from that specimen. Although it is not impossible that future discoveries may prove their specific identity, the following points suggest that the two forms are distinct. In *P. middridgensis* the rachis is not known to fork; the pinnae are mostly narrower at the base and taper to a pointed apex; the veins are more delicate; and the cuticle appears to have been thinner. Most of the pinnae in the present specimens are incomplete owing to fracture of the rock, and their apparent truncation elsewhere may in some cases be due to breakage before fossilization. There is, however, no indication that a single one tapered to a point, and in one case the impression of what appears to have been the undamaged apex can just be seen to be bluntly rounded.

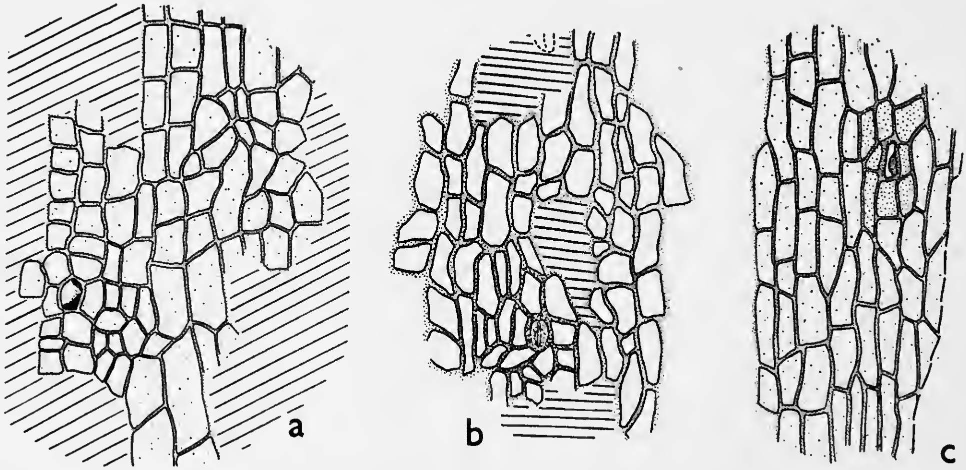

Fig. 9. ? *Psygmophyllum cuneifolium* (Kutorga) Schimper. Cuticle. Marl Slate, Middridge, British Museum (Natural History); (*a*), no. V.35133; (*b*), no. V.35134*a*; (*c*), no. V.35134*a*. All × 150.

These specimens much resemble a figure of *Psygmophyllum cuneifolium* published by Zalessky (1937) and are therefore referred with a query to that species. Previously described specimens are from the Permian of Russia, where the species is well represented although the cuticle has not been described. It is questionable whether *Psygmophyllum* is the best generic name for the species (cf. Arber, 1912), and it might be transferred to Zalessky's genus *Bardia*.

Genus ***SCHÜTZIA*** Geinitz, 1863

Schützia ? sp.

(Pl. 37, figs. 7–12)

Occurrence and material. Hilton Plant Beds of Hilton; several specimens, B.M.N.H. and G.S.M.

Remarks. The specimens illustrated look like the cup-like sporangial aggregates of *Schützia anomala* figured from the Lower Permian by Geinitz (1863), Göppert (1864), Schuster (1911) and Gothan (1937). It is not, however, possible to prove that they are of this nature. Compression has distorted many of them in various ways. Gothan thought that *S. anomala* belonged to the species *Sphenopteris germanica* Weiss, and the present specimens could belong to *S. bipinnata*, with which some were found associated.

Genus ***SPHENOBAIERA*** Florin, 1936

Sphenobaiera digitata (Brongniart) Florin

(Pl. 38, fig. 6; Text-figs. 10, 11)

1828 *Fucoides digitatus* Brongniart, p. 69, pl. 9, fig. 1.
1862 *Zonarites digitatus* (Brongn.) Geinitz, p. 336, pl. 26, figs. 1–3.
1876 *Baiera digitata* (Brongn.) Heer, p. 7, pl. 21, figs. 1, 2.
1880 *Schizopteris digitata* (Brongn.) Geinitz, p. 16, pl. 6, figs. 13, 14.
1928 *Baiera digitata* (Brongn.): Weigelt, p. 476, pl. 11, figs. 1–19; pl. 12, figs. 1–16.
1932 *Baiera digitata* (Brongn.): Weigelt, p. 148, pl. 4, figs. 1–3.
1936 *Sphenobaiera digitata* (Brongn.) Florin, p. 108.

Occurrence and material. Marl Slate of Middridge, Durham; 3 specimens (Hancock Museum). Hilton Plant Beds, Hilton Beck; several specimens (B.M.N.H. and author's coll.).

Description. Relatively good leaves from Middridge are shown in Text-fig. 10*a* and Pl. 38, fig. 6; unfortunately their cuticles are not preserved. Some recognizable although less perfect leaves (Text-fig. 10*b*) were found at Hilton and some of these retain their cuticles. The cuticle proved delicate; Text-fig. 11 shows parts of prepared fragments. The cuticle has the rather elongated cells and ring of subsidiary cells seen in many Ginkgoales. The stomatal pit is partly overhung by blunt papillae but the ordinary epidermal cells have none.

A curious structure found at Hilton (Pl. 38, fig. 4), looking like a capsule on a stalk, rather resembles the groups of microsporangia of the Rhaetic species *Baiera münsteriana* Heer figured by Schenk (1884: 261, fig. 180*b*), but it is larger. The nature of the specimen was not determined, and although it was found in the same bed as leaves of *Sphenobaiera digitata* there is no proof that it belongs to that species.

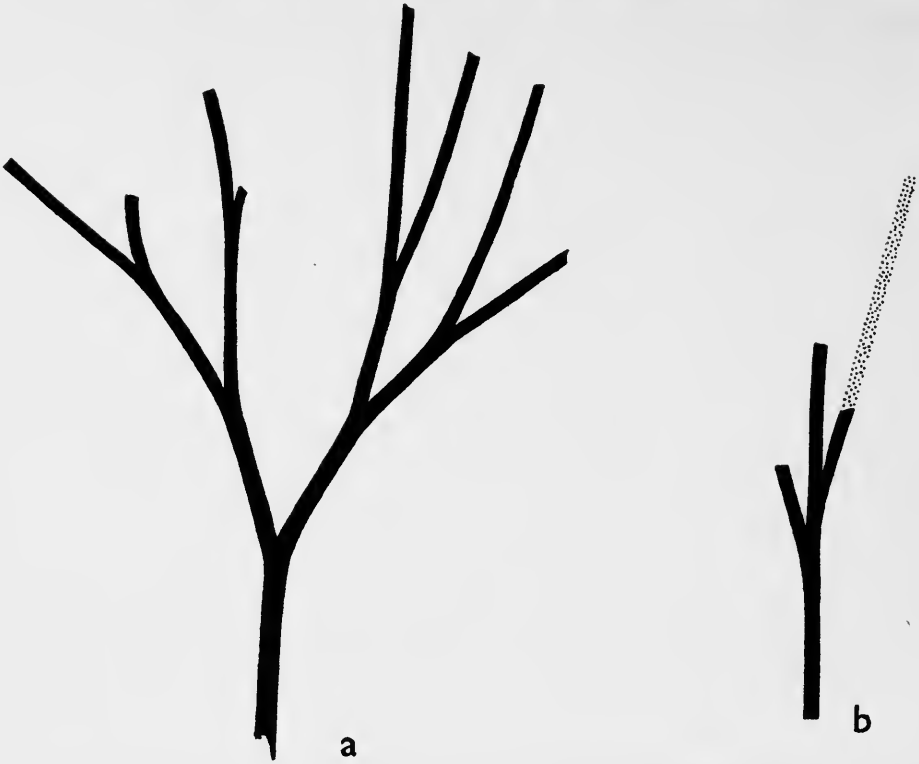

FIG. 10. *Sphenobaiera digitata* (Brongniart) Florin. (*a*), Marl Slate, Middridge. Hancock Museum; (*b*), Hilton Plant Beds, Hilton. British Museum (Natural History), no. V.35118. Both × 1.

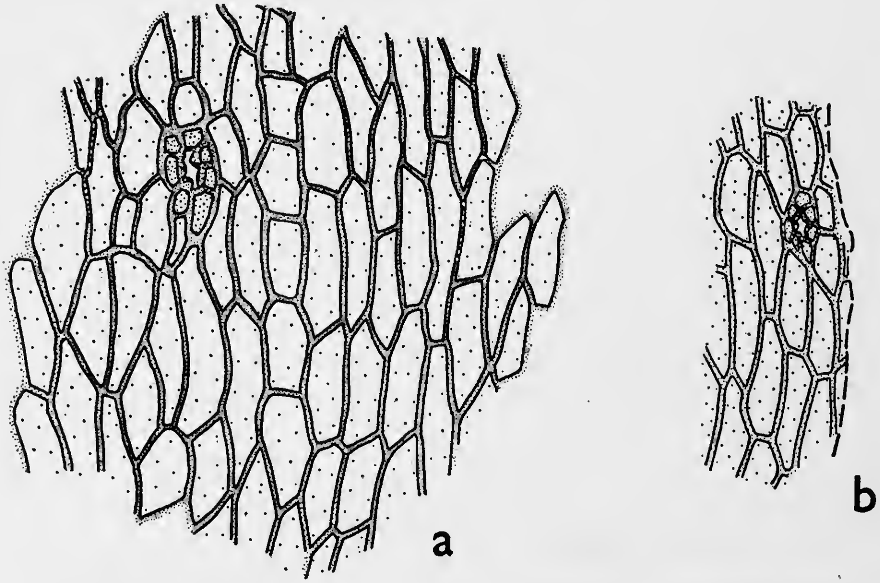

FIG. 11. *Sphenobaiera digitata* (Brongniart) Florin. Cuticle. Hilton Plant Beds, Hilton. (*a*), British Museum (Natural History), no. V.35135; (*b*), British Museum (Natural History), no. V.35136. Both × 200.

Genus *CORDAITES* Unger, 1850

cf. *Cordaites aequalis* (Göppert) Zalessky

(Pl. 38, fig. 3)

1845 *Noeggerathia aequalis* Göppert, p. 385, pl. 27, fig. 7.
1879 *Rhiptozamites Goepperti* Schmalhausen, pp. 32, 49, 81, pl. 4, figs. 2–4 ; pl. 7, figs. 23–27 ; pl. 15, figs. 1–11.
1912 *Cordaites aequalis* (Göppert) Zalessky, pl. 1, figs. 1, 3 ; pl. 2 ; pl. 3, figs. 1, 1*a*, 3, 3*a*, 4 ; pls. 4, 5 ; pl. 6, figs. 1–3 ; pl. 7, fig. 1.
1914 *Cordaites aequalis* (Göppert) : Zalessky, p. 71, pl. 2, figs. 8, 8*a*, 10, 10*a*, 11–14, 6 *bis*, 6*a*.

OCCURRENCE AND MATERIAL. Fackley Hill (p. 299), probably from basement beds of Magnesian Limestone Series ; a leaf impression in cream-coloured limestone (G.S.M. no. 76680).

DESCRIPTION. The specimen (Pl. 38, fig. 3) is the impression of the upper part of a leaf with the base missing. It shows some obscure longitudinal ridges (visible in the figure) and also fine longitudinal cellular striations. There are impressions of similar but smaller bodies on the same piece of rock. No organic substance remains.

The specimen resembles leaves from the Russian Permian figured by Zalessky, although with such scanty material the identification is not very convincing. If it can be confirmed by the discovery of more material it will be interesting as *C. aequalis* is unknown in the German Zechstein.

Genus *PSEUDOCTENIS* Seward, 1911

Pseudoctenis middridgensis sp. nov.

(Pl. 38, fig. 5 ; Text-fig. 12)

DIAGNOSIS. Leaf as a whole broadly lanceolate, typically about 18 cm. × 6 cm.; midrib straight, bearing pinnae laterally at an angle of 45° ; pinnae typically 40 mm. × 4·5 mm., widely spaced, with lower margin strongly decurrent on rachis, contracted just above the base, and with upper part tapering from the middle to an acute point ; base of pinna with two veins, each forking once or twice near the pinna base to give about 6, which continue without branching or anastomoses to the apex ; cuticle of upper side of rachis with straight-walled elongated cells, that of other parts of leaf unknown.

OCCURRENCE AND MATERIAL. Marl Slate of Middridge, Durham ; holotype only (Hancock Museum).

REMARKS. This specimen, catalogued by Howse (1890) under the *nomen nudum Ctenis permiana*, is probably the best preserved fossil plant ever found at Middridge. It is interpreted as consisting of two leaves on the same bedding plane, one lying across the other. Detached and disarranged pinnae surround the lower end of the rachis of the larger leaf. Parts of some pinnae are represented only by their impressions on which the venation is faintly visible, and the remaining parts by a thin carbonaceous film. The veins have no cross-connections. The cuticle is ill-preserved. A few frag-

FIG. 12. *Pseudoctenis middridgensis* sp. nov. Marl Slate, Middridge. Hancock Museum. × 1.

ments of cuticle from the upper side of the lamina were prepared, but the only ones showing any structure were from the rachis. These have elongated cells 20 μ wide in bands alternating with bands of less elongate cells very variable in size and shape. No stomata could be recognized. The ordinary epidermal cells have simple anticlinal walls which do not undulate, showing that the species does not belong to the Bennettitales.

This specimen resembles various Mesozoic leaves placed in *Pseudoctenis*, but in the absence of adequate knowledge of its cuticle its reference to that genus must be considered provisional, and it is also not definitely separable from *Pterophyllum*, though in typical species of that genus the pinnae arise rather above the lateral margins of the rachis. No comparable leaf is known from the Zechstein, but several from the Upper Carboniferous and Lower Permian have been referred to *Pterophyllum*. They differ in their more crowded, parallel-sided pinnae, which are almost at right angles to the rachis. The Permian leaf *Ctenis renaulti* Zalessky (1928 : 153) has broader and more crowded pinnae. *Plagiozamites* Zeiller (1894), from the Carboniferous and Permian, differs considerably in its crowded, broadly lanceolate pinnae.

CONIFERALES

Genus ***ULLMANNIA*** Göppert, 1850

Ullmannia bronni Göppert

(Pl. 38, figs. 1*a*,*b*, 2 ; Pl. 39, figs. 3, 4)

1828 *Cupressus Ullmanni* Bronn, p. 526, pl. 4, figs. 1–7, 9 (?), 10 (for figs. 8, 11 see *Strobilites bronni*).
1850 *Ullmannia Bronnii* Göppert, p. 185, pl. 20, figs. 1–19, 23*b* (for figs. 20–22, 23*a*, 24–26 see *Strobilites bronni*).
1862 *Ullmannia Bronni* Göppert : Geinitz, p. 154, pl. 30, fig. 2 ; pl. 31, figs. 22–27 (*non* figs. 11, 21, 28–30).
1876 *Ullmannia Bronnii* Göppert : Heer, p. 8, pl. 21, figs. 3–5.
1880 *Ullmannia Bronni* Göppert : Geinitz, p. 23, pl. 4, figs. 8–11, 14.
1884 *Ullmannia Bronnii* Göppert : Solms-Laubach, pp. 13–28, pl. 2, figs. 11–15.
1922 *Ullmannia Bronni* Göppert : Gothan & Nagalhard, p. 443, pl. 5, figs. 1, 2 ; pl. 6, fig. 1.
1928 *Ullmannia Bronni* Göppert : Weigelt, p. 564, pl. 35, figs. 1–5, 9.
1954 *Ullmannia Bronnii* Göppert : Florin, p. 2, pl. 2.

Occurrence and material. Marl Slate of Raisby Hill quarries (p. 298), one fine specimen (King's College, Newcastle-on-Tyne), and of Middridge, one specimen (G.S.M.). Isolated leaves (some as cuticle preparations) from Marl Slate of Cinderhill (p. 300) (B.M.N.H.) and of Calverton Colliery shaft (p. 301), depth 402–456 ft., (B.M. N.H.) ; from Lower Marl of Bentley Colliery (p. 300) (Wollaton Hall Mus.) and of Sutton borehole (p. 300), depth, 1,085 ft. (B.M.N.H.) ; from Lower Limestone or Lower Marl of Doddington borehole (p. 300), depths 2,300, 2,303 and 2,310 ft. (G.S.M.), and of Wellow borehole (p. 301) (B.M.N.H.) ; and from Hilton Plant Beds of Hilton (B.M.N.H.), Belah Brook, and Little Salkeld (Carlisle Mus.).

Description. The specimen from Raisby Hlll (Pl. 38, figs. 1*a*, *b*) which is nearly 35 cm. long, consists of a main stem about 20 mm. wide and 20 cm. long which divides into four secondary branches about 13 mm. wide, two of which ultimately bifurcate. Two of the secondary branches cross as they lie flattened on the bedding plane. The main stem and branches are densely covered with imbricating leaves, the impressions of which are clearly preserved. The leaves, have the broadly lanceolate form and bluntly angular extremity characteristic of *Ullmannia bronni.* Their median keel and longitudinal striations are visible in places. The leaves on the main stem are about 4·5 mm. wide and twice as long and there are about five to the width of the stem. The size of the leaves decreases towards the distal end of each branch, but their proportions remain the same. No cuticle is preserved.

There is a poorly preserved specimen of *U. bronni* from Middridge, but most specimens from that locality so labelled in museums belong to *U. frumentaria* or to *Hiltonia rivuli.* Many of the isolated leaves from the borings and colliery shafts have well-preserved cuticles. The preparations show characteristic dark bands with stomata in single files, and agree with the cuticle of *U. bronni* as figured by Gothan & Nagalhard (1922) and Florin (1944, 1954) from German and Belgian specimens, and as prepared by myself from German material.

Göppert was not justified in changing the trivial name of this species when founding the genus *Ullmannia,* but his name *bronni* is here retained in accordance with long-established usage.

Ullmannia frumentaria (Schlotheim) Göppert

(Pl. 39, figs. 1, 2 ; Text-figs. 13, 14)

1820 *Carpolithes frumentarius* Schlotheim, p. 419, pl. 27, fig. 1.
1828 *Fucoides selaginoides* Brongniart, p. 72, pl. 9, fig. 3.
1836 *Voltzia Phillipsii* Lindley & Hutton, p. 123, pl. 195.
1850 *Caulerpa ? selaginoides* (Brongn.) King, p. 3, pl. 1, figs. 3, 3*a*.
1922 *Ullmannia frumentaria* (Schloth.) : Gothan & Nagalhard, p. 445, pl. 5, fig. 3 ; pl. 6, figs. 3, 4. (See this for further literature.)
1928 *Archaeopodocarpus germanicus* Weigelt, pp. 485–553, pl. 2, figs. 24, 25 ; pl. 3, figs. 1, 4–6, 8 ; pl. 4, figs. 1, 2, 7, 11–13 ; pl. 6, figs. 3–12 ; ? pl. 13, figs. 7, 11, 13, 15, 17 ; pls. 23–38 (most figs.) ; pl. 31, figs. 1–3, 6, 7, 11.
1928 *Strobilifer frumentarius* (Schloth.) Weigelt, p. 553, pl. 30, figs. 1, 2, 11–17, 28–31, 34 ; pl. 35, figs. 10 *a*, *b*.
1944 *Ullmannia frumentaria* (Schloth.) : Florin, p. 447, pl. 169/170, figs. 10–12 ; p. 449, text-figs. 44*a*, *b* (microspores).
1944 *Ullmannia Bronnii* Göppert : Florin, p. 484, text-fig. 52 ; pl. 179/180, figs. 17–19 ; pl. 181/182, figs. 1, 2.

Occurrence and material. Marl Slate of Cullercoats, Middridge, Ferryhill, Thickley, Claxheugh, and Cinderhill ; numerous specimens in the chief collections studied. Hilton Plant Beds, Hilton Beck and Belah Brook, fragments of shoots and isolated leaves (B.M.N.H. and G.S.M.). Isolated leaves, some now as cuticle preparations, from Lower Marl of Sutton borehole (p. 300), depth 1,085 ft. (B.M.N.H.) ; from Lower Limestone or Marl of Doddington borehole (p. 300), depth 2,327 ft. (G.S.M.), and of Thoresby Colliery shaft (p. 301) (B.M.N.H.) ; and from Hilton Plant Beds of Little Salkeld (Carlisle Mus.).

Description. Text-fig. 13*c* shows a shoot apex with densely overlapping leaves ; Pl. 39, fig. 2, the lower part of a shoot with more widely spaced leaves ; and Text-

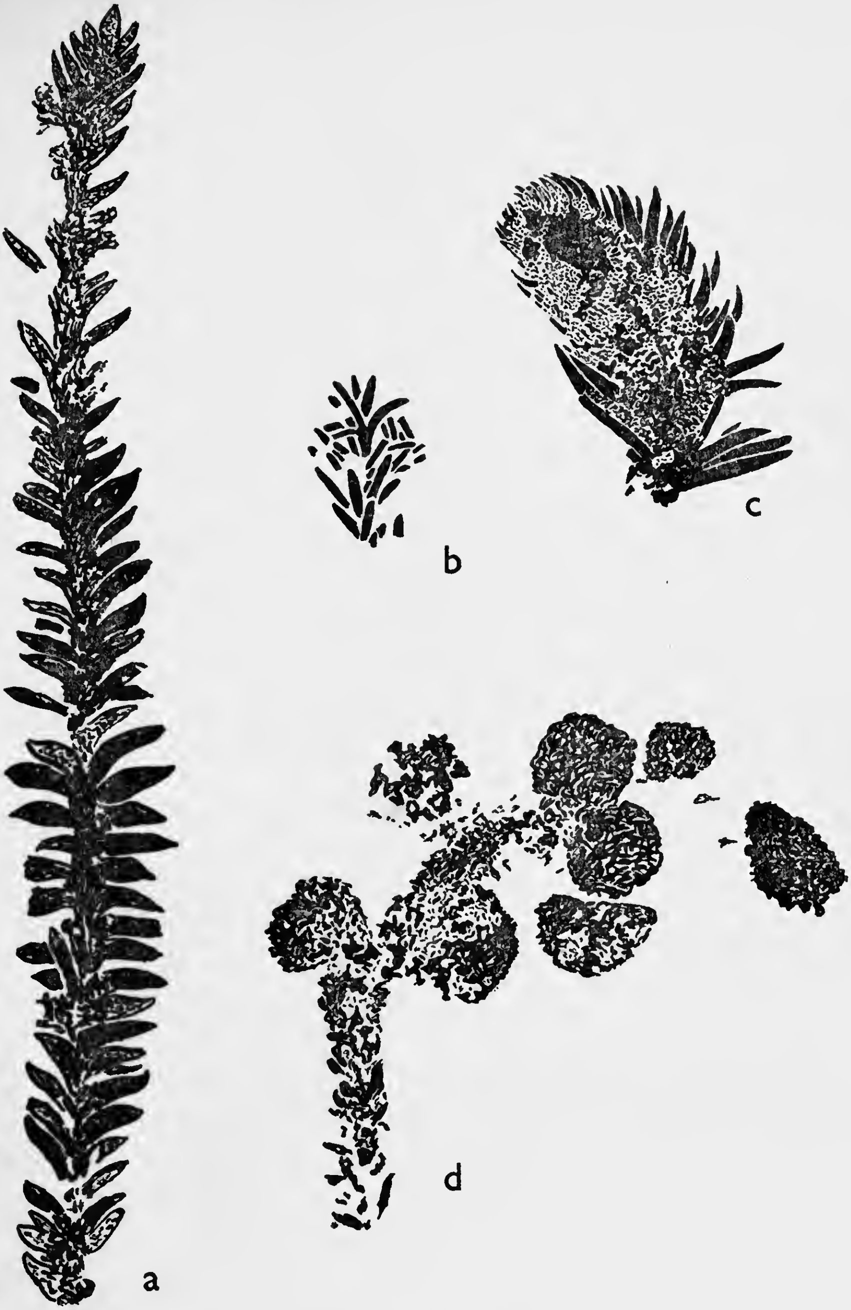

Fig. 13. *Ullmannia frumentaria* (Schlotheim) Göppert. (*a*), Marl Slate, Middridge. British Museum (Natural History), no. V.35130 ; (*b*), Hilton Plant Beds, Hilton. Geological Survey, no. 19075 ; (*c*), Marl Slate, Thickley. British Museum (Natural History), no. V.32390 ; (*d*), Marl Slate, Co. Durham. Dorman Memorial Museum, Middlesbrough. All × 1.

fig. 13*a* a shoot with rather short spreading leaves. It is noticeable that in some of the compressed shoots the leaves look less regular than in others. There are considerable differences in the size of the leaves on different shoots. Text-fig. 13*d* and Pl. 39, fig. 1 show fertile shoots similar to those from Germany described by Florin (1944). Unfortunately no details of the structure of the female cones can be made out. These fertile shoots and the majority of sterile ones from Durham are unsuitably preserved to give cuticle preparations. Rather poor preparations were obtained from a specimen from Cullercoats and good ones from isolated leaves from Thoresby Colliery shaft and from Hilton Beck. The details are like those of *U. bronni ;* the stomata are in single files along strips darker than those between the files. The structure agrees with that of the German specimens described by Gothan & Nagalhard (1922) and by Kräusel (1923).

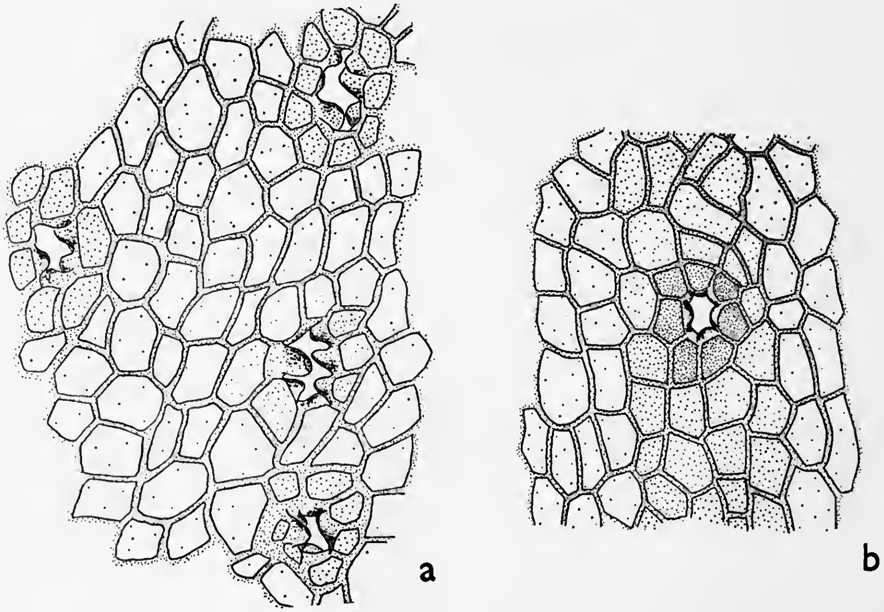

FIG. 14. *Ullmannia frumentaria* (Schlotheim) Göppert. Cuticle. (*a*), Marl Slate, Cullercoats. British Museum (Natural History), no. V.35137. × 150 ; (*b*), Magnesian Limestone Series, Thoresby Colliery shaft. British Museum (Natural History), no. V.35138. × 200.

The English specimens had previously been identified in museums as *U. frumentaria, U. selaginoides,* and *U. bronni.* The second was considered a synonym of *U. frumentaria* by Gothan & Nagalhard (1922), whose views are here accepted. The difference between *U. bronni* and *U. frumentaria* lies in the shape of the leaves. In *U. bronni* these are broadly lanceolate and mostly obtusely pointed, although some have rounded tips ; their length does not exceed 2½ times their width. In *U. frumentaria* they are relatively and often absolutely longer and the apex is acute. There has, however, been some disagreement about the boundary between the two species.

By the criterion stated, most English specimens labelled as *U. bronni* belong to *U. frumentaria*.

The holotype of *Voltzia phillipsii* Lindley & Hutton, an early synonym of *U. frumentaria*, has not been traced; it came from the Marl Slate of Whitley, Durham.

Genus ***PSEUDOVOLTZIA*** Florin, 1927

Pseudovoltzia liebeana (Geinitz) Florin

(Pl. 40, figs. 1, 4, 6; Text-figs. 15, 16)

1862 *Cyclopteris Liebeana* Geinitz, p. 140, pl. 26, figs. 4–6.
1880 *Voltzia liebeana* (Geinitz) Geinitz, p. 26, pl. 5, figs. 1–8, 10–25 (*non* figs. 9, 26).
1928 *Voltzia Liebeana* (Geinitz): Weigelt, p. 565, pl. 5, fig. 4; pl. 16, figs. 4, 8, 9; pl. 31, figs. 4, 5, 8–10; pl. 32, figs. 1–29; pl. 33, figs. 1–19; pl. 34, figs. 1–11.
1929 *Voltzia Liebeana* (Geinitz): Walton, p. 1, pl. 1; text-fig. 1.
1929 *Pseudovoltzia liebeana* (Geinitz) Florin, p. 257, pl. 4, fig. 10.
1944 *Pseudovoltzia Liebeana* (Geinitz): Florin, p. 413, text-fig. 26*a*; p. 479, text-figs. 50, 51; pl. 179/180, figs. 1–15.

Occurrence and material. Marl Slate of Thickley (B.M.N.H. and King's College, Newcastle-on-Tyne), of Ferryhill (G.S.M.), of Middridge? (Hancock Museum), and of Kimberley (B.M.N.H.). Lower Marl, Sutton borehole (p. 300), depth 1,085 ft. (G.S.M.) and Markham Moor borehole (p. 300), depth 1,105 ft. (G.S.M.). Lower Magnesian Limestone, Wressell borehole (p. 300), depth 1,982–1,984 ft. (G.S.M.). Hilton Plant Beds, Hilton (B.M.N.H. and G.S.M.), Belah Brook, and Birkshead Mine.

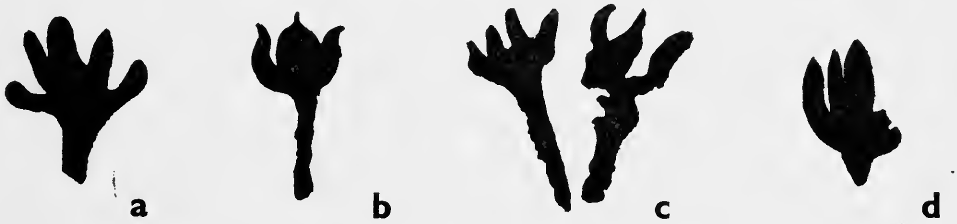

Fig. 15. *Pseudovoltzia liebeana* (Geinitz) Florin. Cone scales. (*a*), Marl Slate, Kimberley. British Museum (Natural History), no. V.35128; (*b*, *c*), Hilton Plant Beds, Hilton. Geological Survey, nos. 19073, 19074; (*d*), Hilton Plant Beds, Hilton. British Museum (Natural History), no. V.35119. All × 1·6.

Description. The English material consists of shoots, isolated leaves, and isolated cone scales. Typical shoots are shown in Pl. 40, figs. 1, 4; fig. 4 represents the largest seen. The leaves in all the specimens are elongated, parallel-sided, and rounded at the apex. Fig. 1 shows the short basal leaves produced when the bud first began growth; as Florin pointed out, this is a character of the species (cf. Geinitz, 1880, pl. 5, fig. 1).

The cuticle has perished in the Durham specimens, but moderately good preparations were made from leaves from the Markham Moor borehole (Text-fig. 16). They look just like the figure given by Florin (1944: 413) and some preparations I made from

German shoots. They are very similar to the cuticles of the two species of *Ullmannia*—so similar, indeed, that isolated fragments not showing the form of the whole leaf cannot be distinguished. There is, however, a possibility (which needs confirmation from further material) that in *Pseudovoltzia* the subsidiary and ordinary cells along the stomatal bands are less heavily cutinized; that the ordinary epidermal cells are often shorter; that the subsidiary cells have a more regularly pentagonal shape; and that the stomata are more often grouped in pairs or in threes. At present, however, the only reliable distinction between leaves of *Pseudovoltzia* and *Ullmannia* lies in their very different shape.

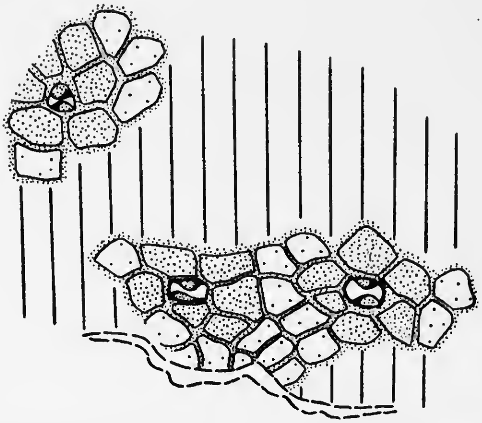

FIG. 16. *Pseudovoltzia liebeana* (Geinitz) Florin. Cuticle. Magnesian Limestone Series; depth 1,293 ft., Markham Moor borehole. Geological Survey, no. PF623. × 200.

An excellent isolated cone scale from the Sutton borehole has been figured by Walton (1929) and Florin (1944, pl. 179/180, figs. 14, 15). Text-fig. 15 shows isolated cone-scales from Hilton and Kimberley preserved in carbonized form; the lobes are strikingly varied.

The specimens from the Manchester Marls preserved in the Manchester Museum as the basis of records of this species by Geinitz (1890 : 549) and Roeder (1892 : 16) are indeterminate.

Genus **HILTONIA** Stoneley, 1956

Hiltonia rivuli Stoneley

1956 *Hiltonia rivuli* Stoneley, p. 714, text-figs. 1–4.

OCCURRENCE. Marl Slate, Middridge, Thickley, and Kimberley. Lower Marl, Haughton Hall borehole (p. 300), depth 1,116 ft.; and of Sutton borehole (p. 300), depth 1,085 ft. Lower Marl or Lower Limestone, Doddington borehole (p. 300), depths 2,310 and 2,330 ft.; of Wellow borehole (p. 301); and of Farnsfield borehole (p. 301). Hilton Plant Beds, Hilton, Belah Brook, Birkshead Mine, and opencast mine near Kirkby Thore.

Genus *CONITES* Sternberg, 1823

Conites sp.

(Pl. 40, fig. 5)

Occurrence and material. Bulcote borehole (p. 301), depth 711 ft. (3 ft. 6 in. above base of Upper Permian beds); one specimen (G.S.M. no. 76681).

Description. The only specimen is shown in the figure. The lateral appendages seem irregularly spaced, but this is perhaps a result of compression of those originally above or below the bedding plane on which the specimen lies. Both main axis and appendages are longitudinally striated. There is nothing to show whether the expanded distal ends of the appendages bore pollen sacs or seeds. The specimen consists of crumbly carbonaceous matter and a fragment yielded no cuticle. The matrix contained no leaf or other plant remains throwing light on its identity.

Remarks. Nothing like this specimen has been previously described from the Permian. There are, however, a good many obscure cones from the Mesozoic which look something like it, and it is referred to *Conites* at the suggestion of Professor T. M. Harris.

Genus *STROBILITES* Lindley & Hutton, 1833

Strobilites bronni Solms-Laubach

(Pl. 40, figs. 7–11).

1850 *Ullmannia Bronnii* Göppert, p. 185 (in part), pl. 20, figs. 20 (?), 21, 22, 23*a*, 24–26.
1884 *Strobilites Bronnii* Solms-Laubach, p. 34, pl. 2, figs. 2, 3, 4 (?), 5–9, 16 (?), 17 (?), 18 (?), 19 (?).
1928 *Strobilites Bronni* Solms-Laubach: Weigelt, p. 474, pl. 10, fig. 5.
1930 *Strobilites bronni* Solms-Laubach: Weigelt, p. 644, pl. 1, fig. 2.
1931 " Rosetten von *Ullmannia bronni* ": Weigelt, p. 106, 108, text-figs. 3*b*, *c*.
1944 *Strobilites Bronni* Solms-Laubach: Florin, p. 447, pl. 169/170, figs. 13–22.

Occurrence and material. Marl Slate, Kimberley; several specimens (B.M. N.H.). Hilton Plant Beds, Hilton; several specimens (B.M.N.H., G.S.M.); also of Belah Brook.

Description. The specimens occur carbonized or as mere impressions. They show no fine details. The figures show the range of form. All can be matched among published figures of German specimens.

Remarks. There has been much doubt about the nature of these curious little fossils, specimens of which from the Upper Zechstein were described as "Sterngraupen" by Waldin (1778) and Ullmann (1802). Heer (1876) and Solms-Laubach (1884) doubted Göppert's assumption that they belonged to *Ullmannia*. Weigelt at first (1928) doubted but later (1931) accepted this view. Florin (1944) interpreted them as isolated segments of *Ullmannia* male cones. They vary so much in form that they may not all be of the same nature

Strobilites ludwigi (Weigelt)

1928 " Weibliche Blüte von *Archaeopodocarpus* ": Weigelt, p. 495, pl. 13, fig. 19.
1930 *Araucarites ludwigi* Weigelt, p. 660, text-fig. 39 ; ? also text-fig. 41 (p. 663).
1931 *Araucarites ludwigi* Weigelt : Weigelt, p. 107, 115, text-figs. 2, 12.

OCCURRENCE AND MATERIAL. Hilton Plant Beds, Hilton ; one specimen (B.M.N.H., C. T. Trechmann Colln.).

DESCRIPTION. The specimen shows three rounded or bell-shaped groups of elongated leaf-like organs and closely resembles the fossil figured by Weigelt. The specimen is carbonized and no cuticle could be obtained from it ; no finer details are apparent.

REMARKS. Weigelt first named his species *Araucarites*, but this generic name has been used by some authors for cones or cone scales which agree in structure with *Araucaria* (e.g. in having one seed on the upper surface of each scale), and nothing of the sort has been proved in this species. Weigelt abandoned his original view that it was the female inflorescence of " *Archaeopodocarpus* " (*Ullmannia*). The non-committal name *Strobilites* is here adopted for it.

Genus ***SAMAROPSIS*** Göppert, 1864

Samaropsis triangularis (Geinitz) Seward

(Pl. 40, figs. 2, 3)

1862 *Cardiocarpon triangulare* Geinitz, p. 145, pl. 31, figs. 11*, 12–15.
1880 *Ullmannia frumentaria* (Schloth.), " Fruchtschuppen mit Abdruck des Samens, früher *Cardiocarpon triangulare* ": Geinitz, p. 22, pl. 3, figs. 11–15.
1884 *Cardiocarpon triangulare* Geinitz : Solms-Laubach, p. 34, pl. 2, fig. 20.
1917 *Samaropsis triangularis* (Geinitz) Seward, p. 338.
1928 *Cyclocarpon triangulare* (Geinitz), " Fruchtschuppen, vielleicht aus Zapfen von *Strobilifer frumentarius* ": Weigelt, p. 560, pl. 30, figs. 23–26.

OCCURRENCE AND MATERIAL. Marl Slate of Kimberley and Watnall ; several specimens (B.M.N.H.).

REMARKS. The English specimens, which seem locally abundant, show the central part of the seed as a solid body surrounded by a flat membrane. The surface of the central part is slightly wrinkled. Geinitz (1880) and later Weigelt (1928) thought that this might be the seed of *Ullmannia frumentaria*, but Florin has found a different kind of seed in the seed-scale complex of that species.

UNIDENTIFIED CUTICLE TYPES

Bulk-macerated material from several boreholes and from the Hilton Plant Beds yielded a number of well-characterized cuticle types distinct from any of those prepared from identifiable plant remains. In some cases it was possible to ascertain the form of the complete leaf, but in others the material consisted only of small fragments. A set of descriptions and illustrations is available for consultation in the British Museum (Natural History), where the cuticle slides are also deposited. The identification of these cuticle types must await future research. More complete remains of the plant species to which the majority belong probably have yet to be discovered and described, although a few of the new types may belong to described species the cuticular structure of which has not yet been investigated owing to lack of suitably preserved identifiable material.

NON-VEGETABLE STRUCTURES WHICH HAVE BEEN REGARDED AS PLANT REMAINS

Guilielmites permianus Geinitz

(Pl. 40, fig. 12)

1858 *Guilielmites permianus* Geinitz, p. 19, pl. 2, figs. 6–9.
1889 *Guilielmites permianus* Geinitz : Geinitz, p. 56 (English specimens).
1890 *Guilielmites permianus* Geinitz : Geinitz, p. 550 (English specimens).
1890*b* *Guilielmitis* (*sic*) *permianus* Geinitz : Roeder, p. 16 (English specimens).

Occurrence and material. Upper Permian Marl of Fallowfield, near Manchester ; specimens recorded by Geinitz and by Roeder are now in the Manchester Museum.

Remarks. First described from the German Rotliegende and originally regarded as a fructification of a palm related to the living *Guilielma*, *Guilielmites* is a peculiar structure now known from many geological formations. Authors who have discussed it include Weiss (1868 : 94 ; 1872 : 211), Carruthers (1871 : 446), Roemer (1880 : 246), Sterzel (1881 : 242), Hoffmann & Ryba (1899 : 102), Potonié (1921 : 16), Pruvost (1930 : 260) and Wood (1935). The best figures are those of Hoffmann & Ryba (1899, pl. 19, figs. 19, 20). Wood attributes such structures to the collapse under pressure of some body, such as a shell or plant fragment, which has been embedded in the sediment. As a result, a series of polished, striated surfaces came into existence owing to local slipping of the rock, which is always a compact, fine-grained shale.

Spongillopsis dyadica Geinitz

1889 *Spongillopsis dyadica* Geinitz, p. 56 (*non S. dyatica* Geinitz, 1862).
1890 *Spongillopsis dyadica* Geinitz : Geinitz, p. 550 (*non S. dyatica* Geinitz, 1862).

Occurrence and material. Upper Permian Marl of Stockport, near Manchester ; the specimen recorded by Geinitz, now in the Manchester Museum.

Remarks. It is doubtful if the short, irregularly curved, occasionally branching wrinkles which stand out on the surface of this specimen of red marl are of the same nature as Geinitz's original *S. dyatica*, itself problematical. The structures are undoubtedly of inorganic origin and the name can be expunged from the list of English Permian plants.

Palaeophycus insignis Geinitz

1861 " Cast of a laterally compressed tube . . . " Kirkby, p. 309.
1862 *Palaeophycus insignis* Geinitz, p. 131, pl. 24, fig. 4.
1890 *Palaeophycus insignis* Geinitz : Howse, pp. 237, 244.
1930 *Palaeophycus insignis* Geinitz : Weigelt, p. 645, text-fig. 1*a*, *b*.

Occurrence and material. Kirkby (1861) described specimens which must have belonged to *P. insignis* from the Lower Magnesian Limestone of Hampole Stubbs, near Doncaster. Howse (1890) recorded *P. insignis* from the Lower Magnesian Limestone of Thickley and the Middle Magnesian Limestone of Tunstall Hill. The only specimen seen by the present writer is from Thickley and is in the Hancock Museum.

Remarks. The specimen from Thickley closely resembles that described by Geinitz, which came from the Dolomitic Zechstein near Gera and was a fragment, 40 mm. long and 7 mm. wide, of a smooth, solid, rod-like body elliptical in cross-section. He listed the species as an alga, but Weigelt (1930), who figured specimens from the Kupferschiefer of Ilmenau, thought that they were the borings of arthropods. There have been various theories as to the origin of other " species ", from different formations, described under Hall's genus *Palaeophycus* (Richter, 1927 : 198, 200 ; Schindewolf, 1928 : 39 ; Wilckens, 1947 : 47 ; Korn, 1932 : 17). No modern authorities consider them to be algae.

Chondrus binneyi King

(Pl. 40, fig. 13)

1850 *Chondrus ? Binneyi* King, p. 2, pl. 1, fig. 1.

Occurrence and material. Upper Permian Marl, just above Collyhurst Sandstone, of a river section at Newton, near Manchester (Binney, 1839 : 55 ; 1855 : 226). The holotype, formerly in the Binney Coll., has not been traced, but a topotype belonging to the Geological Survey has been examined. The specimen (G.S.M. no. Bc 4081) from the Ulleskelf Nurseries boring recorded as " cf. *Chondrus binneyi* King " (Edwards *et al.*, 1950 : 42) has also been examined.

Description. On the bedding planes of the red marl, in the topotype, are numerous irregularly scattered circular structures, each about 2 mm. in diameter and having the form of a raised ring with a central depression, or (as seen on the reverse surface) of a central boss surrounded by a moat-like depression. Between these structures each bedding plane is covered with sinuous fibrous markings, the general direction of which varies considerably. The structures are composed of the same material as the rest of the marl and carbonaceous matter is absent. They were regarded by King (1850) as " seed vessels " sessile on a " broad frond ", but there is little doubt they are of inorganic origin. They seem comparable to the " pit and mound " structures described by Kindle (1916), Shrock (1948 : 132) and other authors.

The Ulleskelf specimen consists of hard grey limestone with comparable structures, which, however, are more variable in size and often larger than in the topotype.

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PLATE 36

FIG. 1. *Algites sternbergianus* (King). Fine filaments are visible on the curved axis. Lower Magnesian Limestone, Westoe, South Shields. Geological Survey, no. 90165. × 1.

FIG. 2. Same species, formation, and locality. Group of axes. Geological Survey, no. 90164. × 1.

FIG. 3. *Piaea anglica* sp. nov. Group of axes. Magnesian Limestone series, depth 1,140 ft., Markham Moor borehole, near East Retford. Geological Survey, no. 76607. × 2 approx.

FIG. 4. *Calathella dictyonemoides* sp. nov. Magnesian Limestone series, depth 1,056 ft., Markham Moor borehole, near East Retford. Geological Survey, no. 76608. × 1.

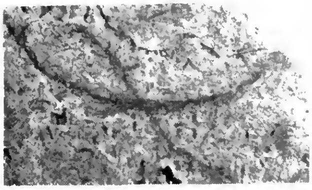
FIG. 5. *Algites sternbergianus* (King). Brush of filaments. Same formation and locality as Figs. 1, 2. Geological Survey, no. 49956. × 2·2.

FIG. 6. ? *Tubulites permianus* (King). Bunched tubes. Upper Magnesian Limestone, Blackhall Rocks, 5 miles N. of Hartlepool. *C. T. Trechmann Colln.*, British Museum (Natural History), no. V.35111. × 3.

FIG. 7. *Tubulites permianus* (King). Upper Magnesian Limestone (concretionary beds), Easington. *C. T. Trechmann Colln.*, British Museum (Natural History), no. V.35113. × 2·4.

FIG. 8. Same species. Transverse sections of tubes. Upper Magnesian Limestone, depth 4,240 ft., Eskdale borehole no. 3, Sleights, near Whitby. Geological Survey, no. PF625. × 5.

FIG. 9. Same species. Longitudinal sections of tubes. Same borehole and depth as the preceding. Geological Survey, no. PF624. × 5.



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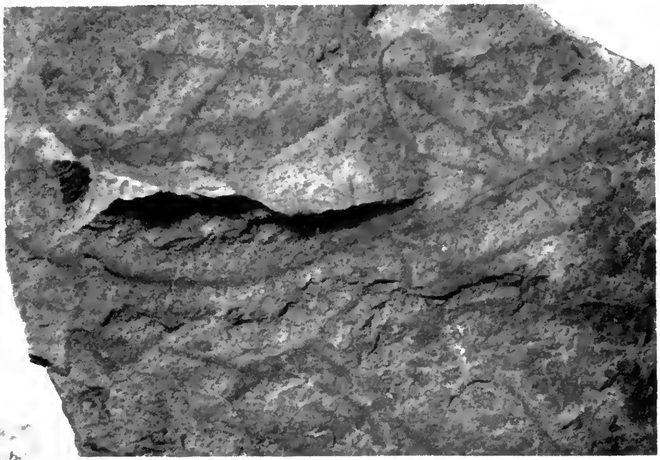

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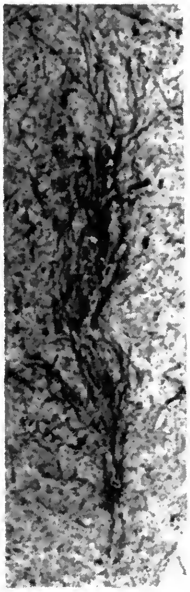

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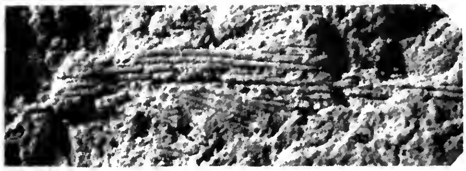

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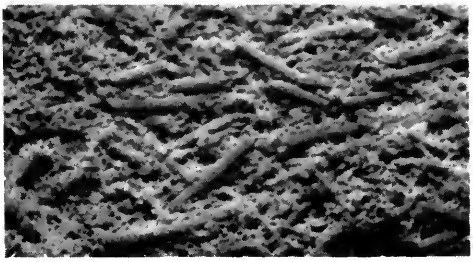

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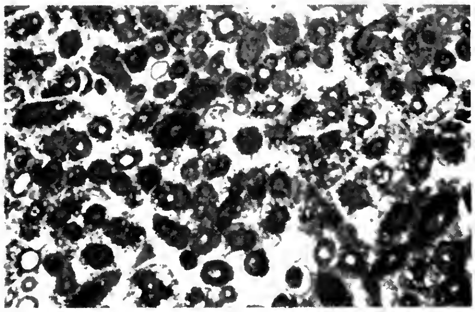

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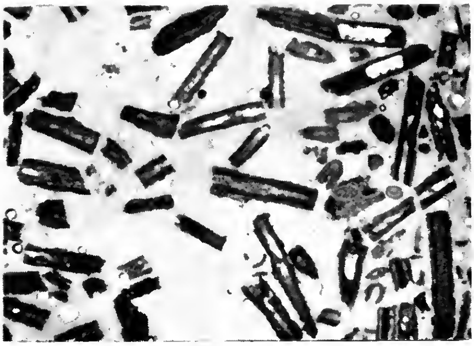

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PLATE 37

FIG. 1 *Paracalamites kutorgai* (Geinitz) Zalessky. Enlarged view of part of flattened stem fragment, with a node near left of figure. Marl Slate, Fulwell Water Works, near Sunderland. Hancock Museum. × 3, approx.

FIG. 2. *Callipteris martinsi* (Kurtze) Zeiller. Cuticle, showing a stoma with a prominent papilla. Marl Slate, Kimberley. British Museum (Natural History), no. V.5963*i*. × 200.

FIG. 3. *Taeniopteris eckardti* Kurtze. Marl Slate, Middridge. Hancock Museum. (*a*) × 1; (*b*) part of specimen, × 2, showing details of veins.

FIG. 4. *Mixoneura* sp. Pinnule from the holotype of *Neuropteris huttoniana* King. Marl Slate, Thrislington Gap, near Ferryhill. University College, Galway. × 2·3.

FIG. 5. *Callipteris martinsi* (Kurtze) Zeiller. The pinnules show a midrib and veins, also, at their base, scars of unknown origin. Marl Slate, Kimberley. British Museum (Natural History), no. V.5960. × 1·5.

FIG. 6. *Sphenopteris bipinnata* (Münster) Geinitz. Hilton Plant Beds, Hilton. British Museum (Natural History), no. V.35116. × 1·4.

FIGS. 7, 8. *Schützia* ? sp. Crushed specimens possibly belonging to the same species as Figs. 9–12, but with the sporophylls (?) relatively few and distinct. Hilton Plant Beds, Hilton. British Museum (Natural History), nos. V.35120–21. × 1.

FIG. 9. *Schützia* ? sp. Two associated cup-shaped sporangial aggregates, preserved almost uncompressed but with their structure obscure. Hilton Plant Beds, Hilton. *C. T. Trechmann Colln.*, British Museum (Natural History), no. V.20554. × 1.

FIG. 10. *Schützia* ? sp. Laterally crushed specimen, with the opened-out sporophylls clearly seen. Hilton Plant Beds, Hilton. British Museum (Natural History), no. V.35122. × 3.

FIG. 11. *Schützia* ? sp. Specimen crushed so as to present much the same aspect as Fig. 10. Hilton Plant Beds, Hilton. Royal Scottish Museum, no. 1957. 15.1. × 3.

FIG. 12. *Schützia* ? sp. Crushed specimen; the under side with a hollow for stalk attachment is seen, but the outlines of individual sporophylls are mostly indistinct. Hilton Plant Beds, Hilton. Geological Survey, no. 19068. × 1.

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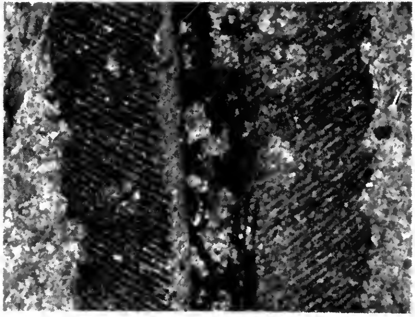
a



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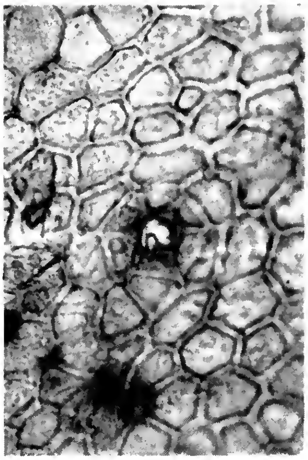

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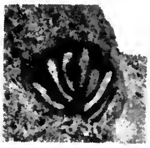

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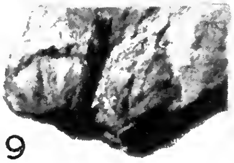

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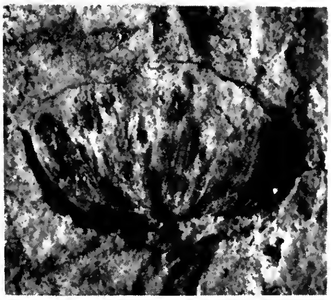

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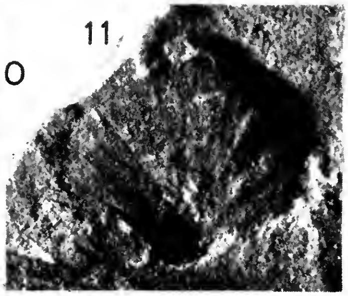

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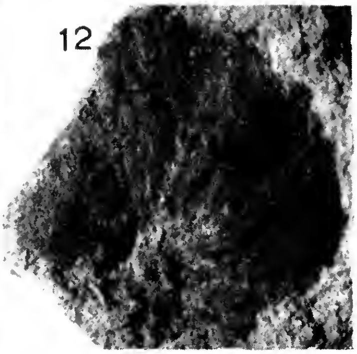

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PLATE 38

FIGS. 1*a*. *b*. *Ullmannia bronni* Göppert. Impression of a forking branch. Marl Slate, Raisby Hill Quarries, near Coxhoe. King's College, Newcastle-upon-Tyne. (*a*) Complete specimen. × 0·38, (*b*) part of specimen, showing densely imbricating leaves. × 0·77.

FIG. 2. Same species. Marl Slate, Middridge. Geological Survey, no. 19067. × 1.

FIG. 3. cf. *Cordaites aequalis* (Göppert) Zalessky. Leaf impression. Basement beds of Magnesian Limestone series, Fackley Hill, near Skegby. Geological Survey, no. 76680. × 1.

FIG. 4. Capsule of uncertain affinities, from bed containing *Sphenobaiera digitata* (Brongniart). Hilton Plant Beds, Hilton. British Museum (Natural History), no. V.35123. × 1.

FIG. 5. *Pseudoctenis middridgensis* sp. nov. Portion of rachis and bases of several pinnae, showing veins. Marl Slate, Middridge. Hancock Museum. × 1·8. (see also Text-fig. 12).

FIG. 6. *Sphenobaiera digitata* (Brongniart) Florin. Marl Slate, Middridge. Hancock Museum. × 1

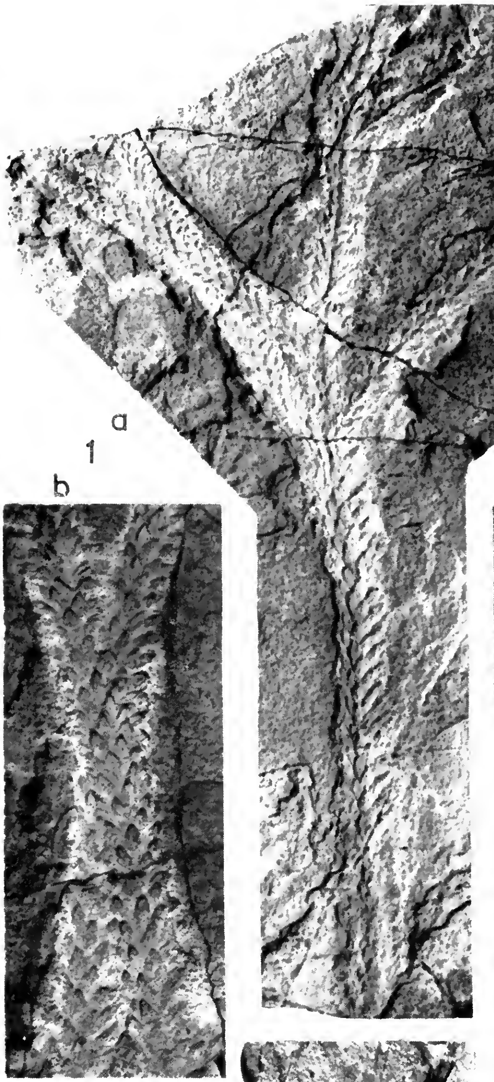

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PLATE 39

FIG. 1. *Ullmannia frumentaria* (Schlotheim) Göppert. Female cone. Marl Slate, Middridge. British Museum (Natural History), no. V.35129. × 1.

FIG. 2. Same species. Marl Slate, Thickley. *C. T. Trechmann Colln.*, British Museum (Natural History), no. V.20553. × 1.

FIG. 3. *Ullmannia bronni* Göppert. Cuticle. Near base of Magnesian Limestone series, Wellow borehole. British Museum (Natural History), no. V.35139. × 150.

FIG. 4. Same species. Cuticle with two stomata. Near base of Magnesian Limestone series, Calverton Colliery shaft. British Museum (Natural History), no. V.35140. × 270.

FIG. 5. *Strobilites ludwigi* (Weigelt) ; also two leaves of *Hiltonia*, near right and left margins. Hilton Plant Beds, Hilton. *C. T. Trechmann Colln.*, British Museum (Natural History), no. V.20555. × 1.


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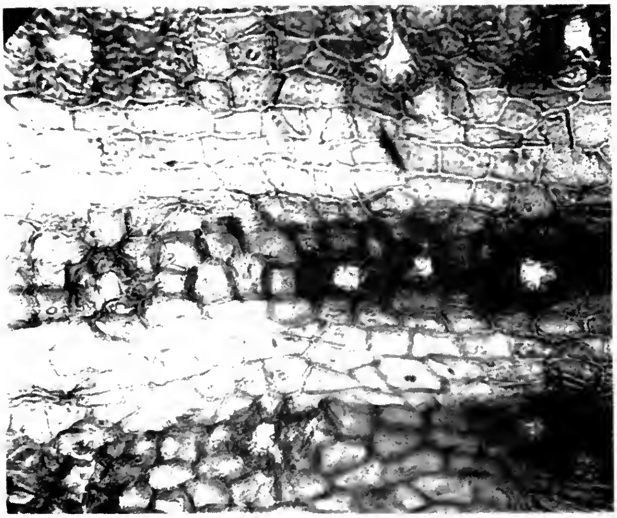
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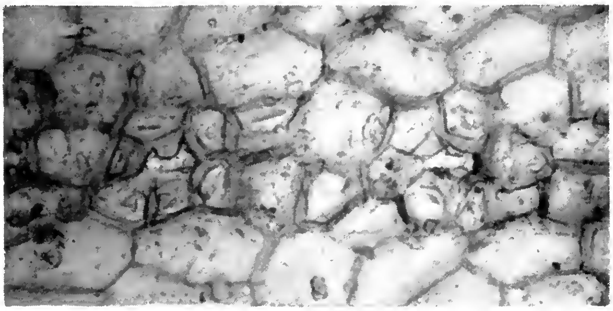
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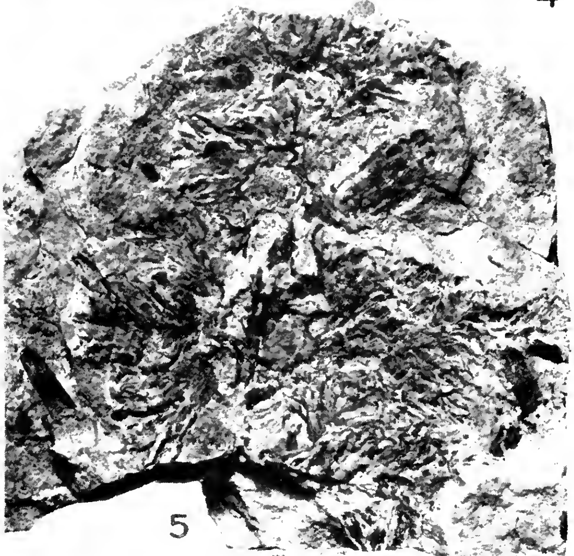
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PLATE 40

FIG. 1. *Pseudovoltzia liebeana* (Geinitz) Florin. Marl Slate, Thickley. King's College, Newcastle-upon-Tyne, no. 2525. × 1.

FIGS. 2, 3. *Samaropsis triangularis* (Geinitz) Seward. Marl Slate, Kimberley. British Museum (Natural History), nos. V.6210, V.6206. × 1.

FIG. 4. *Pseudovoltzia liebeana* (Geinitz) Florin. Marl Slate, Thickley. British Museum (Natural History), no. 46651. × 1.

FIG. 5. *Conites* sp. Near base of Upper Permian Beds, Bulcote borehole, near Nottingham. Geological Survey, no. 76681. × 2.

FIG. 6. *Pseudovoltzia liebeana* (Geinitz) Florin. Impression of cone scale. Marl Slate, Kimberley. British Museum (Natural History), no. V.6228. × 1.

FIG. 7. *Strobilites bronni* Solms-Laubach. Carbonized specimen. Hilton Plant Beds, Hilton. British Museum (Natural History), no. V.35124. × 1·5.

FIG. 8. Same species. Impression in sandstone. Hilton Plant Beds, Hilton. British Museum (Natural History), no. V.35125. × 1.

FIG. 9. Same species. Marl Slate, Kimberley. British Museum (Natural History), no. V.35126. × 1.

FIG. 10. Same species. Hilton Plant Beds, Hilton. Geological Survey, no. 19070. × 1.

FIG. 11. Same species. Marl Slate, Kimberley. British Museum (Natural History), no. V.35127. × 1.

FIG. 12. *Guilielmites permianus* Geinitz. A non-vegetable structure. Manchester Marls, Fallowfield. Manchester Museum, no. L.707. × 3·5.

FIG. 13. *Chondrus binneyi* King. A non-vegetable structure. Manchester Marls, Newton, Manchester. Geological Survey, no. 19048. × 1·7.

FIGS. 14, 15. ? *Psygmophyllum cuneifolium* (Kutorga) Schimper. Cuticle. Marl Slate, Middridge. British Museum (Natural History), nos. V.35133–34. × 150.


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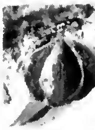
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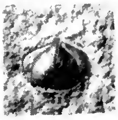
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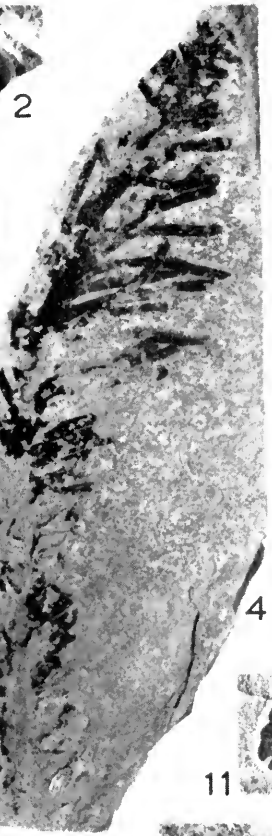
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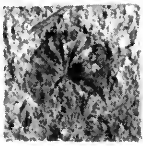
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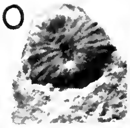
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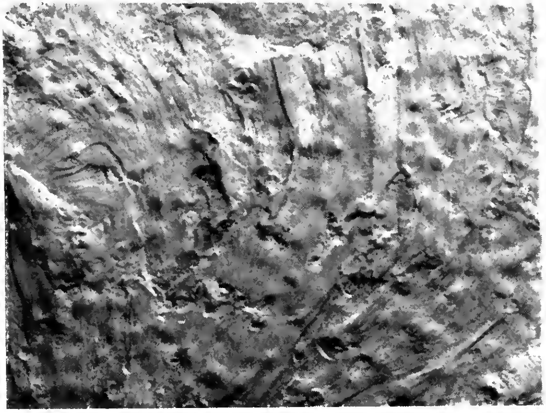
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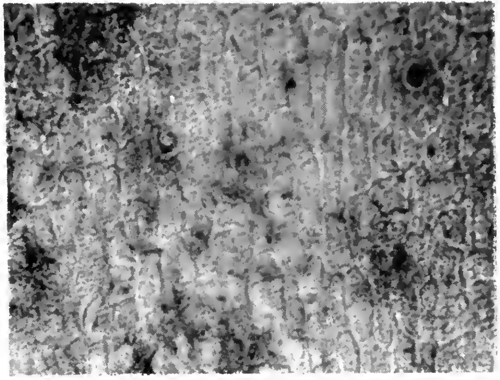
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BLUE-GREEN ALGAE FROM THE MIDDLE DEVONIAN OF RHYNIE, ABERDEENSHIRE

W. N. CROFT and E. A. GEORGE

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 3 No. 10
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BLUE-GREEN ALGAE FROM THE MIDDLE DEVONIAN OF RHYNIE, ABERDEENSHIRE

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Pp. 339–353 ; *Plates* 41–44

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BLUE-GREEN ALGAE FROM THE MIDDLE DEVONIAN OF RHYNIE, ABERDEENSHIRE

By the late W. N. CROFT AND E. A. GEORGE

SYNOPSIS

Three new blue-green algae, *Langiella scourfieldi* nov. gen. et sp. (Stigonemataceae), *Kidstoniella fritschi* nov. gen. et sp. (Stigonemataceae) and *Rhyniella vermiformis* nov. gen. et sp. (incertae sedis) are described from the Middle Devonian Rhynie Chert Bed in Scotland. The material is well preserved and details of the sheath, cell wall, cell contents and heterocysts are clearly seen. It supports the view that the Myxophyceae are an ancient stock and indicates that the Stigonemataceae which are generally regarded as being among the most advanced members of the class existed as early as the Devonian age.

I. INTRODUCTION

SINCE the classical memoirs of Kidston & Lang (1917–21) on the vascular cryptogams and thallophytes of the Rhynie Chert Bed, no further work has been published on the plants of this deposit.

Archaeothrix (Kidston & Lang, 1921) is the only fossil so far described from this chert which could reasonably be placed within the blue-green algae. The material on which the present account is based confirms the presence of Myxophyceae in the deposit and adds very materially to the knowledge of the fossil history of this important group of plants.

The specimens, placed in three new genera, occur in a single small chip of the chert. This was found labelled " ? Blue-green alga " in D. J. Scourfield's collection which was bequeathed to the British Museum (Natural History) in 1950.

The rarity of remains of blue-green algae in the deposit is in contrast with the abundance of other plants, especially fungi. It is the more striking when it is remembered that these algae are generally abundant at the present day in warm springs in which siliceous material is being deposited. It suggests that the habitat was little favourable to their growth, but is in no way contradictory to the well founded view that the peat bog was overwhelmed by flooding (Kidston & Lang, 1921 : 892).

The method adopted for studying the plants in the chip was that used by Scourfield (1926 : 154) for the crustacean remains ; direct examination in oil with an oil-immersion objective. Examination and illustration of the plants are rendered difficult by the thickness of the chip and the amount of debris contained in it. It was often necessary to readjust the setting of the substage mirror even for examination of different parts of the same plant. Moreover the cell walls often contrast little with the matrix and the outlines and visibility of the cells and of the sheaths vary considerably with the setting of the mirror and the width of the illuminating cone.

II. DESCRIPTION OF THE MATERIAL

The chip is about 1 mm. thick and nearly 5 mm. across. The topography of the two sides is shown at a magnification of × 14 in Pl. 41, figs. 1, 2. In the upper right-hand corner of fig. 1 numerous trichomes of *Langiella*, including the type specimen, are present. They tend to be similarly orientated (Pl. 43, fig. 17). Numerous trichomes of the same species are seen in the same corner of the chip from the other side (Pl. 41, fig. 2), but they are not aligned. Near the middle of the upper edge of the chip (Pl. 41, fig. 1) is the only specimen of *Rhyniella*. Associated with it are a few filaments of *Langiella*. Running obliquely through the lower right-hand portion of the chip in Pl. 41, fig. 2 is part of what is presumed to be a vascular axis about 1·4 mm. in diameter. Along the edge of this axis and partly detached from it is a narrow zone of trichomes of *Kidstoniella*. As suggested below (p. 348) the plant probably grew epiphytically upon this axis. A few trichomes showing branching, near the middle of the face of the chip (Pl. 41, fig. 1) may belong to the same species. Many fragments of plant tissue are present together with abundant fungal hyphae. These latter are occasionally branched and rarely septate. Spores have not been observed.

The occurrence of these three species in such close proximity is not unlike present-day communities of Myxophyceae. Mats and cushions consisting of several species or genera almost inextricably interwoven are a characteristic covering of damp surfaces to-day.

That so much has been learnt of the algal flora of the Rhynie Chert from one small chip encourages the hope that further fortunate discoveries may add still more to our knowledge.

III. SYSTEMATIC DESCRIPTIONS

MYXOPHYCEAE

Order STIGONEMATALES

Family STIGONEMATACEAE

Genus ***LANGIELLA*** nov.

Diagnosis. Mature thallus heterotrichous. Prostrate axis multiseriate, cells large and moderately thick-walled with both transverse and longitudinal divisions, also rounded cells in small aggregations, branches few, heterocysts absent, sheaths thin. Erect filaments essentially uniseriate, unbranched, trichomes more or less strongly torulose, cells generally smaller and except in the proximal region of some filaments, thinner-walled than those of the prostrate system ; sheaths generally thin, but thicker in middle and upper parts of some filaments ; in the upper parts of some filaments trichomes much narrower with more elongate cells or no clear evidence of cell walls ; ends of some filaments multiseriate with cells formed by oblique divisions. Heterocysts, at or near the base of most erect filaments, absent from the basal system, walls refractive, contents depleted, shape subspherical to cylindrical. Reproduction by fragmentation of erect filaments at heterocysts, probably by single akinetes formed in basal system, possibly by catenate akinetes formed in lower part of erect filaments, possibly by hormogonia released from the tips of erect filaments.

Diameter of prostrate axes, 22 μ to 40 μ; diameter of prostrate axes cells, 12 μ to 20 μ.

Length of erect filaments about 100 μ to 300 μ.

Maximum width of trichome (lower part), 16 μ. Minimum width of narrowest trichome, 8 μ.

Length of heterocysts, 6 μ to 10 μ; width 6 μ to 8 μ.

TYPE SPECIES. *Langiella scourfieldi* n. sp.

Langiella scourfieldi n. sp.

(Plate 41, figs. 1, 3–8, 10; Pl. 42; Pl. 43, figs. 17, 19–24)

DIAGNOSIS. As for genus.

HOLOTYPE. Specimen No. V.32409, Palaeont. Dept. Brit. Mus. (Nat. Hist.)

OCCURRENCE. Middle Devonian (Old Red Sandstone); Muir of Rhynie, Aberdeenshire, Scotland.

General morphology. The holotype (Pl. 41, fig. 10 and Pl. 42, fig. 12) is markedly heterotrichous and the same habit is indicated by some of the obscurely seen specimens alongside it (to the left in Pl. 41, fig. 1). A multiseriate basal system, curved round into the shape of an asymmetrical horse-shoe, gives rise on its outer edge to a number of uniseriate branches. Most of these, including two or three apparently detached filaments are subparallel, similarly orientated and lie in almost the same plane. Some at least of the uniseriate branches were probably fertile. Possibly the basal system was originally more or less straight and creeping with erect branches arising on the side opposite the substrate. Most of the specimens in the chip are, however, clearly unattached and there is no direct evidence that they ever were attached to a substrate. A description of a few associated forms follows that of the holotype (p. 346).

Basal system. The compacted cells of the basal system are generally broader and thicker-walled than those composing the erect filaments. They are not arranged in regular transverse rows as is usually the case in present-day species of *Stigonema.* The left-hand portion of the basal system (Pl. 41, fig. 10) attains a thickness of about 40μ. A row of broad thick-walled cells formed by transverse and longitudinal divisions, up to 18 μ across, is clearly seen on its surface. Beneath these, at a deeper focus, a few small cells with polygonal outlines suggesting mutual pressure are visible. The dense right-hand portion shows a row of three large thick-walled cells 20 μ in diameter. The middle, curved portion of the basal system consists of rounded cells one of which with a thick wall and a diameter of about 18 μ is suggestive of an akinete (Pl. 42, fig. 12). Some of the cells of the basal region may be " chroococcoid ", but this is uncertain; heterocysts seem to be quite absent from the basal system.

Branches Nos. 12 and 14 (Pl. 41, fig. 10) are dark like the basal system and are probably branches of it. Unlike the erect branches they are crooked and lack heterocysts. The status of branch No. 1 is uncertain. The cells are rather short in branch No. 12 and a few of them are wedge-shaped. The distal portions of branches Nos. 1 and 14 are narrow and composed of elongate cells similar to those of the hair-like terminations of a few of the erect branches.

Erect system.—The erect filaments of *Langiella* are quite unbranched and essentially uniseriate. Though generally curved or slightly sinuous they give the appearance of being somewhat rigid. The longest filament measures about 300 μ.

The cells of the filaments present some diversity of size and shape. Many of the cells are slightly wider than long, others nearly twice as broad as long, while others are depressed globose, cask-shaped or truncate ovoid. In some filaments there are cells once to twice as long as broad, wedge-shaped cells also occur. The small cells which are clearly heterocysts also show a diversity of form ; they are described in detail below (p. 345). The trichomes are generally markedly torulose and may be nearly moniliform. The two short branches, Nos. 4 and 9, are of nearly uniform width throughout and the end cells are subspherical. The larger branches, however, show a more or less clear differentiation into a proximal portion resembling these two branches and a distal portion which usually has an elongate cell at the base. The distal portions are of two main types. In one type it is hair-like and slightly club-shaped with comparatively long and narrow cells giving the whole branch a somewhat tapering form, e.g. Nos. 2 and 5. The other type is composed of cells which are shorter and thinner-walled than those of the proximal portion and the apex may include a few rather large cells or cells formed by oblique divisions, e.g. Nos. 3 and 7. There is a tendency for the end cells of all the filaments to be somewhat longer than the penultimate cells and they are always rounded, never pointed or attenuate. The sheath surrounding the proximal part is thin, usually fairly dark and well defined and often slightly torulose. That around the distal cells, however, is less distinct but thicker and at the thickest part the width of the filament may be nearly twice that of the trichome (Pl. 42, figs. 13, 15).

Basal portion of erect filaments. The catenate basal cells of some of the erect filaments are large and torulose with well-defined walls and a dark narrow sheath. A good example of this is seen in branch No. 8 (Pl. 42, fig. 12) where the basal heterocyst is succeeded by a row of seven cells which contrast rather sharply with the less well-defined, less torulose and generally smaller cells of the distal portion. These proximal cells have a diameter of about 10 μ and those of other filaments from 9 μ to 12 μ. They recall the lower cells of the uniseriate filaments of certain Rivulariaceae, lying next to the heterocyst which as in the fossil is not enclosed in the sheath. In filament No. 11 the four cells lying between the two heterocysts are unusually large and well defined, and the dark sheath closes round the end cells. The largest has a diameter of 13 μ. It is possible that these are resting cells (akinetes) as developed in e.g. *Nodularia.* They may, however, merely be thick-walled older cells like those met in the filaments of *Stigonema* and *Hapalosiphon.* If they are resting cells it seems possible that the basal cells of some of the other filaments may be incipient akinetes.

Distal portions. The modifications shown by the distal portions of the filaments have already been briefly noted. The hair-like form is well shown in filament No. 11 (Pl. 42, fig. 15) in which the end four cells are considerably smaller, though unchanged in shape, giving a sudden reduction by about one-third in the width of the trichome. The basal cell of the four is subcylindrical and about twice as long as broad, whereas the remaining cells are subspherical. The hair-like terminal portions of branches

Nos. 2, 5 and 10 also have elongate basal cells and increase slightly in width towards the apex where two or three rounded cells can be faintly seen. The cells in the middle part of the trichome are long and attenuated. The sheath around these latter trichomes is very faintly seen and is narrow, whilst that of filament No. 11 is more distinct and also wider.

Branch No. 3 is an example where the trichome does not end in a hair-like portion. The swollen apex which follows after a series of rather small cells with indistinct walls, consists of perhaps six or eight cells formed partly by oblique divisions. Their walls are not all distinct and it is impossible to say whether any of them are ruptured. The sheath around the terminal portion of the trichome which is separated from the proximal portion at an intercalary heterocyst is ill-defined but apparently of moderate width. The last few cells of branches Nos. 6 and 7 include some wedge-shaped sublateral cells probably indicating an early stage in the development of a multicellular termination like that of branch No. 3. However there is a rather similar wedge-shaped cell at the proximal end of branch No. 10 which can hardly be interpreted thus. At the end of branch No. 13 a short length of trichome, about 35 μ long with five rather ill-defined partitions, appears to be detached from the rest of the filament and to be emerging from the end of the sheath (Pl. 42, fig. 14). Its maximum width (13 μ) is somewhat greater than that of most of the trichome. Proximal to it is a shorter piece of trichome, apparently consisting of two cells, which is similar to that near the end of filament No. 8. It is possible that these pieces of trichome, especially the first, had a propagative function like that of hormogonia.

The sheaths of filaments Nos. 8 and 13 are rather wide and increase gradually and markedly in width from the lowest cell of the terminal portion of the filament as is well shown in Pl. 42, fig. 13. A similar contrast between the sheaths of the basal and of the terminal portion is shown by branch No. 11. In each of these three filaments the sheaths taper both proximally and distally and the widest part, where the filament is nearly twice the width of the trichome, occurs nearer to the apex than to the base. The hair-like termination of filament No. 11 is enclosed by the sheath. In filament No. 8 (Pl. 42, figs. 13, 16) and more clearly in the isolated piece of trichome shown in Pl. 43, fig. 23 there are indications of dark, more or less transverse lines or bars in the sheath, the only indications of lamination to be observed.

Heterocysts. All the erect filaments, with the possible exception of No. 10, have a heterocyst at or near the point of origin of the filament from the prostrate system. In two branches (Nos. 3 and 11) there is also a second, intercalary, heterocyst near the middle of the branch. The basal heterocyst is usually more or less symmetrically placed in relation to adjoining cells. In filament No. 4, however, the heterocyst is somewhat wedge-shaped and in a rather lateral position. The heterocyst may be ovoid to cylindrical, spherical or subquadrate, the long axis is usually parallel to that of the trichome. Examples of cylindrical trichomes are seen in filament No. 2 and in the isolated piece of filament shown in Pl. 43, fig. 24. These heterocysts, which are always distinctly smaller than the adjoining cells, range in diameter from 5 μ to 8 μ and in length from 5 μ to 10 μ. In several instances the heterocyst is broader and flatter at the proximal pole. The heterocysts are characterized chiefly by the hyaline nature of the wall, giving the appearance of a thin bright line. As may be seen in Pl. 43, fig. 22, the inner boundary of the wall is defined by a dark line, perhaps formed by deposits on the wall. The outer boundary of the wall is more faintly demarcated. In no case does the heterocyst appear to be enclosed in the sheath. The absence of a sheath would no doubt facilitate fragmentation of the trichome at the heterocyst. That fragmentation did occur is clearly shown by the isolated filament in Pl. 43, fig. 23 and by filament No. 2. This last example suggests that fragmentation normally took place distal to the heterocyst and this is supported by the observation that the distal end of the heterocyst is more often pointed than the other. Branch No. 6 which has no basal heterocyst was quite possibly detached in this way. The isolated filament in Pl. 43, fig. 24 shows that the heterocyst may permit considerable displacement of the filament without fragmentation occurring.

Cell contents. In some cells of a few branches of the erect system there are indications of cell contents. These consist of slightly darker central areas with a defined, rounded outline which often follows the outline of the cell wall. These areas appear minutely granular. The diameter is usually less than half that of the containing cell. In several examples the area lies slightly to the left of the centre. In a cell near the middle of filament No. 6 the faintly granular contents are but slightly contracted away from the cell wall and there are also signs of partial contraction in the cell next but one below it. The prominent black dendritic contents in branch No. 4 (Pl. 43, fig. 19) largely disregard the boundaries between the cells. It is probable that these, like the irregular black markings in a few other cells of the plant (Pl. 42, figs. 12, 15, 16) are merely inorganic, probably pyritic, deposits like those scattered through the matrix.

The heterocysts are scarcely paler than most of the other cells of the filaments. A few of them have irregular black deposits on the inner side of the wall. The example illustrated in Pl. 43, fig. 19 is the only heterocyst to show clear indications of a central dark area. This also may be inorganic.

It should be noted that in *Archaeothrix* Kidston & Lang (1921 : 875) from the same geological deposit the cell contents are also preserved.

Other specimens of Langiella. Closely associated with the holotype and clearly belonging to the same species are numerous filaments, few of which can be seen clearly. Most of them are uniseriate. A few are straight uniseriate filaments with heterocysts like those of the erect system of the holotype (Pl. 43, figs. 23, 24). The majority are more or less crooked (Pl. 41, figs. 3, 6, 7 ; Pl. 43, figs. 20, 21) and resemble branches Nos. 12 and 14 of the holotype which are regarded as vegetative branches of the prostrate system. They include small intercalary cells which, because of their size, are possibly incipient heterocysts. But they lack the distinctive characters of those of the erect system, especially a hyaline wall and elongation parallel to the axis of the filament. Also they are more or less clearly enclosed in the sheath, which is usually rather well developed. A few of the cells show cell contents as a dark central area, as in the holotype. These additional specimens do not include any cells which can definitely be recognized as akinetes or hormogonia and do not give any further evidence as to the methods of propagation or of the growth of the plant. They do, however, provide additional evidence of the modes of cell division and of branching.

The smallest group of cells seen, consisting of a row of three cells of graded size with a definite sheath, is shown in Pl. 41, fig. 5; whether they were formed by germination of a spore or by fragmentation is uncertain. Pl. 41, fig. 8 shows a short row of rather wide cells up to 16 μ in diameter. The small basal cell, which does not appear to be enclosed in the sheath is probably a heterocyst. Of particular interest is the fact, clearly demonstrated by focussing at different planes, that the distal cell has undergone a longitudinal division, and one of the daughter cells is further divided in a plane at right angles to the previous division. The piece of filament in Pl. 41, fig. 4 shows at its widest part a pair of collateral cells, presumably formed by division of an apical cell rather than by longitudinal division of an intercalary cell. The bent piece of filament in Pl. 41, fig. 7 shows a small cell at the bend formed by oblique division. The specimen in Pl. 41, fig. 6 and Pl. 43, fig. 21 appears to consist of two short filaments crossing one another. The large dark-walled cell near the centre may possibly be an akinete which has germinated. Lastly in Pl. 41, fig. 3 the upper filament appears to be branching out of the more horizontal filament. The downwardly directed filament appears to originate at the junction of the filaments. The upper filament shows what is perhaps an incipient heterocyst where the filament bends.

Discussion. As is general in the filamentous blue-green algae, the cell division in *Langiella* is predominantly transverse. In the Stigonematales, where true branching occurs, the branches arise from the longitudinal division either of an apical cell or of an intercalary cell. Branches produced in this latter way push through the sheath of the filament and increase in length by the usual transverse divisions. In the holotype and the other fossil material examined this type of longitudinal division of an intercalary cell is nowhere conclusively shown. Presumably such must have occurred both to increase the thickness of the prostrate axis and to produce the numerous erect filaments arising from it. It is considered unlikely though not impossible that all these arose from apical cells.

Elongation of the erect filaments was probably in part at least from intercalary divisions in the distal portion of the filaments. In branches Nos. 3, 7 and 8 a series of short cells suggests recent cell divisions, such cells are not found in the proximal, presumably older, parts of the filaments. The subterminal lengths without cross-walls in filaments Nos. 2, 5 and 10 recall the filaments of Recent species of *Fischerella* (Geitler, 1932, text-figs. 296–299) where hormogonia are in the process of leaving the sheath of the parent filament. However it seems that this is not the case here, as the non-septate portion appears not to be an empty space but more like an attenuated cell. The possibility of necrotic lengths of trichome must also be considered, especially as Kidston & Lang (1921 : 835) report necrotic and wound areas in *Rhynia*.

An interesting feature clearly shown by the holotype and other specimens is the prevalence of wedge-shaped cells, often small and lying at a bend of the filament; they were presumably formed by the oblique division of an apical or perhaps an intercalary cell. This is especially well shown by the ends of branches Nos. 6 and 7 in the holotype where several cells are cut off by oblique walls.

Genus ***KIDSTONIELLA*** nov.

DIAGNOSIS. Thallus heterotrichous, epiphytic. Basal system consisting of a mass of cells, some of which are polygonal, forming thin parenchymatous tissue, others larger, rounded and thicker-walled. Erect branches uniseriate, straight, more or less strongly torulose, once or twice unequally branched by longitudinal division of the apical cell, or unbranched. Intercalary transverse divisions rare or absent. Cells variable in shape and size, mostly somewhat wider than long, end cells subspherical. Sheath seldom well preserved. Heterocysts small, nearly spherical, intercalary in erect filaments. Cell contents conspicuous in many cells of the thallus. Method of reproduction uncertain.

Cells of pseudoparenchymatous tissue of basal system 10 μ to 14 μ broad; large rounded cells of basal system 16 μ broad; erect filaments up to 160 μ long and up to 24 μ broad; length of mature cells 5 μ to 14 μ; heterocysts 5 μ to 6 μ long and 6 μ to 7 μ broad.

TYPE SPECIES. *Kidstoniella fritschi* n. sp.

Kidstoniella fritschi n. sp.

(Pl. 41, figs. 2, 9; Pl. 44)

DIAGNOSIS. As for genus.

HOLOTYPE. Specimen No. V.32409, Palaeont. Dept. Brit. Mus. (Nat. Hist.).

OCCURRENCE. Middle Devonian (Old Red Sandstone); Muir of Rhynie, Aberdeenshire, Scotland.

GENERAL MORPHOLOGY. As noted above (p. 342), this species appears to have grown epiphytically. Pl. 44, fig. 29 shows a dark band of multiseriate filaments forming a basal layer lying parallel to, but partly detached from the edge of an oblique section through a nearly opaque plant axis. A number of uniseriate filaments, a few of which are branched, arise from this basal layer and stand away from it at a wide angle. It seems likely that the axis, perhaps growing more or less erect, formed the substrate for the heterotrichous thallus of the alga.

Basal system. Much of the basal system shown in Pl. 41, fig. 9 is composed of a dense mass of rather ill-defined cells. Some of these are rather large, spherical or ovate, with thick walls and clear indications of dark rounded contents. These cells attain a diameter of 15 μ. In part of the basal system a number of cells which are smaller than those forming the erect filaments have become polygonal through mutual pressure and form a thin pseudoparenchymatous tissue which in part at least seems to be monostromatic. Another part of the basal system is formed of imperfectly seen rounded cells up to 16 μ in diameter. There is little or no evidence of any mucilaginous sheath around the basal system.

Erect system. The more or less erect branches are essentially uniseriate and often strongly torulose. The cells vary considerably in shape and size. They are mostly somewhat wider than long, and may be twice as wide as long, ranging in shape from discoid or wedge-shaped to depressed—or truncate-globose. A few are slightly longer than wide, cask-shaped or ovoid. The end cells are rounded and when mature, subspherical. The filaments range in width from about 8 μ to 14 μ. An unusually large cell in filament No. 1 is 15 μ in diameter.

A feature of special interest is the unequal dichotomous branching shown by two of the erect filaments. In filament No. 1 the two divisions are but slightly divergent. The shorter and narrower division consisting of shorter but more numerous cells, is less developed than the other. In filament No. 2 the very short right-hand division is indistinctly preserved but appears to be multiseriate. The terminal cell of the left-hand division is itself divided by a faint but definite longitudinal wall (Pl. 44, fig. 27). From the fortunate preservation of the filament at this stage of growth it may be inferred that the other dichotomous divisions have also resulted from the longitudinal division of an apical cell. There is no clear indication in the thallus of the longitudinal or transverse division of an intercalary cell and it might therefore be concluded that growth was wholly apical. However, in filaments Nos. 1 and 4 there are rather short cells which might be products of recent intercalary divisions. The large end cell of filament No. 2 seems to be in process of dividing longitudinally, for the contents consist of two rounded bodies in place of the usual one. In the left-hand filament in Pl. 44, fig. 25 the distal end of the filament is divided into a number of imperfectly seen cells somewhat reminiscent of the multicellular tips seen in *Langiella.* The large end cell of the next filament seems to be in the process of dividing longitudinally for two rounded bodies are seen inside it. Springing from the right-hand side of this filament is a short club-shaped body whose contents are divided into three or four very small portions not obviously separated by septa. This appears to be an incipient branch and may be compared with the branch of very short cells in filament No. 1. The pair of cells just below the branch in filament No. 2 may have resulted from a transverse intercalary division.

The erect filaments have few and discontinuous pieces of a surrounding sheath. The clearest examples are round the distal parts of filaments Nos. 2 and 3 and around filament No. 4.

Heterocysts. The small nearly spherical cells indicated in filaments Nos. 3 and 4 are possibly heterocysts. Their diameters are about 6 μ. Like those in *Langiella* they are small and have a hyaline wall delimited by dark lines of which the inner seems to be the darker. A few of the normal sized cells, for instance those on each side of the heterocyst in filament No. 4, also have hyaline walls, though in these the outer limiting line seems to be the darker. Most of the cells having a thin dark wall in optical section, show a similar shining wall at a slightly higher focus. In shape and appearance these two cells resemble the small intercalary cells thought to be heterocysts in some of the filaments of *Langiella.*

In Pl. 44, fig. 27 several of the cells, notably in filament No. 3, show a clear wall bounded internally by a fine dark line. The small intercalary cell in this filament recalls by its size the cells which are regarded doubtfully as heterocysts in filaments of *Langiella.* The wall, however, is not hyaline, cell contents are present and the sheath appears to enclose it. This may well be an example of a small cell which has not yet developed into a heterocyst.

Cell contents. In most of the cells in the uniseriate filaments, as well as in the basal region, there are more or less clear indications of contents (Pl. 44, figs. 27–29).

As in *Langiella*, these consist of darker, central areas with a rounded outline. As a rule the larger bodies are found in the larger cells. The shape of the central area corresponds generally with that of the cell, being wedge-shaped in wedge-shaped cells and transversely elongate in discoidal cells. The central areas are particularly well defined in the distal regions of filaments Nos. 1 and 2. In the main division of branch No. 1 the central areas of four cells are more or less sharply delimited and surrounded by a narrow clear zone or halo which is paler than the outer zone. In certain cells in filament No. 2 the clear zone appears to be delimited from the outer, slightly dark, contents of the cell by a fine line. This suggests that the zones outside the central dark area may represent mucilaginous or other contents of the cell. With the highest resolution which could be used the dark central areas appear to be finely granular. The cell immediately below the dichotomy in filament No. 1 appears to be empty and to be ruptured on its left side.

MYXOPHYCEAE

INCERTAE SEDIS

Genus ***RHYNIELLA*** nov.

DIAGNOSIS. Thallus filamentous, essentially uniseriate, vermiform, non-heterotrichous. Trichomes mainly sinuous within a mucilage sheath, often two or three sharing a common sheath, branching doubtful, heterocysts doubtful, some with multicellular apices. Cells usually broader than long, wedge-shaped at the sharper bends in the trichome. Terminal cells rounded or rarely bluntly pointed. Method of reproduction unknown.

Trichome up to 140 μ long; cells 4 μ to 10 μ long and 10 μ to 14 μ broad.

TYPE SPECIES. *Rhyniella vermiformis* n. sp.

Rhyniella vermiformis n. sp.

(Pl. 41, figs. 1, 11; Pl. 43, fig. 18)

DIAGNOSIS. As for genus.

HOLOTYPE. Specimen No. V.32409, Palaeont. Dept. Brit. Mus. (Nat. Hist.).

OCCURRENCE. Middle Devonian (Old Red Sandstone); Muir of Rhynie, Aberdeenshire, Scotland.

GENERAL MORPHOLOGY. The species represented in Pl. 41, fig. 11 is found near the middle of the upper edge of the chip in Pl. 41, fig. 1 and does not appear to be present elsewhere in the chip. It consists of numerous subparallel trichomes many of which are distinctly vermiform. The drawing is considerably condensed, but the thickness of the bundle of trichomes is much less than the width. The cells are typically broader than long; wedge-shaped cells are found at the sharper bends in the trichome. Several trichomes are more or less isolated and enclosed in their own sheaths. Some of the trichomes, however, are closely associated for part of their length and it is practically certain that they share a common sheath. No clear case of branching has been observed. Nor are heterocysts certainly present, though one cell may be of this type.

There is no defined basal system ; the multicellular, and presumably distal, terminations of many of the filaments are, however, with one exception similarly orientated and the direction of growth was probably to the right in Pl. 41, fig. 11.

Trichomes. Some of the more distinct trichomes attain a length of 140 μ, and vary in width from 10 μ to 14 μ. A few of the indistinctly seen trichomes are nearly straight, but the majority are sinuous, and a few are bent at right angles. All but the terminal cells are shorter than wide and many are twice as wide as long. At the bends in the trichome the cells are more or less markedly wedge-shaped, in some instances not reaching across the full width of the trichome. There are generally distinct constrictions at the septa. The end cells vary considerably in shape, they may be segmental, hemispherical, subspherical or spherical. If spherical two or more may form a group. A few of the hemispherical cells are bluntly pointed. At A (Pl. 41, fig. 11) a trichome is terminated by an unequal pair of rounded cells : and at B the penultimate cell is divided longitudinally. At C an unusually large, oval-shaped end cell (length 20 μ ; breadth 14 μ) appears to be dividing. The various groups of terminal cells may have had a propagative function.

To the left of the centre of Pl. 41, fig. 11 there is a small cell almost surrounded by a curved piece of trichome. This cell is subquadrangular and measures 5 μ by 6 μ. It is distinctive not only because of its size and shape but because the wall is hyaline and marked on its inner boundary by a heavy dark line. These features characterize those cells of *Langiella* which are confidently regarded as heterocysts ; this cell must therefore be regarded as quite possibly a heterocyst. Its position in the thallus is, however, unusual and its true nature is uncertain.

Some of the trichomes are divided into lengths composed of from 4 to 12 cells. The longest piece of trichome without such a segmentation has 18 cells. The end cells of each segment are usually hemispherical or subspherical. There may be a small, nearly spherical cell connecting two segments as in the central trichome in the lower part of Pl. 41, fig. 11. These small cells do not have a hyaline wall.

In a few places, the trichomes are closely parallel for part of their length indicating that they share a common sheath. The mode of branching, if this does occur, is not clearly demonstrated at any point.

Cell contents. As indicated in Pl. 41, fig. 11 a few of the cells show rounded contents. Though indistinct, they do not appear to differ significantly from those in the associated species.

Sheaths. The trichomes are enclosed in more or less clearly defined sheaths which vary in thickness from a quarter to a half of the trichome width. In one or two places where the edge of the sheath is clearly defined it is irregularly sinuous. The sheaths also show indications of longitudinal folds. Two of the more isolated trichomes are completely enclosed in their own individual sheaths. The majority of the trichomes appear to share a common sheath, at least over part of their length.

DISCUSSION AND COMPARISON. *Rhyniella* differs from the other two genera in the apparent absence of heterotrichy, of heterocysts and in its shorter and less rounded cells. It calls to mind forms like *Tolypothrix elenkinii* and *Scytonema* (*Diplocolon*) *crustaceum* (Geitler, 1932 : 738, 784). Both these Recent species are heterocystous and non-heterotrichous with many contorted trichomes in a common sheath. However the possibility must not be overlooked that this specimen grew from a basal system which is not now in evidence. From its general appearance and cell morphology it could not be part of either *Langiella* or *Kidstoniella* which, however, it resembles in the possession of multicellular apices. Nothing quite like these structures occurs in present-day members of the class.

IV. CONCLUSIONS AND GENERAL DISCUSSION

It is now evident that in Middle Devonian times the blue-green algae had reached an evolutionary grade which is generally regarded as advanced among Recent forms, namely a heterotrichous thallus with a pseudoparenchymatous basal system. The enigma of the heterocyst, so well presented by Fritsch (1951) is no nearer solution, but it is clear that the evolutionary origin of the heterocyst must be sought in still older fossils.

The multicellular tips to the trichomes seen in *Langiella* and *Rhyniella* and rarely in *Kidstoniella* are of considerable interest in that they have no close parallel in present-day forms. Rather similar structures in *Stigonema dedroideum* were described by Frémy (1930) as conidia, but there the cells are rounded and separated within mucilage. It is of course possible that the fossil structures are an early stage, either phylogenetically or ontogenetically, in the development of such conidia.

There is a certain similarity in general appearance between *Langiella* and *Kidstoniella* but it is considered most unlikely that they belong to the one species or even the same genus. *Langiella* has unbranched erect filaments with distinct heterocysts and occasional multicellular tips, while *Kidstoniella* shows true branching of the erect filaments which have few multicellular tips and doubtful heterocysts. How constant these characters were in the living population one cannot say but on the present evidence and in accordance with taxonomic practice, both in phycology and in palaeobotany they must be considered separate genera. There can be little doubt that these two genera belong in the Stigonematales (Geitler, 1925; Fritsch, 1942) and there are no characters on which one could satisfactorily found a new family apart from the Stigonemataceae.

The position of *Rhyniella* is less certain. On the present probably incomplete evidence it is non-heterotrichous and unbranched, suggesting a position in the Nostocales (Geitler, 1925; Fritsch, 1942) and perhaps within Oscillatoriaceae but the presence of multicellular tips as in *Langiella* suggests Stigonematales and possibly a close relationship with *Langiella*. This difficulty in assigning a taxonomic position to a blue-green alga is by no means limited to fossil forms; there is wide lack of agreement over the classification of present-day forms (see Papenfuss, 1955).

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PLATE 41

Langiella scourfieldi, Kidstoniella fritschi and *Rhyniella vermiformis*

FIG. 1. Drawing of the chip showing position of the fossils, in particular *Langiella scourfieldi* (top right-hand corner) and *Rhyniella vermiformis* (centre). × 15 (V.32409).

FIG. 2. The same, reverse side, to show position of *Kidstoniella fritschi*. × 15.

FIGS. 3–8. Drawings of isolated filaments of *Langiella scourfieldi* associated with the holotype. × 280.

FIG. 9. Drawing of the holotype of *Kidstoniella fritschi* constructed from photographs and direct observation. × 280.

FIG. 10. Drawing of the holotype of *Langiella scourfieldi* constructed chiefly from photographs at different focal levels, but partly from direct observation. × 280.

FIG. 11. Drawing of the holotype of *Rhyniella vermiformis* from photographs and direct observation. × 280.

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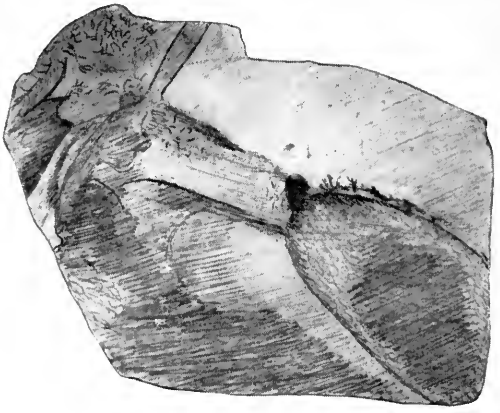

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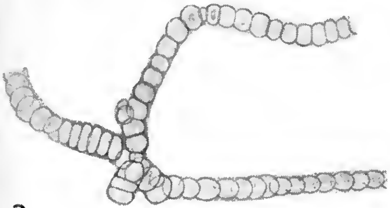

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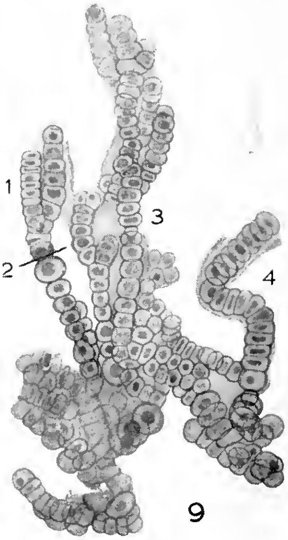

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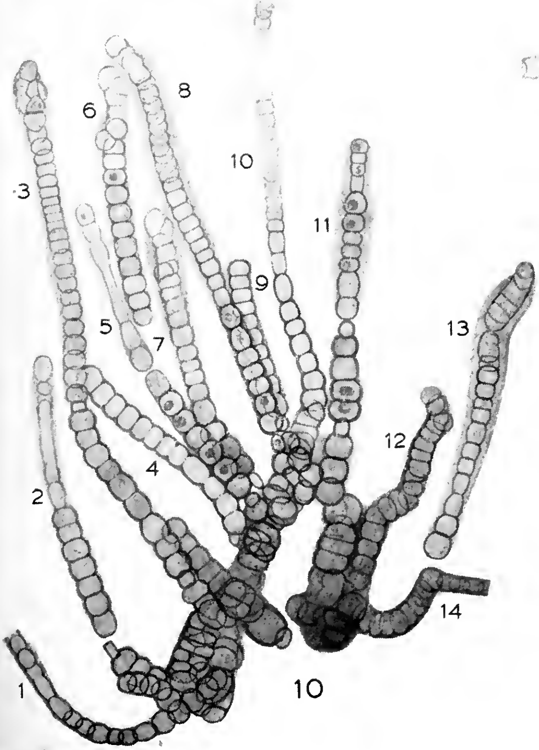

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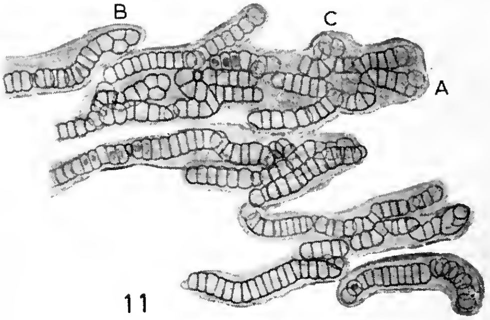

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PLATE 42

Langiella scourfieldi sp. nov.

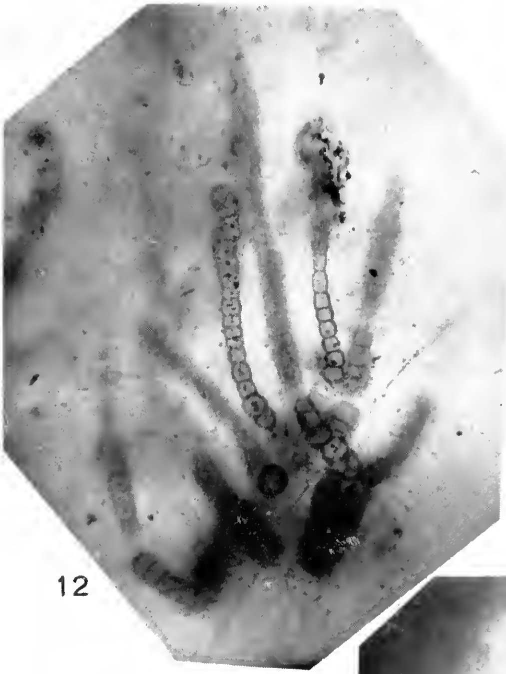
FIG. 12. A supposed akinete near the base of filament No. 4 (latter not in focus) and pyritic granules in filament No. 7; also filament No. 10. × 230 approx.

FIG. 13. Filaments Nos. 4 and 8. × 230 approx.

FIG. 14. Terminal portion of filament No. 13. × 560.

Fig. 15. Filaments Nos. 9 and 11. × 230 approx.

FIG. 16. Filaments Nos. 4 and 8 and cells of the basal system. × 375 approx.



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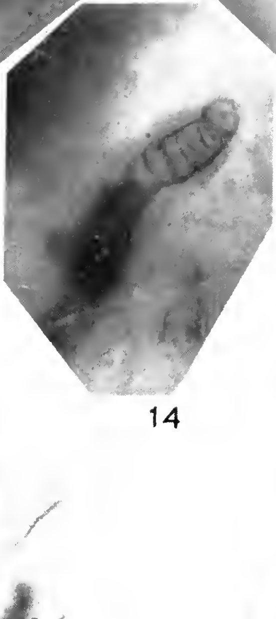

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PLATE 43

Langiella scourfieldi and *Rhyniella vermiformis*

Fig. 17. Holotype of *Langiella scourfieldi* showing habit. × 44.

Fig. 18. Holotype of *Rhyniella vermiformis*. × 375 approx.

Fig. 19. *Langiella scourfieldi* showing branches Nos. 4 and 8. × 560.

Figs. 20, 21. Isolated filaments of *Langiella scourfieldi*. Fig. 20 × 105, Fig. 21 × 185.

Fig. 22. *Langiella scourfieldi*. Two heterocysts in filament No. 11 and one in filament No. 9. × 560.

Fig. 23. *Langiella scourfieldi*. Isolated piece of erect filament showing break at the heterocyst and laminated sheath. × 560.

Fig. 24. *Langiella scourfieldi*. Isolated fragment of filament with a cylindrical heterocyst showing displacement at the heterocyst. × 560.

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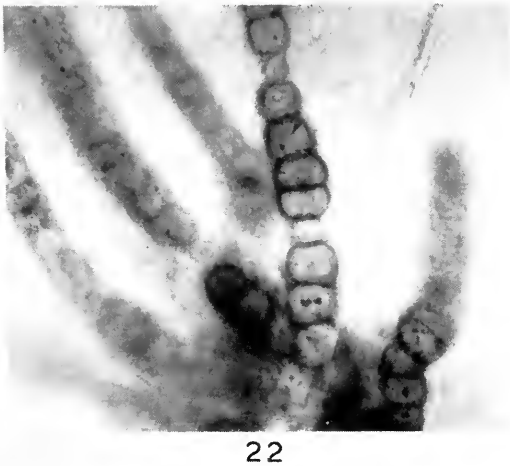

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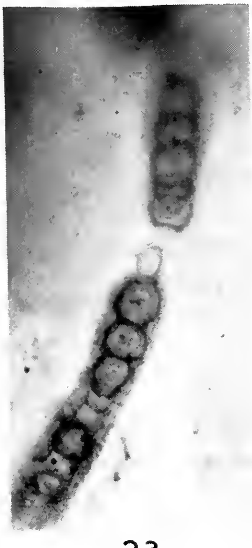

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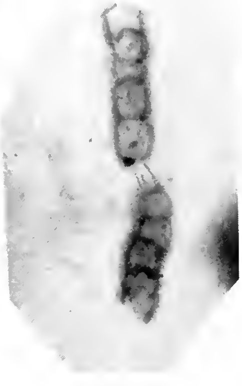

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PLATE 44

Kidstoniella fritschi sp. nov.

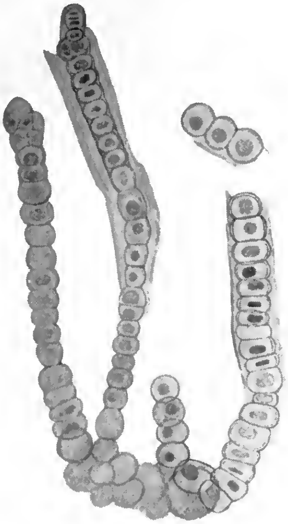
FIG. 25. Drawing of paratype. The distal end of the left-hand filament is divided into a number of obscurely seen cells. × 280.

FIG. 26. Holotype. Right branch of filament No. 1 and a divided apical cell of filament No. 2. Note the granular contents. × 435 approx.

FIG. 27. Photograph showing general features of holotype including the basal system and granular cell contents. × 435 approx.

FIG. 28. The left branch of filament No. 1 and the apical cell of the right branch. × 435 approx.

FIG. 29. Photograph showing habit. × 44.



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